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European and Northwest African Middle Pleistocene Hominids¹

by F. Clark Howell

THE SPARSE REPRESENTATION of human skeletal remains from the Middle Pleistocene has always been one of the greatest gaps in human-paleontological knowledge. At first, Southeastern Asia was unique in having provided remains from the Trinil beds in Java, but the significance of this poorly preserved skull-cap was confirmed and greatly amplified by subsequent discoveries (Von Koenigswald 1940) of better preserved specimens at other localities of similar age, as well as in the still older Djetis beds. Still truly unique in all the world is the somewhat younger occupation site of Locality 1 Choukoutien, with its extraordinarily abundant, probably cannibalized, human remains in association with hearths, stone implements (Choukoutienian chopper/chopping-tool complex), and remains of slaughtered animals.

For many years, the only such find from the West was the enigmatic human mandible from the Grafenrain gravel pit at Mauer in the Rhineland. Then, within a few years in the mid-thirties, three additional specimens came to light in western Europe (Steinheim), Britain (Swanscombe), and northwest Africa (Rabat, Morocco). In the last several years, further Middle Pleistocene human remains were found in northwest Africa, both in Algeria (Ternifine) and in Morocco (Sidi Abderrahman). All these discoveries (Fig. 1) have excellent paleontological associations, and, in three cases (Swanscombe, Ternifine, Sidi Abderrahman), there are associated stone implements (Acheulean of various stages). However, no occupation site is yet

known from the Middle Pleistocene of Europe or Africa with *in situ* human skeletal remains, stone implements, and the bones of slaughtered animals.

These human skeletal remains, taken in conjunction with those from the Middle Pleistocene of eastern and southern Asia, have an important bearing on interpretations of the course of human evolution. The significance of these discoveries has been obscured by the preoccupation of some human paleontologists with other human remains either *suspected* to be of Pleistocene antiquity or questionable due to an extraordinary complex of morphological features (the famous hoax of Piltdown). Largely as a consequence of this, there have grown up two main interpretations of man's phylogeny in the Pleistocene, one depending on the possible importance of the suspicious "fossils," and the other depending only on the scanty, but well-dated, human fossils enumerated above. The former interpretation recognizes an early, at least earlier, Middle Pleistocene separation of a morphologically modern (*sapiens*) lineage. The latter postulates progressive transformation of primitive and variable Middle Pleistocene human populations into diverse "Neanderthal" and related, geographically distinctive, groups, as well as into incipiently *sapiens* peoples. The purpose of this paper is to discuss the significance of the Middle Pleistocene human remains from Europe and North Africa for the resolution of this basic problem in the study of human phylogeny.

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HOWELL has undertaken field and other studies on early man in Europe (1953, 1956) and in Africa (1954, 1957-58, 1959), and made a recent brief visit to Israel (1959). He has published various papers on human paleontology, especially as regards the Neanderthal problem, and on early man and the Pleistocene in general.

Prior to submitting the present paper to CURRENT ANTHROPOLOGY, HOWELL sent it, for comment and criticism, to three colleagues, of whom W. W. Howells and Kenneth P. Oakley responded. The response was primarily commendatory, and except for HOWELL's addition of some paragraphs along lines recommended by Oakley, the paper stands as first written.

COMPARATIVE STRATIGRAPHY AND ASSOCIATIONS

THAMES RIVER: SWANSCOMBE

The Swanscombe human remains were recovered from gravel deposits exposed in the Barnfield pit, between Dartford and Gravesend, on the south bank of the lower Thames River valley. Marston (1937) discovered a complete occipital in June, 1935, and a left parietal in March, 1936. Twenty years later Wymer recovered the right parietal of the same individual. The three fragments occurred in the same seam of sandy

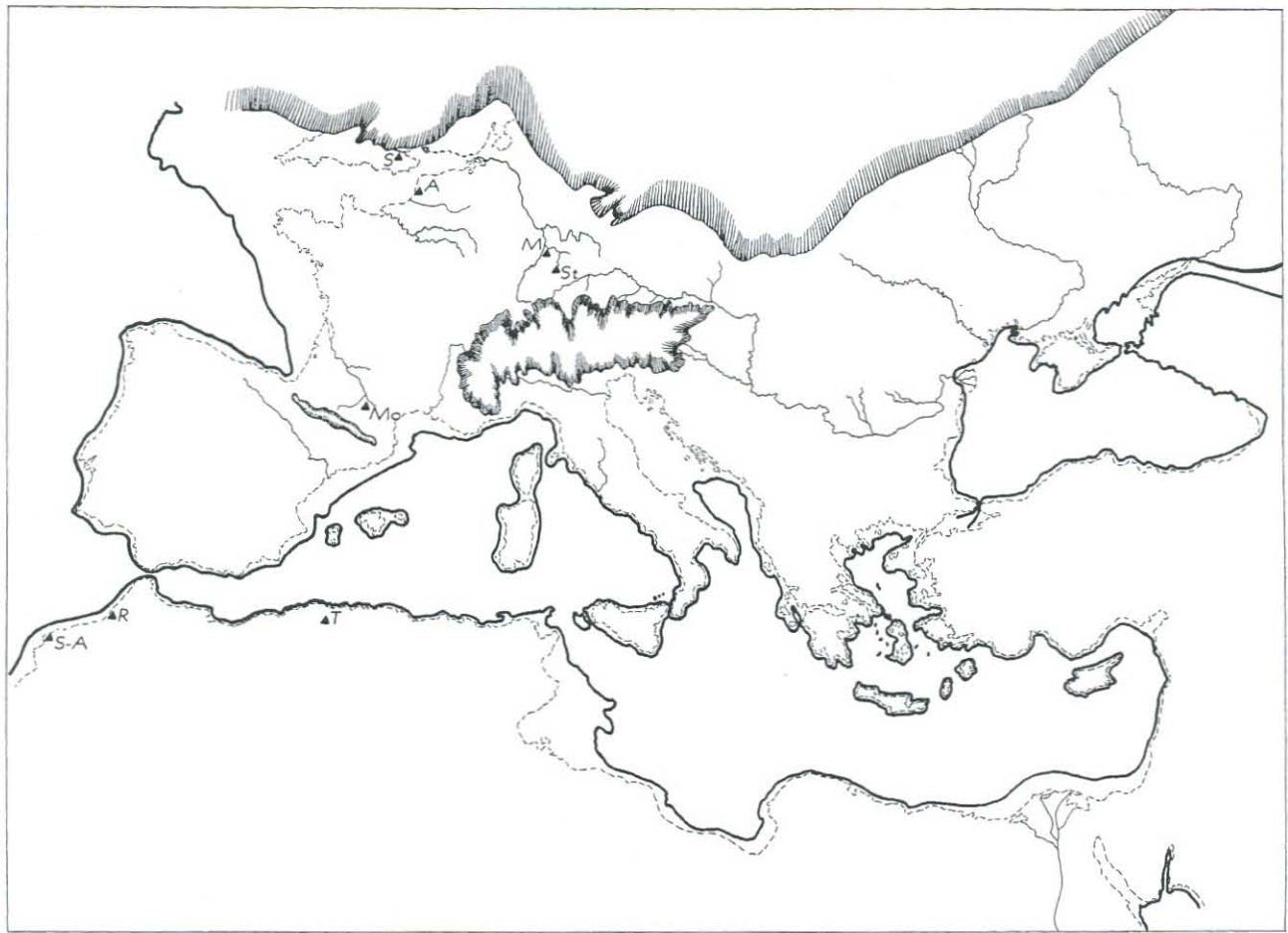


FIG. 1. Outline map of Europe and the circum-Mediterranean regions. The continental outlines are those of the earlier Middle Pleistocene during the extensive Romanian regression, correlative with the first major continental glaciation (Elster) and the Mindel glaciation of the Alps. Key to abbreviations: S = Swanscombe; A = Abbeville; M = Mauer; St = Steinheim; S-A = Sidi Abderrahman; R = Rabat; T = Ternifine.

gravel, "the position of the three fragments forming a triangle with sides 51, 49 and 24 ft." apart (Wymer 1955). These gravels and sands represent fluvial accumulations within the High (100 feet) or Boyn Hill Terrace, which extends as a nearly level feature for some fifty miles (Fig. 2) (Smith and Dewey 1913; Dewey 1932; Wooldridge and Linton 1955). At the time of the aggradation, the river flowed in a wide, meandering course, successively cutting, filling, and then abandoning channels. The Barnfield pit exposes some thirty-five to forty feet of gravels, sands, and loams that filled in one such ancient channel, its base at seventy-five feet, cut into the local bedrock (Thanet Sand and Chalk) (Fig. 3).

The human remains occurred in an obliquely-lying gravel seam at the base of the Upper Middle Gravel, some sixteen to twenty feet of current-bedded reddish-yellow sands (below) passing upward into pale yellow cross-bedded sands with some silty layers. Above these "gravels," a thin wedge of soliflucted rubble is interposed at the base of the three to four feet of thick sandy Upper Loam. These deposits fill a small channel cut during a minor erosional phase into the underlying Lower Middle Gravel (and sands), the Lower Loam, and in part the Lower Gravel. The skull fragments appear to have reached the base of this channel shortly after it was cut and still dry, quite clearly prior to the deposition by floodwaters of the successive seams of Upper Middle Gravels and sands. The stone tools associated with the human remains, including numerous

hand axes, flake tools, and many waste flakes but rarer cores, constitute a Middle Acheulean industry (Acheulean III-IV of the Somme classification of Breuil) (Smith and Dewey 1913; Swanscombe Committee 1938). This same industry is present also in the underlying Lower Middle Gravels as well as on the surface of the Upper Loam. However, Wymer's (1958) recent work at Swanscombe indicates that ovates and cleaver-forms of bifaces, as well as tortoise cores, are lacking in the skull-layer, whereas the former are present on a land surface of the Upper Loam. He has also found traces of fire, including reddened and crackled flints and small pieces of charcoal, in the skull-layer.

It has been suggested that the Middle Gravels and Upper Loam constitute a recognizably distinct depositional stage, the Middle Barnfield or Late Boyn Hill stage, separated by an erosional interval (represented in certain localities) from the Lower Gravel and Lower Loam, the Lower Barnfield or Early Boyn Hill stage of King and Oakley (1936). Judging from the molluscan faunas, the Thames and Rhine rivers were separate during the earlier stage, whereas, in the Late Boyn Hill

stage, species of freshwater Rhenish mollusca began to penetrate into the Thames River valley (cf. Oakley 1952). The Lower Loam, a silty deposit laid down in reed-filled swamp conditions, was probably weathered during that interval. A very rich Clactonian industry (Clactonian II of the classification of Breuil 1932), comprising many flake tools, cores, and core-choppers (but no hand axes), is present in the Lower Gravel (Smith and Dewey 1914; Chandler 1930, 1931, 1932, 1935). The mammalian fauna from these latter gravels is especially rich, with two forms of elephant (*Elephas antiquus*, *El. trogontherii*), broad-nosed rhinoceros (*Rhinoceros merckii*), hippopotamus (*Hippopotamus amphibius*), wild boar (*Sus scrofa*), deer (*Cervus elaphus*, *C. browni*), wild ox (*Bos primigenius*), wild forest horse (*Equus caballus*), giant beaver (*Trogontherium cuvieri*), and various small rodents and voles. The faunal assemblage from the series of Middle Gravels is similar, but lacks giant beaver, oxen, and wild boar, and includes two extinct fallow deer (*Dama clactoniana*, *Megaceros* sp.),

one a giant form; also, in a silty layer in the Upper Middle Gravels, small mammals occur, including extinct voles (*Microtus agrestis-arvalis*, *M. ratticepoides*) and a lemming (*Lemmus* sp.) (Schreuder 1950). The composition of the fauna in both gravel series is typically interglacial (Swanscombe Committee 1938; Oakley 1952, 1957b). The fluorine content of the human skull fragments and of the animal remains is similar, confirming that the Swanscombe cranium is of the same age as its containing deposit (Oakley 1951, 1953).

Several distinct lines of evidence permit quite accurate relative dating of these deposits within the framework of the Pleistocene succession of Britain (King and Oakley 1936; Oakley 1952, 1957b). It is clear that one,

FIG. 2. Terraces of the lower Thames Valley and the location of Swanscombe (redrawn after Wooldridge and Linton 1955).

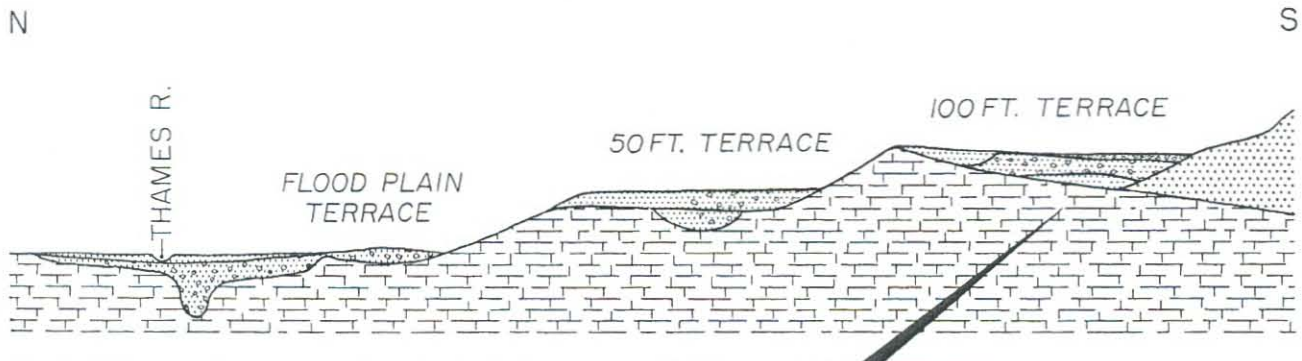
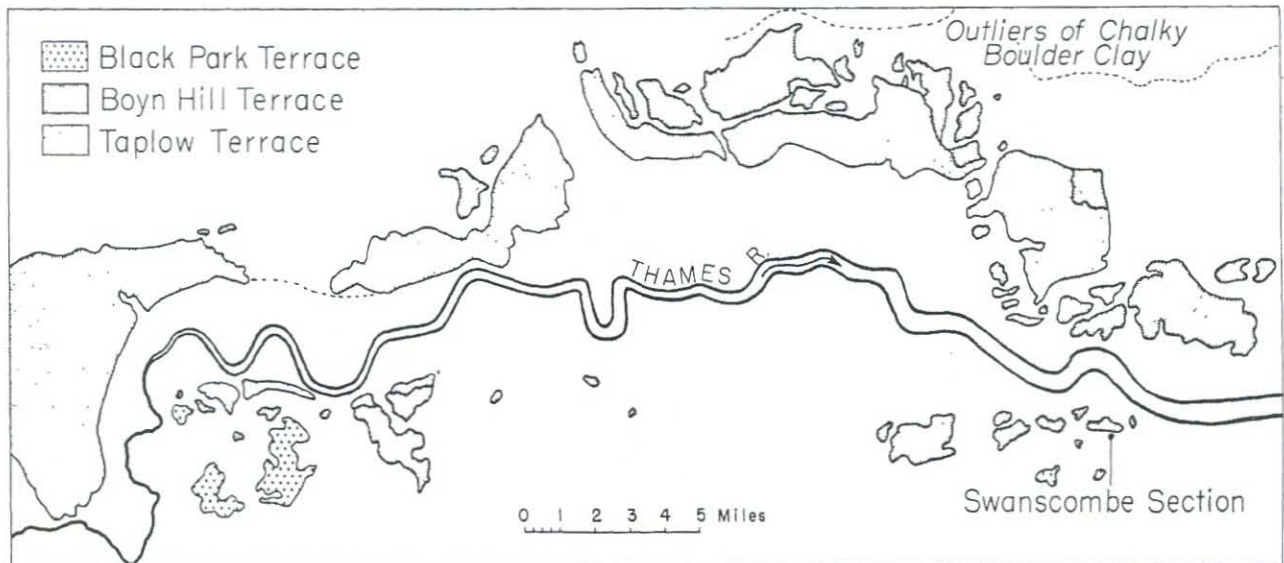
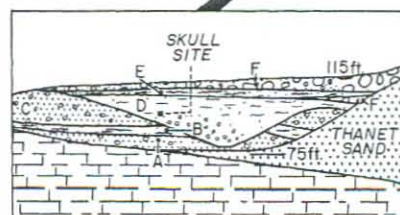


FIG. 3. Diagram of terrace relationships in the lower Thames Valley with (inset) the filling of the Barnfield channel of the Boyn Hill Terrace (redrawn after Dines in Swanscombe Committee Report 1938).



and more likely several, glacial advances preceded the aggradation of the deposits that constitute the Boyn Hill Terrace, since: (1) within the gravels, far-traveled glacial erratics are found, attributed by Baden-Powell (1951) to the Lowestoft (Lower Chalky Boulder Clay) Glaciation; (2) the Thames River flowed at the time in its present terraced valley, previously having been diverted southward from more northeasterly courses by glacial advance(s) (Wooldridge 1938, 1957; Wooldridge and Linton 1955); (3) such gravels overlie glacial boulder clay at certain other exposures (Hornchurch); and (4) the great thickness of the Swanscombe gravels indicates a considerable rise in sea level during their aggradation, a rise, in fact, of approximately 107 feet, corresponding with the extent of the Tyrrhenian I marine transgression of the Mediterranean. The initial point is of particular importance, since the southeasterly-directed Lowestoft glacial advance preceded the southerly-directed Gipping glacial advance and was separated from it by a major interglacial stage (Baden-Powell 1948; West and Donner 1956). This interglacial stage, termed the Hoxnian (West 1955), equates with the Needian of the marine succession of the Netherlands, and with other continental localities of Great Interglacial age on pollen-analytical grounds (West 1956). The Gipping Glaciation is equivalent to the continental Saale Glaciation; the preceding Hoxnian interglacial is the equivalent of the Great Interglacial, that is, the Mindel-Riss stage of the Alpine succession. Thus, on geological grounds the deposits that constitute the Boyn Hill Terrace are of Great Interglacial age, and this is further substantiated by the faunal and stone tool assemblages.

The exact position within the admittedly long Great Interglacial is a more difficult matter. Oakley (1952; Oakley and Leakey 1938) attempted to show that the later Barnfield deposits (Late Boyn Hill stage) represented the latter half of this interglacial, probably equating with the earlier part of the marine Drenthian of the Netherlands. It is now clear that the Middle Acheulean assemblages from the Barnfield pit at Swanscombe, and the silted-up Hoxne lake basin, belong to the same industrial stage (West and McBurney 1954). If the Hoxne pollen sequence (West 1956) is utilized as a measure of the climate during this interglacial, such an Acheulean industry was practiced at the onset of a deterioration of climate (end of Early Temperate stage 2) marked by deforestation (high nontree pollen; decline in elm, oak, and hazel; increase in pine and birch), which followed on a long phase of mixed-oak forest, presumably representing the interglacial maximum. This same shift in climate is probably reflected in the solifluction wedge between the (Upper) Middle Gravels and Upper Loam in the Barnfield pit.

The type site of the Clactonian, Clacton-on-Sea (Essex), representing an old channel filled with two lower freshwater beds (the lowermost yielding Clactonian implements in great quantity, a yew-wood spearpoint, as well as fauna and flora) overlain by estuarine beds (Warren 1923, 1924, 1932, 1951, 1955), was generally assumed to correspond with the interval represented in the weathering of the Swanscombe Lower Loam (King and Oakley 1936; Oakley and Leakey 1938; Oakley 1952; Warren 1955). The recently published pollen dia-

gram from Clacton (Pike and Godwin 1953) indicates a mixed-oak forest (oak, elm, and linden, in decreasing order of abundance) extending from the upper part of the freshwater series well into the estuarine series, where it is replaced by a coniferous forest phase particularly high in silver fir. West (1956: 340) has pointed out that "this forest development exactly parallels that of Stage III (= Late Temperate) at Hoxne, with the component trees the same." However, the basal freshwater beds are not represented in the diagram, and it is presumed that these would fall into an earlier Early Temperate stage, very likely even older than the Swanscombe Middle Gravel series. Thus, this evidence does not necessarily contradict the former relative dating of the Clactonian from the Clacton channel to a phase earlier than the Late Boyn Hill stage. These different types of stone industries do not necessarily imply that morphologically distinct peoples were responsible for the Acheulean and the Clactonian. Oakley (1952: 291) has suggested that it is very probable that "the hand-axe people . . . were mainly adapted to life in open grassland, rather than to wooded country," whereas the Clactonian industry "represents the facies of Lower Palaeolithic culture which was more related to forest life." While this is not yet proved, and may very well be extremely difficult ever to prove, it is evident that man's tools, his way of life, and the environments in which he lived are all inextricably linked, and that this is the most productive manner in which to approach the problem.

Table 1 illustrates the specific succession under discussion, and relates it to the general Pleistocene sequence of Britain (King 1955; West 1958) and also that of the Netherlands (Van der Vlerk 1950, 1953; Van der Vlerk and Florschütz 1953; Zagwijn 1957). The well-defined interglacial stages are used as marker horizons (cf. Van der Vlerk 1955, 1956; West 1955). No attempt has been made to offer a correlation with the still inadequately known *earlier glaciations* of the Alpine region. The complex nature of the post-Villafranchian but pre-Great Interglacial stratigraphy is especially to be noted (cf. Boswell 1931, 1936; King 1955). Prior to the well-defined and distinctive Hoxnian (= Needian) interglacial stage, there were *at least* two warmer phases, the earlier represented by the well-known Cromer Forest Bed (Norfolk) (Sainty 1929; Boswell 1958), and the later by the fossiliferous marine sands of the Corton Beds (Baden-Powell and Moir 1942); the latter might represent only an interstadial, although the series cover an interval of erosion, weathering, and marine transgression. The industry of the old Caversham channel, containing a high proportion of Abbevillian and early Acheulean types, was tentatively referred to this stage (Treacher *et al.* 1948), but Wooldridge (1957) agreed that it might be slightly later, and Oakley (in West and Donner 1956: discussion) now considers that it is unquestionably *no earlier* than Great Interglacial. The Forest Bed series is distinct from the Hoxnian, both on faunal (Newton 1882; Osborn 1922; Azzaroli 1951)² and floral (Reid 1890; Reid and Reid 1908; Thomson in Woldstedt 1949; Rein 1955) grounds, and is generally agreed to represent a full "interglacial stage." However, the Forest Bed is clearly post-Villafranchian (post-Tegelen), and also underlies the

river then made a great bow to the west and returned northward, following the same course as the present northward-flowing Elsenz River (Sauer 1898, 1909; Thürach 1909; Rüger 1928*b*). To the north, the two branches of this uncommonly long, parallel-sided loop were separated by the Hollmuth horst or upland. A fairly substantial basin, particularly favorable for extensive fluvial deposition by a sluggishly-moving stream, lay in the bow of the meander at the south end of the loop. The latter coincided with the boundary of the uplifted Odenwald Buntsandstone shield and the Kraichgau depression (northern Mulden flank).

The tectonic instability of the Rhine Valley in general, and of this region in particular, is well known, and various workers (Schmitthener 1922; Kolb 1931; Wagner 1929*a,b*, 1950; Becksmann and Richter 1939) have stressed the important role of tectonic movements in the formation of ancient meanders. This Hollmuth meander of the Neckar follows closely the course of the two, parallel north-south trending, fault zones. The Neckar River, which originally ran near its present course over the earlier-Pliocene surface (Salomon 1924), was apparently forced southward due to terminal Pliocene-basal Pleistocene uplift of the Hollmuth horst along this unstable zone (Becksmann 1950). Some

traces of the earliest fluvial accumulations within the meander are present in the so-called "Wiesenschotter": these lie at high levels, varying from 200 to 150 meters (a.s.l.), and at some localities are known to rest on the eroded shelly limestone bedrock (*Muschelkalk*). The Wiesenschotter, predominantly Buntsandstone, differ from the Mauer gravels proper in the relative absence of limestone elements (probably originally present, but removed by weathering), in the loamy nature of the gravel matrix, and in their brownish color. Becksmann (1950), in stressing the importance of these deposits, pointed out that, at two pits (Ziegler's and Schafer's) in the vicinity, there is evidence of erosion of the Wiesenschotter prior to subsequent burial by the overlying Mauer Sands. The uplift of the Odenwald, which must have largely ended by late Pliocene times, took place prior to the aggradation of the Wiesenschotter series, and subsequent to the erosional phase that developed the Pliocene surface.

The succession exposed in the Grafenrain pit comprises (1) a lower series of fluvial deposits of the ancient Neckar River, overlain by (2) a loessic complex with intercalated weathering horizons (Fig. 5). The lower or fluvial series (Mauer Sands) consist of a basal sandstone gravel followed by a thick accumulation of

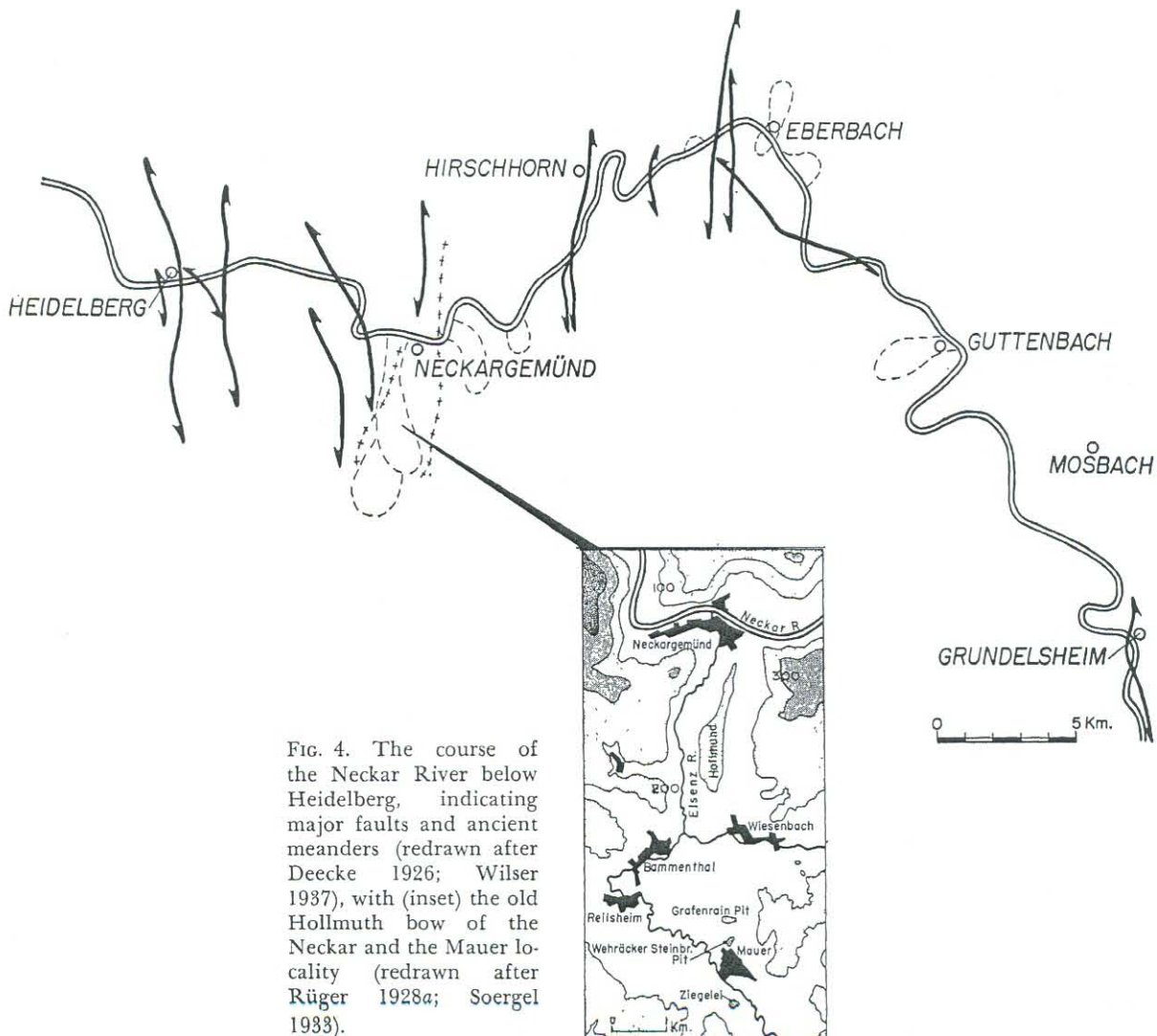


FIG. 4. The course of the Neckar River below Heidelberg, indicating major faults and ancient meanders (redrawn after Deecke 1926; Wilser 1937), with (inset) the old Hollmuth bow of the Neckar and the Mauer locality (redrawn after Rüger 1928*a*; Soergel 1933).

yellow or gray sands, within which occur thin clay lenses (*Lettenbank*). Another sandstone gravel of slight thickness caps these sands. All these sands and gravels, the latter composed largely of quartz, shelly limestone, and red sandstone (Soergel 1928, 1933), are lacking in glacial erratics, and must therefore antedate the first extensive continental glaciation, the Elster (Mindel). The human mandible was found within the Mauer Sands, at a depth of some twenty meters from the top of the pit. These sands have also yielded a particularly abundant and well-preserved mammalian fauna, including, in decreasing frequency, extremity bones, mandibles and teeth, portions of skulls, but only one complete skeleton, that of a young red deer (Rüger 1931, also 1928*b*). The fossils occur in a completely unrolled and fresh condition (cf. Salomon 1926), and are present discontinuously throughout the thickness (c. 5 meters) of the sands. It is clear that at the time of deposition the stream must have been relatively slow-moving and sluggish, with numerous marshy and ponded places where animals came to drink and where Mauer man probably took full advantage of opportunities for hunting. The faunal assemblage, in contrast to that from other such sites, is neither derived nor mixed, but represents a faunal unity and a good sample of local mammals of the time at which the sands were accumulated.

According to the figures first published by Soergel (1923; cf. Wurm 1912*d*, 1913; Freudenberg 1914), seventy per cent of the fauna is comprised of Eurasian rhinoceros (*Rh. etruscus* = 20.5%) (Wurm 1912*b,c*), red deer (*C. elaphus* = 18%), straight-tusked elephant (*El. antiquus* = 18%) (Soergel 1912), and bison (*Bison priscus* = 14%) ; a further eighteen per cent is made up by moose (*Alces latifrons* = 5.5%), roe deer (*C. capreolus* = 6.5%), and horse (*Eq. mosbachensis*). More rare, each constituting 2% to 3% of the assemblage, are remains of a primitive bear (*U. arvernensis* = *U. stehlini* of Heller 1949), both primitive (*T. cuvieri*) and modern (*Castor fiber*) beaver, and wild boar (*S. scrofa*). The list is completed by rarer specimens of various felids (*Felis leo*, *F. catus*, *F. pardus*, *F. issidorensis*) (Wurm 1912*a*; Rüger 1928*a*; Voelcker 1930), a sabretooth tiger (*Homotherium crenatidens* = *Machairodus latidens*) (Rüger 1929; Voelcker 1929), a primitive wolf (*Canis mosbachensis*), primitive hyena (*Hyaena arvernensis*), another bear (*U. arctos deningeri*), and hippopotamus (*H. amphibius*) (Voelcker 1931), and a microfauna including voles (*Arvicola greeni*, *A. mosbachensis*, *Dolomys episcopalpis*) and moles (*Talpa gracilis*, *T. praeglacialis*) (Heller 1934, 1939). This assemblage, as well as the invertebrate fauna (Geyer 1910, 1913), indicates a woodland biotope, probably a deciduous mixed-oak forest (remains of oak do occur in the Mauer Sands), which is widely agreed to be of interglacial age.

The Mauer fauna is post-Villafranchian, and thus constitutes the oldest truly "interglacial" assemblage in continental Europe. On comparative paleontological grounds, its relative age can be fairly well determined, since it is bracketed between an older and a younger steppe fauna (Adam 1952, 1953). The fauna from the Mauer Sands is recognizably younger than the warm-steppe fauna represented by earlier (Stage I) assemblages, characterized by *El. meridionalis-trogotherii*,

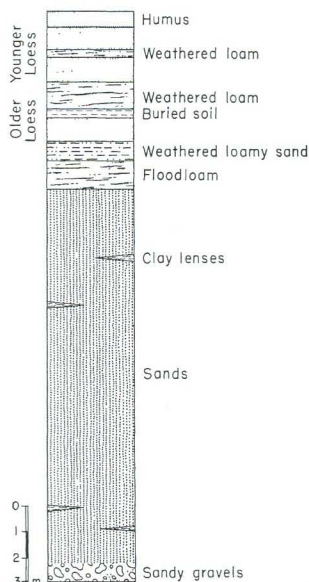


FIG. 5. Stratigraphic succession exposed in the Grafenrain pit at Mauer (redrawn after Müller-Beck 1957).

from the not far distant sites of Mosbach (near Mainz, Rheinhessen) and Jockgrim i.d. Pfalz.³

The Mauer fauna is older than the later (Stage II) fauna from Mosbach. It is also older than the fauna from the high-level (50-70 meters) gravels at Süssenborn, situated about five kilometers east of Weimar, in an old meander of the Ilm River. Both these sites are older than the main faunal assemblage(s) from Steinheim (see below).⁴

There is a good primitive hyena here, from the apparently fully interglacial Mauer assemblage, through to the semi-periglacial steppe assemblage of Süssenborn, the main Mosbach fauna being more or less intermediate. The Süssenborn fauna is widely regarded as of Elster (= Mindel 2 of some authors) glacial age (Soergel 1923, 1924, 1939*a*; Adam 1952, 1953; Zeuner 1945). The full advance of this glaciation extended as far south as Thuringia and the Mittelgebirge (Woldstedt 1950, 1954-8). The Mauer Sands were accumulated in the bow of the Hollmuth meander during an earlier interglacial phase, but the difficult question is to determine which phase. Frequently, since they were known to be "pre-Mindel," the Mauer Sands and their contained fauna have been referred to the so-called "First Interglacial," the Günz-Mindel or Antepenultimate Interglacial of Zeuner; this view was held by Soergel (1933), although he (1928) had earlier held the view that an interstadial

age within the Mindel Glaciation was more probable (accepted by Zeuner 1937, 1945, 1952). Since there is no straightforward way of linking these deposits with the Alpine Pleistocene succession, and since the "First Interglacial" of the Alps has been equated by some authors (cf. Movius 1949b) with the Cromerian stage, it is simpler to avoid such an attempt at correlation.

In terms of the sequence of interglacial stages discussed earlier, the problem might be best framed as follows: Is the Mauer fauna, which is manifestly post-Villafranchian (i.e., specifically post-Val d'Arno, post-Tegelen, etc.) and pre-Great Interglacial, of Cromerian (Bilshausen of northern Germany) age or of still later interglacial/interstadial age?

The fauna from the freshwater and estuarine horizons of the Cromer Forest Bed, studied in the last century by Newton (1882; summary in Osborn 1922, and in Zeuner 1937), is clearly mixed and derived from several sources (Azzaroli 1951; cf. Zeuner 1945). Nevertheless, even when allowance has been made for such mixture, and considering that the North Sea Drift that overlies the Forest Bed series represents a pre-Elster glaciation which is not certainly known in the continental succession, the Mauer fauna is post-Cromerian (Table 2). This is evident from the composition of the bulk of the fauna and is clear also from Heller's (1936, 1939) study of the rodent remains (replacement of *Mimomys* by *Arvicola* at Mauer). It would appear most likely that the Mauer Sands were accumulated during a warmer interval within the marine Taxandrian, a period of extended duration and with a still poorly known series of climatic oscillations. It is altogether likely that this interval corresponds with the Corton Beds, which may be fully interglacial and not merely interstadial (although these terms have limited usefulness at this early time level). As shown before, this was a warmer transgressive phase between the Norwich Glacial and the Lowestoft Glacial advances in eastern Britain. This interpretation is in full agreement with all the available evidence, and avoids the uncontrollable correlation with the Alpine glacial/interglacial stages. If it could be shown that the Mindel does indeed correspond (broadly) with the Taxandrian, then the Mauer Sands and their fauna would correspond to an interglacial/interstadial amelioration within this glacial stage.

Overlying the Mauer Sands is a sandy and calcareous flood-loam succeeded by another thick (2.5 meters) brownish loess-like loam, the upper part of which was consequently weathered and denuded. Soergel (1933) stressed the hiatus above this flood-loam, and concluded that erosion was followed by weathering, a considerable lapse of time being involved. However, as Zeuner (1945) has suggested, it is equally likely that denudation and weathering took place simultaneously.

Above these fluvial deposits are a succession of loesses and weathering horizons. These were regarded by Soergel (1928) as representative of the Older (Penultimate Glaciation = Saale) and Younger (Last Glaciation = Weichsel) loesses. They are separated from the lower fluvial deposits by a discordance, above which are reddish Neckar sands about one meter thick and showing signs of sludging (solifluction). The so-called "Older Loesses" are three-fold, with a major interval of weathering between the basal and middle

elements of the complex. Soergel (1928, 1933, 1939a) concluded, and most workers agree, that this lowermost Older Loess is of Elster age, and was weathered during the Great Interglacial. The overlying, double Older Loess, split by a period of considerable weathering and erosion, undoubtedly constitutes the well-defined Saale and Warthe phases of the Penultimate Glacial stage. These are separated from the typical (for the Rhineland) two-fold Younger Loesses of Last Glacial age by a well-developed loam at the top of the Older Loess; the latter is characteristic of the Last Interglacial throughout western and central Europe. This unique succession provides additional clear-cut geologic confirmation of the age of the Mauer Sands.

Buntsandstone pebbles and flakes, supposedly showing traces of human workmanship, have been discovered by Rust (1956a,b) in the Mauer Sands. However, neither Oakley (1957a) nor the author, who have examined all or some of these specimens, accept that they show clear proof of human tool-making activity. Similarly, a pointed fragment of horse or elk tibia, reported by Voelcker (1933a,b) as a humanly fashioned spearpoint, is of questionable authenticity, just as are the pointed bone fragments from the Mosbach Sands (Schmidtgen 1929, 1931). However, the Mauer mandible is still the oldest proved trace of early man on the European continent, and indications of his stone tools should eventually be discovered, given the proper geological circumstances.⁵

STEINHEIM

The Steinheim skull came to light in July, 1933, among ancient gravels of the river Murr, a tributary of the Neckar River, exposed in the Sigris pit on the northern edge of the village of Steinheim, twenty kilometers north of Stuttgart. As in the case of the Swanscombe cranial fragments, the exact position of the skull is known, since it was left in place within the gravels by the discoverer, K. Sigris, Jr., and only subsequently removed by the late Berckhemer (1933b) of the Naturhistorisches Museum, Stuttgart. The skull was overlain by gravels (5.5 meters) and loess (1.5-2 meters), and underlain by other gravels (up to 9 meters). The specimen lay in a thin, brown, fine sandy-clay (*Letten*) horizon, intermixed with sand, which in places contained coarse pebbles; within the matrix that filled the cranial cavity were small angular limestone fragments. Immediately below the skull horizon was a light, pure sandy level, the sand being derived from weathering of the basement sandstone; immediately above it was another such light sand containing numerous pebbles. These deposits (see below) are highly fossiliferous, including snails (Geyer 1913). Only two days before the skull was discovered, an *El. antiquus* molar was found about 120 centimeters above, and a *Rh. merckii* molar was found a meter below, the skull horizon; two meters above the skull, a mammoth tusk (*El. primigenius*) was also recovered. Subsequently, at the same height above the skull as the aforementioned *El. antiquus* molar, further remains of straight-tusked elephant were found, including additional molars, six tusks, two skull fragments, and a mandible (Berckhemer 1934, 1938).

Upstream from Steinheim, the Murr River flows at a marked gradient through a narrow limestone-walled

valley that widens (up to six hundred meters) and loses gradient for several kilometers between Murr and Steinheim; below Marbach, it is again narrow before it empties into the Neckar River. Between Steinheim and Murr, where the stream gradient has reduced due to the less resistant bedrock (*Lettenkohle*), the river eroded and filled a wide, meandering valley with sands and gravels during the Middle Pleistocene (Fig. 6). The aggraded deposits are of variable thickness, up to fifteen meters, with no trace of a continuous terrace: this suggests the influence of tectonic factors in this deepest part of the valley, probably due to sinking (of the Pleidelsheim basin). Presumably, as Wagner (1934; also 1929a, 1950) has pointed out, the steeply flowing river brought down much rubble and sand from its upper course and deposited its load in this widened valley,

creating gravel accumulations, spits, sand bars, and ponded waters. Such a situation, probably not too unlike that in the earlier Middle Pleistocene bow of the Hollmuth meander at Mauer, would provide maximum opportunity for the preservation of mammalian fossils, and also afford ideal localities for encampments of early man. The animal remains appear to be largely *in situ*, bones of the skeleton often being found together (known for *Bison*, *Bos*, *Cervus*). Traces of rolling are

TABLE 2. Provisional correlation of Middle Pleistocene stratigraphy in the Neckar Valley and the glacial sequence of northern Germany, with correlative stages in the Netherlands marine succession.

NETHERLANDS		NORTH GERMANY	NECKAR and RHINE VALLEY SITES
DRENTHIAN		WARTHE GLACIAL ADVANCE	<i>El primigenius</i> gravels
		OHE INTERSTADIAL	M
		SAALE GLACIAL ADVANCE	I <i>El primigenius-trogontherii</i> gravels
NEEDIAN	HOLSTEINIAN	HOLSTEIN SEA	E
			H
			N <i>El antiquus</i> gravels (<i>Homo</i>)
			I
TAXANDRIAN		ELSTER GLACIAL ADVANCE	E
			T
			S <i>El trogontherii</i> gravels MOSBACH 2; SÜSSENBORN (Thüringia) warm → cool steppe fauna
			MAUER; GRAFENRAIN PIT (<i>Homo</i>) woodland fauna
			MOSBACH 1; JOCKGRIM I warm steppe fauna
Zones of Sterksel— Budel—Woensel— Weert	CROMERIAN	BILSHAUSEN	

The loesses that overlie the Steinheim gravels have been carefully studied by Freising (1952). In the Sigrist pit, there are some five meters of light, yellowish loess, representing the Main Würm, at the base of which is a loamy sandy-clay, representing the well-known Göttsweiger interstadial horizon. In the neighboring Sammet pit, the same general sequence is evident from the basal *antiquus*-bearing gravels through the two *trogotherii-primigenius*-bearing sandy-clay levels, overlain by (presumably Last Interglacial) bedded reddish sandy-clays, and Early and Main Würm flood-loesses; the latter are subdivided by the Göttsweiger loam and an overlying solifluction horizon. This succession confirms the Great Interglacial age of the straight-tusked elephant-gravels, and the Saale Glacial age of the overlying mammoth-gravels.

+60 meters altitude) is represented by conglomerates and beach sands, overlying Cretaceous marls and pre-Cambrian quartzites, in the basal portion of the section. This deposit contains rolled pebble chopping tools and some typologically Chellean (Abbevillian) hand axes, not unlike the assemblages in the lower limits of Bed II at Olduvai Gorge (northern Tanganyika). On its surface an unrolled assemblage was found (described by Neuville and Ruhlmann 1941) that reveals incipient

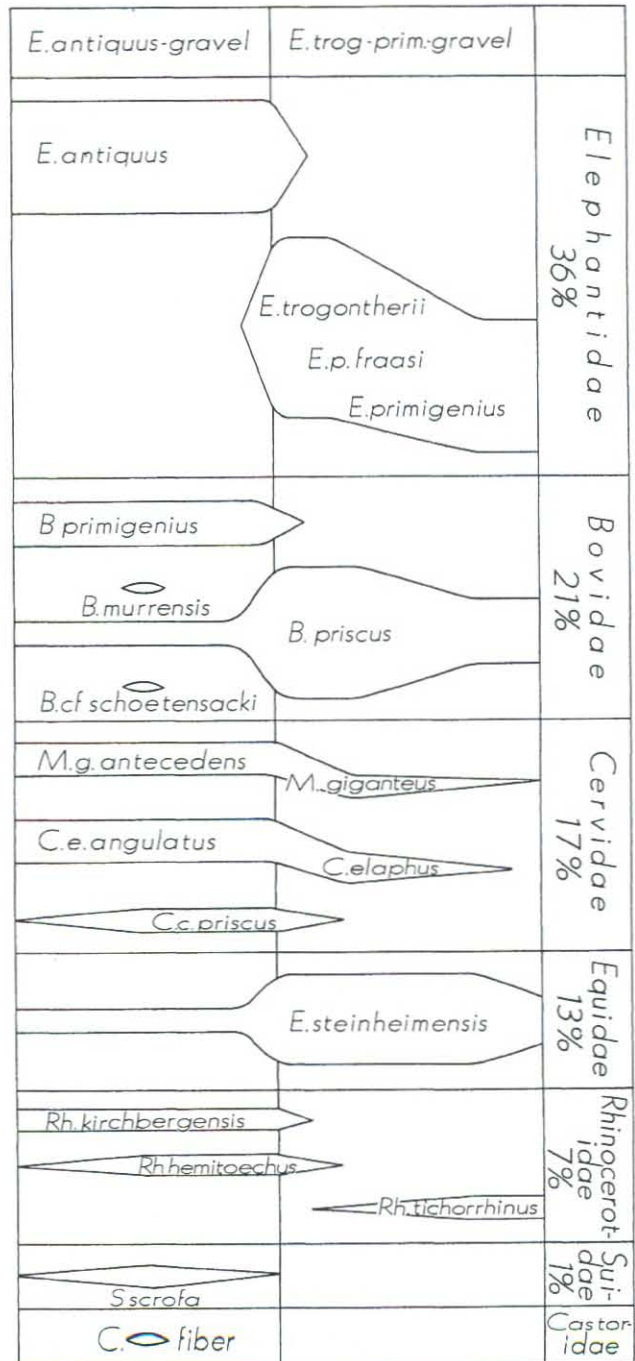
ATLANTIC COAST OF MOROCCO

SIDI ABDERRAHMAN

The Atlantic coast of Morocco, a region relatively stable since the final Tertiary (in this regard unlike the Mediterranean littoral of the Magreb; cf. Dalloni 1940, 1954), has preserved one of the best known Pleistocene successions (for general discussion, see Balout 1955; Vaufrey 1955; also Alimen 1955; Choubert 1956, 1957; Gigout 1957; Gigout and Raynal 1957). The littoral, subject to alternative fluctuations of sea level as ocean water was successively locked up in ice during continental glaciation and later returned to the sea as meltwaters during interglacial deglaciation, is characterized by a series of well-developed ancient marine beaches, intercalated with which are continental formations. The highest of these marine deposits, either two or three in number, range up to +300 meters for the oldest, and +100 to +60 meters for the next younger. These are generally attributed to the Calabrian (probably including the Emilian) and the Sicilian transgressions of the earlier Pleistocene (Lecointre 1952). The former, which in fact represents a progressively regressive sea, analogous to the Waltonian-Weybournian Seas of Britain and the Netherlands, is surely contemporaneous with the continental Villafranchian; the latter corresponds perhaps with the Netherlands Tiglian, but most likely with the younger Cromerian stage. More important for consideration here is the well-developed and often continuous beach of the +30-meter marine transgression, with an invading molluscan fauna that includes *Purpura haemastoma* and *Patella safiana* (in the Mediterranean, *Strombus bubonius*). This represents the Tyrrhenian I (= Tyrrhenian *sensu strictu*) of the Mediterranean marine Pleistocene succession, upon the Great Interglacial age of which practically all workers concerned are in agreement.

One of the localities where littoral accumulations of this sea and related continental formations are best exposed is Sidi Abderrahman, a few kilometers south of Casablanca, where a number of commercial quarries have been opened (Fig. 8). In 1954 one of these quarries, long known for its richness in Acheulean implements, provided a portion of a human mandible in an unusually well-dated context (Biberson 1955, 1956). The terminal or regressive phase of the Sicilian (+55 to

FIG. 7. Distribution of fauna (excluding carnivores) in the interglacial straight-tusked elephant gravels (2) and the glacial Main Mammoth gravels (3) of Steinheim (after Adam 1954a).



traces of a true cylinder-hammer technique for working hand axes; the assemblage contains hand axes and numerous flakes and the first true cleavers in the Moroccan succession (Biberson 1954). This would indicate a transitional Chelleo-Acheulean industry, like that represented, for example, by stages 4-5 in the uppermost part of Bed II at Olduvai Gorge (Leakey 1951).

These conglomerates are overlain by beach sands grading into continental calcareous sands of aeolian origin that make up the prominent Great Dune formation. These sands were subsequently consolidated into sandstone during the Romanian marine regression (Bourcart 1943), a time corresponding broadly with the first major continental glaciation (Elster) in northern Europe. During the initial phases of the Tyrrhenian (I), a transgressive sea carved out a tortuous coastline in this dunar cliff, and percolating waters eroded out karstic caves (Fig. 8, inset). The caves and fissures were periodically occupied by cave-dwelling animals (bears and hyenas), and also were from time to time inhabited by early man; however, the high seas of the Tyrrhenian disturbed and rearranged these continental accumulations at the base of the caves and buried them under marine sediments.

In general, the stone tool assemblages from these caves extend from earliest Middle Acheulean of proto-Levallois technique (stage 1), represented in basal Tyr-

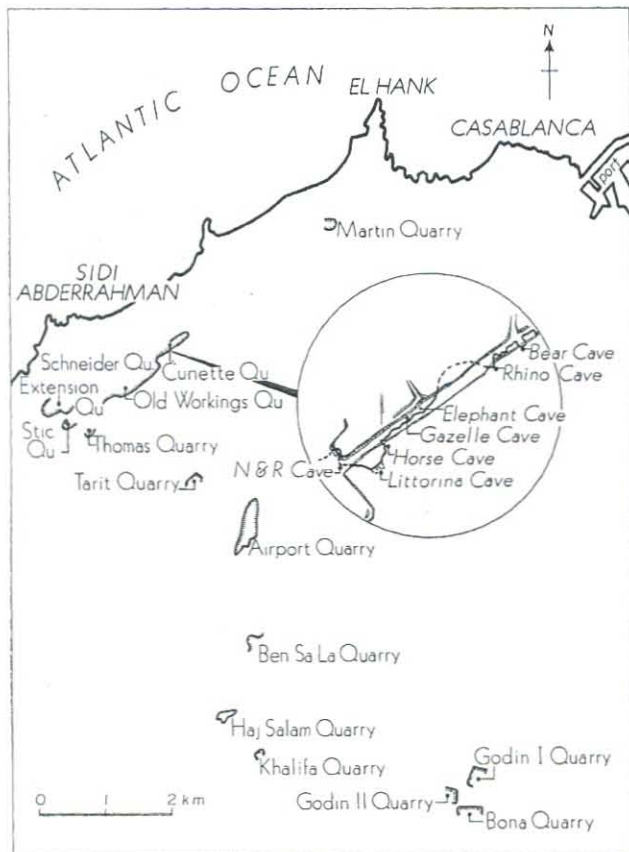


FIG. 8. The Atlantic littoral of Morocco indicating the main quarries of paleoanthropological interest, with (inset) the Schneider quarries at Sidi Abderrahman (redrawn after Biberson 1955, 1956).

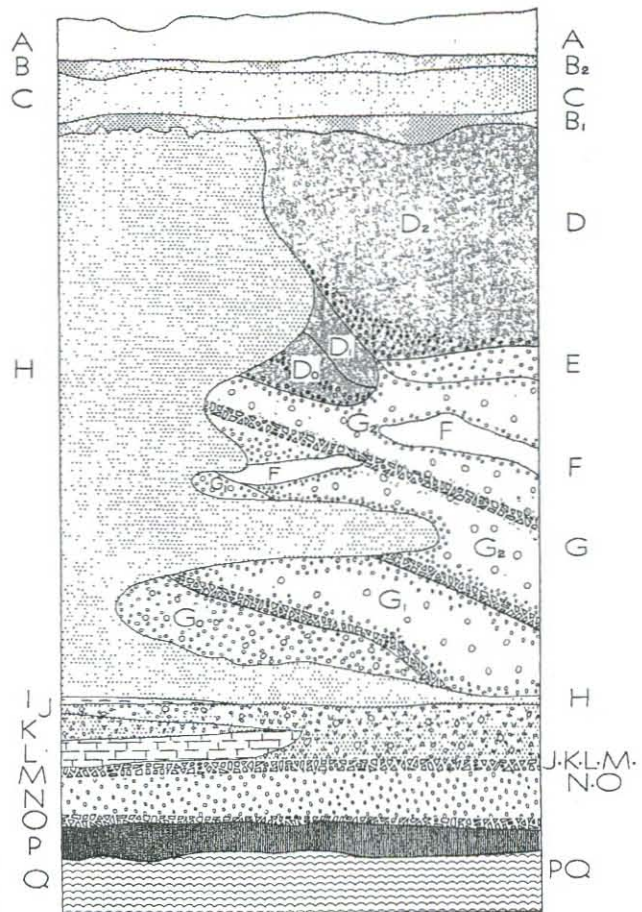


FIG. 9. Succession of deposits exposed in the Sidi Abderrahman (Cunette) quarry (left), and the deposits filling the karstic cave cut into the great consolidated dune H (right). The nomenclature on the left is that of Neuville and Ruhlmann (1941); that on the right is the nomenclature currently employed by Biberson (redrawn after Biberson 1955).

rhenian levels in the Cave of the Bears, through a more developed Middle Acheulean (stage 2), represented in the Littorina Cave, into later expressions (stages 3 and 4) of Middle Acheulean, represented in the S.T.I.C. quarry and the Sidi Abderrahman extension, all of which are of post-Tyrrhenian regressive age. A final Acheulean or Micoquian is also known from calcareous crust formations formed at the time of the ensuing interpluvial (= Tyrrhenian II transgression, or Eemian of the Netherlands).

The Littorina Cave (Fig. 9), which has provided the portion of human mandible (Arambourg and Biberson 1955), reveals a series of basal Tyrrhenian marine deposits (G_0 - G_1 - G_2), consisting of gravels, pebbles, and sands that contain molluscan shells, derived mammalian remains, and Acheulean implements; sometimes there are also intrusive marine sandstone lenses, redistributed by running waters as slope wash. A series of continental deposits (D_0 - D_1 - D_2), sandy and clayey with pebbles, and the topmost brecciated, overlie these marine deposits unconformably, an interval of erosion separating the accumulation of the two series. The fauna from these two series of beds is typically tropical

African, and includes remains of *El. iolensis*, *Rh. simus*, *Eq. mauritanicus*, *H. amphibius*, various antelopes (*Hippotragus*, *Connochaetes*, *Alcelaphus*) and gazelles (*Gazella atlantica*, *G. dorcas*), several hyenas, a fox, wild dog, and ostrich; there is also wild boar (*S. scrofa*) and wild ox (*B. primigenius*).

The human mandible was found in a sandstone lens (F = D₀) at the base of the continental series of deposits. The associated stone tools represent a Middle Acheulean (stage 2) assemblage, numbering 254 pieces (114 of which are waste). More than fifty per cent of the tools were made with stone-on-stone technique, the flake tools being struck from unprepared pebble cores. The proto-Levallois technique, present in the earlier Tyrrhenian deposits in the Cave of the Bears, is entirely absent in this *Littorina* Cave assemblage. The latter comprises numerous hand axes (72), mostly pear-shaped and lanceolate with only rare ovates, rare cleavers (3), a considerable number of pebbles (34) worked into chopping tools and crude bifaces, unifacial tools (13), bifacially worked side-scrapers (2), rare hammerstones (3), cores (3), and bifacially trimmed discs (10) (Biberson 1956).

The *Littorina* Cave human mandible and the associated Acheulean industry is thus clearly dated to the termination of the Tyrrhenian (I) transgression, corresponding in time to the very onset of the post-Tyrrhenian regression and the Penultimate North African pluvial stage. This corresponds with the Drenthian of the Netherlands and the Saale Glacial of northern Germany).

RABAT

In 1933 the Rabat sandstone, or "Great Dune," exposed in the Khebibat (or Mifsud-Giudice) quarry on the sea front of Rabat, provided the first Middle Pleistocene human remains ever found in northwest Africa. The specimen, perhaps a nearly complete human skull originally, was exposed by blasting in the quarry, but was later reburied by the local workmen. Marçais (1934) was eventually able to recover twenty-three fragments, aside from the original portion of mandible given him by the quarry manager.

As at Sidi Abderrahman, the consolidated sandstone of the "Great Dune" forms a prominent feature of the topography of the Rabat littoral (Bourcart 1943). Jaranoff (1936) noted some years ago that this sandstone was complex, with two dunes being separated by a purely marine horizon. This conclusion was confirmed by subsequent investigations (Choubert and Marçais 1947;

Bourcart, Choubert, and Marçais 1949). Between the Khebibat quarries and Chellah hill to the northeast, the lower part of this marine sandstone, with alternating pebbly molluscan (*Littorina*) beds, overlies a submerged basal conglomerate containing *El. cf. meridionalis*. These appear to represent, just as at Sidi Abderrahman, marine formations of the Sicilian transgression. In the Khebibat quarry the surface of this sandstone has been eroded, and, according to Neuville and Ruhlman (1942; also Ruhlman 1945a,b), is overlain unconformably by a shelly (*P. haemastoma*) marine conglomerate, above which is another consolidated calcareous sandstone, some eight to ten meters thick (Fig. 10). The human remains were found in the middle portion (the exact level is unknown) of the upper Rabat sandstone. This sandstone has yielded also a typically tropical African faunal assemblage, including *Rh. simus*, *Eq. mauritanicus*, *H. crocuta spelaea*, *H. amphibius*, *B. primigenius*, *G. atlantica* and *Bubalus boselaphus* (Arambourg 1938; also 1952).

It seems quite clear that the Rabat lower sandstone is of post-Sicilian (I) age. Sometimes this has been referred to as an horizon of "Milazzian" age; however, this marine horizon is distinct not even in the type locality. As at Sidi Abderrahman, this marine formation was exposed to weathering and became consolidated during the Romanian regression (= Amirian pluvial). Lecomte (1952, 1953) earlier stated that the human remains were correspondingly of this same age, since they post-dated the *Littorina* conglomerate, and were earlier than the *P. haemastoma* conglomerate; he did not believe that a conglomerate with *P. haemastoma* occurred below the upper sandstone, except in places where there was infilling, which he attributed to an Upper Pleistocene or Ouljian (cf. Gigout 1957) transgression. However, such a shelly conglomerate is present, as Choubert (1955) has demonstrated, so that the "Great Dune" at Rabat is not wholly of the same age as that at Sidi Abderrahman. The upper portion of the sandstone represents a Tyrrhenian I dune. The human remains and the mammalian fauna must be contemporary with the post-Tyrrhenian (I) regression, or, under the newer ter-

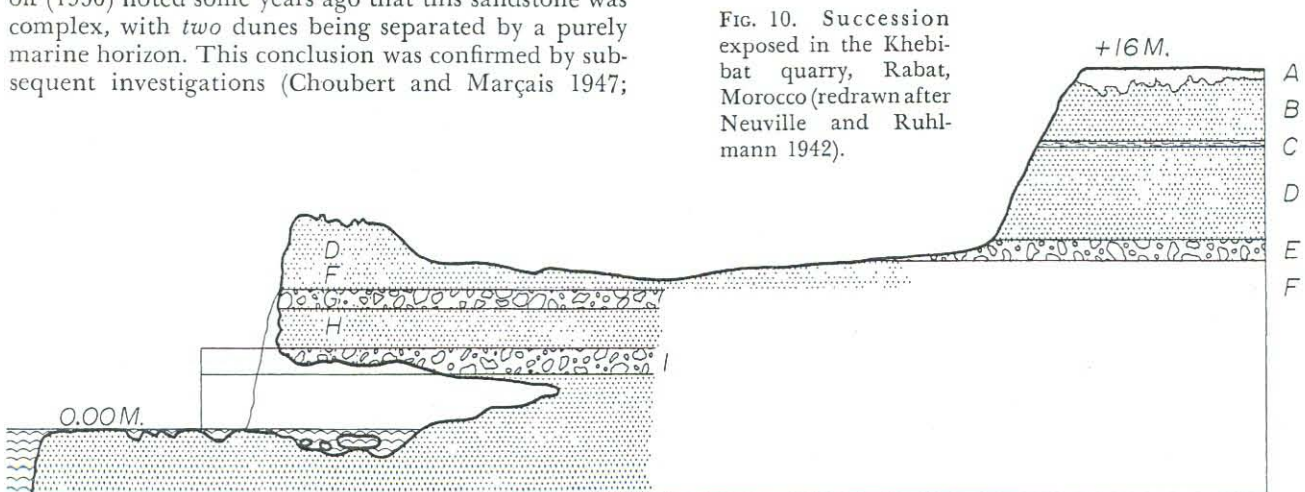


FIG. 10. Succession exposed in the Khebibat quarry, Rabat, Morocco (redrawn after Neuville and Ruhlmann 1942).

minology, with the Tensiftian pluvial (Biberson and Lecoindre 1956). The human remains are, therefore, broadly contemporaneous with those from the Littorina Cave at Sidi Abderrahman.

ALGERIAN PLATEAU: TERNIFINE

The Algerian site of Ternifine (or Tir'enfin) is a large sand pit situated several hundred meters west of the village of Palikao, twenty-two kilometers east of Mascara, department of Oran. Commercial working of a large hill of sand opened the pit in 1872. Shortly thereafter, it yielded the first of a considerable series of mammalian fossils (Pomel 1879), and subsequently yielded also stone tools (Tommasini 1883; see Balout 1955 for an excellent summary of the earlier investigations at the site). In 1886 and 1888, Pallary (Pomel and Pallary 1888) carried out investigations in the upper levels and recovered considerable fauna, much of it being described in the paleontological memoirs by Pomel (1893-98). This work, restricted to the zone above water level, exposed two main horizons, from two to three meters in thickness, within each of which were several sandy horizons, some sterile and others containing stone tools (pebble tools, bifaces, cleavers, and flakes) and/or mammalian fossils.

The true nature of the site was first revealed by Arambourg (unpublished) in 1931; further work in 1954 and 1955, in the lower flooded levels, provided additional fauna, stone implements, and the first human skeletal remains (Arambourg 1954*b,c*; Arambourg and Hoffstetter 1954). The site is a small lake basin filled during the Middle Pleistocene with fossiliferous and implementiferous sands. During the existence of the lake, the plain of Eghris in which it is situated was some twelve meters higher than at present, which indicates that extensive erosion and denudation took place during the later Middle and Upper Pleistocene. As in the present-day neighboring Lake Palikao, the waters are of artesian origin, and the lower levels remain submerged (necessitating the use of pumps in the recent excavations). The uppermost levels of the profile (Fig. 11) exposed at Ternifine are sandstone bands, hardened by surface exposure as the waters of the ancient lake evaporated; these deposits cap and preserve the softer, underlying, unconsolidated, siliceous clayey-sands. All the beds of sand are horizontally disposed, or reveal a very slight concavity, and their margins can be defined at the edge

of the small basin. Arambourg's (1954*a*) work now indicates that there is no evidence to support Pomel's view that the sands were carried up by artesian waters and deposited around active springs.

The mammalian faunal assemblage from the site is a very rich one, and is particularly important for determining the relative geological age of the site. Many of the bones are broken, especially those with large medullary cavities, and it is likely that the activities of early man are to some extent responsible; cranial remains are distinctly rare, although a complete elephant skull was found in 1954. The typical African savannah fauna includes very abundant hippopotamus (*H. amphibius*), zebra (*Eq. mauritanicus*), hartebeest (*Alcelaphus*), wildebeest (*Connochaetes*, *Gorgon*), gemsbok (*Oryx*), buffalo (*Bubalus*), sheep (*Ovis*), gazelle (*Gazella* sp.), giraffe, camel (*C. thomasi*), elephant (*El. atlanticus*), rhinoceros (*Rh. mauritanicus-simus*), carnivores (*Felis* sp., *H. crocuta spelaea*, *C. anthus*, and a sabretooth, *M. latidens*), as well as a giant wart-hog (*Afrochoerus* sp.), and a giant baboon (like *Simopithecus*). This fauna, considerably different from that of the North African Villafranchian (cf. Arambourg 1949), is characterized by some elements absent from, and also lacks some elements present in, later Middle Pleistocene faunas (such as those at Rabat and Sidi Abderrahman) (Arambourg 1952). This would suggest an earlier Middle Pleistocene age, either before or very early in the Tyrrhenian (I) stage. This conclusion is broadly confirmed by the assemblage of stone tools in quartzite or dolomite, recovered from the Ternifine Sands. It comprises choppers and chopping tools, rare polyhedral spheroids, block-on-block flakes some retouched as scrapers and borers, and hand axes and cleavers. The hand axes are numerous; they are made of pebbles or fragments of pebbles, and are thick and often show traces of cortex. Long or more pointed piriform shapes are uncommon, and most are roughly pear-shaped. There are few cleavers, and they are made with block-on-block technique from unprepared cores or pebbles. This assemblage, as recently described by Balout and Tixier (1957), is homogeneous and represents an early Acheulean industry, like stages 1 and 2 (the "Clacto-Abbevillian" of Neuville and Ruhlmann 1941) of the S.T.I.C. site at Sidi Abderrahman (cf. Balout 1955). The latter, resting on the surface of the Sicilian conglomerate, dates toward the end of the Romanian re-

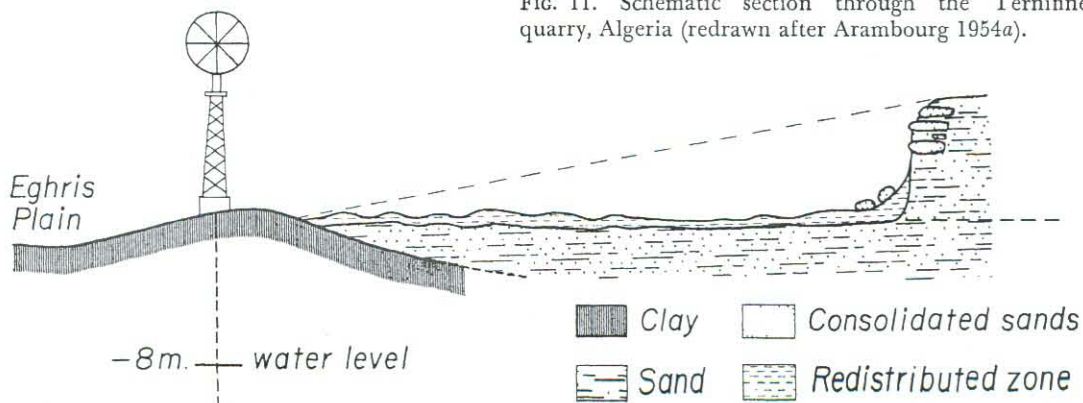


FIG. 11. Schematic section through the Ternifine quarry, Algeria (redrawn after Arambourg 1954*a*).

gression, as has been noted previously. Thus, on these grounds, the Ternifine human skeletal remains are the oldest known from Northwest Africa.

The temporal interrelationships of the Middle Pleistocene human remains from northwest Africa are shown in Table 3. Gigout and Gourinard (1956) have recently offered a correlation between the Moroccan Atlantic and the Algerian Mediterranean littorals. The correlation offered here is in general agreement with

theirs, except for the present writer's subdivision of a two-fold Sicilian marine stage (cf. Choubert 1956, 1957).

GENERAL CONCLUSIONS

Human skeletal remains earlier than the Upper Pleistocene are but sparsely represented from widely scattered sites in Britain, westernmost Germany, and the Atlantic and Mediterranean littorals of northwest Africa. The scarcity of human fossils is due largely to a dearth of actual occupation sites and to the apparent general absence of burial practices among these primi-

TABLE 3. Provisional correlation of Middle Pleistocene stratigraphy of the Moroccan littoral and the Algerian littoral, with correlative stages in the Netherlands marine succession.

NETHERLANDS	ATLANTIC MOROCCO		ALGERIA	
	CASABLANCA	RABAT	LITTORAL	INLAND
DRENTHIAN	V D ₂ Sidi-Abd Extension IV continental sands, loams and gravels III D ₁ II → Homo D ₀ (=F) ←	Consolidated dune (<i>Homo</i>)	post-TYRRHENIAN REGRESSION TYRRHENIAN REGRESSION	evolved M. Acheulian Clairfontaine Lac Karar Champlain
	← M. Acheulian → Karstic caves developed in Great Dune I ←	marine gravels and sands Marine conglomerate		
TAXANDRIAN	Amirian L. Acheulian I Great Dune consolidated		ROMANIAN REGRESSION ROMANIAN REGRESSION	L. Acheulian I Ternifine lake beds
	SICILIAN II Conglomerate - +55 to +60 meter shore line <i>Littorina littorea</i> , <i>Purpura lapillus</i>			
	Saeletian			
Zones of Sterksel - Budel - Woensel - Weert	SICILIAN I	+80 to +100 meter shore line <i>Trochatella trochiformis</i> , <i>Acanthina crassilabrum</i> , <i>Cyprina islandica</i> , <i>Mya truncata</i>		

tive peoples. In the cases of the Mauer and Steinheim specimens, local geological factors, related to tectonics and the meanderings of the Neckar River and its tributary the Murr, afforded favorable circumstances for the accumulation of skeletons of Middle Pleistocene animals, including a human skull. At Swanscombe, there is every indication of actual occupation sites of peoples of the Acheulean, adjacent to the small tributary channels of the sluggishly meandering Thames River. At Ternifine, the situation is less clear, the human remains and other mammalian bones, as well as earliest Acheulean implements, being found in fresh condition at the base of a small depression once occupied by a mere or small lake. Primitive hunting-and-gathering peoples of the Acheulean presumably occupied the margins of this body of water, and it may be that the occurrence of unrolled bones and tools in the floor of the basin is a reflection of man's activities in discarding rubbish (also the opinion of C. Arambourg, personal communication). Only at the Littorina Cave, and perhaps at Swanscombe, is there evidence of a probable occupation site originally *in situ*, but in each case subsequently disturbed. None of these occurrences is comparable to an occupation site like Locality 1 at Choukoutien, or to the open-air habitation sites of eastern Africa represented by localities in Olduvai Gorge and at Isimila in Tanganyika, or at Ologesailie and Kariandusi in Kenya. Torre in Pietra, a littoral occupation site of peoples of the Acheulean that is situated west of Rome, has provided stone tools and fauna (largely horse) from an ancient land surface (A.C. Blanc, personal communication), but human skeletal remains are lacking, as they are generally at the otherwise rich eastern African sites.

All these human remains are of broadly Middle Pleistocene age, but their relative datings are in fact spread over a considerable range of this span of time.

The famous Mauer mandible is of the greatest antiquity, and dates from an "interglacial" interval prior to the Elster Glaciation. This interval presumably corresponds with the ameliorative phase between the North Sea (Norwich) and the Lowestoft Glacial advances. It seems likely that this interval is represented in certain sections by the second regressive phase of the Sicilian transgressive stage (sometimes termed "Milazian"). Somewhat younger are the recently recovered human remains from the Ternifine sand pit, found in

association with an archaic Middle Pleistocene fauna and an early Acheulean industry. On faunal grounds, these remains are pre-Tyrrenian (1). They date broadly from the same stage as the well-known fossils of Java man (*Homo erectus*) from the Trinil beds. The earlier Javan hominids from the Djets beds, *H. modjokertensis* and "*Meganthropus*," are pretty clearly post-Villafranchian, but presumably still older than the Mauer jaw. This conclusion is based on Hooijer's (1952, 1957; Hooijer and Colbert 1951) recent analyses of the faunal succession in Java, work of great importance for correlation of the Pleistocene sequence established there.

The two well-preserved, but damaged or incomplete, skulls, from Steinheim and Swanscombe, are representative of European peoples of the latter part of the Great Interglacial. In the latter case, the industrial association is broadly Middle Acheulean; the assemblage is considerably advanced in comparison with that found in association with the Ternifine human remains. It is strange that no stone implements have ever turned up either at Steinheim or at Mauer. The Steinheim and Swanscombe specimens are broadly contemporaneous with the people of the renowned site of Choukoutien, Locality 1, found in association with the Choukoutien chopper/chopping-tool industry (Movius 1944, 1949a).⁶

Somewhat younger are the human remains from the Littorina Cave at Sidi Abderrahman and from the Rabat sandstone. Both are clearly dated to the early post-Tyrrenian (1) regressive stage. They thus correspond to the onset or early phase of the Penultimate Glaciation (Tensiftian Pluvial).

MORPHOLOGY OF THE SKELETAL REMAINS

EARLY MIDDLE PLEISTOCENE

Skeletal remains of pre-Great Interglacial peoples from Europe and Mediterranean Africa are restricted to mandibles and the lower dentition; a single parietal bone from Ternifine represents the only portion of cranium known. The general lack of cranial remains complicates comparisons with the southeastern Asian peoples from the Djets and Trinil beds of Java, which, with the exception of the Sangiran B mandible fragment (from the Djets beds), are known nearly wholly

TABLE 4. Some measurements of Middle Pleistocene hominid mandibles.

	Sangiran B	Choukoutien G ₁	Choukoutien H ₁	Mauer	Ternifine 1.	Ternifine 2.	Ternifine 3.	Sidi Abderr.	Montmaurin
Symphysial ht.	39	40	32.5	34	39	35	39	—	(29)
Body ht. (behind M ₁)	31.1	33.2	25.4	34.3	35	34	38	34.5	(31)
Body thickness (behind M ₁)	18.9	18.8	16.6	22	19	16	20	17	(16)
Ramus ht.	—	74	77	71	—	72	93	—	(70)
Ramus breadth	—	40.7	39.7	52	—	45	48	—	(45)
Mandibular angle	—	97°	108°	105°	—	98°	111°	—	110°
Total length	—	103	94	120	110	110	129	—	(116)
Bicondylar breadth	—	150	102	133	—	—	158	—	(137)

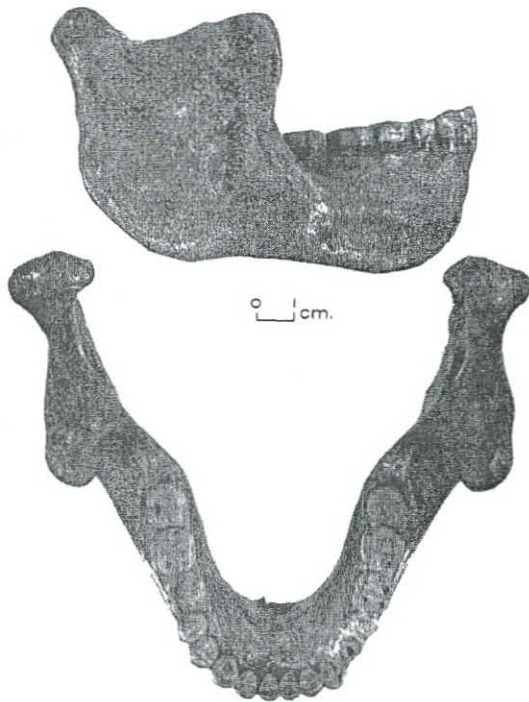


FIG. 12. Right lateral and occlusal views of the Mauer mandible. (Photographs courtesy of B. Engels, Geologisch-Palaeontologisches Institut, Universität Heidelberg.)

from crania. However, aside from the Sangiran B mandible, the remains of the later Choukoutien Locality 1 people provide some materials for comparison.

The Mauer mandible (Schoetensack 1908; Wust 1951) is still the earliest known human fossil from either Europe or Mediterranean Africa. In common with other early men, it is massive and robust (Table 4), the mental foramina are multiple (3 right, 2 left), the symphyseal region is posteriorly inclined, and the alveolar arch is characteristically parabolic. However, it has certain unique features, including (1) the extraordinary breadth of the ramus, massive-rounded-off and low coronoid process, and related shallow sigmoid notch; (2) the extreme depth of the prelacteal segment of the body, related to the marked inferior extension of the marginal torus and anterior marginal tubercle (resulting in the formation of a cupid's-bow shaped submental incisure); and (3) the relatively moderate size of the dentition compared to the massiveness of the mandible (Fig. 12). In these aspects of its morphology, the Mauer specimen is distinguished from broadly contemporaneous peoples of southeastern Asia as well as from the somewhat younger northwest African Ternifine people. There are also some minor differences, compared to the Choukoutien mandibular morphology, in the architecture of the ramus: on the lateral surface the mandibular angle is scarcely everted and a true masseteric fossa is absent, both features being related to the pattern of development of the masticatory musculature; the ectocondyloid crest (and lateral sub-condyloid tubercle) is absent; on the medial surface the attachment area for the internal pterygoid muscle is extensive,

but the superior and inferior pterygoid tubercles are not especially developed.

As in all hominids, the anterior dentition is reduced relative to the posterior. However, this reduction largely affects the crowns of the teeth, and the roots of the canines and incisors are still robust and long (Fig. 13). Consequently, as Weidenreich (1936, also 1934) has clearly shown, the symphysis is thick, the alveolar plane well-developed, the superior transverse torus is massive with a marked genioglossal fossa below it, the alveolar and basal arches are scarcely separable (only a faint depression corresponding to the anterior symphyseal incurvature), and a bony chin (*mentum osseum*) is altogether absent (Fig. 14); the presence of a true mental trigone is difficult to confirm, but a low rounded protuberance marks the symphyseal tuber. The digastric fossae, separated anteriorly by a rounded basal trigone, are broad and relatively short (rather than long and narrow as in the Choukoutien folk), and, although extensive anteriorly, are also directed backward onto the basal arch.

The Mauer incisors show a basal lingual tubercle and slight marginal ridges. The canine, unfortunately much worn, is swollen buccally, and exhibits a basal lingual tubercle as well as a median, and marginal lingual ridges. The molar series is not, as is sometimes claimed, especially small, except in comparison with the massiveness of the mandible. The dimensions of these teeth fall fully within the range of variation of the Choukoutien Locality 1 people, as well as of most of the Middle Pleistocene peoples of northern Africa (Table 5).

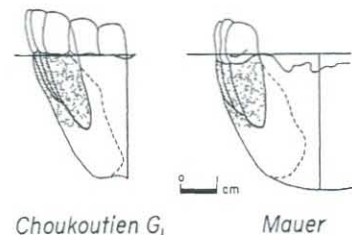


FIG. 13. The symphyseal region and emplacement of anterior teeth in the Mauer and Choukoutien G₁ mandibles (redrawn after Weidenreich 1936).

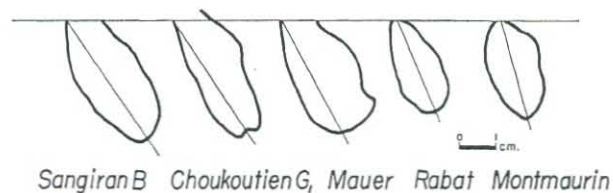


FIG. 14. Mid-sagittal sections through the symphyseal region of some Middle Pleistocene hominid mandibles (redrawn after Von Koenigswald 1940; Weidenreich 1936; Vallois and Roche 1958).

The crown of P_1 is asymmetrical, consequently its transverse axis is obliquely oriented, with full and prominent buccal cusp, from the apex of which ridges extend mesially and distally, and a small buccally-situated lingual cusp; a median ridge extends between the cusps, and the anterior and posterior foveae are well developed; there is slight buccal swelling of the crown but no true cingulum. The crown of P_2 is symmetrically rounded, and the prominent buccal and small lingual cusps are joined by an enamel ridge; the anterior, and particularly the posterior, foveae are well defined. The molars, moderately taurodont, are longer than wide, the third molar being reduced and the second molar the largest of the series, as is frequently the case in other early hominids. A cingulum, or even traces of it, is lacking. The cusp pattern is of the dryopithecine sub-Y5 (M_1) or +5 (M_2 , M_3) pattern, with a well-developed hypoconulid and prominent metaconid and hypoconid; probably M_3 , and certainly M_2 , possessed a sixth cusp. In M_1 and M_2 the hypoconid-metaconid contact is evident, but in M_3 the enlarged entoconid is in contact with the protoconid.

Lack of additional human skeletal material from this time level limits generalization, since it is impossible to control the range of variability within the population of which the Mauer specimen is an isolated sample. Nevertheless, there are fundamental differences, expressed in both the mandibular and dental morphology, between the Mauer individual and such eastern Asian forms as the individual (B) from the Djetis beds at Sangiran (Von Koenigswald 1940; Weidenreich 1945) and the younger Choukoutien Locality 1 population (Weidenreich 1936, 1937). A considerable period of genetic isolation was clearly required to produce such divergences, if these respective peoples were commonly derived from a primitive hominid radiation, such as might be represented by an unspecialized form of australopithecine.

The recent discovery of three human mandibles (Arambourg 1954c, 1955a,b,c, 1956), other isolated teeth, and a parietal bone (Arambourg 1955d) at Ternifine ranks as an event of prime importance in human paleontology. The need for caution in arriving at far-reaching conclusions from isolated specimens is indicated by the morphological variability of these remains.

The three Ternifine mandibles are all extremely robust and massive (Table 4). No. 3 (Fig. 15) is the largest, its length and (bicondylar) breadth exceeding even that of the Mauer mandible. In all specimens, the borders of the body are parallel; in No. 1 (Fig. 16), there is a prominent marginal torus (less developed than in Mauer, however), with anterior and posterior marginal tubercles. The marginal torus and anterior marginal tubercle of No. 3 are also prominent; the former is delimited by a well-defined inter-toral sulcus. This development of the torus accentuates a prominent circumflex-formed submental incisure. As in other early hominids, there is a tendency for multiple mental foramina, two in No. 1, and two (right) or three (left) in No. 3; in No. 2 the foramen is single; the foramina are situated either below the second premolar (No. 3) or between the premolars. In all specimens, the symphysis is thick and inclined posteriorly; its anterior face, in both No. 2 and No. 3, and as in the Choukoutien people, reveals the presence of a slight mental trigone, but no *mentum osseum*. The lingual symphyseal surface is strongly inclined backward, and the alveolar plane is markedly developed (especially in No. 2 and in No. 3) and slightly concave. Only in No. 3 is there development of the superior transverse torus; but this structure is much less pronounced than in the specimen from Mauer, and approaches the reduced condition found in the Sangiran B specimen and in those from Choukoutien Locality 1. In No. 2 there is a slight genioglossal fossa, at the base of which the foramen supra-spinosum opens; in No. 3 the fossa is more clearly delimited and deeper; below it the genial tubercles are united in a salient submental spine. In the Choukoutien folk there is no pit, but a "real mental spine" with upper tubercles for the genioglossi and fused lower tubercles for the geniohyoid muscles (Weidenreich 1936). In No. 1 and No. 2, the digastric fossae are relatively short, but much more extensive in No. 3; in Nos. 1 and 3, these occupy only the ventral face of the basal arch, but in No. 2 there is a tendency for expansion obliquely backward onto the lingual face of the body.

TABLE 5. Dimensions of lower premolar and molar teeth in Middle Pleistocene hominids and in the australopithecines (*Australopithecus* and *Paranthropus*).

		Sterkfontein	Swarthkrans	Sangiran B.	Choukoutien Loc. 1	Mauer		Ternifine 1.	Ternifine 2.	Ternifine 3.	Sidi Abderr.	Rabat	Montmaurin	
						r	l						r	l
P_1	b	11.7-11.8	10.6-12.9	—	8.9-10.8	9.0	—	9.0	11.2	10.0	9.6	10.0	—	—
	l	9.0-9.2	9.2-10.5	—	7.9-9.8	8.1	7.3	8.5	9.0	8.0	9.0	9.0	—	—
P_2	b	11.6-11.7	12.0-17.0	11.0	8.0-11.1	9.2	—	10.0	10.5	10.0	—	—	—	—
	l	9.8-10.1	10.3-12.5	9.2	8.5-9.2	7.5	—	8.0	9.5	8.2	—	—	—	—
M_1	b	11.2-13.9	13.0-15.2	13.0	11.1-12.6	11.2	—	12.0	13.0	11.8	11.6	11.0	10.5	10.7
	l	13.0-15.1	14.3-16.1	12.5	11.3-13.6	11.6	11.1	12.8	14.0	12.0	13.0	13.0	12.5	12.5
M_2	b	13.2-15.3	13.9-16.2	13.2	11.4-12.9	12.0	—	13.7	13.7	12.1	11.4	11.3	11.0	11.0
	l	14.3-16.8	15.0-17.4	13.0	11.9-12.9	12.7	12.9	13.0	14.2	12.0	14.4	12.5	12.0	12.5
M_3	b	12.7-14.8	12.9-16.5	12.5	10.0-12.4	10.9	11.3	12.5	12.5	11.5	11.2	10.6	10.7	11.0
	l	13.5-16.7	15.4-18.5	14.5	10.0-12.9	12.2	11.5	12.0	13.2	8.0	12.2	12.0	13.0	13.0

As is the case in the Choukoutien people, there is fairly marked variability in the form of the mandibular ramus. In No. 2 (Fig. 17) the ramus is relatively broad, but low, with short truncated coronoid and shallow mandibular (sigmoid) notch. However, in No. 3 the ramus is not only broad, nearly attaining the dimensions of the Mauer specimen, but extremely high and more posteriorly inclined; the coronoid process is extraordinarily prominent and massive, exceeding the condyle in height, with an attendant narrow and deep sigmoid notch. All these features are reminiscent of the smaller G_1 specimen from Locality 1 at Choukoutien. The mandibular angle (111°) is truncated in No. 3, as it is in Mauer, with a very thick margin that is slightly everted in its lower portion but twisted inward in its upper half; this also corresponds rather closely to the morphology of the Choukoutien G_1 specimen. The masseter and internal pterygoid insertion areas are especially salient, the ectocondyloid crest is pronounced, and a thick ridge is developed throughout the vertical extent of the thickened anterior margin of the coronoid; in No. 2, on the other hand, these features are either absent or much attenuated.

In all three specimens, the dental arch is parabolic, being most rounded in No. 2; but, in No. 3, the pre-lacteal portion projects farther anteriorly due to the robust canine-incisor series (Fig. 18). The form of the arch in the Ternifine specimens approximates closely to that of the Choukoutien people; however, among the former the arch is more posteriorly divergent, reflecting some differences in the form of the palate and the structure of the facial skeleton. The Mauer arch is smaller, especially its pre-lacteal portion, which is also more gently and symmetrically curved.

The teeth of the Ternifine peoples are relatively macrodont, as in the case of most other early Middle Pleistocene hominids (Table 5). It is interesting to note that the extremely robust No. 3 mandible has, in general, smaller teeth than the other two specimens, especially No. 2, which has the largest teeth, but a more gracile mandible. The incisors are unknown, except for a very worn right lateral in No. 3, which is small-crowned; however, the dimensions of the sockets for these teeth indicate that there was some tendency for root reduction. The canines, a very worn example of which is preserved in No. 3, were evidently large-crowned with robust and deep roots, as in the Choukoutien folk.

The premolars are large, both absolutely and relative to the size of the molars. In Nos. 1 and 2, the crown of P_1 shows a large compressed main cusp on the buccal margin, from the apex of which ridges extend mesially and distally; a smaller lingual cusp is situated somewhat distally on the lingual margin. Both anterior and posterior foveae are well developed. The crown is asymmetrical, there being poor development of the mesio-lingual margin, so that the transverse axis through the cusps passes obliquely to the plane of the mesio-distal axis. On the mesial and distal edges of the crown, there are well-defined oblique cingular ridges. The same basic structure is evident in the more worn right P_1 of specimen No. 3. The root system is semi-bifid, with separate pulp chambers. In general, the crown and root structure of this tooth in the Ternifine remains is remarkably

similar to that of the Choukoutien folk. This morphology is also present, in a more primitive condition, in the Villafranchian hominid, *Australopithecus*, as Robinson (1956) has so clearly shown.

The crown of P_2 is symmetrically shaped, and rectangular, or sub-rectangular, with rounded buccal margin. In No. 2, in which this tooth is least worn, there are numerous wrinkles on the occlusal surface. This is a double-rooted tooth, at least in the No. 3 individual. The buccal cusp is very large, with a well-defined prominent mesial ridge passing inward from its apex. The lingual cusp, of considerable size in specimens Nos. 1 and 2 especially, is situated opposite the buccal cusp on the mesial half of the crown. The anterior fovea is evident, but the posterior fovea is particularly prominent and large; a low triangular ridge extends buccolingually between these cusps, and separates the foveae. The anterior and posterior walls bounding these foveae are in general well developed. The talonid is relatively large, especially in Nos. 2 and 3 in which a cusp is nearly formed on the disto-lingual margin (a condition found in some modern human populations). Mesial and distal oblique cingular ridges are clearly evident on the buccal faces of the teeth. This basic crown pattern, present in the australopithecines (Robinson 1956), is also common in the eastern Asian hominids from Java (Sangiran B mandible) and Choukoutien (however, in the latter the crown of P_2 is rather more rounded, and approaches more closely the shape found in the mandible from Mauer).

The lower molars of the Ternifine mandibles are in general large, although there is a fair range of variability in the three specimens (Table 4). The second molar is the largest in the molar series, and reduction of M_3 is evident in all three individuals. This condition is also characteristic of the Choukoutien population, but the earlier Sangiran mandible from the Djetis beds lacks such reduction, and this tooth is the largest of the series. In No. 2, all the molars are longer than wide; but, this feature is not general, since M_2 and M_1 of specimen No. 1, and M_2 and M_3 of specimen No. 3, are wider than long (Table 4). This same variability is evident, however, in the Choukoutien people, and in the older remains from the Djetis beds. The Ternifine lower molars exhibit a dryopithecine Y5 or +5 cusp pattern, with predominance of the metaconid and a characteristic metaconid-hypoconid contact. However, the cusp pattern of the molars is rather variable and perhaps in the process of change; for example, in individual No. 2, the last two molars are considerably squared-off, and the hypoconulid somewhat reduced in size, indicative of the modification antecedent to the +4 pattern. A sixth cusp occurs in M_2 and M_3 of individual No. 2, and perhaps in M_3 of individual No. 3. Extensive crenulations of the occlusal surface, so well known in the Choukoutien Locality 1 folk, were probably characteristic (judging from the least worn P_2 and molars of individual No. 2). Traces of a cingulum on the swollen buccal surfaces of the molars are evident in the No. 2 specimen, and also on M_1 and M_2 of the No. 3 specimen. Nearly all these features are characteristic of the Middle Pleistocene peoples of eastern Asia.

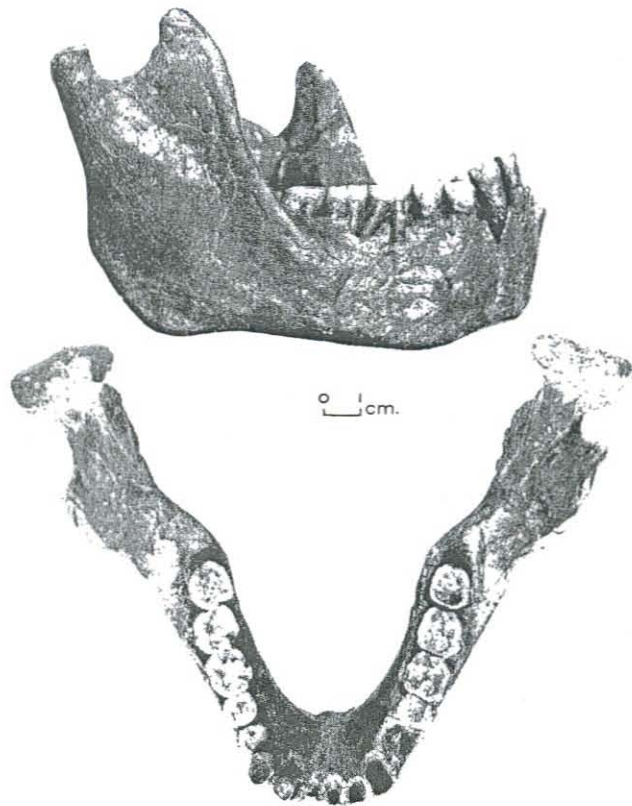


FIG. 15. Right lateral (slightly oblique) and occlusal views of the Ternifine 3 mandible. (Photographs courtesy of C. Arambourg.)

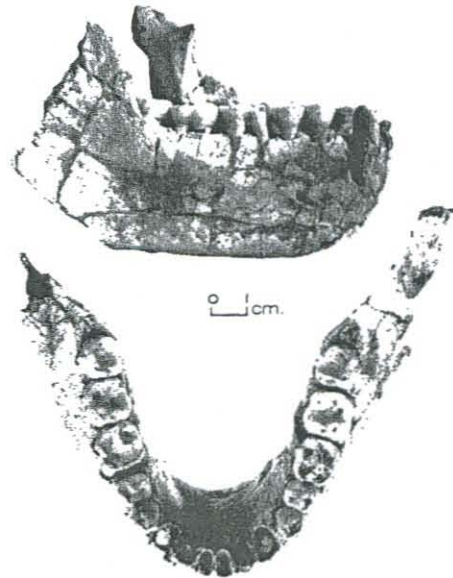


FIG. 16. Right lateral and occlusal views of the Ternifine 1 mandible. (Photographs courtesy of C. Arambourg.)

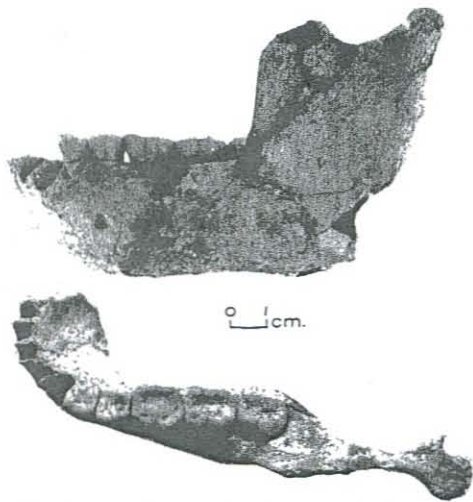


FIG. 17. Left lateral and occlusal views of the Ternifine 2 mandible. (Photographs courtesy of C. Arambourg.)

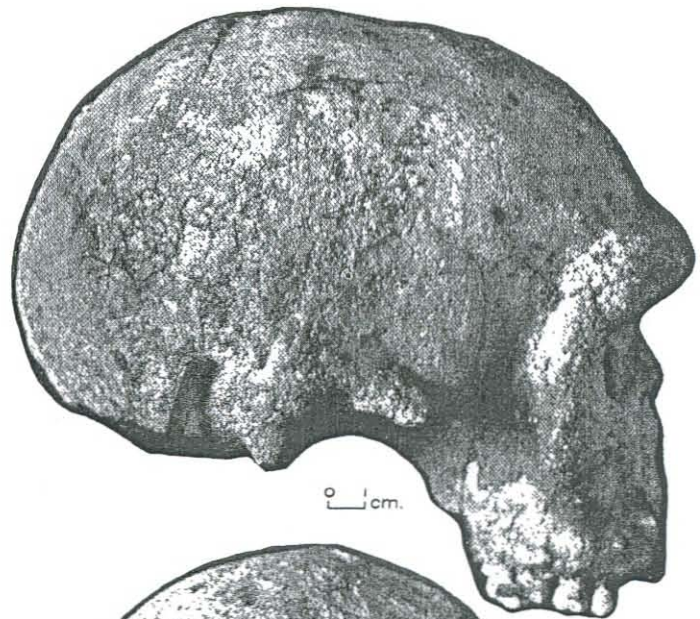


FIG. 20. Right lateral and frontal views of the Steinheim cranium (after Berckhemer 1934; Weinert 1936).



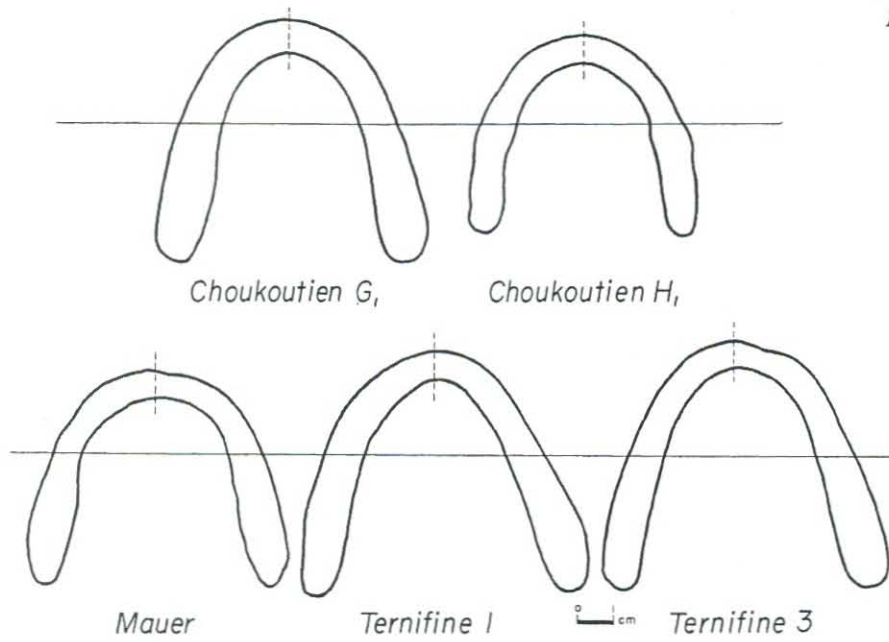


FIG. 18. Outlines of the mandibular arches of some Middle Pleistocene hominid mandibles (redrawn after Weidenreich 1936; Arambourg 1955b).

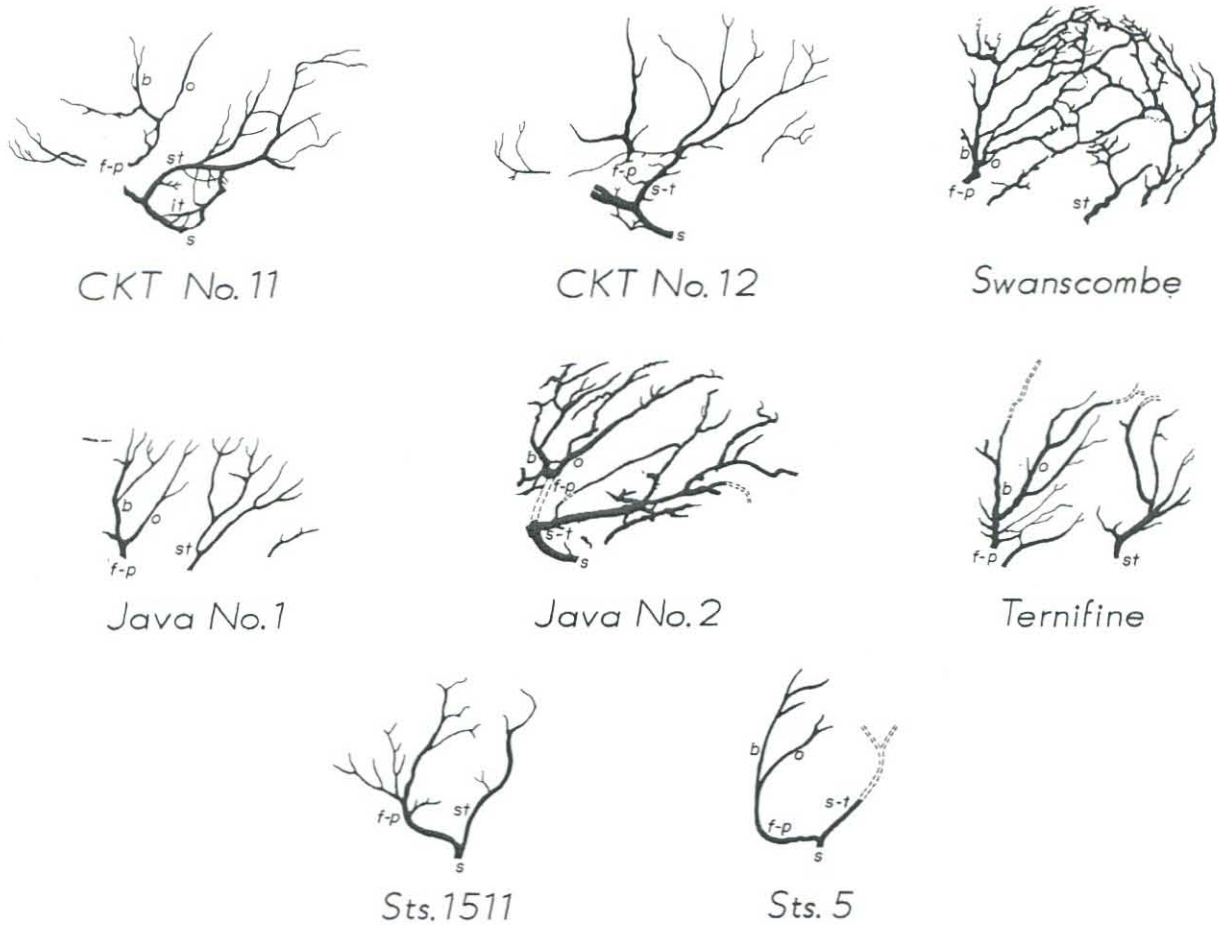


FIG. 19. Patterns of ramification of middle meningeal vessels in an australopithecine (*Australopithecus*) and in some Middle Pleistocene hominids (redrawn after Broom, Robinson, and Schepers 1950; Weidenreich

1938; Arambourg 1955d; Le Gros Clark 1938). Key to abbreviations: s = stem; fp = fronto-parietal; b = bregmatic; o = obelionic; st = superior temporal; it = inferior temporal.

A single right parietal (Arambourg 1955*d*) constitutes the only part of the vault of the Ternifine peoples found thus far. It represents a relatively young individual, the sutures being still open and the thickness of the bone corresponding approximately to that of a modern adult. The parietal curvature suggests a relatively low-vaulted skull, with the greatest transverse diameter situated below the squamous (temporo-parietal) suture. The superior temporal line is quite well delineated, especially for a non-adult individual. The well-preserved endocranial surface reveals a distinct and prominent Sylvian crest, extending upward from the antero-inferior angle. The postero-inferior angle is thickened (11 mm.) into a prominent angular torus. Both these features are typical and well developed in the eastern Asian hominids (Weidenreich 1943, 1947*a*). The pattern of the middle meningeal vessels (Fig. 19) reveals an initial bifurcation before penetration into the parietal region. The anterior branch crosses the area of the Sylvian crest and ramifies into anterior (bregmatic) and median (obelionic) branches; the posterior (lower temporal) branch, comparable in size to the anterior, extends over the postero-inferior margin of the parietal, but it is scarcely ramified, and its subdivisions are minor. This basic pattern, characterized by (1) the importance of the lower temporal branch and its premature separation from the common meningeal trunk, and (2) the weak development of the anterior (bregmatic and obelionic) branches, is typical of the Choukoutien folk (Weidenreich 1938), and is found in the earlier Java specimens from the Trinil beds (Von Koenigswald 1940). This pattern is also evident in the (earlier known) endocranial casts of the australopithecines described by Schepers (in Broom and Schepers 1946). It differs rather markedly from patterns in anatomically modern peoples, in which extensions of ramifications of the median and bregmatic branches predominate, the temporal branch is reduced, and a generally more completely ramified and secondarily anastomotic pattern is characteristic. It is likely, as Weidenreich (1938) has suggested, that the former pattern was a basic feature of primitive hominids.

Certain significant differences have been noted between the dental and mandibular morphology of the Mauer and the Ternifine hominids. The former shows no close resemblance to the eastern Asian Middle Pleistocene peoples, whereas the morphology of the Ternifine group is markedly similar to the latter. Any differences are of a minor variational sort, and are at most of racial significance; thus, there are no differences between the Ternifine and Choukoutien Locality 1 people which might not be expected within a single polytypic species, populations of which were widely separated geographically. The extent of the distinctiveness in the case of the Mauer individual, unfortunately based on only a single mandible and adult dentition which is assumed to be representative of its population, is difficult to account for on these same grounds. Consequently the conclusion must be that the evolutionary history of such European people must have been quite different from that of the northwest African and eastern Asian populations. The implications of this conclusion will be considered below.

Europe has provided two human skulls in deposits of Great Interglacial age, from Swanscombe and from Steinheim. The Steinheim specimen (Fig. 20) is of particular importance, since not only is the cranium largely complete, but the facial skeleton is preserved as well as a premolar and six molars of the upper dentition. The right side of the Steinheim specimen is perfectly preserved, although Weinert (1936) wrongly emphasized the distortion of this side, and permits accurate reconstruction of the whole skull (cf. Berckhemer 1937). The left side is badly damaged in the fronto-sphenoidal region, and the left side of the face is broken away except for the portion of frontal with the supraorbital torus, as is the whole anterior segment of the maxilla. The anterior and middle portions of the base are excellently preserved, but the base of the occipital is broken away. A detailed description of this specimen has never appeared, although preliminary notes were published by Berckhemer (1933*b*, 1934, 1937, 1938); and, a more lengthy discussion and reconstruction were attempted by Weinert (1936) from a cast and after a brief examination of the original skull (prior to its being fully cleaned). A full description of the skull will be published by W. Gieseler (Tübingen).

The facial skeleton of the Steinheim specimen is relatively small, all sides of the facial triangle being relatively short and non-prognathous (Table 6). The suprafacial (supraorbital) torus is prominent, and separated from the forehead by a marked supraglabellar fossa; the torus is thick (22 mm.) in the midline, where a pronounced and extensive frontal sinus is developed. The torus is bipartite and curved on either side, rather than forming a continuous straight (Java man of the Trinil beds), or more arched, bar (Choukoutien people); it is thickest medially (supraciliary area), and decreases in robustness laterally (supraorbital area). The space between the orbits is very wide, and the nasal bones are raised into a pronounced saddle and distinct from the frontal bone, a deep depression being present at the nasal root. The orbits are small and semi-rectangular, being deeper (vertically) laterally than medially. The nasal aperture, although very short, is uncommonly broad, and its lateral walls project forward markedly. The infraorbital zygo-maxillary region is considerably angulated, and thus differs substantially from the mid-facial morphology of the Choukoutien people. There is an incipient depression corresponding to the position of a canine fossa, although a true fossa (in the anatomically modern sense) is not developed. The structure of the middle face of Steinheim resembles in a general way that of European early Neanderthal peoples, and approaches that of anatomically modern man; it is quite different from the specialized facial structure so characteristic of classic Neanderthal folk (Howell 1951).

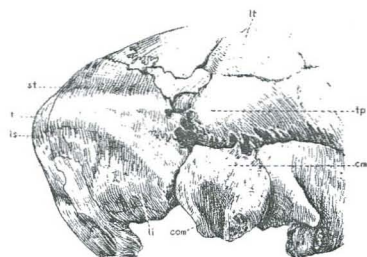
The complete upper molar dentition of this individual, a young adult, is little worn and perfectly preserved. The right premolar is also present; its crown is short (7 mm.), but wide, with well developed buccal cusp and small lingual cusp symmetrically arranged. The first molar is the largest of the series; M^3 is markedly reduced toward a sub-rounded form, with the

hypocone most affected. The crowns of the first and second molars are asymmetrically square, the mesial margin sloping backward lingually, and the distal sloping the same direction due to the prominent development of the large hypocone. The buccal cusps (paracone and metacone) are large, and the protocone is relatively reduced. These teeth are moderately (M^2) to markedly (M^1 , M^3) taurodont; and, M^1 and M^2 also show quite well-developed prismatic root formation (cf. Berckhemer 1937).

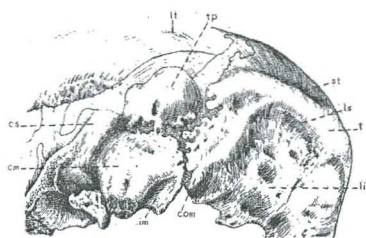
The Steinheim cranial vault is long and narrow and fairly low (highest point near bregma) and, in general, relatively small (Table 6). The cranial capacity has been variously estimated, the figure of 1070 cc. offered by Weinert (1936) being cited most frequently. However, this figure is almost surely too low, and it is much more likely that the actual value approaches 1150-1175 cc. The cranial bones are only moderately thick, considerably less so than any of the earlier or broadly contemporaneous eastern Asian peoples; the thickness approaches, but does not always attain, that of some portions of the Swanscombe specimen. The difference between the outer and inner cranial dimensions is nonetheless considerable. In contrast with the eastern Asian folk, it is due not to the development of massive cranial superstructures, but to an extraordinarily large frontal sinus (a formation that is extremely small in the Choukoutien group). The greatest vault breadth is situated rather high, at the inferior margin of the parietal, as it is in the Swanscombe specimen, rather than at the auricular

level, as in the eastern Asian peoples. Thus, in posterior view, the vault has a quadratic form with rounded margins. The frontal bone, with marked postorbital constriction, is long and low, but exhibits (as does that of the Choukoutien folk) a distinct frontal tuber some 50 mm. above the supraorbital margin. The curvature of the parietal is broken by a faint prelamdboid depression. The temporal lines are only barely delimited. The temporal squama is expanded and curved superiorly, a condition similarly present in Swanscombe; the sphenoid is in articulation with the parietal (over a distance of c. 9 mm.). The mastoid process is relatively small, with an open, moderately shallow mastoid incisure posterior to it. The external auditory meatus is vertically elliptic in shape, with a well-developed, vertically oriented anterior portion, separated from the glenoid cavity by a prominent thick postglenoid ridge, and a smaller but thick posterior portion; these are separated by a small, lateral vaginal ridge. The occipital bone is well-rounded, rather than angulated as in the eastern Asian Middle Pleistocene peoples, and lacks the massive occipital torus formation so characteristic

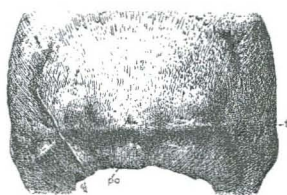
FIG. 21. Occipital torus structure in the east Asian hominid from Choukoutien and in the west European hominids from Swanscombe and Steinheim (after Weidenreich 1940). Key to abbreviations: ds = supratoral fossa; ls = superior nuchal line; po = external occipital protuberance; t = occipital torus.



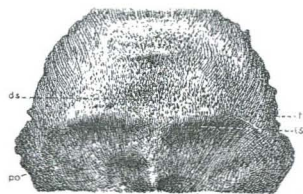
CKT 11



CKT 12



Steinheim



Swanscombe

of the latter (Weidenreich 1940, 1943). The occipital torus (Fig. 21) is low, and extends laterally as far as the asterionic region, but there is no development of the

angular torus such as in the Asian peoples. The torus is tripartite in structure, with more salient lateral segments and a wide, flattened medial portion; superiorly,

TABLE 6-A

Martin's Nos.	Calvarial Measurements	Great Interglacial							Post-
		Pre- Java 2	Choukoutien 10	Choukoutien 11	Choukoutien 12	Choukoutien range (10, 11, 12)	Steinheim	Swanscombe	
1(2)	Maximum length (g-op)	176.5	199	192	195.5	192-199	185	—	(181-2)
1d	Nasion-opisthocranium length (n-op)	—	194	185	192	185-194	177	—	182
3	Glabella-lambda length (g-l)	159?	186	169	174	169-186	172-4	—	(155-73)
3a	Nasion-lambda length (n-l)	—	184	166	175	166-184	167-9	—	(161-76)
4	Inner skull length	148	173	167	168	167-173	156	—	—
—	Difference between 1(2) and 4	28.5	26	25	27.5	25-27.5	29	—	—
5(1)	Nasion-opisthion length (n-o)	134?	—	145	147	145-147	(135-40)	—	135
8	Maximum (parietal) breadth (eu-eu)	131	138?	135	139?	135-139	132-3	(142)	142
9	Least frontal breadth (ft-ft)	79	89	84	91	84-91	102	—	101
9(1)	Post-orbital breadth	83?	98?	93	95	93-98	102	—	102
10	Greatest frontal breadth (co-co)	102?	110?	106	108	106-110	118-9	—	116
11	Biauricular breadth (au-au)	129?	147	143	151	143-151	116	—	125
12	Biauricular breadth (ast-ast)	120	111?	113	115	111-115	106-8	123.5?	(117)
13	Bimastoid breadth (ms-ms)	102	—	103?	—	—	93.4	—	102
17	Basi-bregmatic height (ba-b)	105?	—	rest.	—	—	(110)	125?	109
20	Auriculo-bregmatic height (po-b)	89	106	94	101.5	94-106	98	—	101
—	Opisthocranium height above n-o (proj.)	37	—	53	41	41-53	50	—	—
—	Inion height above n-o (proj.)	37	—	53	41	41-53	29	—	—
—	Distance between internal & external inion	25	38	34	35	34-38	—	15	—
24	Auriculo-bregmatic arc (po~po (b))	262	310	280	280	280-310	300	—	282
25	Median sagittal arc (n~o)	302?	—	332	337	332-337	341-2	—	338?
26	Nasion-bregma arc (n~b)	107?	129	122	124	122-129	120	—	(110)?
27	Bregma-lambda arc (b~l)	94	113	92	102.5	92-113	107-9	115.5?	(121)
28	Lambda-opisthion arc (l~o)	101?	—	118	118	—	(113-4)	116	(107)
29	Nasion-bregma chord (n-b)	90?	115	106	113	106-115	(98-100)	—	105.5
30	Bregma-lambda chord (b-l)	91	106	86	91	86-106	(96-9)	107.5?	112
31	Lambda-opisthion chord (l-o)	75	—	86	86	—	(88-9)	94	87
32(1)	Frontal inclination angle I (b-n \angle n-op)	—	46.5°	42°	44°	42°-46.5°	47°	—	52°
33(lb)	Occipital inclination angle II (l-op \angle op-g)	62.5°	68°	57°	61°	57°-68°	76°	—	—
33(4)	Occipital curvature angle (l-op \angle op-o)	103°	104°?	105°	98°	98°-105°	112°	—	102°-09°
	Cranial capacity (in cc)	775	1225	1015	1030	1015-1225	(1150-75)	(1325)	1175

a fine supratatorial sulcus differentiates it from the occipital squama; inferiorly, the superior nuchal line is fully evident. This structure, marking the level of inion, is about 18 mm. below the position of maximum cranial length (opisthocranion); in the eastern Asian peoples of the Middle Pleistocene, these points coincide. The supramastoid crest, unconnected with the torus, is only moderately developed, and terminates abruptly at the squamosal suture; a faintly depressed area above it presumably represents a supramastoid sulcus.

The Steinheim skull, although small and exhibiting a number of related primitive features, differs markedly from the crania of eastern Asian peoples of the Middle Pleistocene. These differences are fundamental rather than trivial, and include the form, thickness, and curvature of vault bones, structure of the cranial base (cf. Kramp 1936), and the development of special cranial superstructures. The preserved portions of the Swanscombe cranium (Fig. 22), representing a fairly young adult individual, bear a very close and detailed resemblance to the corresponding portions of the Stein-

heim skull. This was demonstrated some years ago by Morant (1938: 97), who noted that "as far as can be seen, the Swanscombe and Steinheim skulls were quite similar, and it is not unlikely that they represent the same Acheulian group." Thus, the real significance of the Swanscombe cranium, aside from its well-dated context and the extremely important association with an Achulean industry, is its confirmation of the fact that this population was relatively widespread in Europe during the Great Interglacial, and that it differed considerably from broadly contemporaneous human populations in eastern Asia.

The Swanscombe parieto-occipital bones are slightly larger, and in places rather thicker (Table 6), than their counterparts in the Steinheim specimen; however, the differences are no more than might be expected within a single variable population and in individuals of different sex, the form and cranial architecture being the same (Fig. 23). Various estimates, made according to different methods, are available for the cranial capacity of this specimen (cf. Morant 1938; Breiting 1955); the most reasonable and likely figure is 1250-1300 cc., but, since the remains are incomplete, it is impossible to be precise.

TABLE 6-A, 6-B. Some dimensions of the Steinheim and Swanscombe crania with comparative figures for some east Asian Middle Pleistocene hominids.

TABLE 6-B

Martin's Nos.	Facial Skeleton Measurements	Great Interglacial		Last Interglacial	
		Choukoutien (reconst.)	Steinheim	Saccopastore 1.	Saccopastore 2.
5	Basilar length (n-ba)	105.5	(96-100)	101.5	114
40	Superior facial length (ba-pr)	114	(108-10)	(114)	117
48	Superior facial height (n-pr)	77	(74-75)	(86)	87
43	Superior facial breadth (above fmt-fmt)	121	117	118	120
43(1)	Inner biorbital breadth (fmo-fmo)	111	—	112	118
44	Biorbital breadth (ek-ek)	111	106	103	116
45	Bizygomatic breadth (zy-zy)	148	(132)	—	140
46	Maxillary breadth (zm-zm)	98?	(98-100)	—	112
48(1)	Alveolar height (ns-pr)	25	(21-4)	25.5	27
50	Anterior interorbital breadth (mf-mf)	25	—	22	25-6
51	Orbital breadth (mf)	44	41	46-47	49
52	Orbital height	36	30	(39)	38-9
54	Nasal breadth	30	(30)	31	34
55	Nasal height (n-ns)	52.5	(32)	59	59-60
60	Maxillo-alveolar length (pr-alv.)	64	59	(60)	63
61	Maxillo-alveolar breadth (ekm-ekm)	71	68	70	72
62	Palatal length (ol-sta)	52	—	53	57
63	Palatal breadth (between second molars)	39	—	40	41
72(5)	Upper facial triangle (nasion \angle)	72°	74°	75°	70°
72(5)	Upper facial triangle (prosthion \angle)	68°	65°	60°	66°
72(5)	Upper facial triangle (basion \angle)	40°	42°	46°	44°



FIG. 22. Left lateral and occipital views of the Swanscombe cranium. (Photographs courtesy of K. P. Oakley, British Museum, Natural History.)

The parietals are relatively thick, except for the obelionic and lambdoid regions, and are slightly curved with a prelambdoid depression; the length is rather small in proportion to the breadth. The slightly curved squamous margin is thickened, not sharp-edged, and the sphenoidal angle only roughly rounded and bent medially. Keith (1938/39) suggested a fronto-temporal articulation here, whereas Marston (1937) and Morant (1938) thought an epipterice bone may have been present, but the exact morphology is difficult to determine since the remains are incomplete. The transverse curvature of the parietal is of the form seen in the Steinheim specimen, and the lateral expansion of the vault reveals the same rounded quadractic shape when viewed from behind. As in the case of Steinheim, the anterior parietal breadth is reduced. The superior temporal lines, situated below the parietal tuber, indicate a

moderately large area of origin for the temporal muscle. There is no Sylvian crest development, in contrast to the massiveness of this structure in the eastern Asian peoples from Java and Choukoutien. The pattern of ramification of the middle meningeal vessels (Le Gros Clark 1938) reveals a primary bifurcation, in the middle cranial fossa, of lambdoid and bregmatic branches; in the upper parietal area, a branch is given off extending toward the obelionic region (Fig. 15). This pattern, corresponding to the type-IV category of G. Ruggieri, is extremely rare in anatomically modern peoples, and also differs from the primitive hominid pattern of the Choukoutien (Weidenreich 1938) and Ternifine (Arambourg 1955*d*) populations.

The biasterionic breadth of this specimen is considerable, and the maximum breadth was estimated by Morant to be even greater and situated markedly low

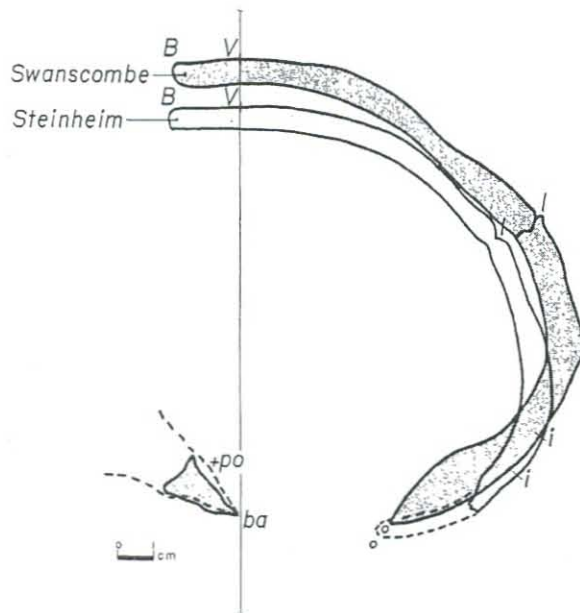


FIG. 23. Mid-sagittal sections of the Steinheim and Swanscombe parieto-occipital bones.

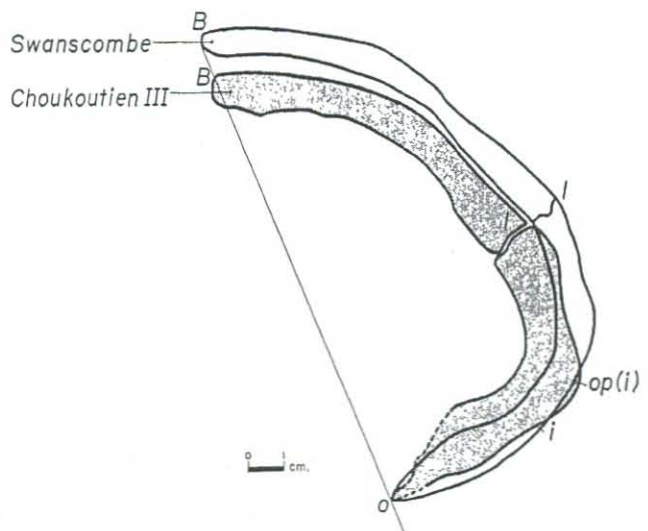


FIG. 24. Mid-sagittal sections of the Swanscombe and Choukoutien Locality I (No. III) parieto-occipital bones.

on the skull. The expanded curvature of the Swanscombe occipital resembles closely that of the Steinheim individual and contrasts markedly with the eastern Asian hominids (Fig. 24). The occipital torus is present only as a transverse, slightly curved ridge, with the lateral portions more salient than the reduced and flattened central segment; a true external occipital protuberance is absent, just as in the Steinheim specimen. The torus, slightly projecting above the depressed nuchal plane with well-developed sites of nuchal muscle attachment, is somewhat less demarcated from the occipital plane than is the case in the Steinheim specimen (Fig. 16); a triangularly shaped, widened depression in the mid-line represents the supratoral fossa. Such minor differences are either individual variation and/or sexually determined. The mastoid angle is entirely flat with no trace of a connection with the occipital torus, although there is some thickening of this area. The cerebellar fossae are small in comparison with the cerebral fossae, and the internal occipital protuberance is situated considerably below (15 mm.) the level of the occipital torus. The sphenoidal sinus was quite extensive, judging from its marked expansion into the basioccipital, especially since the individual was still youthful.

Certain authors (see below) have concluded that the Swanscombe cranium offers proof of the Great Interglacial age of anatomically modern man. However, it is difficult to understand this conclusion in view of the close similarity in cranial form and architecture between the Steinheim and Swanscombe specimens, a similarity that Morant called attention to, but failed to stress, in his original description of the Swanscombe cranium. This conclusion is of course meaningful if both individuals are referred to *H. sapiens*. However, Roginskii (1948) has emphasized that a number of the cranial proportions of the Swanscombe specimen are duplicated among some, especially early, Neanderthals and, correspondingly, differ from those of morphologically modern human groups. Stewart (1959) has recently noted the same similarity in the inferior projection of the masto-occipital process, suggesting a small mastoid, and resembling the Neanderthal rather than the anatomically modern conditions. Sergi (1953) and Breiting (1952, 1955) have reached essentially the same conclusion. Breiting, in a careful study of the proportions and interrelationships of cranial elements of the Swanscombe skull, has demonstrated that an anatomically modern frontal and facial region is in fact highly improbable for that individual. The preserved portions of the Swanscombe specimen indicate that this individual closely resembles in its cranial morphology the individual from Steinheim, and that both represent the same hominid variety. However, in a number of features, including (1) the shortness and flatness of the parietal, (2) the length and curvature of the occipital squama and the relative shortness and flatness of the occipital region and length of the foramen magnum, (3) the marked biasterionic breadth and reduced anterior diameter of the parietal, and (4) the moderate cranial height, both specimens deviate from the anatomically modern morphological pattern and, instead, are allied with early Neanderthal peoples.

It seems very likely that the Montmaurin mandible

(Fig. 25) should be attributed to a population like that represented by the Steinheim and Swanscombe crania. Except for a slight difference in size, it fits closely the Steinheim skull, as Vallois (1955, 1956, 1958) has noted in his preliminary descriptions of the specimen. This specimen, discovered in 1949, was recovered from the Montmaurin caves, situated in the limestone cliffs bordering Montmaurin, thirteen kilometers northwest

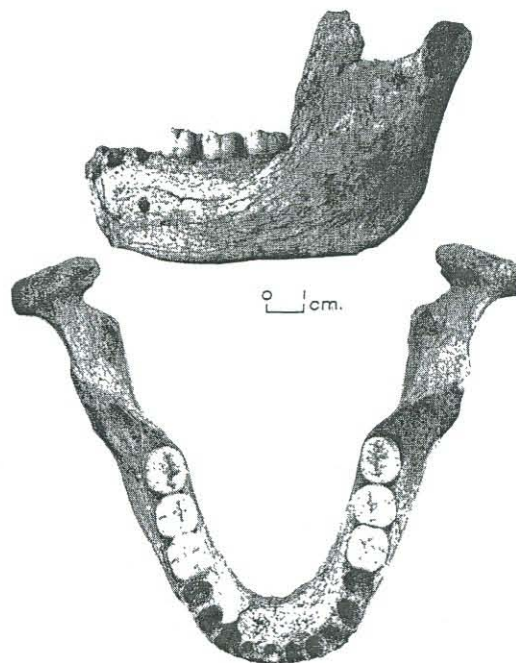


FIG. 25. Left lateral and occlusal views of the Montmaurin mandible (after Vallois 1958).

of Saint-Gaudens (Haute-Garonne). It was found in the lower portion of a collapsed vertical shaft (termed La Niche), the filling of which was unstratified, but contained a so-called warm fauna (mostly red deer; no reindeer), and a pre-Mousterian type of flake assemblage. Its age, based on the fauna and on geological studies by Bonifay, is either late in the Great Interglacial or within an interstadial phase of the subsequent (Saale = Riss) glaciation. The adjoining Coupe-Gorge cave (Baylac *et al.* 1950), with Micoquian and Upper Paleolithic occupation horizons, shows cold maxima interpreted as end-Riss and early Würm (Bonifay 1957), and the filling of La Niche occurred evidently during an earlier, warmer stage. The several Montmaurin sites have been known for many years. Boule (1902) and, later, Saint-Périer (1902) presented lists of an interesting warm fauna (*Rh. mercki*, *Eq. caballus*, *S. scrofa*, *Bos cf. primigenius*, *C. elaphus*, *C. capreolus*, and various carnivores including the sabretooth, *M. latidens*) collected, first from work by E. Cartailhac, from remnants of breccia adhering to cave walls.

The body of the Montmaurin mandible is very robust, in this respect resembling the Mauer specimen. However, the borders are essentially parallel, and the

lower border is broad with well-defined posterior marginal tubercle. The digastric fossae are extremely well developed, extending along the lower border to the level of the first molar. The buccal surface is swollen behind the double mental foramen. The lingual surface is raised below the mylo-hyoid line; a sub-lingual fossa is not present. The anterior symphyseal face is retreating, lacking any trace of a bony chin; the posterior face is marked by a very oblique planum, below which is a marked torus situated above the widely depressed zone in which an oblong crest represents the genial tubercles (Fig. 12). The rami are not particularly broad, considerably less so than Mauer, and the mandibular angles describe a regularly rounded, weakly angulated curve. There are low, but marked crests on both faces of the ramus, a marked triangular torus, continuous with the alveolar ridge on the lingual face, and an oblique torus on the buccal face. The large condyles, markedly long and broad with oval articular surfaces, project notably outward as in the Mauer mandible. The sigmoid notch, on the other hand, is more pronounced than in the latter specimen. The alveolar arch is parabolic in shape and markedly divergent.

The incisor, canine, and premolar teeth are missing from the specimen, but the full permanent molar series is present. The root of the canine was long and the premolar root single, judging from the sockets. The molars are large, M_3 being the largest tooth and M_2 slightly smaller than M_1 . In all the molars the buccolingual dimension is smaller than the mesio-distal dimension. There is no trace of a cingulum, but the molar crowns are swollen on the buccal surface. The cusps present a dryopithecine pattern, with a hypoconulid and also with a *tuberculum sextum*. The crown is considerably wrinkled on the least worn M_3 . The molar pulp cavities show a moderate degree of taurodontism, as do those of most other Middle Pleistocene hominids.

LATER MIDDLE PLEISTOCENE

Human skeletal remains from the Penultimate Glacial/Pluvial stage are extremely rare. At present, only incomplete lower and upper jaws, with portions of the mandibular and maxillary dentition, are known from Littorina Cave (Sidi Abderrahman) and from the Rabat sandstone.⁷ The Littorina Cave specimen (Arambourg and Biberson 1956) comprises a portion of the right mandibular body with three molars, and a part of the left post-symphysial region with P_1 and the alveoli of the canine and lateral incisor. The Rabat remains (Vallois 1945, 1946; cf. also Briggs 1948, 1955), representing an adolescent individual, include the lower part of a right maxilla (with incisors, canine, premolars, and first two molars), the anterior half of a mandible (with full dentition except for the unerupted M_3), and twenty-one small fragments of the cranial vault (which are impossible to reconstruct).

The body of the Littorina Cave mandible (Fig. 26) is robust, with the ventral and alveolar borders parallel. The ventral border, although rounded and thick, lacks a marginal torus; the alveolar border is also smooth and devoid of any torus development, including the lateral prominence of the buccal side, which is weakly expressed. The heavily worn P_1 is single-rooted, with a

slight longitudinal depression on the distal face (a condition found in those Choukoutien folk in which the root is not bifid). There is no true cingulum, although traces of vertical cingular folds occur on the distal and mesial borders, and the buccal face of the crown is rather swollen. The crown shape is asymmetrical, with the bucco-lingual axis oblique to the mesio-distal axis; thus, the larger buccal cusp forms the whole buccal wall, whereas the smaller lingual cusp is displaced slightly distally. The anterior fovea is small, while the posterior fovea is quite large. In all these features, the morphology of this tooth resembles closely that of the Ternifine people.

The molars, the crowns of which are quite heavily worn, are large; as in Ternifine, M_2 is the largest of the molar series. The crown of M_1 is subrectangular, with a Y5 cusp pattern, the large metaconid being in contact with the hypoconid. An anterior fovea is faintly evident between the protoconid and metaconid. M_2 is somewhat more elongated—rather elliptical—with a similar cusp pattern, except that there is a closer approach to

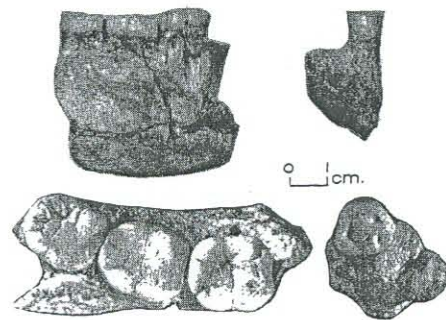


FIG. 26. Lateral and occlusal views of the Littorina Cave mandible fragments (after Arambourg and Biberson 1956).

the +5 shape, and a sixth cusp is present buccally between the entoconid and hypoconulid. M_3 , smallest of the series, reveals a Y5 pattern, probably with an additional sixth cusp; the unworn portion of its occlusal surface is covered by secondary wrinkles.

The Rabat mandible is robust and broad, with a moderately low body. The mental foramina are double, as in Ternifine and other Middle Pleistocene peoples. The relatively large digastric fossae are restricted to the ventral surface of the body. The symphysis is retreating, and on its lingual surface there is a moderate superior transverse torus; below the torus is a broad fossa, representing the site of the upper genial tubercles, whereas the lower genial tubercles are fused below as a median ridge. The incisors and canines are not arranged in an arc, but are more transversely positioned. The canines are incisiform. The lingual cusp of P_1 is relatively well developed, and the crown exhibits the characteristic asymmetry noted in the Ternifine and the Choukoutien peoples. P_2 is double-rooted with a well-developed talonid, as in the Ternifine folk. The molars are large, show traces of a buccal cingulum, and exhibit considerable taurodontism. The cusp pattern of M_1 is of the Y5 variety, with the large metaconid in contact

with the hypoconid. In M_2 , which is larger than M_1 , there is a +5 pattern and an additional sixth cusp.

The Rabat maxillary fragment exhibits considerable prognathism, lacks a mid-facial depression (canine fossa formation), and the palate is relatively large. The upper incisors show considerable development of marginal ridges, producing a shovel-shaped crown, and have pronounced marginal tubercles. The canine is large, projects slightly past the occlusal plane, and has a large cingulum on the buccal face and a marked median crest on the crown. P^1 is double-rooted and P^2 single-rooted, the crown patterns of each resembling homologous teeth of the Choukoutien folk. As in the lower dentition, M^2 is larger than M^1 , and a well-marked cingulum is present, as is basal swelling of the crown. There is a well-developed hypocone, and accessory cusplets obscure the basic crown pattern; on M^1 the normal transverse ridge (paracone-protocone) is absent, and on M^2 the oblique ridge (metacone-protocone) is similarly lacking. Both these and other features are typical of the Choukoutien Locality 1 population.

In so far as preserved, the Littorina Cave mandible and dentition bear a marked resemblance to those of the Ternifine people. Moreover, as Arambourg (in Arambourg and Biberson 1956) has pointed out, there are specific dental characteristics (the dryopithecine cusp pattern, traces of sixth cusp, predominance of protoconid over metaconid, trace of a cingulum on molars and premolars, and shape and pattern of the crown of P_1) which indicate affinities with the Middle Pleistocene peoples of eastern Asia. There are also certain differences (such as narrower molars, more elliptical M_2 , and greater reduction of M_3) which must indicate geographical variation. The resemblance of the Rabat morphology to that of both the Choukoutien people and also various Neanderthals of Europe has been noted by Vallois (1945); however, he doubted whether this individual represented a member of a specifically Neanderthal group. In fact, as indicated above, the Rabat remains are of the same Middle Pleistocene group as the Littorina Cave specimen, and both are closely allied with the earlier Ternifine population.

SOME PHYLOGENETIC IMPLICATIONS

In spite of incomplete preservation and the limited number of specimens, sufficient is known of the Middle Pleistocene peoples of northwest Africa and western Europe to permit some assessment of their relationships with other broadly contemporaneous peoples elsewhere. Several important conclusions emerge from a consideration of human populations from two major blocks of the Middle Pleistocene: (1) the pre-Great Interglacial range (early Middle Pleistocene) and (2) the Great Interglacial and subsequent early phase of the Penultimate Glacial range (later Middle Pleistocene).

(1) In Europe there is no trace of the so-called "pithecanthropine" peoples so characteristic of the whole of the Middle Pleistocene of eastern Asia. In the latter area, a series of populations has been recognized from the basal (Djetis beds) and earlier (Trinil beds) Middle Pleistocene and extending into a stage that probably corresponds broadly with the European Great Interglacial (Choukoutien Locality 1). The only European

human fossil from the earlier Middle Pleistocene range of time, the Mauer mandible, is sufficiently different to be regarded tentatively as very likely specifically distinct from the eastern Asian lineage. The European evidence is admittedly tenuous, since human crania are lacking, but if the dental and mandibular morphology is indicative (as it is in the Asian populations), then this conclusion is warranted. The Ternifine people, however, in the morphology of their teeth and jaws, bear a (perhaps unexpected) close resemblance to the eastern Asian populations. Any slight differences are of probably no more than subspecific significance, and are not wholly unexpected between specifically similar, but widely separated, natural populations.

(2) No human skeletal remains are known from the Great Interglacial stage in northern Africa, but the slightly younger remains from the Littorina Cave and Rabat appear to testify to the persistence of populations like Ternifine into the earlier phases of the Penultimate Glacial/Pluvial. This is paralleled in eastern Asia by the continuation of the "pithecanthropine" lineage represented by the people of Choukoutien Locality 1.

In Europe "pithecanthropine" peoples are absent also from the Great Interglacial range. The Steinheim and Swanscombe crania, exhibiting a number of incipiently anatomically modern features, establish the fact that at that time human populations of the area differed markedly in cranial morphology from contemporaneous peoples of eastern Asia (and presumably of northwestern Africa). The evidence would suggest that two distinctive hominid lineages were differentiated within the Middle Pleistocene, one represented by eastern Asian and northwest African populations, and the other by European populations.

These lineages correspond closely to the "vertical" lines of evolutionary development to which Le Gros Clark (1955) has attributed generic status: *Pithecanthropus* and *Homo*, respectively. He states that members of the former "comprise a group whose morphological characters are held by most anthropologists to be sufficiently consistent and distinctive to justify their generic separation from *Homo*" (p. 105); and, further, that "the cranial and dental differences (as well as the even more significant contrast in cranial capacity) appear to be as well marked as those which are commonly accepted as justifying a generic distinction between gorilla and chimpanzee" (p. 106). The writer doubts that "most anthropologists" (human paleontologists) have ever expressed an opinion on this matter, other than merely accepting the existing terms of reference without examining the full taxonomic implications of the terminology. Moreover, although no clear-cut definition of a genus is possible, as it is in the case of species and species-groups (cf. Cain 1956), it is generally recognized that genera testify to the achievement of special adaptive plateaus (in S. Wright's sense), characterized by well-established behavior patterns and morphological adjustments toward definite habitats, specifiable in nature as well-delineated ecological zones. It is questionable whether such far-reaching distinctions are recognizable within the known hominids of the Middle and Upper Pleistocene.

The writer's own proclivity, and broadly in agreement with Mayr (1950) (except in the case of *Australopithecus*, which he has granted specific status within the genus *Homo*, but which is more likely generically distinct), is to reduce these to paleospecies representing phyletic lineages. The paleospecies, discussed by Cain (1956: 103; also 1954), represents "a time series of populations known (or believed) to be connected successively by descent, reproductively separate from all other forms co-existing during the same period, and sufficiently homogeneous on comparative criteria to be included under a single specific name." Simpson (1951: 289) has pointed out that "a phyletic lineage (ancestral-descendant sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, is a basic unit in evolution"; and that "the genetical definition [of a species] tends to equate the species with such an evolutionary unit." The morphological evidence does not appear to warrant recognition of separate genera; certainly there is complete overlap in range of variation in cranial capacity, a character to which Le Gros Clark has attached considerable importance. Nor, taking into consideration Simpson's (1954: 32-33) remarks on mammalian generic origin rates (*c.* five to seven million years as an approximation), has there been sufficient time for generic differentiation, even allowing for an extraordinarily rapid evolutionary rate. The original dispersal and subsequent evolution of hominids from a primitive australopithecine group, probably not unlike *Australopithecus*, most likely occurred within a single genus (*Homo*). The earliest phases within the formation of that genus are difficult to define, owing to the incomplete record. Oakley's (1951) emphasis upon tool manufacture and its use as a criterion *may* prove to be correct, although at least *some* australopithecines were tool-makers.

The eastern Asian hominids provide a classic example of phyletic evolution within a paleospecies (*H. erectus*). The detailed morphological patterns have been analyzed by Weidenreich (1941, 1943, 1946, 1947*b*). There is evidence of development within the lineage during the early Middle (Djetis and Trinil varieties) and the later Middle (Choukoutien variety) Pleistocene and probably into the earlier Upper (Ngandong variety) Pleistocene. The fossil record is inconclusive as to the subsequent history of the group, but it is not unlikely that the lineage became extinct prior to, or when, anatomically modern australoid peoples expanded throughout the Southeast Asian area during the later phases of the Upper Pleistocene. All the evidence available tends to confirm Movius' (1949*a*: 411) conclusion that "it seems very unlikely that this vast area could ever have played a vital and dynamic role in early human evolution, although very primitive forms of Early Man apparently persisted there long after types at a comparable stage of physical evolution had become extinct elsewhere."

It is a matter of considerable interest that in north-western Africa, where such persistence apparently also occurred, cultural (= industrial) transformations did take place, as evidenced by the widespread adoption in the earlier Middle Pleistocene of the Chelles-Acheul hand-ax/cleaver and associated flake traditions. In the

far easterly and southerly regions of Asia, the earlier Pre-Chelles-Acheul tradition was maintained, as the chopper/chopping-tool tradition, with only slight modification into the Upper Pleistocene (*cf.* Movius 1949*a*). The continued existence of this industrial complex, undoubtedly derived from the early African "pebble-tool" tradition the Villafranchian age of which is well established, is a striking instance of human conservatism, undoubtedly caused in large part by isolation from western Asia, Europe, and Africa. Only in certain portions of India is there any real evidence of overlap between these traditions and their industrial expressions.

The cranial morphology of the human populations of the Great Interglacial of Europe suggests a distinctive new lineage, markedly different from that of eastern Asia and northern Africa, and whose origins are still entirely unknown. Some workers, notably Vallois (1949, 1952), Heberer (1950, 1951), and also Kälin (1952), have attempted to show a primary bifurcation into distinct "neanderthal" and "*sapiens*" lines within the European hominid populations at this early date. This implies subsequent coexistence of these lineages in Europe until extinction of the terminal classic Neanderthal population by the middle phase of the Last Glacial stage (*cf.* Howell 1957). The essential similarity in morphology of the only two European crania of Great Interglacial age, those of Swanscombe and Steinheim, fails to confirm this interpretation. In general, and as Le Gros Clark (1955) has also recognized, the over-all morphological pattern of such early European peoples closely approaches, in certain aspects, that of the anatomically modern species *H. sapiens* (so much so, in fact, that Le Gros Clark refers the remains to that species). Whether this taxonomy is fully justifiable or not, the European populations of the Great Interglacial provide an ideal ancestral stage for the subsequent varieties of Upper Pleistocene Neanderthal peoples and the incipiently and fully anatomically modern peoples who were subsequently to replace the last "Neanderthals" during the interstadial between the Early and Main phases of the Last Glacial. This later evolutionary history of the lineage has been discussed in some detail recently by the present author (Howell 1957; also 1951, 1952) and by Breitingner (1957).

The origins of these lineages are still largely a matter for future research. The fossil record leaves little doubt that the initial, basic hominid manifestation, representing new adaptations toward a bipedal ground-dwelling way of life in a new unexploited environment, was essentially African (*cf.* Bartholomew and Birdsell 1953). Its primary formative phases are unknown, due to the inadequacy of the hominid fossil record, but may very well have been linked with the terminal Miocene and earlier Pliocene desiccation during the Kalahari Stage which markedly affected the extent of the semi-arid central African bushy and wooded grassland. The Villafranchian australopithecines, already adapted to the upright posture and fully bipedal locomotion, and long since differentiated into two distinct (probably sub-generic) lineages, testify to the nature of this primary adaptive radiation (Howell 1959).

This radiation gave rise to primitive tool-making hominids whose dispersal by the earlier Middle Pleistocene probably extended throughout the tropical and

subtropical zones of Africa and Asia. This initial, primary human (*Homo*) dispersal probably occurred during the later Villafranchian stage, for the earliest Southeast Asian hominids associated with them, the Djetis fauna in Java, show considerable differentiation from the presumably ancestral australopithecine group. From the occurrence early in the Middle Pleistocene of both human skeletal remains and stone tools, it is clear that this dispersal was unaffected and unretarded in most areas by the major isolating factors of characteristically Pleistocene glacial climate and related vegetation zones resultant from the first major continental stage of glaciation (Elster = Cracovian = Oka).

The archaeological record would suggest that this initial dispersal was essentially African, both north and south of the Sahara, and eventually southern Asian. Evidence is lacking from the intervening western Asian zone, but distribution was presumably broadly continuous, at least originally, across the Mediterranean African-southwest Asian-Indian semi-arid grasslands, and into the then peninsular Sunda Shelf. The comparative morphology of the Ternifine and eastern Asian representatives of *H. erectus*, populations at the most western and eastern extremes of the range, tends to confirm their relationships and common origin from this primary dispersal.

It would appear, although the evidence is admittedly incomplete, that continental Europe was not penetrated by this primary dispersal. There are no traces of hominids, either skeletal remains or stone tools, in the European Villafranchian. Such evidence does not appear until well along in the earlier Middle Pleistocene. The circumstances whereby Europe was not populated earlier by man are still difficult to ascertain. It is likely that the high sea levels of the earlier (Calabrian) and later (Sicilian I) Lower Pleistocene may have been a major factor which inhibited dispersal. The Mediterranean was greatly enlarged, and the otherwise narrow water-gaps (or potential land bridges during later regressive phases of glaciation) in the western (Gibraltar) and northeastern (Bosporus, Dardanelles) reaches of the basin were submerged. It is tentatively suggested here that the primary dispersal did not pass 35°–40° N, the barriers being formed in the westerly zone by (a) the Mediterranean basin, and (b) the Taurus-Zagros mountain chains; in the easterly zone, the northern limit presumably did not exceed, or in places attain, 30° N, the barriers being formed by the great Hindu-Kush-Karakorum-Himalayan arc. However, in the latter regions there is clear evidence of the presence of man at the end of the earlier Middle Pleistocene (at Locality 13, Choukoutien) and more complete evidence later from the Great Interglacial (Locality 1), both proving distribution as far as 40° N.

A variety of evidence indicates hominid penetration north of latitude 40°, into the temperate European continent, only well along in the earlier Middle Pleistocene. This northward expansion in hominid distribution coincides in time approximately with the maximum lowering of sea levels during the Romanian regression (cf. Fig. 1), coincident with the first major Scandinavian glaciation, which extended into southern Britain and central Europe as far as latitudes 51°–52°. Such evidence as there is from that time, including the

Mauer mandible and sporadic assemblages of an Abbevillian industry, seems to be of peoples different from those representing the primary dispersal. It is (difficultly) suggested that new technical refinements and additions to human tool-making capabilities, including the establishment of the Chelles-Acheul tradition, but probably also others which are unknown due to incompleteness of the record, re-enforced the effectiveness of such a dispersal into a previously unoccupied zone. The source of this expansion is still unknown; the central-eastern African region is a reasonable probability.⁸ At any rate, and most important, there is no evidence at present to indicate an eastern Asian center. It is necessary to emphasize that the extent of this initial occupation of Europe by man must have been relatively slight, at least judging from the relative paucity of early Chelles-Acheul assemblages compared with sub-Saharan Africa. However, for the subsequent Great Interglacial stage, there is every indication of broadened and intensified occupation in the course of the Acheulean and, in some regions, other non-hand-ax industries (Clactonian).

It is at this later time that Europe reveals clear evidence of a lineage distinct from that of *H. erectus*. However, the origins of this lineage are still unknown, and there is a real problem as to relationships with the first Middle Pleistocene populations of Europe, fossil remains of which are represented only by the Mauer mandible. It is impossible to arrive at any solution to the problem until either mandibles of the Steinheim-Swanscombe people, or a cranium of the Mauer people, can be discovered. The Montmaurin mandible is of some interest in this regard since its morphology is in some respects like that of the Mauer mandible, in other respects like that of early Neanderthal peoples. Tentatively, the most economical hypothesis is that Mauer was merely an early representative of the same lineage. The major climatic amelioration which brought on the Great Interglacial undoubtedly permitted a major expansion of populations of gathering and hunting peoples into previously restricted or unavailable biotopes; but, the extent to which this represented only intra-continental expansion and shiftings, as opposed to more extensive movements of extra-European peoples, is impossible to ascertain from existing evidence.

There has been a tendency among certain workers to deny speciation within the Pleistocene evolution of the hominids. This was the opinion of Weidenreich (1943, 1946), and it was accepted and expanded upon by Dobzhansky (1944: 261-62), who stated that "all the phylogenetic transformations within the *Hominidae* were always taking place within a single genetic system, a species consisting of geographically, but not reproductively, isolated races." The same point has been made by Mayr (1950: 112), who concluded that "all the available evidence can be interpreted as indicating that in spite of much geographical variation, never more than one species of man existed on the earth at any one time." The genetical definition of species, as "actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1949: 371), cannot be directly applied to pale-

ontological species, but, as Simpson (1951: 286) has noted, "actual or potential interbreeding is continuity and reproductive isolation is discontinuity." Thus, such taxonomy is arbitrary, in Simpson's terms, since the hominid fossil record of the Middle Pleistocene reveals morphological discontinuities, and the forms "are placed in a single group although essential discontinuity is indicated." Moreover, this general point of view fails to take into consideration the extent of various isolating mechanisms operative on Pleistocene human populations, in the same manner as on other mammals, although human cultural capabilities undoubtedly

served as a buffering agent. Factors of isolation, about which very considerable is known for the Upper Pleistocene, must have played a very considerable role in the distribution of such early peoples, whose cultural capacities and capabilities for adaptation to varied Middle Pleistocene biotopes were relatively restricted. The hominid fossil record indicates how extensive such isolation must have been within the Middle Pleistocene. It is essential that in the study of human evolutionary problems in the future, paleoanthropologists take into account more fully the whole matter of distributions and environmental adaptations.

Notes

1. The writer is deeply grateful to a number of colleagues whose cooperation has made this paper possible. Dr. K. P. Oakley (British Museum, Natural History, London) made available the Swanscombe cranial remains. He also accompanied the author on a visit to the Barnfield pit at Swanscombe. Prof. C. Arambourg (Museum National d'Histoire Naturelle, Paris) made available the Ternifine and Sidi Abderahman human remains. Prof. H. V. Vallois (Institut de Paléontologie Humaine, Paris) permitted the author to examine the human remains from Rabat and Montmaurin. Prof. W. Gieseler (Universität Tübingen, Tübingen) permitted the author to examine the Steinheim skull. Dr. K. D. Adam (Naturhistorisches Museum, Stuttgart) accompanied the author on a visit to the pits at Steinheim, and has also discussed with the author certain problems of Pleistocene faunas, their interpretation and correlation. Similarly, certain problems of the Pleistocene paleoanthropology of Morocco have been discussed with my colleague P. Biberson (Musée de l'Homme, Paris). The Mauer mandible was studied at the Geologisch-Palaeontologisches Institut, Universität Heidelberg, in 1956, and the author is grateful to the staff there for their assistance. The writer is also grateful to the Wenner-Gren Foundation for Anthropological Research, Inc. (New York), for grants-in-aid which made possible a study tour in sub-Saharan Africa in 1954, and another in Europe in the Summer of 1956. In Africa, Dr. J. T. Robinson (Transvaal Museum, Pretoria) and Prof. R. A. Dart (Medical School, University of the Witwatersrand, Johannesburg) generously made available for study all the australopithecine skeletal material.

2. The Cromer Forest Bed, overlying the Weybourne Crag (in places), is a complex three-fold formation, composed of Lower and Upper Freshwater Beds—both of which are discontinuous,

variable in facies, and often not preserved—and the practically continuous Middle or Estuarine Bed (= Forest Bed *sensu strictu*). The fauna is clearly mixed (cf. Zeuner 1937). Many of the fauna collections were made years ago, and it is no simple matter to unravel the particular provenance of the specimens, since different "Forest Bed" localities preserve different portions of the Forest Bed and hence different faunas (cf. Azzaroli 1951, 1953). There is pretty clearly both a later Villafranchian fauna, probably derived from the shelly Weybourne Crag (and basal Freshwater Bed), and a Middle Pleistocene assemblage, probably derived from the Upper Freshwater Bed, which closely resembled the later Great Interglacial assemblages of early Drenthian age, such as Swanscombe. However, the fauna of the Forest Bed *sensu strictu* is of intermediate age, comparable with the so-called "preglacial" St. Prestian fauna. In view of the geological evidence, it is difficult to agree with Azzaroli's (1953) conclusion that the two later (post-Villafranchian) faunas are both of Great Interglacial age.

3. The Jockgrim fauna, studied first by Freudenberg (1909, 1911) and later in greater detail by Soergel (1925; also 1912, 1923), is derived from a series of clay horizons (underlain and overlain by gravels and sands) exposed in pits in a low terrace along the left bank of the Rhine River, near Karlsruhe. The section studied in detail by Schwegeler (1935; also Thürach 1899) reveals seven clayey loam levels, totaling some four to six meters in thickness, and broken in the middle by an erosional disconformity. It is capped by the eroded remnant of a lignite horizon with deciduous forest pollen (frequent oak, hazel, spruce, and alder; infrequent fir and pine; rare maple, linden, willow, and larch; notable is the presence of hemlock and the Asian wing-nut *Pteryocarya*). Kuss (1955) has recently shown that the mammalian fossils are found throughout the clay horizons in three different pits; in contrast to Schwegeler, Soergel, and Adam, he believes the as-

semblage is a faunal unity and covers a relatively short span of time. This fauna (= lower series of Adam) is characterized by *El. meridionalis-trogontherii* (straight-tusked elephant is known from the gravelly sands that unconformably overlie the lignitiferous level), *B. priscus*, rare deer (*C. elaphus*, *C. capreolus*), *Rh. etruscus*, *H. amphibiis*, and *T. cuvieri*; also known are recent beaver (*C. fiber*), very rare moose (*A. latifrons*), giant fallow deer (*Megaceros verticornis*), *C. nescherensis*, *U. deningeri* (= *arctos*), *Desmana*, and *Emys*, but their position in the profile is uncertain.

4. The Süssenborn assemblage (Soergel 1926, 1936, 1939b, 1941; also Wust 1900) is found in gravels suggesting at least incipient periglacial conditions in Thuringia, and is basically a cool-steppe fauna (Soergel 1924, 1939a). This fauna (Kalke 1954) is characterized by abundant steppe elephant (*El. trogontherii*), horse (mostly *Eq. süssenbornensis*, 24%; also, *Eq. aff. hemionus*), grassland-loving bison (*B. priscus*, 17%), a variety of deer and elk including large-antlered forms (*Megaceros*, 20%; *Alces*, 5%) as well as roe (*C. capreolus*, 7%) and red deer (*C. elaphus*, 5%), fairly numerous rhino (*Rh. etruscus*, 9%), some beaver (both *T. cuvieri* and *C. fiber*, 4%), and rare wild boar (*S. scrofa*, 1%); both tundra reindeer (*Rangifer articus*, 4–5 individuals) and musk-ox (*Ovibos moschatus*, 1–2 individuals) are also present, but in very low frequency, as are various large (*Epimachairodus*, *H. crocuta* and *H. brevirostris*, *Canis mosbachensis*, *U. arctos deningeri*) and small (*Mustela*, *Lutra*, *Meles*) carnivores and other small mammals (including *Spermophilus*).

The main (II) Mosbach fauna (Schroeder 1898; Soergel 1923) is very similar in composition, but contains (c. 10%) both straight-tusked (*El. antiquus*) and much more frequent (c. 90%) steppe (*El. trogontherii*) elephants (Soergel 1916, also 1912; Schmidtgen 1927), frequent horse (*Eq. mosbachensis*), rhinoceros (*Rh. etruscus*, *Rh. merckii*) (Schroeder 1903), and several additional large and small carnivores

(Von Reichenau 1906, 1910); there are also small mammals, including water voles (*A. mosbachensis*, *A. greeni*) and mice (*Microtus*, *Pitymys*) (Heller 1933; also Schmidgen 1911).

A slightly worn, sub-ovate hand ax, typologically perhaps Middle Acheulean, has been found at Mosbach in the floor of the Bogger pit (Kutsch 1953). This is very likely derived from a remnant of an interglacial deposit yielding *El. trogontherii-primigenius*, interbedded between the earlier Mosbach gravels and the overlying Last Glacial loess complex. Hence the hand ax is presumably of Great Interglacial (Hoxnian) age.

5. The Abbevillian industry, often regarded as of "First Interglacial" age (cf. Zeuner 1952), might be considered to antedate the Mauer mandible. This is, in fact, not the case, as an examination of the most typical occurrence of this industry, in the Somme River valley at the Porte du Bois, near Abbeville (Commont 1910; Breuil 1939), will indicate. The Abbevillian assemblage, found in association with a typical early Middle Pleistocene fauna (which includes *El. meridionalis-trogontherii*, *Rh. etruscus*, *Rh. merckii*, *Hippopotamus* sp., *S. scrofa*, *Equus* sp., *C. elaphus*, *C. capreolus*, *B. prisus*, *Hyaena* sp., *M. latidens*, *Ursus* sp., *T. cuvieri*, etc.), has been found in a whitish marl with sandy horizons at the base of the High (40 meters) Terrace, underlain by an ancient gravel capped by marly and shelly sand. This marl, deposited under conditions of deep-water sedimentation, was deeply channeled during a subsequent phase of low sea level. The channels were later filled with gravels and sands (containing Acheulean), aggraded during a time of marine transgression corresponding to the Tyrrhenian I stage of the Great Interglacial. The erosion of the channels must have occurred during the later phase of the Romanian regression, and thus at a time corresponding to the maximum extension of the Elster Glaciation. The underlying marl, and the Abbevillian, is thus quite clearly of pre-Elster date, and very probably has a relative age corresponding broadly with the Mauer Sands. The Plateau Gravels and main High Terrace of the Somme have long been thought to be devoid of humanly-flaked stone artifacts. However, some traces of human occupation are recorded (by F. Bordes and H. Breuil, unpublished) from the c. 50-55 meters lower High Terrace. Most recently Agache and Bourdier (1959) have reported flint flakes, some trimmed and retouched as implements, and having a porcellanized appearance (due to fire?), from gravels of the upper High Terrace (+ 60-65 meters) at Montières (near Amiens).

6. In several recent, very stimulating papers, Kurtén (1956, 1957a, b) has drawn attention to the ecological replacement in the Pleistocene of the giant hyena (*H. breivrostris*) by the spotted hyena (*Crocuta crocuta*). This replacement is well-recorded at Choukoutien Locality 1 (Pei 1934), where only the former species (*H. b. sinensis*) is present in the lower sandy brecciated horizons (Zone II), and only the latter species (*C. c. ultima*) is present in the upper ashy, travertine horizons (Zone I). It is also instanced, though less clearly, at Süssenborn, where both *H. b. breivrostris* and *C. c. spelaea* are recorded, and in a number of faunal assemblages referred to the Forest Bed series, and hence of presumed Cromerian interglacial age. Kurtén, on carefully reasoned evidence, regards the replacement as having been roughly simultaneous in western Europe, eastern Asia, and southern Africa, and thus dates a number of such sites, like Choukoutien Locality 1, Kromdraai, Swartkrans (where *C. c. ultra* occurs), to the Cromerian stage. The question of "whether this European replacement can be correlated with the East Asian" seems to him justified since "it seems that the species evolved in India from *C. sivalensis* [recorded with *H. b. neglecta* in the Pinjor zone of the Upper Siwaliks] and spread from there. . . ." It is necessary, however, to point out that Süssenborn is later early Middle Pleistocene (= end-Mindel of the Alpine succession) in age, and the replacement in Europe is at least post-Cromerian (*sensu strictu*). Neither at Mauer nor at Mosbach is *Crocuta* in evidence, although *H. perrieri* is characteristic. Moreover, there is a real question as to whether the Norfolk faunal localities, referred to as contemporaneous with the Cromer Forest Bed, are indeed contemporaneous; the present writer believes them to be later (Mindel) in age. It is of course altogether possible, on other grounds, that the Swartkrans-Kromdraai localities are of Cromerian age, but one would still wish for a better understanding of the Villafranchian and, especially, Pliocene hyaenids of Africa before excluding them from *Crocuta crocuta* ancestry.

7. Since this was written, Vallois and Roche (1958) have announced the discovery of human remains from Contrebandiers Cave at Témara, a few kilometers southwest of Rabat. The cave is cut into a cliff of Ouljian age, and the remains were found in remnants of breccia adhering to the walls, all that remains of the first infilling of the cave. The specimen, consisting of a nearly

complete body of a mandible with most of the left, and bits of the right, ramus, and full dentition, dates from the early Upper Pleistocene. It does not particularly resemble the earlier Sidi Abderahman or Rabat specimens, although there are some very general similarities, but seems more likely to represent a member of a North African early Neanderthal group.

8. Aside from the Villafranchian australopithecines, the Lower and Middle Pleistocene of sub-Saharan Africa has still to provide hominid skeletal remains of much use in solving the problems discussed here. However, it is necessary to mention briefly two occurrences that are suggestive and have a bearing on these problems:

(a) The breccias bearing australopithecines at Swartkrans, of either later Villafranchian (Howell 1955) or early Middle Pleistocene (Oakley 1954) age, provide clear-cut, though fragmentary, evidence of co-existence of two distinct hominids: one a large australopithecine (*Paranthropus*), and another (termed "*Telanthropus*") which is certainly different. The latter, represented by the type mandible with six molars and a first premolar (Sk 15 = No. I) (Broom and Robinson 1949, 1952), another fragment of mandible with the first two molars (Sk 45 = No. II) (Broom and Robinson 1950, 1952), and a fragment of maxilla including some heavily worn or broken premolars (Sk 80 = No. III) (Robinson 1953), is still too poorly known to determine its exact affinities. From a careful study of the original specimens, as well as from the published descriptions (esp. Broom and Robinson 1952; Robinson 1953: 477), it is clear that Robinson is completely justified in his statement that these remains differ "in so many respects from those of *P. crassidens*, without any intermediate specimens, that these forms could not have been members of the same population even though they lived simultaneously in the same area." There are no specific detailed resemblances of these specimens with the eastern Asian hominids of the *H. erectus* group; however, some features of the dentition as well as of mandibular morphology are not unlike those found in the Mauer individual. While it is possible to state (negatively) that the former is the case, it is not possible, due to the fragmentary preservation and general lack of material, to be more positive about either the morphology of this form or its phylogenetic affinities. Nevertheless, merely its discovery and the proof of co-existence with the most recent australo-

pitheciene (*Paranthropus*) is of great importance in further understanding of the dispersal of the genus *Homo* and of the relationships of the latter to *Australopithecus* and the species of the latter radiation.

(b) The only human remains from sub-Saharan Africa of earlier Middle Pleistocene age are two deciduous teeth from a Chellean stage-1 living site (BK II) in Bed II at Olduvai Gorge in northern Tanganyika. One specimen, a left lower milk canine, is very heavily worn and provides little useful information. The other, which may be an upper deciduous molar, but is identified by Leakey (1958) as a left m_2 , is well preserved and more useful for comparative purposes. This scarcely worn specimen is extremely large-crowned (length 15 mm.; breadth 14 mm.) and exceeds in size its homologue in australopithecines. There are six main cusps, three buccal and three lingual, with a large accessory cusp and traces of cingulum. The pattern is somewhat unique, but there are general points of resemblance both with australopithecines and with the Choukoutien hominid (*H. erectus*).

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