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CURRENT PROBLEMS IN RESEARCH

The Villafranchian and Human Origins

Man's bipedalism and the use of tools appeared during times of faunal change in the early Pleistocene.

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Few people lack curiosity about their ancestors, their genealogy, and the ways of the world in the past. This curiosity extends to the ancestry and history of all mankind. In the last hundred years theological explanations have—especially in countries of Western cultural tradition—tended to be replaced by a more rational approach to the matter. This approach is the concern of human paleontology, and its inception is closely linked with the name of Darwin.

A century ago only a few early human skeletal remains were known, and these only from Western Europe. These represented either the approximately 35,000-year-old Cromagnon people or the (then scarcely recognized) 50,000-year-old "classic" Neanderthal folk. Much understanding of the course of human evolution has been gained since Darwin's time, and especially within the past quarter century (*1*). There are still some extraordinary gaps in the fossil record of the family Hominidae with respect both to specific ranges of Pleistocene time and particular geographic areas. Some such gaps, like the middle Pleistocene range in Mediterranean Africa, have become known only in the last decade, as investigations have been vigorously pursued in the field. However, fossil hominid specimens are still almost entirely unknown from this range of time in Western Asia and in sub-Saharan Africa. The most striking hiatus, particularly since stone artifacts are far from uncommon, is the complete absence of hominid skeletal remains from the Pleistocene in the Indian subcontinent.

In spite of these deficiencies in knowledge, a good deal is known of the major evolutionary stages in hominid phylogeny for the latter half of the Pleistocene. Several distinct, largely geographically restricted lineages are recognized to have existed during the middle, and to have persisted into the early upper, Pleistocene; these probably represented paleospecies (*2*), although some workers consider them to have been generically distinct (*3*). From a portion of one such (*not* Asian) lineage, anatomically modern man (*Homo sapiens*) evolved, but the details of this transformation are still largely obscure (*4*). This best documented aspect of human paleontological knowledge encompasses only the later phases of man's evolution. It is well known largely because of its recency and because there are apparently more abundant traces of human occupation in datable Pleistocene contexts, especially since these can often be linked with effects of the extensive continental glaciations of the Northern Hemisphere. This record thus begins, broadly, during the time of the first of these great continental ice sheets, variously named in Germany (*5*), Britain (*6*), Poland (*7*), and European Russia (*8*).

The main lines of hominid evolution were set during an earlier segment of the Pleistocene. The mammalian faunas of that time range, in Europe, Asia, and Africa, reveal the first appearance of new and modern genera in an otherwise often archaic assemblage. This was an extended period of fluctuating, but generally cooler and more temperate, climates compared with the late Tertiary (Pliocene), leading to mountain glaciation and changing biotopes and biotas. It was a time marked by extensive mountain building, faulting, and upwarping to the extent of several thousand meters, as seen in the Alps, Pyrenees, Caucasus, Atlas, and Himalayan ranges (*9*). This long interval, representing the lower Pleistocene and often termed the Villafranchian after its characteristic fauna, encompasses a time probably as long as the whole of the middle and upper Pleistocene. Half a million years is perhaps a modest estimate. The recent work by Emiliani (*10*), who employed oxygen isotopes in the analysis of climatic change from ocean-bottom cores, gives some promise of providing an "absolute chronology" for the Pleistocene. However, the published climatic curves appear to encompass only the latter half of the Pleistocene—that is, the three major continental glaciations and the intervening Great and Last interglacial stages, the stratigraphy of which closely parallels the core profiles.

The lower Pleistocene represents perhaps the most crucial period for future research in human paleontology. Such efforts promise results of great significance to the understanding of formative phases of hominid phylogeny and the elucidation of those distinctive associated patterns of behavior which differentiated the first hominids from other higher primate (pongid) antecedents and collaterals. I have attempted in this article to indicate a part of what is known of the Villafranchian stage from traces of hominids of this period.

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Villafranchian: Europe and Asia

The base of the Pleistocene is best defined by three lines of evidence: tectonics, climatic deterioration, and the appearance and distribution of new forms of animal life. In the majority of stratigraphic sections, an unconformity, representing an interval of uplift and erosion, separates terminal Pliocene deposits from overlying marine or continental (Villafranchian) sediments of the basal Pleistocene. The first signs of marked cooling are evident in the appearance of north temperate or arctic forms (such as *Cyprina islandica* in Mediterranean waters) in marine invertebrate faunas, and in vegetation changes demonstrated by palynology or by the particular conditions of sedimentation. Continental deposits of basal Pleistocene age contain mammalian assemblages referred to as Villafranchian, from the type locality of Villafranca d'Asti in the upper Po river drainage basin (*11*). Such faunas are characterized by the first appearance of the modern genera *Elephas* (*Archidiskodon*), *Bos (Leptobos)* and *Equus* (and, in some areas, *Camelus*), but in association with a number of other typically late Tertiary species (*12*). The term *Villafranchian* has also often been extended to apply to this basal Pleistocene interval as well as to the fauna. The termination of the interval is ill defined; it is probably best taken as the base of the Cromerian "interglacial" stage (*13*) or its marine equivalent in the Mediterranean basin, the Sicilian (*14*). This stage immediately precedes the first major continental glaciation.

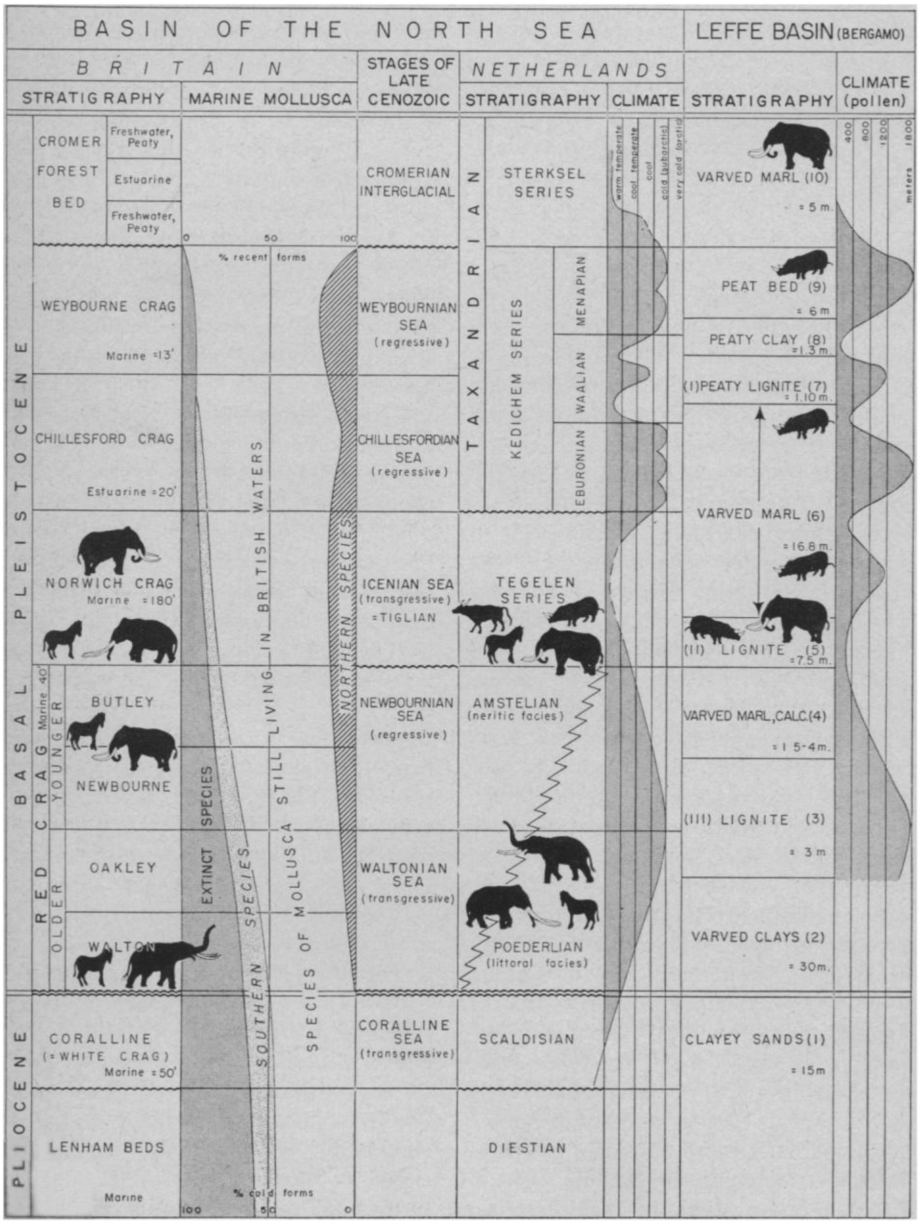


Fig. 1. Villafranchian stratigraphy and climatic change in the North Sea basin and the Leffe lake basin (Tuscany). The silhouettes indicate some of the characteristic species in particular faunal assemblages. The Leffe climate curve, based on palynological evidence, is expressed in terms of present altitude corresponding to vegetation; Leffe is 400 meters above sea level. [Compiled from various sources; see text citations]

In western and southwestern Europe (*15*), evidences of fluctuating sea levels, both transgressive and regressive, and of variably cooler climates, unlike the preceding Pliocene (*16*), are recognized at a number of localities. The tilted deep-water Plaisancian and brackish Astian sediments of the (later) Pliocene sea, which flooded many areas of lowland southern Europe which are continental at present, are unconformably overlain in a number of regions (in southern France and Italy) by the marine deposits of the basal Pleistocene Calabrian sea (*17*). The Calabrian, a transgressive sea which was subsequently regressive [compare the Po valley; also the Emilian stage of *Emilia* (*18*)], has as its continental equivalent, developed in unsubmerged and emergent uplands, a series of fluviolacustrine sands and gravels with a markedly cool temperate flora and a characteristic Villafranchian mammal fauna. The contrast with the subtropical vegetation and archaic mammal faunas of the Pliocene is striking and clearly delineated.

The comparable successions afforded by the North Sea basin, in East Anglia (*19*) and the Netherlands (*20*), and by the polliniferous clays and lignites of the lacustrine basin of Leffe (Bergamo, Tuscany) (*21*) illustrate the main pattern of climatic change during the Villafranchian in western and southern Europe (Fig. 1). The evidence would seem to indicate at least two major colder stages, the latter double, prior to the well-defined Cromerian interglacial stage. These two colder stages are separated by the still inadequately known Tiglian "interglacial" stage (*22*). This sequence is paralleled in the Rome region by the Acquatraversan and Cassian phases of colder climate which precede the transgressive Sicilian sea and the extensive eruptions of the Sabatino volcanoes (*23*). A very considerable body of evidence indicates several phases of fairly extensive mountain glaciation during this interval, very probably including the Donau (*24*) and Günz stages in the northern Alps. The first Himalayan glaciation is perhaps the Asian equivalent. However, there is a dearth of evidence of direct correlation of these subalpine stages either with continental Villafranchian deposits in the lowlands or with equivalent marine horizons.

The European Villafranchian lacks any trace of higher primates, and there are no stone implements testifying to occupation of the continent by hominids (*25*). This was probably a consequence of two factors: (i) Europe was not a primary center in the original hominid radiation, and (ii) the extent of the Mediterranean and Black seas (*26*), not only in the Pliocene but also during the Calabrian and Sicilian transgressions of the early Pleistocene, created impassable water gaps which effectively isolated Europe. The first evidence of hominid occupation of the European continent is well along in the earlier middle Pleistocene. It corresponds to the time of the Romanian regression (*27*) of the Mediterranean, when eustatic lowering of sea level attendant upon the first major continental glaciation evidently permitted expansion into Europe of those peoples [probably represented only by the Mauer (Heidelberg) mandible] responsible for the Abbevillian hand-axe industry (*28*).

In eastern Asia the continental Villafranchian is best known in northern China and in the southern foothills of the Himalayas (*29*). In northern China (*30*), the Pliocene, a period of dry subtropical-to-tropical climate with extensive lakes between stretches of desertic country, was terminated by diastrophic movements resulting in extensive erosion (Fenho erosion interval). These formerly widespread lakes were consequently displaced, and rejuvenated rivers and streams greatly enhanced their fluviatile activities. In the synclinal basins of Nihowan (Hopei), Taiku, and Yûshe (Shansi), to mention only the best known, this erosion surface underlies a torrential lacustrine series of basal conglomerates overlain by sands, marls, and clays (lower Sanmenian series); the clays include a plant bed with cool dry flora (Taiku basin), and the series is capped with sands and silts which yield a characteristic Asiatic Villafranchian fauna (*31*). The entire series was tilted and is separated unconformably (by the Huangshui erosion interval) from the early middle Pleistocene red loams (upper Sanmenian series). No evidence of hominid fossils or of tool-making activities have been recorded from the earlier, Villafranchian, beds. The first evidence of hominid occupation is revealed at locality 13, Choukoutien, correlative with the upper Sanmenian series on faunal grounds, which has yielded a single small chert chopping tool but no human skeletal remains.

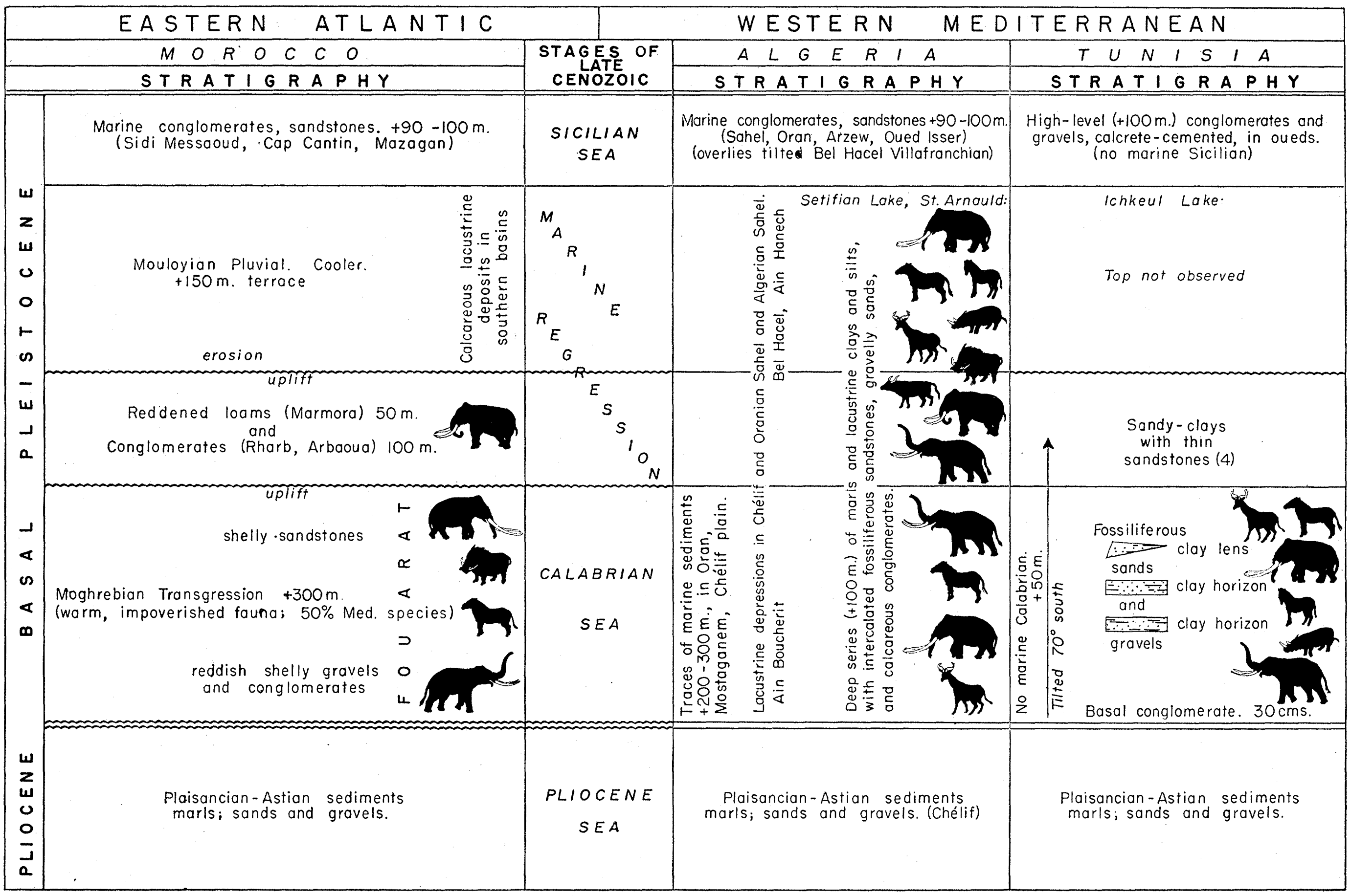
The entire Pliocene and lower Pleistocene succession is magnificently represented in sub-Himalayan northwest India, both in the Potwar region (Punjab) to the northwest and the Siwalik Hills to the east (*32, 33*). The Pliocene, exposed in the middle Siwaliks series, is represented by fresh-water sandstones and shales, 6500 to 10,000 feet in thickness, deposited under tropical to subtropical climates trending toward increased aridity. The entire series was tilted during a major phase of mountain building followed by an interval of severe erosion at the end of the Pliocene. These movements, either through the development of anticlines or as a result of faulting, created a series of depressions trending northeast-southwest which were filled during the lower Pleistocene with great thicknesses of alluvial sediments (upper Siwaliks series) derived from the adjacent uplands. The earlier Tatrot zone of this series is characterized by a thick (100-foot) basal conglomerate overlain by nearly a thousand feet of coarse sandstone; interspersed silty or conglomeratic horizons contain a (still inadequately known) fauna which is characteristically Villafranchian (*34, 35*). The overlying Pinjor zone, some 1000 to 1500 feet of laminated silts and sands, clearly distinguished lithologically from the Tatrot zone, appears to have been deposited under warmer and more temperate conditions by sluggishly meandering streams, in contrast to the great alluvial activity that accompanied the deposition of the preceding Tatrot. A rich Villafranchian fauna is represented in the Pinjor zone (*34, 36*). However, neither the Tatrot nor the Pinjor provide hominid remains, nor is there evidence of stone tools testifying to hominid occupation. Such tools first appear, as the "Pre-Soan" (Punjab flake industry) chopper–chopping-tool assemblage (*33, 37*), in the overlying boulder conglomerate, attributed to the second Himalayan glaciation, of early middle Pleistocene age.

Discussion of the southeast Asia area of the Sunda shelf, an extension of the mainland in middle and later Pleistocene time, is less pertinent here because of the extensive Pliocene submergence. Only isolated mountain peaks were emergent along the southern (Zuider Mountains) and northern (Kendeng Hills) coasts in eastern Java, and some few uplands in the western region (*38*). A Villafranchian fauna is known from fresh-water sandstones and coarse conglomerates at several localities where these overlie Pliocene marine beds (*39*). However, skeletal remains of two distinct hominids (*Meganthropus, Homo modjokertensis*) first appear only in the early middle Pleistocene (*40*). Sundaland, including Sumatra, Java, and Borneo, and much of the present ocean floor had become largely continental by that time as a result of further uplift and marine regression consequent upon continental glaciation in the Northern Hemisphere. There is no evidence to suggest hominid occupation of the Sunda shelf during the Villafranchian stage.

The present evidence would appear to indicate that continental Eurasia was not occupied by hominids during the lower Pleistocene—that is, the Villafranchian stage. The evidence is admittedly and necessarily of a negative nature, and further field investigations, particularly in the sub-Himalayan Siwaliks, are sorely needed. The important fact is that the available evidence does not bear out the opinions of certain earlier workers (*41*) that Asia, or central Asia in particular, was a primary center for hominid (or higher primate) origin and dispersal. Such a conclusion is contradicted not only by our understanding of higher primate relationships, based on comparative anatomical and paleontological studies, but also by biogeographical and paleogeographical conditions. On the other hand, a variety of evidence shows that the Villafranchian stage in Africa was crucial in the earlier phases of hominid evolution.

African Villafranchian

Mediterranean Africa. Several lower Pleistocene localities with Villafranchian faunas are known in northwestern Africa (*42*) (Fig. 2). One of the best stratified localities is Fouarat (near Port Lyautey, Morocco), along the southern border of the Rharb plain. A Villafranchian fauna is present here in coarse sands and sandstones representing a littoral facies of a Calabrian gulf which in places filled depressions in Pliocene marine sediments (*43*). Hominid occu-



	EASTERN ATLANTIC		WESTERN MEDITERRANEAN	
	MOROCCO	STAGES OF LATE CENOZOIC	ALGERIA	TUNISIA
	STRATIGRAPHY		STRATIGRAPHY	STRATIGRAPHY
BASAL PLEISTOCENE	Marine conglomerates, sandstones. +90 -100 m. (Sidi Messaoud, Cap Cantin, Mazagan)	SICILIAN SEA	Marine conglomerates, sandstones +90 -100 m. (Sahel, Oran, Arzew, Oued Isser) (overlies tilted Bel Hacel Villafranchian)	High-level (+100 m.) conglomerates and gravels, calcrete-cemented, in oueds. (no marine Sicilian)
	Mouloyian Pluvial. Cooler. +150 m. terrace Calcareous lacustrine deposits in southern basins erosion	MARINE REGRESSION	Setifian Lake, St. Arnauld: Lacustrine depressions in Chélif and Oranian Sahel and Algerian Sahel. Bel Hacel, Ain Hanech Deep series (+100 m.) of marls and lacustrine clays and silts, with intercalated fossiliferous sandstones, gravelly sands, and calcareous conglomerates.	Ichkeul Lake: Top not observed
	uplift Reddened loams (Marmora) 50 m. and Conglomerates (Rharb, Arbaoua) 100 m.			Sandy-clays with thin sandstones (4)
	uplift shelly sandstones Moghrebian Transgression +300 m. (warm, impoverished fauna; 50% Med. species) reddish shelly gravels and conglomerates FOUARAT	CALABRIAN SEA	Traces of marine sediments +200-300 m., in Oran, Mostaganem, Chélif plain. Ain Boucherit	No marine Calabrian. +50 m. Tilted 70° south Fossiliferous clay lens sands clay horizon and clay horizon gravels Basal conglomerate. 30 cms.
PLIOCENE	Plaisancian-Astian sediments marls; sands and gravels.	PLIOCENE SEA	Plaisancian-Astian sediments marls; sands and gravels. (Chélif)	Plaisancian-Astian sediments marls; sands and gravels.

Fig. 2. Villafranchian stratigraphy in northwestern Africa. The silhouettes indicate some of the characteristic species in particular faunal assemblages. [Compiled from various sources; see text citations]

pation of the area is perhaps first recorded at a slightly later stage, probably corresponding to the regressive Emilian. Flaked pebbles, thought by some to represent primitive pebble tools, have been collected from the Arbaoua conglomerates, of basal Pleistocene age (*44*). These deposits, like the reddened Marmora sandy loams, mantle this region and (broadly) represent the continental equivalent of the Calabrian (Maghrebian) transgression (*45*). However, the artificial nature of the specimens is difficult to confirm when they are discovered in this gravel con-

The Villafranchian fauna of North Africa is more adequately known in Tunisia (Garaet Ichkeul), and particularly from old lake basins in northern Algeria (Bel Hacel; St. Arnaud). The base of Lake Ichkeul (near Ferryville) comprises southerly tilted deep-water Plaisancian and lagoonal Astian marine sediments which are overlain by fresh-water lake beds of basal Pleistocene age. The lower sands and gravels of the latter, separated from the Pliocene sediments by a thin conglomerate, are richly fossiliferous (*46*); a mild temperate flora, but with substantial boreal elements, occurs in intercalated, more or less sandy, clays (*47*). However, the full succession at Ichkeul is still poorly known, and the faunal assemblage is incomplete, since the beds are only partially exposed during times of low water, on the northern foreshore of the present lake. At Bel Hacel (*48*) emergent dune sandstones, which concordantly overlie transgressive Plaisancian-Astian sediments, are eroded and filled with alluvial, weathered and reddened, conglomerates which contain terrestrial and fresh-water molluscs and a Villafranchian fauna. The more than 100-meter-high Sicilian beach rests horizontally and unconformably on the tilted and compressed series.

On the Constantine-Setifian plateau near St. Arnaud the earlier Pleistocene is exposed in deep ravines dissecting thick marls and other calcareous clayey sediments, with intercalated gravel and conglomeratic horizons, which fill old marshy or lacustrine depressions. In the Oued Boucherit (*49*), two horizons, separated by a meter of sterile brown clay, contain a Villafranchian mammal fauna. The lower horizon (Ain Boucherit) is a coarse calcareous conglomerate, and the upper horizon (Ain Hanech), a cracked clay, rather sandy or with light gravels at the base. A quantity of undoubtedly primitive stone implements have been recovered here, largely from the upper horizon (*50*). These specimens (Fig. 3) are fashioned from naturally worn dolomitic limestone pebbles, exhibiting fresh, concave flaking scars and ranging in size from that of a tangerine to that of a good-sized orange. They are either battered over most of the surface to a multifaceted polyhedral form (boules) or are flaked along a margin unilaterally or bilaterally to produce an irregular sinuous edge characteristic of choppers or chopping tools. Unfortunately, the Ain Hanech site has been worked only briefly, since both political circumstances and the proximity of a Moslem cemetery have prevented extensive excavations.

No hominid skeletal remains have yet come to light in the formations of the North African Villafranchian. There is unquestionable evidence of hominid occupation of this region during the terminal phases of the Villafranchian, and a site such as Ain Hanech might one day provide fossilized remains of the creatures themselves.

Sub-Saharan Africa. The central African Pleistocene was initiated by prolonged and extensive uplift, 1000 to 1500 feet at least, accompanied by downwarping in adjacent areas and by fracturing along ancient troughs. Extraordinary volcanic explosions, especially of tuffs and ashes, also took place along the eastern Rift Valley. As a consequence, the mid-Tertiary surface of erosion, whose relief was relatively gentle even during the end-Tertiary phases of valley incision, was severely deformed, and drainage systems were disrupted and even reversed (*51, 52*). Extraordinary depths of lacustrine deposits and subaerial, partially volcanic-derived, sediments were accumulated. These are particularly well preserved in the western (Albertine) and eastern (Gregory) rift valleys and represent good exposures of the continental Villafranchian (Fig. 4).

The Villafranchian, with an overlying middle Pleistocene series (Rawe beds), is also represented along the southern shores of a minor rift valley trending east-west, now Kavirondo Gulf, an eastern embayment of Lake Victoria (*53*). At Kanam, along the north and northeast slopes of the extinct volcano which forms Homa mountain, a great thickness (more than 100 feet) of lacustrine brown clays, with intercalated fine, laminated stony tuffs from intermittent volcanic explosions, have provided a good Villafranchian assemblage. A few pebble tools have also been recovered from such horizons. A small fragment of a hominid mandible is also known (*54*); although it was once believed to date back to the lower Pleistocene, it is now known to be of considerably more recent age.

In the Albertine rift valley an extensive lake existed in the basal Pleistocene, as indicated by the massive (at least 1500 to 2100 feet, to judge from borings) tilted and contorted beds of the Kaiso series (*55*). These are particularly well exposed along the margins of Lake Albert and its southern tributary, the Semliki River, as well as along the northern shores of Lake Edward (*56*) and in the region south of the latter adjacent to the volcanic highlands north of Lake Kivu. The beds seem to attain their maximum exposed thickness in the southerly reaches of Lake Albert and at the adjacent mouth of the Semliki valley; thinner exposures in the upper Semliki and the northern reaches of Lake Edward may merely reflect earlier, more prolonged and intense subsidence of the rift floor in this region.

The Kaiso series is complex, and three main stages of sedimentation have been distinguished (*57*). Only the basal stages are generally regarded as lower Pleistocene; the upper stage is thought to be earlier middle Pleistocene. The lower stage (100 to 120 feet thick in the northern reaches of the valley) is largely silty, with some minor gravel horizons. In some localities this stage is found to overlie a basal ironstone horizon capped by unstratified sands; the ironstone seems to represent a laterite capping the down-faulted peneplain surface and provides an important datum point. This earlier stage is essentially nonfossiliferous. The middle stage (300 to 600 feet thick in the lower reaches of the valley) is predominantly clayey, with selenite evaporites and zones of gypsum. It is characterized by fine sands and sandstones and by discontinuous ironstone horizons and limonite lenses thought to represent desiccated pools. These horizons occasionally provide silicified wood and have yielded a typical, though small (13 species), Villafranchian mammal fauna. Several such ironstone "bone-beds" appear to be present, though they are restricted largely to the middle Kaiso stage (*58*). However, another, perhaps lower, bed is also present in the lower Semliki valley. The site of Kanyatsi (*59*), along the northern shore of Lake Edward just east of the Semliki outflow, has yielded traces of worked stone implements adjacent to an ancient subaerial soil horizon within the middle Kaiso stage. The specimens represent fresh flakes of quartz and quartzite, but the cores from which these were struck are apparently absent, and no pebble choppers or chopping tools have yet been found.

The central region of the Gregory rift valley has failed to provide certain evidence of lower Pleistocene formations; this is perhaps because there was extensive uplift during the later Pleistocene, or because there was relatively little deposition but considerable volcanic activity. The northern and southern reaches of the valley do afford such exposures. The tilted and step-faulted beds of the Omo series, just north and northwest of Lake Rudolph, testify to an ancient and extensive lower Pleistocene lake. A rich Villafranchian fauna occurs in extraordinary profusion in sandstone horizons intercalated in a massive succession of lacustrine vol-

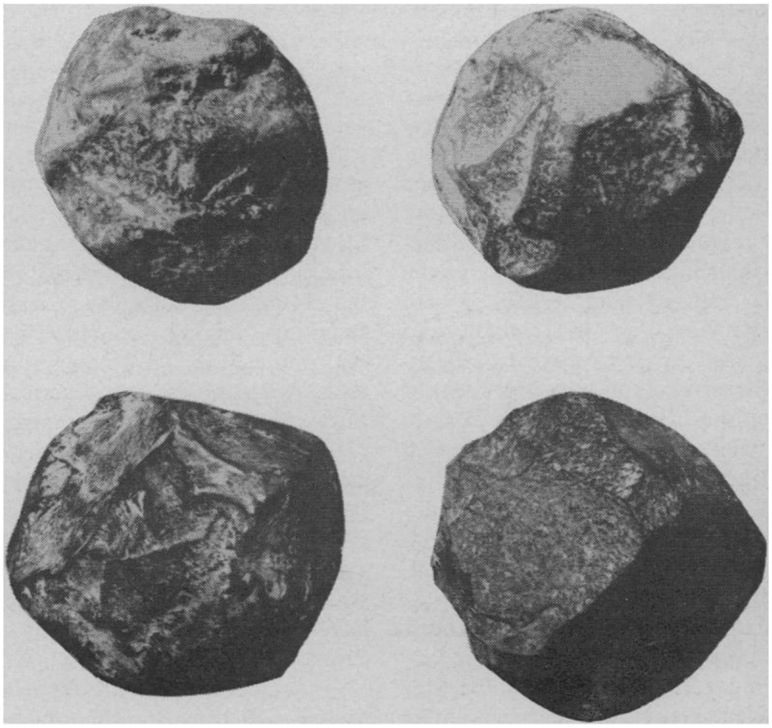


Fig. 3. Pre-Chelles-Acheul implements from the site of Ain Hanech (Algeria). (× ½) [Courtesy C. Arambourg]

canic clayey tuffs (*60*). Neither hominid skeletal remains nor primitive stone implements have been recovered from the Omo series, which, since their discovery by the Bourg de Bozas expedition in 1902-1903, have only been worked during one relatively brief field season. Further investigations in this most inaccessible region are surely warranted, especially since this year I recovered Pre-Chelles-Acheul artifacts from the eroded sandstones.

In the southern reaches of this rift valley the lower Pleistocene is exposed along the tributary Eyasi trough and the adjacent region to the west of the Crater Highlands. At Olduvai Gorge (*61*), which extends from Lake Lagarja on the Serengeti plains some thirty-five miles to the western boundary faults of the Balbal depression, the magnificent lacustrine series of the middle Pleistocene is underlain by a flow of olivine basalt, which buries or obscures earlier horizons. Slightly to the south, in the Vogel river region on the northwest escarpment high above the Eyasi graben, are the Laetolil beds, a series of upfaulted subaerially deposited tuffs (*62*). These appear to be earlier than, as well as in part contemporaneous with, the Olduvai series. The upper Laetolil beds have yielded a rich Villafranchian assemblage of mammals, including some microfauna (*63*). The lowest horizons are also fossiliferous, but the fauna is very poorly known. Pebble tools and a hominid maxilla fragment (*64*), the latter believed to resemble the australopithecine (*Australopithecus*) (*65*), attributed to these beds may in fact be of later Pleistocene age. The basal bed (Bed I) at Olduvai Gorge is now known to contain a Villafranchian faunal assemblage comparable to that from Omo rather than of middle Pleistocene affinity. Pre-Chelles-Acheul stone implements of the Oldowan industry were first found here nearly 30 years ago. In July Dr. and Mrs. L. S. B. Leakey recovered a beautifully preserved skull of a new form of australopithecine from this bed in association with an occupation surface rich in such artifacts and with the bones of small game taken by this creature (announced at the 4th Pan-African Congress on Prehistory, Leopoldville, August 1959).

Central and eastern Africa afford some of the richest Villafranchian faunal localities in the world, coupled with an excellent Pleistocene succession. The faunas from these sites differ somewhat in composition, that from the Laetolil beds being probably the youngest, overlapping basal Olduvai, and that from Kaiso being perhaps the oldest. The Omo fauna overlaps both Laetolil and Kaiso, and that from Kanam is probably broadly equivalent (*52, 66*). As yet it is impossible to determine the magnitude of the climatic change that occurred during the Villafranchian of central Africa because of the effects of tectonics in this unstable region. At present only a broad block correlation with other areas of the Old World, on the basis of faunal content, can be made. Future detailed investigations of the sediments in these basins, particularly of nonsequences and old soil horizons, coupled with palynological research, promise to throw some light on this problem.

At three such localities, Kanyatsi (Lake Edward), Kanam (Kavirondo, Kenya), and Olduvai Gorge, there is clear evidence of hominids, sometimes in the form of skeletal remains and, in all cases, in the form of deliberately fashioned stone tools. Few open habitation sites of the hominids themselves have yet come to light; however, this is largely a result of too little field work in difficult regions. There is every indication that such sites will be forthcoming in the future with concentrated work by prehistorians and Pleistocene geologists. Very complete evidence of such early hominid forms, including abundant skeletal remains, is afforded by the australopithecines of southern Africa (*67*).

Australopithecine Sites

The australopithecines now rank among the most numerous and best known of all Pleistocene hominids. Usually classified as a distinctive subfamily (Australopithecinae) (*68*) of the Hominidae, but quite probably representing merely a distinct genus, *Australopithecus* (*69*), the group contains two probably subgenerically distinct forms, (*Australopithecus*) and (*Paranthropus*). On the basis of the associated faunal assemblages, it appears that the australopithecines are all probably late Villafranchian (*70*); however, there is a possibility that the younger form (*Paranthropus*) may have persisted into the early middle Pleistocene (*71*).

Australopithecines are known from five sites at three localities (Fig. 5) in southern Africa (*72*). With one exception (Taungs) they occur in fossiliferous breccia, composed of calcite-cemented dolomite soil, which infills former caves, formed by solution or subsidence along ancient fracture planes in dolomitic limestones of the Transvaal system. Studies of the mode of formation and the sequence of infillings of these caverns has demonstrated the significance of the degree of communication of the cavern with the outside in the accumulation of sediments (*73*). Travertines and intercalated bands of thin gray marly breccia, representing residual calcified material from dissolution of the dolomite, accumulate prior to the formation of any substantial opening to the surface. Subsequently, as the opening becomes progressively enlarged, surface-derived material collects in sufficient quantity to represent a state of equilibrium with outside conditions. Such breccia accumulations may serve as climatic indicators, through analysis of the sand fractions of breccia residues, minus the carbonate cement derived from roof drip, and comparison with modern dolomite soils in regions of differing rainfall in southern Africa. Very satisfactory results have been thus achieved for the Sterkfontein, Swartkrans, and Kromdraai (site A) sites; the method is not directly applicable to the Limeworks Cave site, Makapansgat, where alluviation or slope-wash, in the higher levels, are complicating factors. In general, the climate appears to have been somewhat drier in this region when (*Australopithecus*) lived and somewhat, or even considerably, wetter when (*Paranthropus*) lived than it is now. Brain (*73*) refers the three older Transvaal sites (Sterkfontein, Limeworks, Swartkrans) to a major dry interpluvial stage (with at least three separate peaks) and the youngest site, Kromdraai, to a succeeding, wetter pluvial stage.

The Taungs site, long since destroyed by quarrying activities, was a cave formed by solution in the capping carapace of a massive basal Pleistocene travertine banked up against a dolomite limestone cliff (Campbell Rand series) (*74*). The filling of the cavity was calcified sandy breccia overlain by contaminated travertine with sandy lenses from which the type australopithecine remains were most probably recovered.

The fauna associated with the australopithecines is not only varied but differs from site to site. In general it comprises other primates (both rare monkeys and abundant baboons), nu-

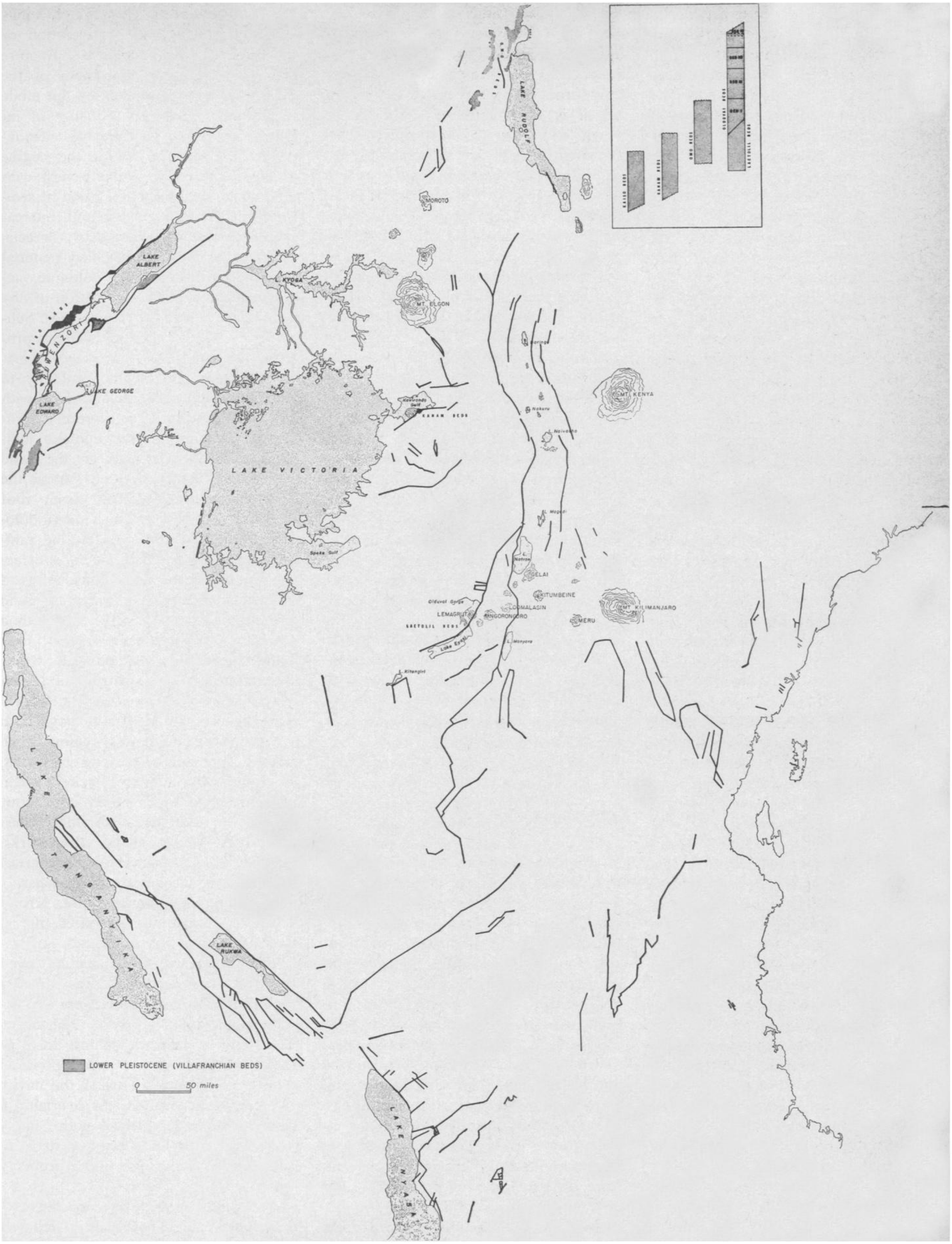


Fig. 4. The Rift Valley system and Villafranchian localities in eastern Africa. [Base map and major faults redrawn from the geological map of East Africa prepared on behalf of the Inter-Territorial Geographical Conference, 1952; stratigraphical inset from H. B. S. Cooke, *52*]

merous rodents, insectivores, hyracoids, lagomorphs, numerous carnivores, including hyaenids and sabretooths, suids, an extinct sivathere, equids, and numerous antelopes. The following frequencies were obtained from counts of over 7000 bone fragments, out of a much larger number, from remnants of the gray marly breccia at Limeworks Cave (*75, 76*): 92 percent, antelope (293 individuals; more than two-thirds medium to small, the remainder large or very small varieties); 4 percent, other ungulates (four zebras, six chalicotheres, five rhinoceroses, one hippopotamus, 20 pigs, six giraffids); 1.6 percent, carnivores (17 hyenas, one leopard, one jackal, one wild dog, one sabretooth, and nine other small and medium species); 1.7 percent, baboons (45 individuals), rare rodents (hares and porcupines), and very rare birds and reptiles (tortoise, water turtle). Five australopithecine individuals represent only 0.26 percent of the total assemblage.

The various segments of the skeleton are very unequally represented at this site. The frequency of cranial fragments is particularly high among the nonbovid ungulates (88 percent), the carnivores (75 percent), the rodents (100 percent), and the primates, including the australopithecines (95 percent). The proportions are lower (34 percent) among the antelopes (of all sizes), and there are interesting differences in frequencies of antelope postcranial elements: cervical vertebrae (7 percent), other vertebrae (5 percent), ribs, and so on (5 percent), scapulae (9 percent), innominates (8 percent), forelimbs (37 percent), hindlimbs (20 percent), feet (6 percent) (these figures do not apply to very small antelopes, which are represented exclusively by cranial elements).

Any consideration of the diet and life habits of the australopithecines must take into account the associated fauna and frequencies of preserved skeletal segments. Hence, such figures are important and are much needed from the other sites. Several possibilities exist as to the manner in which the australopithecines and the associated fauna came to be incorporated into the breccias. The sites might have been (i) natural crevices into which animals fell; (ii) crevices into which bone accumulations were swept by natural agencies; (iii) carnivore lairs into which prey or scavenged carcasses were carried; (iv) rubbish heaps; or (v) actual occupation sites of the australopithecines. There is no evidence at any of the sites to support (i) or (ii), although the gravelly breccia at Limeworks Cave was partly fluviatile in origin; there is also evidence of stratification in the upper brownish breccia at Swartkrans, probably due to deposition in isolated pools but certainly not the consequence of stream activity. It will always be difficult to decide between (iv) and (v), but the important and still unsettled question is whether the sites were occupied and the bones were accumulated by carnivores, in particular sabretooths or hyenas, or both, or by carnivorous australopithecines.

It is necessary to bear in mind that these sites are known because of commercial lime-quarrying activities. In most cases such efforts were directed toward the basal travertines, formed largely when the caves were still solution cavities. In the case of Taungs the cave was discovered as a consequence of such mining in the massive cliff-forming travertines at Buxton, in one of which the cave happened to be situated. All the fossil mammals at the Limeworks Cave, Makapansgat, have been obtained by sorting through the extensive dump heaps left behind by the miners. Only in the case of Swartkrans (*77*) (in part) and some of the excavations at Sterkfontein have investigations been carried out which would permit some comprehension of the fossiliferous breccias as they existed *in situ.* However, the extreme consolidation of the fossil cave earths, a consequence of calcareous cementation, necessitates the use of explosives, so results are definitely limited with respect to details of the pattern of association and the arrangements of bones in the deposits. In the present state of knowledge it is indeed doubtful if the matter can be definitely settled until a new site can be excavated, with every attempt made not to disturb the stratigraphy and fossil associations.

Dart (*75, 78*) has repeatedly maintained that the extraordinary accumulations of mammalian skeletal remains in the fossiliferous breccias are a direct consequence of the predatory and carnivorous habits of australopithecines. Such remains represent in his opinion not only slaughtered prey but also scavenged carnivore kills; many of the bones were useful as tools and weapons for pounding, cleaving, scraping, stabbing, and slicing. On the basis of the preserved remains inventoried at Limeworks Cave, specialized functions have been attributed to specific bones and portions of animal skeletons that were put to use by those "flesh-eating, skull-cracking and bone-breaking, cave-dwelling apes."

There are in fact two distinct issues involved here. The question as to whether the bones were employed as implements and weapons by australopithecines presupposes that these creatures were carnivorous and were therefore responsible for the fossiliferous accumulations. The use of these bones is extremely difficult to verify, since none of the sites yield any trace of specimens which have been deliberately worked or shaped. There is no doubt that the jaws and teeth, horns, and shattered or damaged limb bones which Dart attributes to an "osteodontokeratic culture" might be employed in the fashions he has so exhaustively and imaginatively outlined. However, as in the case of the so-called "bone and antler industry" from the Choukoutien locality in northern China, attributed by Breuil (*79*) to the middle Pleistocene hominid found there, this is extremely difficult to confirm scientifically, even though both claims may prove entirely valid.

The question of the carnivorous habits of australopithecines is a separate matter and one which should be resolved from existing evidence. The parts and proportions of the animal skeletons preserved do coincide closely with remains at carnivore kill sites in the open, even after the usual scavengers have been at work (*80*). Moreover, although contrary claims have been made (*81*), both brown and spotted hyenas may eat and accumulate bones in and about their lairs, at least at times (*82*). Nonetheless, this possibility does not account for the enormous concentration of bones at the sites. Also, there are discrepancies between the proportion of cranial and postcranial elements of the antelopes compared with the other ungulates, the carnivores, and the primates.

Two main points are important in connection with the dietary habits of these creatures: (i) the evidence from Taungs, Sterkfontein, and Limeworks Cave of baboon skulls bearing evident signs of localized depressed or radiating fractures, smashed-in walls or tops of the cranial vault, openings in the vault or base, and twisted facial skeletons all testify to predatory activities which are those of a hominid rather than any hyaenid or felid carnivore; and (ii) the substantial quantity of various antelope and other long bones which are not only broken and smashed but also split longitudinally, and which usually fail to reveal any traces of carnivore gnawing, is further testimony to hominid habits.

Such evidence has been convincing not only to me, but also to other workers (*83*) who have examined the specimens in question. Moreover, it seems very likely, on the basis of the Taung evidence, that eggs, crabs, turtles, birds, rodents, and smaller antelopes were a not insubstantial part of australopithecine diet. The former such items are easily collected, and it is not particularly difficult to kill members of the other species of smaller mammals. The australopithecines were very probably carnivorous predators as well as scavengers of the kills of other carnivores (of which there was then an abundance of forms long since extinct). The marked disproportion between the bovid and nonbovid ungulates and the relatively few carnivores in the Limeworks Cave inventory may merely be a reflection of this latter fact and of the limited hunting capabilities of such creatures. Such a conclusion does not preclude the possibility that carnivores also, at least periodically, occupied such sites and contributed to the bone accumulations. This can hardly be denied until careful excavations have been carried out which prove the situation to have been otherwise.

Until recently none of the australopithecine sites were known to contain artifacts. Consequently, many workers asserted that such primitive creatures, although admittedly hominids, were incapable of making, and perhaps even of using, tools. Quite possibly this lack of stone implements has also convinced some workers that bone, horn, and teeth of other animals were used by australopithecines as weapons and implements. A few split and flaked dolomite pebbles from the calcified stony and sandy fluviatile horizon which overlies the pink and gray breccias at Limeworks Cave (*84*) suggest but do not afford conclusive proof of tool-making activities. However, there is no doubt about the validity of the implements (Fig. 6), referred to a pebble-tool (Pre-Chelles-Acheul) industry, recovered recently from the Sterkfontein locality (*85*). The specimens derive from a reddish-brown breccia at the extension site first thought to be broadly contemporary with the basal pink australopithecine-bearing breccia of the type site. Robinson's (*86*) more recent investigations indicate, however, that these breccias are separated unconform-

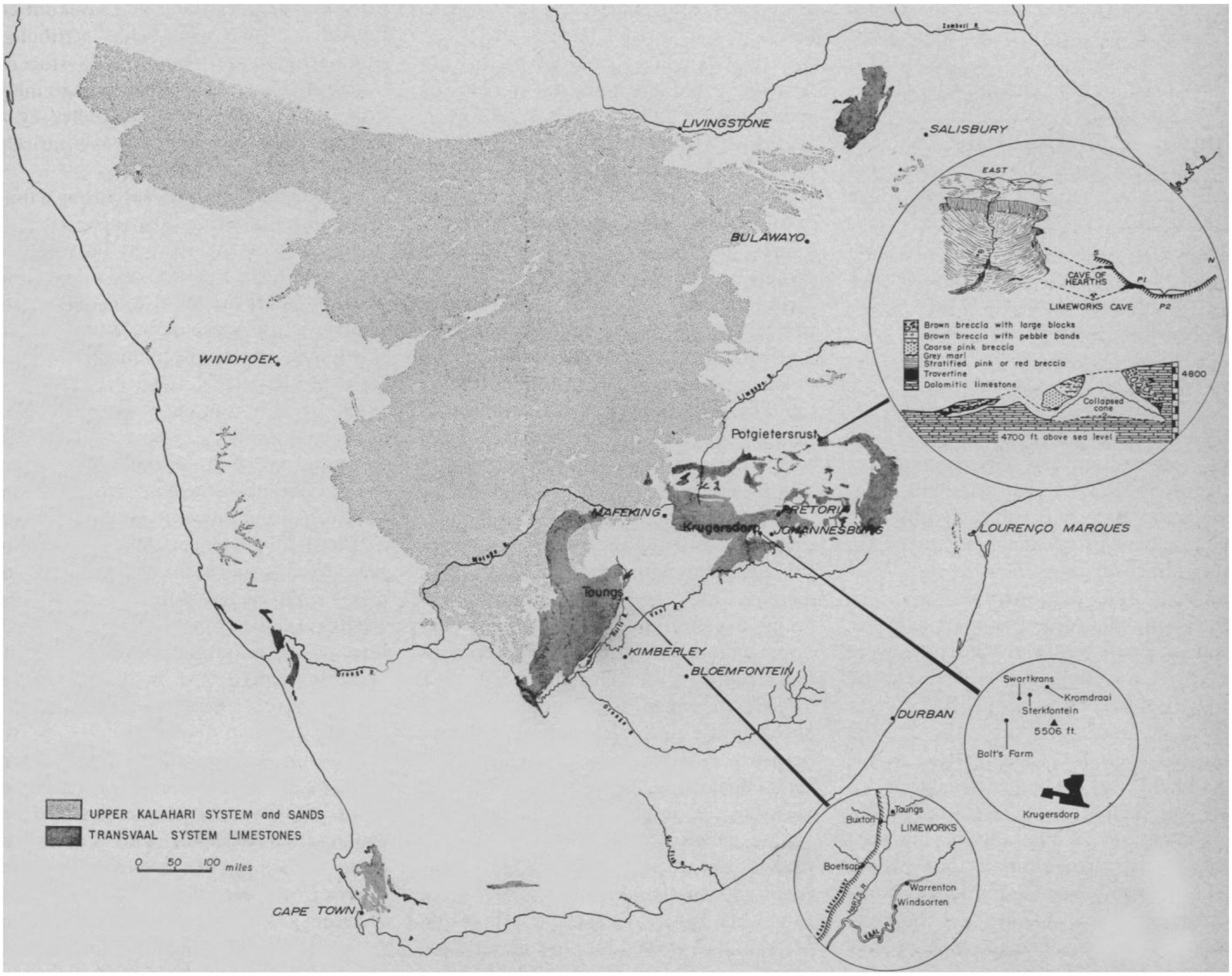


Fig. 5. Australopithecine localities in southern Africa. [Base map redrawn from the geological map of southern Africa in A. L. du Toit, *The Geology of South Africa*, ed. 3, 1954; insets adapted from G. B. Barbour, H. B. S. Cooke, J. T. Robinson, and F. E. Peabody]

ably, as a consequence of subsidence, and that the latter pink breccia underlies the reddish-brown breccia of the extension site. The latter contains the foreign and worked stones as well as some fauna (including *Equus*, absent in the type site basal pink breccia) and some remains (isolated permanent teeth, a juvenile maxilla fragment with several teeth) referred to *Australopithecus*.

The specimens recovered from Sterkfontein include pebble- and core-choppers (8), a chopper-hammerstone (1), and rough retouched end-struck flakes (2). Quartz, quartzite, chert, and diabase pebbles foreign to the deposit were also found; about half (24) of these were plain, and the other half (23) exhibited evidence of fracture from use. The small flakes struck from the choppers and cores are missing and indicate that the specimens were collected and worked elsewhere, near streams where raw material was available, prior to being carried to the site for use. Some of the specimens show extensive battering rather than careful flake removal, suggesting either hard use or, according to J. D. Clark (*87*), poor workmanship. The implements are fresh and unweathered and cannot have been washed in from the outside, since the breccias must have accumulated under an overhanging roof, and since the breccias fail to reveal such conditions of deposition. The artifacts seem to be concentrated at the western end of the site near the original entrance to the cave and were undoubtedly left behind by the hominids who occupied this end of the cavern.

The recovery of pebble tools in association with australopithecines is a momentous discovery. There now seems little doubt that these primitive creatures were already capable of using and manufacturing implements of stone and, presumably, of other nonpreserved materials as well. The extraordinary concentration of other mammalian bones would indicate that these creatures were capable of killing the moderate- and smaller-sized species; probably they also scavenged carnivore kills. There is no indication that they had the ability, the equipment, or the organization necessary for killing very large mammals, in contrast to middle Pleistocene peoples. Such carnivorous habits would have required some sharpened stone implements, such as flakes and chopping tools, for cutting open the hide of kills to obtain meat. There is no trace of the use of fire at this early time.

Clark (*87*) has recently suggested that the availability of water in the cave systems may have been an important factor in their having been occupied. Except for small and seasonally dry streams, cave and fissure systems, and springs related to them, provide the best source of water in such limestone country. Such sources of water would have attracted game and australopithecines alike and would have provided ideal conditions for the latter to prey on antelopes, pigs, baboons, and other animals which came to drink there. This also readily accounts for the profusion of animal bones accumulated in the cave and for the presence of implements necessary to butcher the slaughtered game.

Australopithecine Morphology

Hominids and pongids (apes) are generally regarded as closely related higher primate groups (hominoids). There are obvious and significant morphological and behavioral differences between the living representatives of the two families. Acceptance of the fact of evolution and the reality of such close affinity indicates, however, that such divergences were fewer and less sharply delineated in the remote past. The *primary* adaptation of the hominid radiation required transformation of the locomotor skeleton to permit fully upright posture and an efficient bipedal gait (*88*). This mode of terrestrial locomotion contrasts markedly with the arboreal or terrestrial quadrupedalism of the lower catarrhine monkeys or with the arboreal brachiation of the pongids, coupled, in the larger pongine (anthropoid ape) species, with semipronograde quadrupedalism. This basic locomotor adaptation of the hominids was doubtless preadaptive for subsequent evolutionary changes which affected the skull—reduction of the facial skeleton and extraordinary enlargement of the cerebral hemispheres and cranial vault. The latter has been linked with enhanced cultural capacities, although the manifold interrelationships between structure and function, and their behavioral significance, are still very largely obscure.

The pelves of four australopithecine individuals are now known. Three represent (*Australopithecus*) and were found at Limeworks Cave (*89*) and Sterkfontein (*90*) (at the latter site, much of an associated vertebral column was also found); (*Paranthropus*) is represented by one incomplete innominate bone from Swartkrans (*91*). These fortunate discoveries demonstrate conclusively that the pelvic structure of these creatures was that characteristic of primitive bipedal hominids. They also greatly add to our understanding of the hominid locomotor transformation, which involved a complex of interrelated structural modifications. These constituted a basic reorientation of the pelvis in relation to the trunk, interrelated changes which permitted an erect trunk and full extension of the lower limbs in stable upright posture (and in the female, maintenance of the bony birth canal).

Such changes involve (i) expansion of the iliac blade, especially the auricular area, coupled with sacral rotation and accentuated lumbar lordosis; (ii) shortening and anterior rotation or "twisting" of the ilium, with attendant development of a sigmoid curvature of the iliac crest; (iii) thickening of the outer bony table above the acetabulum (to aid in balance and weight support); (iv) development of an iliac cristal tubercle, in line with the strengthened supra-acetabular region (related to differentiation and expansion of the iliotibial tract as an aid in stabilization of the hip and knee joints in standing and walking erect); (v) enlargement and approximation to the acetabulum of the anterior inferior iliac spine (related to the size of the straight head of the *rectus femoris* muscle, as part of the general enlargement of the *quadriceps femoris* muscle group in bipeds); (vi) shortening of the ischium and altered form of the ischial tuberosity (the full significance of this is obscure, but it is apparently related to the position of the extensor, or hamstring muscle, lever arm); (vii) enlargement and displacement of the *gluteus maximus* muscle as a powerful extensor (rather than a lateral rotator as in apes and monkeys); and (viii) altered function of *gluteus medius* (and *minimus*) muscles as abductors (to maintain lateral stability in walking erect).

There are accompanying interrelated modifications in the proximal head of the femur. These include: (i) enlargement of the femoral head; (ii) development of the lesser trochanter (related to an altered disposition of the *psoas major* muscle); (iii) development of the anterior segment of the greater trochanter and the intertrochanteric line (related to the attachment of the Y-shaped ligament of Bigelow and the joint capsule); (iv) development of the *linea aspera;* (v) shift of *gluteus maxi-*

mus to a posterior rather than a lateral insertion, as in apes, in the place of *adductor minimus* and expansion of *vastus intermedius;* and (vi) notable reduction of the *quadratus femoris* muscle. Other modifications of the distal end of the femur, including the obliquity of the shaft, the marked depth of the patellar surface, the configuration of the intercondylar notch, and the enlargement of the lateral condyle, were apparently associated in large part with enhanced stability of the knee joint in orthograde progression.

The basic morphological pattern characteristic of hominid bipedalism is apparent in the australopithecine lower limb skeleton so far as it is known (*92*). There are a number of minor differences—for example, in the form of the ischial region—from the pelvic morphology of *Homo sapiens*, a not unexpected finding in a primitive lower Pleistocene hominid. The australopithecine lower leg and foot, except for a talus of (*Paranthropus*), is still largely unknown.

The morphological pattern of the australopithecine dentition is also hominid rather than pongid (*93*). In the deciduous dentition this is evident in (i) the evenly curved dental arch, lacking diastemata; (ii) the small milk incisors; (iii) the small, nonprojecting spatulate milk canines; (iv) the quadricuspid upper first milk molar; (v) the nonsectorial, quinticuspid lower first milk molar with well-developed anterior fovea and cusps of approximately equal height. In the permanent dentition this is evident in (i) the evenly curved (parabolic) dental arch; (ii) the small incisors; (iii) the small, nonprojecting spatulate canines, lacking a talonid and with the internal cingulum forming a basal tubercle; (iv) the double-rooted upper first premolar; (v) the nonsectorial, bicuspid lower first premolar; and (vi) the replacement sequence, in which both the permanent canine and medial incisor tend to erupt relatively early.

The related structure of the facial skeleton is also primitively hominid, and this is paralleled in a number of structural details of the cranial base and the occiput. The brain, in proportion to body size, in certain aspects of its form and proportions, and in its tendency toward delayed maturation, approaches a primitive hominid rather than a pongid condition.

There are consistent morphological distinctions between the earlier form (*Australopithecus*) and the younger form (*Paranthropus*) (*94*). These are evident not only in the deciduous and permanent dentitions and the facial skeleton but also in the structure of the cranial base and vault, as well as in the known portions of the postcranial skeleton. (*Australopithecus*) was a small, gracile bipedal creature, weighing certainly no more than 75 to 85 pounds in the larger males. (*Paranthropus*), on the other hand, was a far more robust and massive creature of probably half again that body weight. Such, probably subgeneric, differences indicate a pronounced bifurcation within a primary australopithecine radiation, at least in the basal Villafranchian and possibly even in the later Pliocene. Unfortunately the general absence of fossiliferous Pliocene horizons in sub-Saharan Africa has thwarted investigation of the earlier evolutionary phases

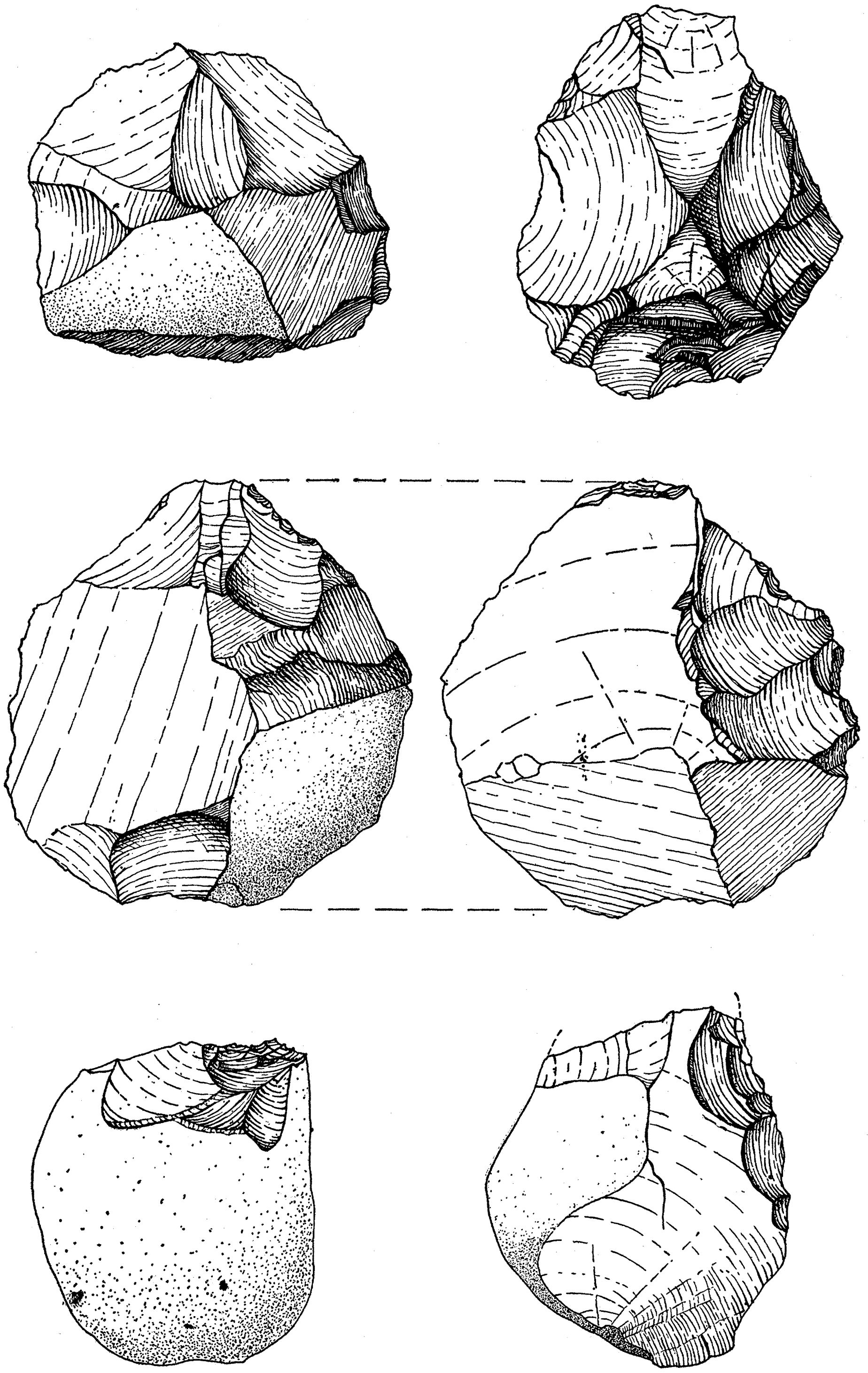


Fig. 6. Pre-Chelles-Acheul implements from the australopithecine-bearing breccias at Sterkfontein (Transvaal). [After J. T. Robinson and R. J. Mason, *85*]

and primitive hominoid antecedents of the australopithecine group.

At Swartkrans another distinct hominid, designated *Telanthropus*, is found in direct association with the australopithecine (*Paranthropus*) (*95*). This form, which is still only very inadequately known, differs markedly from (*Paranthropus*) in dental and mandibular morphology and in certain features of the maxilla (in particular in the structure of the nasal floor). In all such characteristics, some of which reveal some resemblances to the earlier australopithecine (*Australopithecus*), this hominid is further evolved morphologically than any known australopithecine and approaches therefore the phylogenetic status of certain earlier middle Pleistocene forms attributed to the genus *Homo*. The full implications of this conclusion cannot be properly evaluated until additional, more complete specimens have been discovered.

Tertiary Hominoids and Villafranchian Hominids

It is significant that the African Villafranchian hominids differ considerably in morphology from later Tertiary hominoids of eastern Africa and Eurasia. Four hominoid genera are recognized from the earlier Miocene of eastern Africa, three and possibly four genera (*96*) are recognized from the middle and late Miocene and the lower Pliocene of peri-Alpine Europe, and four genera are recognized from the (upper) lower and middle Siwaliks of Asia (Fig. 7).

In both Africa and Europe primitive hylobatids (gibbons) are already evolved in the lower half of the Miocene. Most of the basic cranial and dental morphology of the group is already established in these forms; in fact the dentition is already basically hominoid in the Oligocene form *Propliopithecus*. However, in some features of postcranial structure and in limb proportions these forms differ significantly from their living representatives (*97*). Similarly, the basic dryopithecine (pongid) dental characteristics are manifest in the earlier Miocene hominoids of eastern Africa, although cranial and facial morphology is distinct from that of evidently specialized living varieties of the group (*98*). Moreover, the fundamental locomotor pattern of the recent large-bodied brachiator is evident in the morphology of shoulder and elbow joints, whereas the skeleton of the hand is distinctly primitive cercopithecoid or monkey-like (*99*). The later Miocene and Pliocene dryopithecine hominoids of Europe and their Pliocene counterparts of Asia, known nearly exclusively from jaws and teeth, are typically pongid in mandibular and dental structure and therein do not differ fundamentally from the living gibbons and great apes.

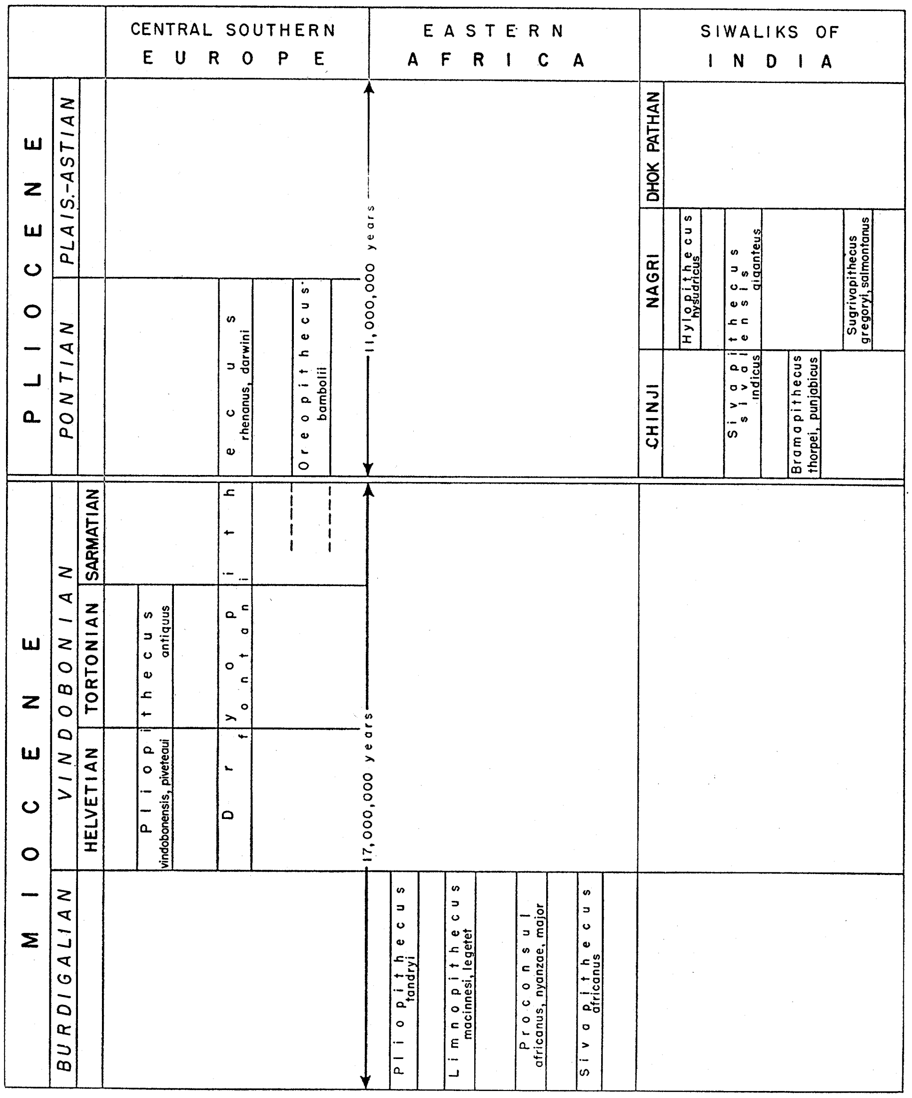


Fig. 7. Temporal distribution of hominoids in the Neogene of Africa, Asia, and Europe.

Oreopithecus, a form known for over three quarters of a century which has received much publicity and been much discussed recently, is a notable exception to this statement. This primate occurs in the Pontian (lower Pliocene) lignites of Tuscany (*100*). It is surely significant that *Oreopithecus* reveals features of dental morphology which are not *typically* pongid, although there can be no question that it is fully hominoid rather than primitive cercopithecoid (cercopithecid) (*101*). A majority of workers tend to agree that the other hominoids of the later Tertiary are typical pongids, with all the attendant dental specializations which would effectively exclude such creatures from hominid ancestry. Hürzeler's (*102*) painstaking reexamination of all the *Oreopithecus* material proves, however, that *all* later Tertiary hominoids were not typically pongid (*103*). Hence, the long-standing argument over the "cercopithecid" (Old World monkey) or "pongid" (anthropoid ape) origin of hominids can be clarified, since many of the more "generalized" hominid features which some workers have regarded as indicative of lower catarrhine affinity are present in either primitive or nonpongid hominoids. Consequently, an oreopithecine hominoid group might well provide the ancestral stage from which orthograde bipedal hominids were subsequently to evolve. It is still premature to assert the correctness of such a hypothesis to the exclusion of all others. The recent and truly important discovery of a nearly entire skeleton of

Oreopithecus from the Grosetto lignites should provide most of the evidence necessary to resolve this problem.

It should be recalled that the whole of the African Pliocene, a span of over ten million years, is still either almost or entirely unknown (*104*). Late Tertiary hominoids surely occupied the more central area of the continent, although fossiliferous deposits of this time range are still unknown. Until some evidences of hominoid varieties are forthcoming from the upper Neogene of sub-Saharan Africa, any hypotheses of hominid origins will lack support. There is widespread evidence of extensive sub-Saharan desiccation, between 1°N and 20°S, from the late Miocene throughout the Pliocene. This was a period of desertification during which great distributions of fine, light, unstratified aeolian sands of the (upper) Kalahari system occurred (*105*). Conditions appear to have been such that, except for rare, and probably small, basins of sedimentation (proto-rift valleys), which are usually obscured by volcanic lavas and other deposits, the preservation of mammalian fossils was literally precluded.

This was certainly a crucial time for mammalian evolution in general as well as for higher primate evolution in particular. Thus, the origins of the incredibly rich eastern-central African grasslands fauna is literally unknown; yet this long interval was probably vital for such a radiation, since the Villafranchian antelopes appear largely referable to existing genera. For the pongid hominoids, whose ecological requirements and habits of locomotion were apparently becoming those of forest-dwelling, vegetarian (or frugivorous) brachiators, such desiccation had profound effects on distribution, which are fully evident today in the sparse and restricted habitats of the African apes. For those hominoids that were preadapted toward terrestrial bipedalism, it was a period of trial in a new and exploitable environment. The Villafranchian stage, as well as the later Pleistocene phases of hominid history, testify to the achievement of this primary radiation.

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22. W. H. Zagwijn, *Geol. en Mijnbouw* **19**, 233 (1957); A. Schreuder, *Arch. néerl. zool.* **7**, 153 (1945).
23. A. C. Blanc, *Quaternaria* **4**, 95 (1957).
24. B. Eberl, *Die Eiszeitenfolge im nördlichen Alpenvorlande* (Filser, Augsburg, 1930); I. Schafer, *Geol. Bavarica No. 19* (1953), p. 13.
25. Supposedly artificially flaked specimens have been reported from the East Anglian "Crags" [see especially J. R. Moir, *The Antiquity of Man in East Anglia* (Cambridge Univ. Press, Cambridge, 1927)]; however, most workers are now convinced that these are natural specimens. See A. S. Barnes, *Anthropol.* **48**, 217 (1938); *Am. Anthropol.* **41**, 99 (1939); S. H. Warren, *Southeast Nat. Antiq.* **53**, 48 (1948) .
26. M. Pfannenstiel, *Geol. Rundschau* **34**, 341 (1944); *Bonner Geogr. Abhandl.* **6**, 1 (1950); S. Erinc, *Rev. Geogr. Inst. Univ. Istanbul* **1**, 85 (1954).
27. A. C. Blanc, *Geol. Meere Binnengewässer* **5**, 137 (1942).
28. It has been maintained that the Abbevillian, at least in the Somme valley where it is best known, is of "first interglacial" (=Günz-Mindel=Cromerian) age. See H. Breuil, *Proc. Prehist. Soc.* **5**, 33 (1939); ——— and L. Koslowski, *Anthropol.* **41**, 449 (1931); ———, *ibid.* **42**, 27, 291 (1932); ———, *ibid.* **44**, 249 (1934). However, a variety of both geological and paleontological evidence indicates that assignment of a younger age is fully warranted, and that this was probably an ameliorative phase within or toward the end of the first major continental glaciation.
29. See the excellent general summary by H. L. Movius, Jr., *Papers Peabody Museum Am. Archaeol. Ethnol. Harvard Univ.* **19**, 1 (1944); also, H. de Terra, *Proc. Am. Phil. Soc.* **77**, 289 (1937).
30. P. Teilhard de Chardin, *Bull. Geol. Soc. China* **16**, 195 (1937); *ibid.* **17**, 169 (1937); *Compt. rend. soc. géol. France, No. 17* (1938), p. 325; *Inst. Géo-Biol., Pekin, No. 7* (1941); ——— and C. C. Young, *Bull. Geol. Soc. China* **12**, 207 (1933); G. B. Barbour, *ibid.* **10**, 71 (1931); H. de Terra, *Inst. Géo-Biol., Pekin, No. 6* (1941).
31. See faunal list in P. Teilhard de Chardin and P. Leroy, *Inst. Géo-Biol., Pekin, No. 8* (1942).
32. H. de Terra. *Proc. Am. Phil. Soc.* **77**, 289 (1937); ——— and P. Teilhard de Chardin, *ibid.* **76**, 791 (1936); G. E. Pilgrim, *Records Geol. Survey India* **40**, 185 (1910); W. D. Gill, *Quart. J. Geol. Soc. London* **107**, 375 (1952).
33. H. de Terra and T. T. Paterson, *Carnegie Inst. Wash. Publ. No. 493* (1939), p. 1.
34. E. H. Colbert, *Trans. Am. Phil. Soc.* **26**, 1 (1935).
35. The interesting and little known pongid *Ramapithecus* is the last Siwalik primate to occur in the Tatrot zone.
36. D. A. Hooijer and E. H. Colbert, *Am. J. Sci.* **249**, 533 (1951); also, D. A. Hooijer *Proc. Koninkl. Ned. Akad. Wetenschap.* **B55**, 436 (1952).

H. L. Movius, *Trans. Am. Phil. Soc.* **38**, 329 (1948); *Cahiers hist. mond.* **2**, 257, 520 (1955).

38. H. de Terra, *Trans. Am. Phil. Soc.* **32**, 437 (1943); R. W. van Bemelen, *The Geology of Indonesia* (Nijhoff, The Hague, 1949).
39. G. H. R. von Koenigswald, *Proc. Koninkl. Ned. Akad. Wetenschap.* **B38**, 188 (1935); *Quartär* **2**, 28 (1939).
40. D. A. Hooijer, *Am. J. Phys. Anthropol.* **9**, 265 (1951); *Proc. Koninkl. Ned. Akad. Wetenschap.* **B55**, 436 (1952); *ibid.* **B60**, 1 (1957); *Quaternaria* **3**, 5 (1956). A contrary opinion is held by G. H. R. von Koenigswald, *Proc. Koninkl. Ned. Akad. Wetenschap.* **B59**, 204 (1956); *Actes congr. assoc. intern. étude quatern., 4^e Congr., Rome-Pise, 1953* (1956), vol. 1, p. 5.
41. D. Black, *Bull. Geol. Soc. China* **4**, 133 (1925); W. D. Matthew, *Climate and Evolution* (N.Y. Acad. Sci., New York, ed. 2, 1939).
42. C. Arambourg, *Bull. soc. géol. France* **19**, 195 (1949); "La paléontologie des vertebrés en Afrique du Nord française," *Congr. géol. intern., 19^e Congr., Algiers*, 1952, *Monogr.* Arambourg distinguishes lower (Ichkeul, Boucherit, Fouarat) and upper (Bel Hacel, Ain Hanech) Villafranchian faunas; the former is more archaic and includes *El. africanavus, Anancus, Stylohipparion*, and *Libytherium*, whereas the latter includes predominantly *El. meridionalis* and *Equus*, with *Libytherium* and, rarely, *Stylohipparion*.
43. G. Choubert *et al.*, *Notes et mém. serv. géol. Maroc, No. 71* (1948), p. 15; G.

Choubert, *Notes et mém. serv. géol. Maroc No. 76* (1950), p. 13.

44. P. Biberson *et al. Compt. rend.* **245**, 938 (1957).
45. G. Choubert and R. Ambroggi, *Notes et mém. serv. géol. Maroc, No. 117* (1953), p. 3; G. Choubert *et al. Compt. rend.* **243**, 504 (1956); G. Choubert, *ibid.* **245**, 1066 (1957); *Actes congr. assoc. intern. étude quatern., 5e Congr. Madrid-Barcelona, 1957* (in press).
46. C. Arambourg and M. Arnould, *Bull. soc. nat. Tunisie* **2**, 149 (1949).
47. C. Arambourg *et al., Compt. rend.* **234**, 128 (1952); *Arch. Mus. nat. hist. natl. Paris, sér. 7* (1953), vol. 2, p. 1.
48. M. Dalloni, *Bull. soc. géogr. archéol. prov. Oran* **61**, 1 (1940); *Actes congr. assoc. intern. étude quatern., 4e Congr., Rome-Pise, 1953* (1956), vol. 1, p. 19; *Bull. soc. hist. nat. Afrique nord* **45**, 134 (1954).
49. C. Arambourg, *Bull. soc. géol. France* **19**, 195 (1949); *Compt. rend.* **229**, 66 (1949).
50. ———, *Compt. rend. soc. géol. France, No. 7* (1949), p. 120; *Bull. soc. préhist. franç.* **47**, 348 (1950); *Compt. rend.* **236**, 2419 (1953); ——— and L. Balout, *Bull. soc. hist. nat. Afrique nord* **43**, 152 (1952). Crude bifaces, referrable to a basal Chellean industrial stage, were discovered in 1952, derived from a higher level at the Ain Hanech site.
51. F. Dixey, *Quart. J. Geol. Soc. London* **102**, 339 (1946); *The East African Rift Valley, Colonial Geology and Mineral Resources Suppl. Ser.* (London, 1956). See especially the recent excellent critical appraisal by H. B. S. Cooke (*52*, p. 60).
52. H. B. S. Cooke, *Annex. Trans. Geol. Soc. S. Africa* (1958).
53. P. E. Kent, *Geol. Mag.* **79**, 117 (1942); E. P. Saggerson, *Geology of the Kisumu District* (Geological Survey, Kenya, Nairobi, 1952).
54. L. S. B. Leakey, *The Stone Age Races of Kenya* (Oxford Univ. Press, London, 1935); compare M. F. Ashley Montagu, *Am. Anthropol.* **59**, 335 (1957).
55. This series is named after the village of Kaiso, the type locality, on the eastern shore of Lake Albert. See, E. J. Wayland *et al., Occasional Papers Geol. Survey Uganda* **2**, 1 (1926); also, K. A. Davies, *Geol. Mag.* **88**, 377 (1951); N. Harris, J. W. Pallister, J. M. Brown, *Geol. Survey Uganda Mem. No. 9* (1956).
56. V. E. Fuchs, *Geol. Mag.* **71**, 97 (1934).
57. J. Lepersonne, *Ann. soc. géol. Belge* **72**, 1 (1949).
58. The particular horizon of the type Kaiso mammal fauna is not clear; possibly it corresponds to the middle or even the upper stage, but this problem may be settled by careful study and comparison of the molluscan faunas within the several stages of the Kaiso series. W. W. Bishop (Geological Survey of Uganda, Entebbe) is now carrying out systematic investigations in the Western Rift, both at Kaiso and in the Lake George-Lake Edward region (see "Proc. Assoc. African Geol. Services, Leopoldville, Belgian Congo, Meeting, July 1958," in press).
59. J. de Heinzelin de Braucourt, "Le fossé tectonique sous le parallèle d'Ishango," *Publ. Inst. Natl. Parcs Nat., Bruxelles* (1950); also, *Proc. Intern. Sci. Sol, 5e Congr. Leopoldville, 1954* (1954), vol. 4, p. 435.
60. C. Arambourg, *Mission scientifique de l'Omo, 1932-1933, I* (Museum Natl. Hist. Nat., Paris, 1935; 1943), vols. **1**, **3**.
61. L. S. B. Leakey, *Olduvai Gorge* (Cambridge Univ. Press, Cambridge, 1951); *Nature* **181**, 1099 (1958).
62. P. E. Kent, *Geol. Mag.* **78**, 173 (1941); also, L. Kohl-Larsen, *Auf den Spuren des Vormenschen* (Strecker and Schroeder, Stuttgart, 1943).
63. W. O. Dietrich, *Palaeontographica* **A94**, 43 (1942); *ibid.* **A99**, 1 (1950).
64. A. Remane, *Z. Morphol. Anthropol.* **42**, 311 (1951); *Am. J. Phys. Anthropol.* **12**, 123 (1954).
65. J. T. Robinson, *ibid.* **11**, 1 (1953).
66. See faunal lists in L. S. B. Leakey, *Olduvai Gorge (61)*.
67. Other riverine situations have provided *selected* assemblages of pebble tools referred to the Pre-Chelles-Acheul industries. The Kafuan industry, generally regarded as the oldest such manifestation, has been recovered from very high-level gravels of the Kafu and Kagera rivers in western and southeastern Uganda, respectively [C. van Riet Lowe, *Mem. Geol. Survey Uganda No. 6* (1952); *Proc. Pan-African Congr. Prehist., 3rd Congr., Livingstone, 1955* (1957), p. 207]. The industry, in a more evolved facies it seems, is probably also represented in the Katanga, southeastern Belgian Congo [G. Mortelmans, "Mélanges en hommage au Prof. Hamal Nandrin," *Publ. soc. roy. Belge anthropol. préhist.* (1952), p. 150; *Actes congr. panafr. préhist., 2e Congr., Alger, 1952* (1955), p. 295; *Proc. Pan-African Congr. Prehist., 3rd Congr., Livingstone, 1955* (1957), p. 214] and in the calcified basal older gravels of the Vaal river in southern Africa [C. van Riet Lowe, *S. African Archaeol. Bull.* **8**, 27 (1953)]. There is little question that some of the selected specimens are indeed artifacts of a very primitive stone industry although this is likely *not* true of those from the Kafu river; until larger assemblages are found *in situ*, preferably on old land surfaces, in clays or other fine sediments, there will always be a considerable measure of doubt concerning their full authenticity.
68. J. T. Robinson, *Am. J. Phys. Anthropol.* **12**, 181 (1954).
69. S. L. Washburn and B. Patterson, *Nature* **167**, 650 (1951).
70. H. B. S. Cooke, *S. African Archaeol. Bull.* **7**, 59 (1951); F. C. Howell, *Am. J. Phys. Anthropol.* **13**, 635 (1955); R. F. Ewer, *S. African Archaeol. Bull.* **9**, 41 (1956); *Proc. Pan-African Congr. Prehist., 3rd Congr., Livingstone, 1955* (1957), p. 135.
71. K. P. Oakley, *Am. J. Phys. Anthropol.* **12**, 9 (1954); *Proc. Pan-African Congr. Prehist., 3rd Congr., Livingstone, 1955* (1957), p. 155.
72. Sterkfontein, Swartkrans, and Kromdraai are situated in a shallow valley about 6 miles northwest of Krugersdorp, southern Transvaal; Limeworks Cave is located in the Makapansgat valley, several miles northeast of Potgietersrust, central Transvaal; the limeworks at Buxton, near Taungs, is just west of the Transvaal border, adjacent to the Kaap escarpment bordering the Harts River, in Bechuanaland (Cape Province).
73. C. K. Brain, *Proc. Pan-African Congr. Prehist., 3rd Congr., Livingstone, 1955* (1957), p. 143; and *Transvaal Museum, Pretoria, Mem. No. 11* (1958), p. 1; also, H. B. S. Cooke, *S. African J. Sci.* **35**, 204 (1938); S. H. Haughton, *Trans. Geol. Soc. S. Africa* **50**, 55 (1947).
74. F. E. Peabody, *Bull. Geol. Soc. Am.* **65**, 671 (1954); also, R. B. Young, *Trans. Geol. Soc. S. Africa* **28**, 55 (1925).
75. R. A. Dart, *Transvaal Museum, Pretoria, Mem. No. 10* (1957), p. 1; *Proc. Pan-African Congr. Prehist., 3rd Congr., Livingstone, 1955* (1957), p. 161; *Am. Anthropol.* **60**, 923 (1958).
76. The recent account by W. I. Eitzman [*S. African J. Sci.* **54**, 177 (1958)] of the original constitution of the Limeworks Cave and the mining activities which largely destroyed it suggests that there were probably three separate fossiliferous breccias, separated by travertines in the lower portion of this great cavern. He states that the lower and middle of these were densely packed with bone, whereas the upper horizon was more discontinuous and far less fossiliferous. It is clear that only a very small proportion of the bone accumulations have been salvaged from the mine dumps and that the great bulk of the fossil mammals (and australopithecines) were consumed in the lime kilns.
77. J. T. Robinson, *Ann. Trans. Museum, Pretoria* **22**, 1 (1952).
78. R. A. Dart, *Intern. Anthropol. Ling. Rev.* **1**, 201 (1953); *Smithsonian Inst. Ann. Rept. 1955* (1956), p. 317; *Am. Anthropol.* **60**, 715 (1958).
79. H. Breuil, *Palaeontol. Sinica, Peking,* **D6**, 1 (1939).
80. S. L. Washburn, *Am. Anthropol.* **59**, 612 (1957).
81. A. R. Hughes, *S. African J. Sci.* **51**, 156 (1954); *Am. J. Phys. Anthropol.* **12**, 467 (1954); R. A. Dart, *Am. Anthropol.* **58**, 40 (1956).
82. J. Stevenson-Hamilton, *Wild Life in South Africa* (Cassell, London, 1954).
83. R. A. Dart, *Nat. Hist.* **26**, 315 (192 [illegible] *Am. J. Phys. Anthropol.* **7**, 1 (1949); see also, K. P. Oakley, in *Appraisal of Anthropology Today,* S. Tax *et al.,* Eds. (Univ. of Chicago Press, Chicago, 1953), pp. 28-30.
84. C. K. Brain *et al., Nature* **175**, 16 (1955); see K. P. Oakley, *Antiquity* **30**, 4 (1956). This horizon has also yielded a fragment of an australopithecine maxilla [R. A. Dart, *Nature* **176**, 170 (1955)].
85. J. T. Robinson and R. J. Mason, *Nature* **180**, 521 (1957); see K. P. Oakley, *Antiquity* **31**, 199 (1957). Foreign pebbles were first reported from this region (at Kromdraai) [illegible] S. H. Haughton, *S. African Archaeol. Bull.* **2**, 59 (1947).
86. J. T. Robinson, *Leech* **28**, 94 (1958).
87. J. D. Clark, personal communication.
88. F. Weidenreich, *Anat. Anz.* **44**, 497 (1913); A. Keith, *Brit. Med. J.* **1**, 451, 499, 545, 587, 624, 669 (1923); S. L. Washburn, *Cold Spring Harbor Symposia Quant. Biol.* **15**, 67 (195 [illegible] L. W. Mednick, *Am. J. Phys. Anthropol.* **13**, 203 (1955).
89. R. A. Dart, *ibid.* **7**, 301 (1949); *ibid.,* in press.
90. R. Broom *et al., Transvaal Museum, Pretoria, Mem. No. 4* (1950), p. 1; R. Broom and J. T. Robinson, *Am. J. Phys. Anthropol.* **8**, 489 (1950).
91. ———, *Transvaal Museum, Pretoria, Mem. No. 6* (1952), p. 1.
92. W. E. Le Gros Clark, *Am. J. Phys. Anthropol.* **13**, 19 (1955); F. C. Howell, in preparation.
93. W. E. Le Gros Clark, *J. Roy. Anthropol. Inst.* **80**, 37 (1952); J. T. Robinson, *J. Dental Assoc. S. Africa* **7**, 1 (1952); *Transvaal Museum, Pretoria, Mem. No. 9* (1956), p. 1.
94. ———, *Evolution* **8**, 324 (1954); *Z. Morphol. Anthropol.* **46**, 269 (1954); also, see the excellent summary by G. Heberer, *Primatologia, I* (1956), p. 379.
95. ———, *Am. J. Phys. Anthropol.* **11**, 445 (1953).
96. See G. H. R. von Koenigswald, *Proc. Koninkl. Ned. Akad. Wetenschap.* **B59**, 318 (1956). This author would distinguish *Paidopithex rhenanus*, of which a complete right femur is known, from the Pontian of Rheinhesse and the Schwäbian lignites, giving it as a separate genus (rather than as a species, as I have done here).
97. W. E. Le Gros Clark and D. P. Thomas, *Fossil Mammals of Africa* (British Museum of Natural History, London, 1951) vol. 3, p. 1; H. Zapfe, *Am. J. Phys. Anthropol.,* in press; J. Hürzeler, *Ann. paléontol.* **40**, 1 (1954).
98. W. E. Le Gros Clark, *Quart. J. Geol. Soc. London* **105**, 225 (1950); ——— and L. S. B. Leakey, *Fossil Mammals of Africa* (British Museum of Natural History, London, 1951), vol. 1, p. 1.
99. W. E. Le Gros Clark, *Proc. Zool. Soc. London* **122**, 273 (1952); J. Napier, *Fossil Mammals of Africa* (British Museum of Natural History, London, in press).
100. H. de Terra, *Science* **124**, 1282 (1956).
101. See A. Remane, *Abhl. Akad. Wiss. Lit. Mainz, Math.-Naturw. Kl., No. 2* (1955).
102. J. Hürzeler, *Schweiz. Palaontol. Abhandl.* **66**, 1 (1949); Eclogae Geol. Helv. **44**, 404 (1951); *Verhandl. naturforsch Ges. Basel* **65**, 88 (1954); *ibid.* **69**, 1 (1958).
103. See W. L. Strauss, Jr., *Quart. Rev. Biol.* **24**, 200 (1949).
104. In Mediterranean Africa the Pontian is little known in southern and northern Tunisia and practically not at all in Morocco. The richest locality, except for primates, is Qued el Hamman, Oran (Algeria). Findings from the later Pliocene are extremely rare; this period is known largely from the Constantine (Algeria) sites of Ain el Bey and Ain el Hadj Baba. A fairly substantial faunal assemblage, probably middle Pliocene, from the Gart el Moluk, Wadi Natrun, in Egypt, is known. The situation is even more discouraging south of the Sahara where a Pliocene fauna is known only from diamond diggings in Little Namaqualand, southwest Africa.
105. L. Cahen and J. Lepersonne, *Mem. soc. géol., paléontol., hydrol. Belg. ser. 8, No. 4* (1952), p. 1; J. de Heinzelin, "Sols, paléosols et désertifications anciens," *Publ. Inst. Natl. Etude Agron. Congo Belge, Bruxelles* (1952).