DUARD L. BONÉ & RONALD SINGER

HIPPARION FROM LANGEBAANWEG, CAPE PROVINCE AND A REVISION OF THE GENUS IN AFRICA

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HIPPARION FROM LANGEBAANWEG, CAPE PROVINCE AND A REVISION OF THE GENUS IN AFRICA[1]

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(With 24 tables, 16 text figures and 13 plates)

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INTRODUCTION

GENERAL

The discovery of the genus *Hipparion* de Christol 1832 in Africa was first mentioned as late as 1878 (Pomel) and then again in 1884 (Thomas), but it was not properly described before 1897 (Pomel). These early papers dealt with specimens found in the Maghreb, North Africa. Additional finds were then made in the Oran and Constantine areas, and, somewhat later, specimens were discovered in Tunisia, in the Nile Valley at Wadi Natrun, in Ethiopia, in the Kaiso Beds of Uganda, and at Cornelia (Uitzoek) in South Africa. The scanty stratigraphical data and faunal associations of these discoveries led to an overmultiplication of genera and species, based mostly on isolated single teeth.

Subsequently more complete discoveries and more detailed descriptions were published. In 1937 Hopwood presented some conclusions of the Oldoway Expedition in a monograph on the fossil Equidae. Dietrich (1942) described an important hipparionid[1] series from South Serengeti, to which Arambourg (1947) added important collections from Omo (Ethiopia). The more extensive material gave rise to a more unified knowledge of the African *Hipparion*. It enabled Gromova (1952), in her revision of the genus *Hipparion*, to point out the characteristic features of the African forms, as well as to sketch their general evolutionary and migratory patterns within Africa.

The lack of stratigraphical correlations and insufficient knowledge of conditions of exposure and of faunal associations at the various sites where hipparionids have been discovered, only permitted attempts at relative dating of the various sites and their fossil horizons. Furthermore, these sites belong exclusively to Upper Pliocene and Pleistocene epochs. Therefore, it was generally accepted that *Hipparion* had appeared in America in Pliocene times

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[1] The term 'hipparionid' refers in a general sense to all forms of African tridactyl equidae. Previously Dietrich (1942, p. 94) erected the sub-family 'Hippariinae' for the same purpose but without taxonomic definition. Furthermore he also used (1942, p. 94) '*Hipparion* de Christol, *i.w.S.*' in a non-generic sense.

As the present authors have come to the conclusion that all African forms belong to a single genus *Hipparion*, the general term 'hipparionid' corresponds to the taxonomic one.

and had migrated to Eurasia where the differentiation of the 'Pontian fauna' had taken place, and that only subsequently, as late as Pliocene times, *Hipparion* had reached Africa as a kind of refuge area. This view was still supported less than ten years ago when material was discovered in lacustrine limestone at Mascara (Arambourg, 1956).

Recently *Hipparion* material was discovered in Algeria in undoubted Upper Miocene beds. This led Arambourg (1959) to propose the relationships between the several African hipparionids, and to reduce drastically the former several genera and species to a more sober and unified taxonomy of three different groups, namely *H. africanum*, *H. sitifense* and *Stylohipparion* sp. These formed a chronological succession from the Upper Miocene through the Upper Pliocene to the 'Villafranchian' or early Pleistocene times. This classification was more satisfactory and had definite merits and advantages which will be commented on later in this paper.

THE LANGEBAANWEG DEPOSITS

Recent discoveries (Singer, 1961) of a fairly extensive series of *Hipparion* teeth at the Langebaanweg fossil sites, from which *Stegolophodon* sp. had previously been reported (Singer & Hooijer, 1958), necessitated a thorough study and comparative review of the African hipparionids. The unique and uniform nature of the Langebaanweg material adds materially to our knowledge of the African hipparionids and also provides new evidence for revising the relationships between the several forms already recognized in the literature.

Thus the purpose of this paper is twofold:

(*a*) to record a description and diagnosis of the *Hipparion* remains from Langebaanweg, and

(*b*) to review and revise the taxonomy of the African hipparionids.

Localization of the sites

The Langebaanweg fossil sites are situated, like the 'Elandsfontein' (Hopefield) site, in the vast Sandveld of the Western Cape, and are located about 75 miles (120 km.) northwest of Cape Town (fig. 1) and 12 miles (19 km.) from the late Middle Pleistocene—early Upper Pleistocene site at 'Elandsfontein'. The former are 150–200 feet (46–62 metres) above sea-level, while the latter are situated at 300 feet (Singer, 1961).

The fossils are mainly located in and around two quarries being commercially exploited for phosphates by the African Metals Corporation (AMCOR). The 'Varswater' site is situated on the farm 'Langberg Suid', and the 'Baard's' site is on the farm 'Remainder of Langberg', the two being subdivisions of 'Langberg' (fig. 2).

History of the discoveries

The first hipparionid teeth were recovered from Baard's Quarry in 1958. In 1961, Mr. Robin Warren, an employee of AMCOR, recovered two excel-

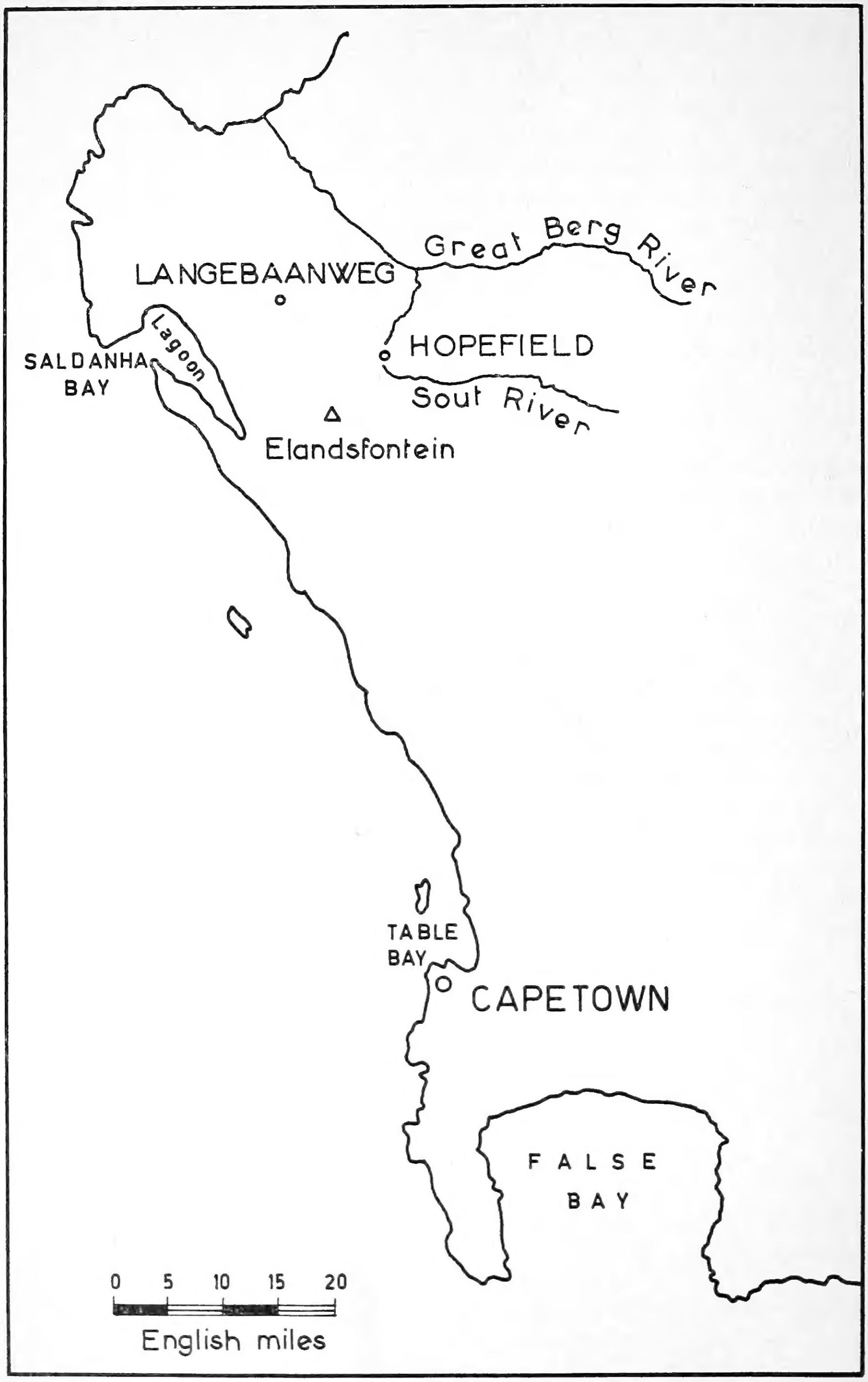

Fig. 1. Map indicating the position of Langebaanweg relative to Cape Town.

lently preserved milk molars at Varswater. Thereafter the remainder of the specimens were found at various sites in the two quarries.

Geology

The geology of the more than 4 square miles of fossiliferous deposits is not easy to interpret. There is little with which to compare it, as virtually nothing is known of the Quaternary geology of the Cape Province.

The surface siliceous sands, possibly aeolian, forms a discontinuous cover of 4 to 5 feet, which may extend to more than 15 feet in a few places. Below this layer, at both quarries, there occurs a *Dorcasia*-type caliche, discontinuous and stratigraphically above the phosphates. There is also ferricrete, younger than the phosphates and intimately associated with them.

The *Dorcasia*-type surface limestone also occurs on the solid calcrete dunes at 'Elandsfontein', at Saldanha Bay, at False Bay (Singer and Fuller, 1962) and elsewhere. The distribution of the caliche is patchy, and is considerably stripped by erosion.

At Varswater the phosphate, a variety of collophane, occurs as the cementing material of the consolidated sand, probably as the result of diagenetic replacement of interstitial limes. There are three main layers which vary laterally in thickness within a range of 3 feet to 6 feet.

At Baards, the phosphate occurs as nodular to bouldery phoscrete (up to 5 feet thick). The phoscrete is a hard, compact mass of phosphatized sand consisting of sand grains which have been cemented and partially corroded by an amorphous calcium phosphate cement. It overlies the phosphatized nodular sands, sandy clays, and clayey sand. The phoscrete and nodular phosphate sands, represent replacement of older shelly sands by phosphate solutions, the phosphate of which is probably derived from guano. A significant feature is that at Varswater the phosphate has remained unaltered as lime phosphate (Singer & Warren, in preparation).

The discovery of shark teeth and other marine forms (*vide infra*) at the same level as and with the land mammals indicates earlier invasion of the area by the sea. Studies on borehole cores and the presence of shelly sands and gravels suggest the formation of sand bars, especially at Varswater, while the clay and clayey sands at Baard's indicates a possible lagoonal stasis. Further studies are being carried out in an attempt to clarify the geological genesis and morphology of the region.

The major portion of the phosphatic deposits is located at both sites at up to 100 feet above sea-level. The archaic fossils are related to or found just above these deposits. The 'rolled' nature of much of the fossil material suggests some transport prior to final deposition. The upper phoscrete and calcrete layers, as well as the clayey deposits, contain the faunal forms represented also at 'Elandsfontein' (*Ceratotherium*, *Equus*, *Sivatherium*, *Homoioceras* and various antelopes), typical of the late Middle Pleistocene—early Upper Pleistocene ('Hopefield Period').

On a comparative basis with other sites, it seems likely that the stegolophodont—stegodont—archidiskodont complex and the hipparionids derive from a period extending from the Lower Pleistocene to the early Middle Pleistocene. The stegolophodont and stegodont specimens together indicate a very early phase of the Lower Pleistocene. Elsewhere (e.g. at Olduvai) archidiskodont material overlaps this phase and extends up to the Middle Pleistocene. It will be demonstrated below that the hipparionids from Langebaanweg belong to the same species as that from the lower layers of South Serengeti, so that their presence is suggestive of the earliest phases of the Pleistocene.

FAUNAL ASSEMBLAGE FROM LANGEBAANWEG

The following identifications have been made thus far:

MOLLUSCA

Trigonephrus sp.

CARNIVORA

cf. *Arctocephalus*
Canis sp.
Hyaena brunnea

PROBOSCIDEA

Stegolophodon sp.
Stegodon sp.
Archidiskodon sp.
Palaeoloxodon sp.

PERISSODACTYLA

cf. *Ceratotherium*
Hipparion (*Hipparion*) *albertense baardi* subsp. nov.
Equus helmei

ARTIODACTYLA

Hippopotamus sp.
Sivatherium(1) *olduvaiense*
cf. *Oreotragus* sp.
cf. *Damaliscus* sp.
cf. *Redunca* sp.
Homoioceras sp.

REPTILIA

cf. *Testudo*

AVES

cf. *Struthio*

SELACHII(2)

Isurus cf. *glaucus*
Lamna nasus
Carcharias sp.
C. ferox
Rhinoptera cf. *dubia*
Glopias vulpes

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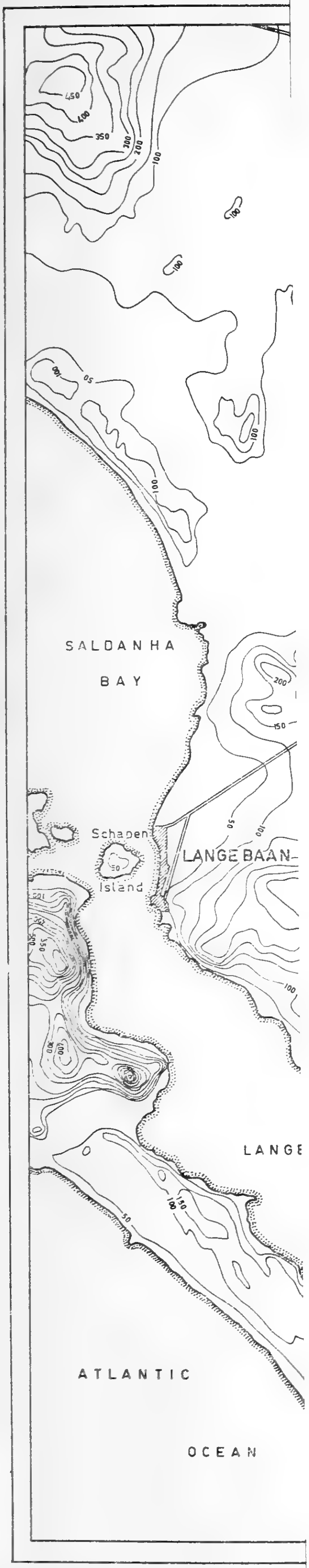
(1) According to Arambourg's recent re-description (1960) of Pomel's type specimen from St. Charles (Oran), *Libytherium maurusium* has precedence (see also Singer and Boné, 1960).

(2) Identified by Dr. B. Schaeffer, American Museum of Natural History, New York.

METHODS AND NOMENCLATURE

For the description of the occlusal surfaces of the teeth, the nomenclatures used by Arambourg (1947, 1959), Cooke (1950), and Sondaar (1961) have been modified (see pp. 325–8) and synthesized (figs. 10, 11).

The measurements of the teeth have been taken according to the method described by Sondaar (1961).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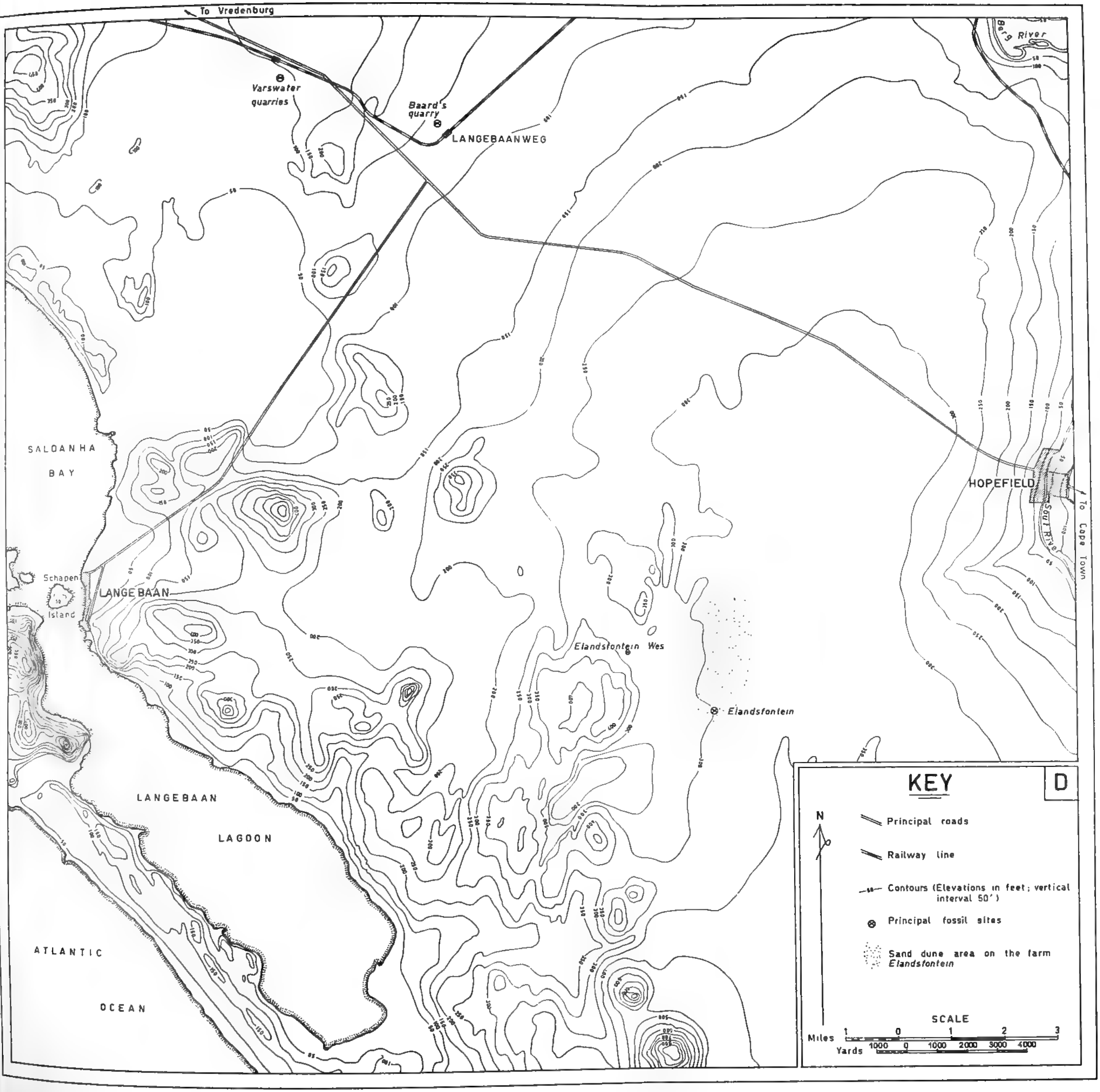

FIG. 2. Contour map showing the location of the quarries at Langebaanweg.

The indices devised by the authors are described at appropriate places in the text.

The following abbreviations refer to the collections and sites of the source material:

Archaeol. Surv. = Archaeological Survey of South Africa, now in the University of the Witwatersrand, Johannesburg, South Africa.
B.M.N.H. = British Museum (Natural History)
C = Cornelia
L = Langebaanweg
M.M.K. = McGregor Memorial Museum, Kimberley
Nas. Mus. = Nasionale Museum, Bloemfontein
Old. = Olduvai
S.A.M. = South African Museum, Cape Town
U.C. = University of California, Berkeley.

GEOGRAPHICAL DISTRIBUTION OF AFRICAN SITES WHERE HIPPARIONIDS HAVE BEEN RECORDED (figs. 3–7)

Site	*Specimen*	*Reference*
MOROCCO		
Camp Berteaux (Gara Ziad)	(*a*) Molar teeth Femur fragment with proximal epiphyses	Bourcart, 1937
	(*b*) Left M^2	Ennouchi & Jeannette, 1954
Oued el Akrech (near Argoub el Hafid)		Ennouchi, 1951
Fouarat (south of Kenitra (Rharb))		Choubert, Ennouchi & Marcais, 1948
ALGERIA		
Tafna (Guiard, Prov. Oran)		Dalloni, 1915
Oued el Hammam	Adult skull no. 141 Adult skull no. 125 Adult skull with dentition no. 116 Juvenile palate with dentition no. 122 Adult mandible no. 143 Adult half mandible no. 89 2 juvenile mandibles with milk teeth nos. 95–96 Several teeth series, juvenile and adult Isolated teeth Humerus, distal fragment no. 159 Radio-ulna no. 123, fragments no. 13, no. 22 and no. 27 Femur: fragment without epiphyses and distal fragment Tibia: distal fragment Pelvic fragment	Arambourg, 1959

Site	*Specimen*	*Reference*
Oued el Hammam (*cont.*)	Astralagus, 2 Calcaneum, 1 Numerous complete metapodials (5 Mc III, 5 Mt III), many (6) of them with lateral digits	
Marceau	P^a and M^a, P_2	Arambourg, 1959
Mascara	Skull fragments of one individual: palate with nearly complete left dental series, and half right dental series; symphysis with incisors	Arambourg, 1956
St. Donat	'Teeth of two jaws'	Joleaud, 1936 Arambourg, 1956
St. Arnaud (Cemetery)	(*a*) upper molars	Pomel, 1897
	(*b*) lower molars	Arambourg, 1956
Aïn el Hadj Baba	Metapodials with developed lateral digits	Thomas, 1884
	Upper teeth: right P^4–M^2 left M^2	
	Lower teeth	
Aïn el Bey		Thomas, 1884
Mansourah		Thomas, 1884
Setif		Thomas, 1884
Beni Foudda (Aïn Boucherit)		Pomel, 1897
Aïn Hanech		Arambourg, 1949
Oran (Puits Kharouby)	M^a, left P_3 or P_4, M_a	Pomel, 1897
Aïn Jourdel	M_3, P	Thomas, 1884
TUNISIA		
Garet Ichkeul		Arambourg, 1949
Tozeur Beds		Roman & Solignac, 1931
Utique		Solignac, 1927
Djebel M'dilla		Solignac, 1927
FAYUM		
Wadi Natrun, Gart el Moluk Hill	Left upper P (P^4 ?)	Andrews, 1902
ETHIOPIA		
Omo Valley	(*a*) 1 incisor, 5 M_a, 1 M^a (brought back by Brumpt from the du Bourg de Bozas Mission, 1903)	Haug, 1911; Joleaud, 1933
	(*b*) right P^2 no. 396 left M^3 no. 395 left M^a fragment no. 370 right M_1 or M_2 no. 3 & no. 4 right humerus fragment	Arambourg, 1947
CENTRAL AFRICA		
Tchad, Koro Toro region Goz-Kerki Koulá Bochianga Quadi Derdeney Koulá Ri Katir (It is not clear at which of these five sites *Stylohipparion* has been found)		Coppens, 1960

Site	*Specimen*	*Reference*
EAST AFRICA		
Uganda: East shore of Lake Albert in Kaiso layers	1 incomplete upper molar BM M12615	Hopwood, 1926
Kenya: Kanam lower beds. Kanjera		
Tanganyika: North-east shore of Lake Eyasi (W. and N. of Mumba Hill)	Teeth	Reck & Kohl-Larsen, 1936
South Serengeti (various localities)	Loose teeth, fragmented mandibles	Dietrich, 1942
Olduvai		Hopwood, 1929, 1937
SOUTH AFRICA		
Cape Province:		
(i) Namaqualand (40 mi. east of Springbok)	Left P_2–M_1 and M_3 Right P_4, M_1, M_2 and part of M_3 (above specimens are S.A.M. 9982)	Haughton, 1932
(ii) (*a*) Sydney-on-Vaal	Left M^3 (MMK 431)	Cooke, 1950
(*b*) Pniel, near Barkly West	Left P_{+} or M_{+} (MMK 5225)	
(*c*) Vaal River at Christiana	Left M^2 or M^3 (Arch. Surv. 113)	
Orange Free State:		
Cornelia (Uitzoek)	(*a*) right M^1 (or M^2) (Nas. Mus. C558) left M^3 (Nas. Mus. C555) left M_1 + M_2 (Nas. Mus. C556)	Van Hoepen, 1930
	(*b*) symphysial fragment and incisors	Van Hoepen, 1930
	(*c*) right M_2 (Nas. Mus. C797) left P_2 (Nas. Mus. C796)	Van Hoepen, 1932
	(*d*) left P_3–M_3 (Nas. Mus. C795)	Van Hoepen, 1932
Transvaal:		
Kromdraai Cave	2 lower teeth (discovered by Broom)	Cooke, 1950
Bolt's Farm		Cooke, 1963
? Makapansgat		Cooke, 1963

NOTE: M^a indicates upper molar; M_a lower molar, etc.

SUMMARY OF PUBLISHED GEOLOGICAL EVIDENCE FROM AFRICAN HIPPARIONID SITES

The present state of our knowledge of the geological evidence from sites in Africa where hipparionids have been discovered indicates that they first appeared in Upper Miocene deposits. A summary of the data is considered useful for the assessment of the status of the Langebaanweg material.

MIOCENE

The continental layers of vertebrate fossils at OUED EL HAMMAM (between Mascara and Mercier Lacombe, upstream from Bou Hanifia,

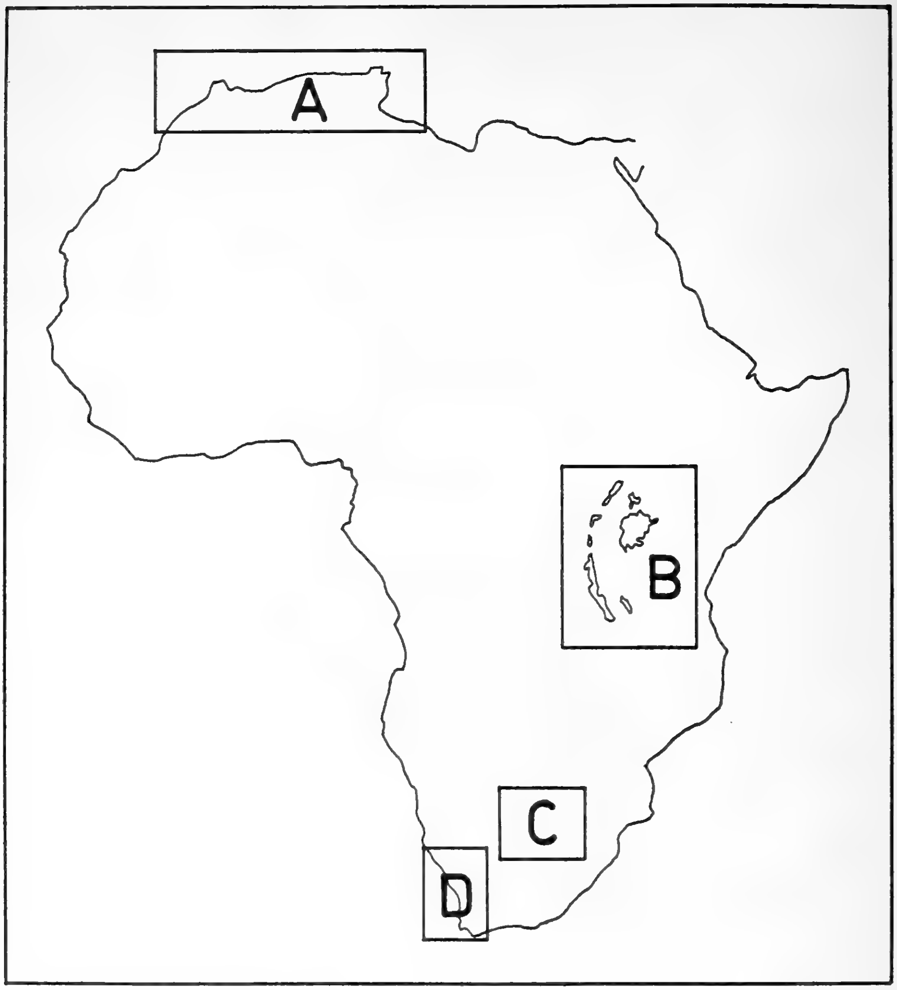

FIG. 3. Map of Africa indicating major areas of discovery of hipparionids. Details of areas A–C are shown in figs. 4–6, while area D is enlarged in fig. 1.

Algeria—figs. 3, 4) occur between two marine horizons, namely, (1) a Burdigalian one, characterized by its mollusc and echinid fauna and (2) an Upper Miocene *Lithotamnium* limestone. On this stratigraphical basis, the *Hipparion* horizon has been dated as Tortonian, i.e. Upper Vindobonian (Late Miocene) immediately antedating the Tortono-Sahelian transgression which occurs at the end of the Miocene marine period in this area (Arambourg, 1959).

The MARCEAU deposit, and especially its lignite and lacustrine clay and limestone which yield the *Hipparion* specimens, are referred to a period anterior to the Pliocene transgression, i.e. they belong to the Upper Miocene and may be equated with Oued el Hammam (Flandrin, 1942).

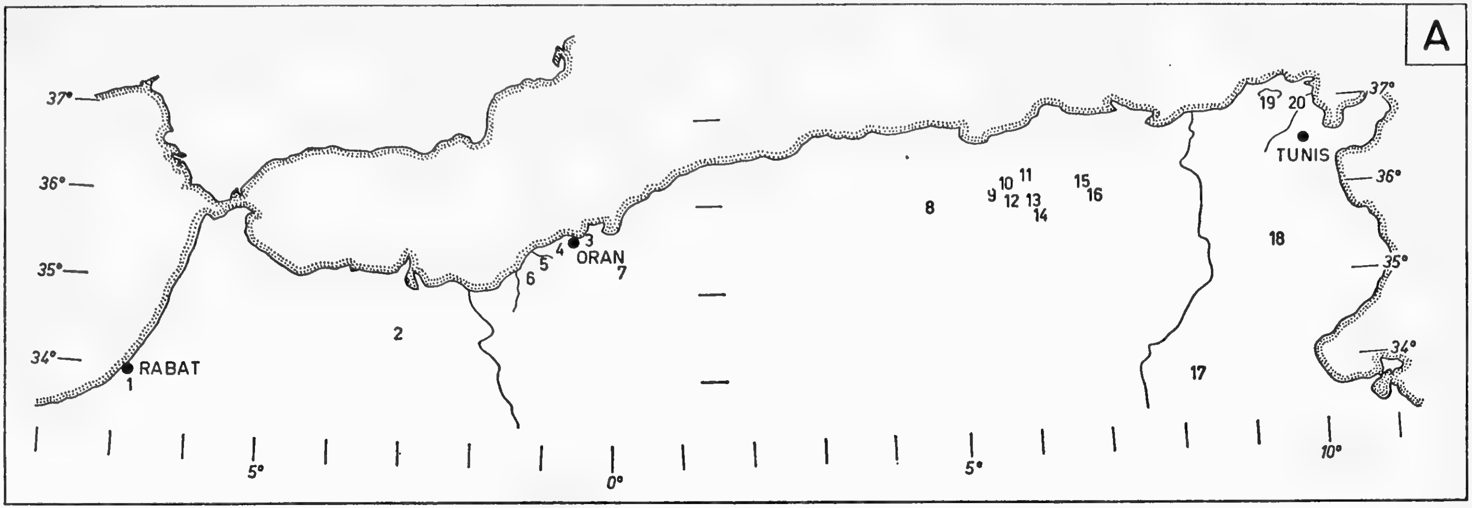

Fig. 4. Map of the Maghreb (A in fig. 3) indicating the localities from which *Hipparion* has been described, namely,

Morocco:

1. Rabat; 2. Camp Berteaux.

Algeria:

3. St. Charles (Oran); 4. Puits Kharouby (Oran); 5. Oued el Hammam; 6. Tafna; 7. Mascara; 8. Mansourah; 9. Sétif; 10. Aïn Boucherit and Beni Foudda; 11. Aïn Hanech; 12. St. Arnaud; 13. St. Donat; 14. Marceau; 15. Aïn Jourdel and Aïn el Bey; 16. Aïn el Hadj Baba.

Tunisia:

17. Tozeur; 18. Djebel M'Dilla; 19. Garet Ichkeul; 20. Utique.

There is good evidence that CAMP BERTEAUX (near Taourirt, Eastern Morocco) belongs to this period. The *Hipparion* layers, from which *Mastodon* cf. *angustidens* has been recovered (Bourcart, 1937), form the base of a lacustrine series of 'argiles smectiques' which are lying on marine horizons with Tortonian fauna and are covered with Pontian deposits. Choubert and Ennouchi (1946) have dated the *Hipparion* layers as Upper Tortonian, being a sub-continental phase at the end of the Miocene period. Thus, they are somewhat younger than those from Oued el Hammam (Arambourg, 1959).

The brack water deposits of TAFNA (near Guiard, Province of Oran) show a 'Sarmatian facies' of the Upper Vindobonian. On faunal and lithological grounds, they were first referred to the 'classical Pontian' (Dalloni, 1914), but recently they were re-studied and correlated with the Oued el Hammam horizon (Perrodon and Tempere, 1953). However, the geological evidence is not clear.

PLIOCENE

Pliocene palaeontological sites are rare in the Maghreb. Some fossiliferous lacustrine formations in the SETIF–CONSTANTINE area have been referred to this period (Middle Pliocene). Included are also the limestone deposits of the ST. ARNAUD Cemetery and of the MASCARA region, AÏN EL BEY, AÏN EL HADJ BABA, ST. DONAT, and possibly UTIQUE in Tunisia.

Most of these exposures correspond to the fluviolacustrine filling of a vast depression between the Tellian and Sahara–Atlas. According to Arambourg (1956) the *Hipparion sitifense* layers of St. Arnaud Cemetery, Aïn el Hadj Baba and Mascara are lithologically different (sands and lacustrine limestones) from the *Stylohipparion* and *Equus numidicus* deposits of Aïn Boucherit and Aïn Jourdel (gray marls and red conglomerate). While these represent the base of the 'Villafranchian' (similar to Lac Ichkeul and Fouarat), they are referred to the Middle Pliocene. No satisfactory geological evidence is available for TOZEUR (Tunisia): it was referred by Boule (1910) and Solignac (1931) to the 'Pontian' stage because of the presence of *Merycopotamus* and *Hipparion.* Now that the occurrence of these forms is known in Upper Miocene deposits in India and North Africa, there is a special need for obtaining better stratigraphical evidence for dating this site.

At WADI NATRUN (Gart el Moluk Hill) in the Nile Valley, fluvio-marine gypsiferous clays (containing, among other rare vertebrates, *Hipparion albertense*) are interbedded with limestones and shales, and deposited in an arm of the Mediterranean in the Nile Valley. On a stratigraphical basis they are dated as Middle Pliocene.

PLEISTOCENE

North Africa

The *Hipparion* fossiliferous horizons in the Maghreb correspond stratigraphically to the marine regression following the major Pliocene extension.

The most significant exposures are St. Arnaud and Oran in Algeria, and Lac Ichkeul, near Bizerta, in Tunisia (figs. 3, 4). The sequence has been extensively described and discussed (Howell, 1959). The general feature is that of a 300-foot series of marls and lacustrine clays and silts, with interbedded fossiliferous sandstones, gravels and calcareous conglomerates.

At LAC ICHKEUL the base is formed by deep-water Plaisancian and lagoonal Astian marine deposits capped with fresh-water beds from the early Pleistocene, with intercalation of a one-foot thick conglomerate.

At BEL HACEL eroded dune sandstones overlying transgressive Astian marls and sands are bearing the 'Villafranchian' fauna: they are further overlain by the 100-metre high Sicilian beach.

In the ST. ARNAUD area, two distinct fossiliferous horizons are visible. The lower one (Aïn Boucherit, i.e. Beni Foudda) is a coarse calcareous conglomerate; the upper one (Aïn Hanech) is a cracked, rather sandy or gravelly clay, intercalated in the thick marl filling the old marshy or lacustrine depression. Faunal and stratigraphical considerations make the St. Arnaud upper deposit somewhat younger than Lac Ichkeul.

At ORAN (ST. CHARLES), where *Libyhipparion* (?) *libycum* was first recovered and named by Pomel (1897), the consolidated dune sandstones and clays are concordantly overlying the calabrian sandstones, of which they represent the regression facies. The calabrian itself is in direct contact with the *Flabellipecten flabelliformis* sands and sandstones of the marine Pliocene; and at the base, the sequence reaches the Tortono-Sahelian marks and red stone of the Upper Miocene (Arambourg, 1960).

Ligniferous clays of the PUITS KHAROUBY near Oran from which *H. massoesylium* Pomel was recovered, has usually been placed—on the basis of its mollusc fauna—in the Upper Pliocene, but there is little geological evidence for it being older than Lower Pleistocene.

East Africa

Most of the fossiliferous horizons of East Africa (figs. 3, 5) are linked with tuffs, ashes or lapilli projected and deposited by volcanic eruptions. This volcanic activity spans over a long period of time, probably from Lower Miocene up to Upper Pleistocene and even to historical times. Therefore it is difficult, on purely geological grounds, to date the different fossil deposits. Usually it is only by convergence of tectonic, stratigraphical, lithological and chemical methods on the one hand, and by faunal studies on the other that it is possible to propose a satisfactory date.

At KANAM, on the slope of the dissected volcanic centre of Homa Mountain, the lacustrine brown calcareous fossiliferous clays, with their interbedded fine tuffs from intermittent volcanic explosions, are commonly referred to the Lower Pleistocene.

The KAISO series is complex. It has been repeatedly studied (Wayland, 1926; Fuchs, 1934), and recently Lepersonne (1949) subdivided it into three

Fig. 5. Map of Central-East Africa (B in fig. 3) indicating the localities from which *Hipparion* has been described, namely, 1. Lake Albert; 2. Kanjera; 3. Mumba Hills, Lake Eyasi; 4. Olduvai Gorge; 5. South Serengeti, Laetolil beds.

main stages of sedimentation, the middle one being highly fossiliferous. It is a clayey deposit, alternating with thin beds of fine sands and sandstones, and discontinuous ironstone horizons and limonite lenses (Kaiso bone beds), containing silicified wood and a high proportion of vertebrates. It overlies a silty lower deposit with some minor gravel horizons, resting on a basal ironstone layer (laterite) capped by unstratified sands above the down-faulted peneplain surface. This lower part of the Kaiso series, including the fossil horizon, is usually placed in the Lower Pleistocene (Howell, 1959; Bishop, 1963).

The OMO beds are lithographically comparable to the Kaiso deposits. The 'Villafranchian' fauna, and the *Hipparion* material in particular, occur in sandstone horizons between lacustrine volcanic clayey tuffs. In the evolution of the Rudolph depression in its Nilotic or open phase, Arambourg (1943) has distinguished two major extensions of the lake during the Pleistocene: (1) the vertebrate beds occur in a sand and sandstone horizon of the lower Omo Valley, representing a first phase of lacustrine deposition prior to the general tectonic uplift of the end of the Lower Pleistocene. (2) Posterior to the tectonic dislocation, the second phase corresponds to the series of horizontal terraces on the slope of the Rudolph Basin—they are not fossiliferous. This distinction, confirmed by the study of the fauna, permits the fossil beds to be dated as Lower Pleistocene, probably younger than Kaiso and Kanam.

It is more difficult to specify the geological location of the SERENGETI *Hipparion* material. The Laetolil beds in the Vogel River area show a sequence of upfaulted subaerially deposited yellow and gray tuffs (Kent, 1941). Unfortunately the fauna collected by Kohl-Larsen 'in den Schluchten und Wasserrissen' of the South Serengeti was probably recovered from various horizons which were altered and mixed-up by subsequent erosion (Dietrich, 1942). The gray tuffs, about 20 m. thick, which appear to contain the 'older fauna' (Kohl-Larsen, 1939), are dated as Lower Pleistocene, more or less contemporary with Omo and Olduvai I. Efforts have been made to identify this stratigraphically older fauna by such means as the type of mineralization and colour. Conclusions based on this method can only be accepted with reserve because of the fact that possible weathering may have altered the original appearance of the fossils. Nevertheless, Dietrich (1942) believed that all his *Hypsohipparion* material derived from the lower gray tuffs.

The vast sequence of stratified beds exposed in the OLDUVAI GORGE (northern Tanganyika) has been extensively discussed in recent years, and lately by Pickering (1960) and Leakey (1963). Independently of the chemical dating of the beds, which provides evidence of a great duration and antiquity of Bed I, dating has also been attempted on studies of the fauna and on a climatological basis. Little has been added from the strictly geological point of view. It is important to note that the major climatic, geological and apparently faunal 'break' occurs near the base of Bed II and not, as was previously thought, between Beds I and II. Most workers agree that Olduvai I belongs to the Lower Pleistocene, being more or less contemporary with (and probably prior to) Omo and Laetolil, while Beds II, III, IV are considered to belong to the Middle Pleistocene.

The KANJERA exposures, on the low cliffs of the Homa Mountain close to Lake Victoria, consist of a tripartite series of basal greenish ash and tuffs, succeeded by clays with limestone and by upper transgressive beds of brown-greenish clay. Most of the fossils are obtained from and in close association with the lower tuff and ash layer, but it is not possible to be certain whether or not all the material came from this source (Kent, 1942). However, there is sufficient evidence that the *Hipparion* may be considered to be more ancient than the human fossil remains which were recovered from the middle beds. The Kanjera faunal beds are referred to the Middle Pleistocene, roughly contemporary with Olduvai IV.

The LAKE EYASI beds are usually referred to an early Upper Pleistocene period, more on a palaeontological than on a geological basis.

According to Reck and Kohl-Larsen (1936), it is probable that the *Hipparion* teeth recovered west and north of Mumba Hill, in the north-east section of the Eyasi basin (*see* p. 283), do not belong to the original beds. Indeed they are very much rolled, which is not the case for the presumably contemporaneous material, and constitute a secondary deposition. If this interpretation is correct, these teeth are probably more ancient than the typical Eyasi fauna, and should be dated to a period prior to the Upper Pleistocene.

South Africa

The only relatively satisfactory stratigraphical information concerning *Hipparion* in South Africa is obtained at the YOUNGER GRAVELS OF THE

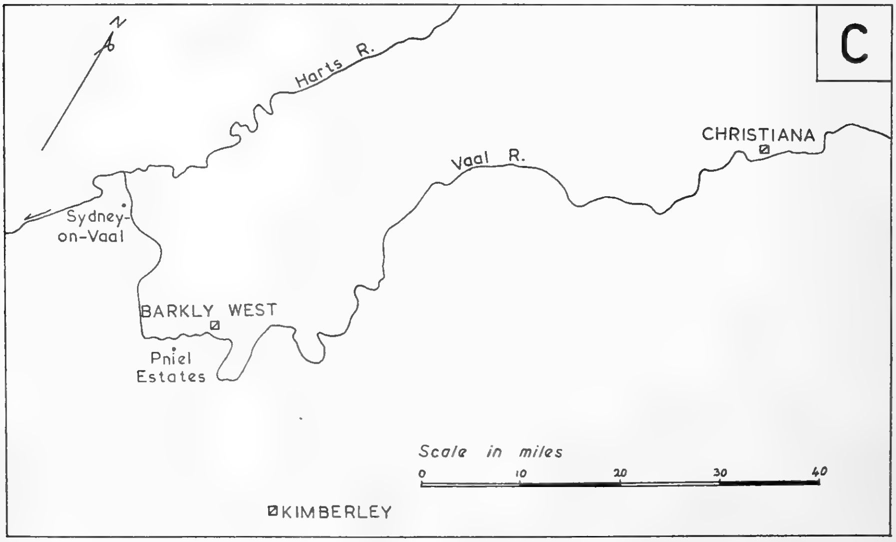

Fig. 6. Map of northern Cape Province, South Africa (C in fig. 3) indicating localities from which *Hipparion* has been described, namely, Sydney-on-Vaal, Pniel and Christiana.

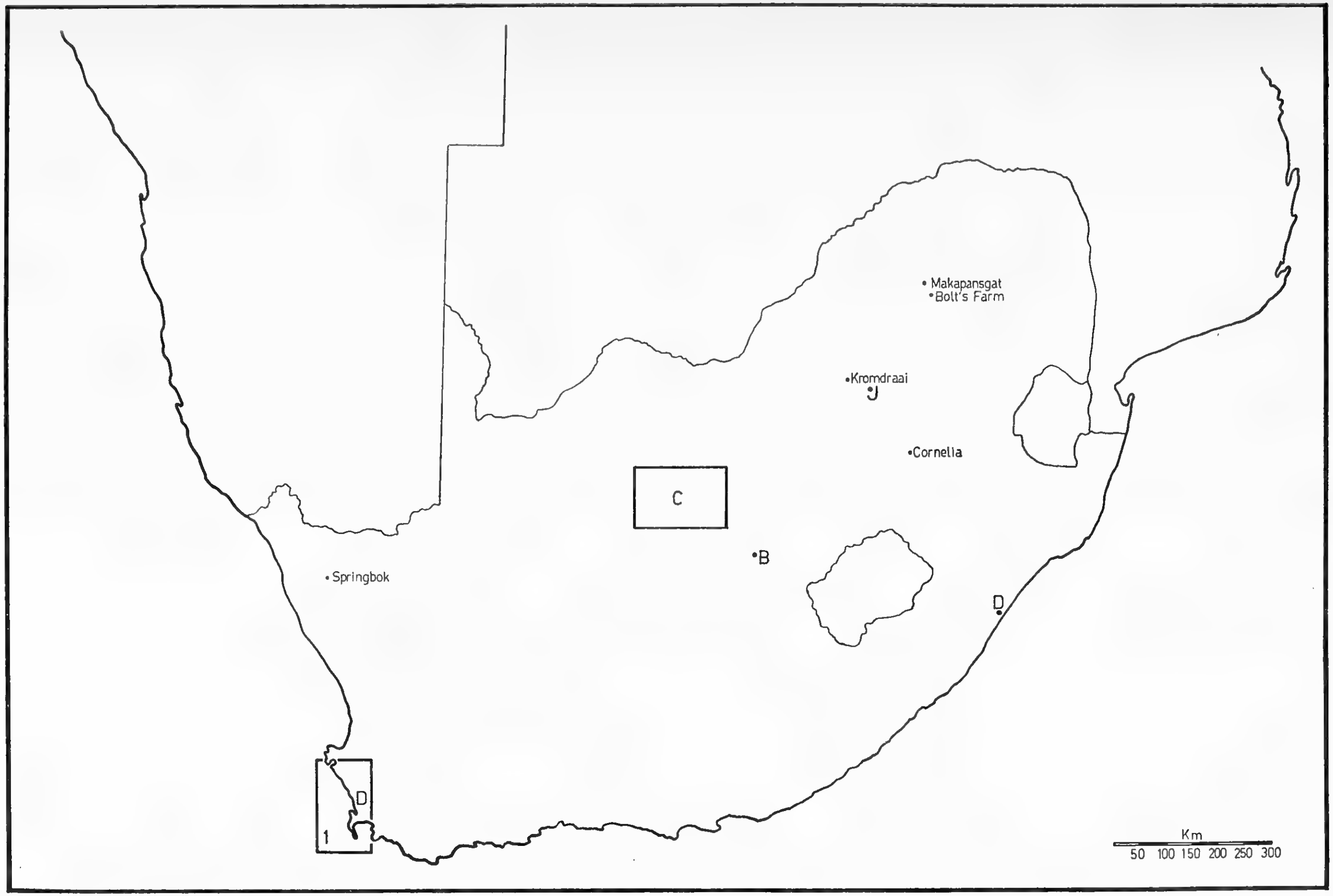

Fig. 7. Map of South Africa indicating certain localities of discovery of hipparionids, in relation to areas C and D of fig. 3. The positions of three cities are shown: B = Bloemfontein; D = Durban; J = Johannesburg.

VAAL RIVER (Christiana; Pniel; Sydney-on-Vaal: fig. 6). In this horizon, which actually presents the first fossil occurrence in the Vaal area (as fossils of the oldest gravels have probably been destroyed), three phases have been recognized from their elevation and their stone artefact associations. However, most of the fossils seem to have derived from Phase II and III, although it is not impossible that the fossils found below Barkly West may have been contained in Phase I of the Younger Gravels (Cooke, 1963). On the basis of a climatological interpretation (Söhnge, Visser and Lowe, 1937; amended by Cooke, 1947, and Lowe, 1952), the Younger Gravels were correlated with the Middle Pleistocene Olduvai Beds II and IV.

The CORNELIA beds, an open site on the farm 'Uitzoek' in the Orange Free State, consists of exposures of clays, gravels and sand, which represent an old 'pan' filling. Oakley (1954) emphasizes the Pleistocene nature of the site by referring to a 'lower Fauresmith industry' from the beds. There is no reliable date based purely on stratigraphy for this site.

At present it is also impossible to make any tentative geological dating for the *Notohipparion* material from NAMAQUALAND. It was recovered from a granite level in a well, 60 feet down in the surface limestone, 40 miles east of Springbok. It is known that the infilling of the valleys with sand has been occurring in Namaqualand from Upper Cretaceous times, with probable breaks in the sedimentation, but there is no information on the actual sequence of gravels and limestone in the well (Haughton, 1932).

The *Hipparion* occurrence in cave fillings at KROMDRAAI, (?) MAKAPANSGAT and BOLT'S FARM has been dated by faunal and climatological methods (Ewer, 1957; Brain, 1958), and nothing further can be added from a purely stratigraphical point of view.

LISTS OF FAUNAL ASSEMBLAGES AT THE AFRICAN HIPPARIONID SITES

It is considered useful to include lists of all the diagnosed, published fauna from the various sites where *Hipparion* has been recovered. Omission of particular sites is due to lack of information, and Hopefield is included because of the richness of fauna and for comparison with contemporaneous sites. The faunal assemblage of Langebaanweg is listed on page 280. The sites are listed according to the order presented on pages 281–3. Wherever possible, generic and specific names are retained as they appear in the publications quoted.

INDIVIDUAL HIPPARIONID SITES

Oued el Akrech (Morocco) (After Arambourg and Choubert, 1957)

PROBOSCIDEA

†*Anancus osiris*
†*Elephas africanavus*

PERISSODACTYLA

†*Stylohipparion* sp.

Oued el Hammam (Oran) and Marceau (Algiers) (After Arambourg, 1963)

PRIMATES

†*Macaca flandrini*

RODENTIA

†*Hystrix* sp.

CARNIVORA

†*Hyaena algeriensis*

TUBULIDENTATA

†*Orycteropus mauritanicus*

PROBOSCIDEA

†*Turicius* sp.
†*Mastodon* sp.

PERISSODACTYLA

†*Dicerorhinus primaevus*
†*Hipparion africanum*

ARTIODACTYLA

†*Palaeotragus germaini*
†*Samotherium* sp.
†*Damalavus boroccoi*
†*Gazella praegaudryi*
†*Tragocerus* sp.
†*Cephalophus* sp.

AVES

†*Struthio* sp.

Aïn Hanech (Algeria) (After Arambourg, 1947; 1949)

CARNIVORA

Hyaena sp.
Canis sp.

PROBOSCIDEA

†*Anancus osiris*
†*Elephas* cf. *planifrons*
†*E.* aff. *meridionalis* or *recki*

PERISSODACTYLA

†*Atelodus* aff. *simus*
†*Stylohipparion libycum*
Equus sp.

ARTIODACTYLA

Hippopotamus amphibius
†*Omochoerus*(1) sp.
Giraffa sp.
†*Libytherium maurusium*
Bos sp.
†*Bubalus* sp.
Oryx sp.
Alcelaphus sp.
†*Gazella sitifensis*

(1) According to Leakey, 1958 = *Mesochoerus*.

Garet Ichkeul (Tunisia) (After Arambourg, 1949)

PROBOSCIDEA

†*Anancus osiris*
†*Elephas* cf. *planifrons*

PERISSODACTYLA

†*Atelodus* aff. *simus*
†*Stylohipparion libycum*
Equus

ARTIODACTYLA

Hippopotamus sp.
†*Libytherium maurusium*
Bos sp.
Oryx sp.
Alcelaphus sp.
†*Gazella* aff. *sitifensis*
Redunca sp.

Tozeur (Tunisia) (After Roman & Solignac, 1934)

PROBOSCIDEA

†*Mastodon* cf. *longirostris*

PERISSODACTYLA

†*Hipparion* sp.

ARTIODACTYLA

†*Merycopotamus* aff. *dissimilis*
†*Capreolus matheroni*
†*Tragocerus amaltheus*
†*Hemitragus perimensis*
Antilopinae

Wadi Natrun (After Studer, 1898; Andrews, 1902; Arambourg, 1947 and 1963)

MAMMALIA

PRIMATES

†*Libypithecus markgrafi*

CARNIVORA

†Machairodontidae gen. sp. indet.
Phocidae gen. sp. indet.
Lutra sp.

LAGOMORPHA

? Leporidae

PROBOSCIDEA

†*Mastodon* sp.

PERISSODACTYLA

†*Hipparion* sp.

ARTIODACTYLA

†*Hippopotamus protamphibius*
†*Sivachoerus giganteus*
Camelidae gen. sp. indet.
†*Libytherium maurusium*
†*Hippotragus* (?) *cordieri*

REPTILIA

Crocodilus
†*Euthecodon nitriae*
†*Sternothaerus dewitzi~~n~~anus*
†*Trionyx pliocaenicus*

PISCES

Protopterus
Synodontis

Omo (After Arambourg, 1947)

PRIMATES

†*Dinopithecus brumpti*

CARNIVORA

†*Homotherium* (?) *ethiopicum*

PROBOSCIDEA

†*Deinotherium bozasi*
†*Elephas* (*Archidiskodon*) *recki*
†*Elephas* (*Archidiskodon*) cf. *planifrons*

PERISSODACTYLA

†*Atelodus* cf. *germano-africanus*
†*Stylohipparion albertense*
Equus cf. *zebra*

ARTIODACTYLA

†*Hippopotamus* (*Tetraprotodon*) *protamphibius*
†*Omochoerus heseloni*(1)
†*Metridiochoerus andrewsi*(2)
†*Notochoerus capensis*(3)
†*Phacochoerus africanus fossilis*(4)
Giraffa camelopardalis
†*Giraffa gracilis*
†*Sivatherium olduvaiense*(5)
†*Menelikia lyrocera*
Kobus (*Kobus*) *sigmoidalis*
Kobus (*Kobus*) sp.
†*Redunca ancystrocera*
Alcelaphus sp.
†*Strepsiceros imberbis*
Aepyceros melampus
Antidorcas sp.
Oryx cf. *gazella*
Tragelaphus nakuae
Taurotragus cf. *procanna*
Gazella praethomsoni
Syncerus aff. *brachyceros*

(1) = *Mesochoerus heseloni* (Leakey, 1958).
(2) = *Pronotochoerus jacksoni* (Leakey, 1958).
(3) = *Notochoerus euilus* (Leakey, 1958).
(4) According to Leakey, 1958 = *Tapinochoerus meadowsi*, but does not belong to the Omo Beds.
(5) See footnote to Langebaanweg fauna (p. 280).

Koro Toro (Tchad) (After Abadie, Barbeau and Coppens, 1949; Coppens, 1960)

MAMMALIA

PRIMATES

- †'*Australopithecus*' sp.

CARNIVORA

- *Hyaena* cf. *striata*

PROBOSCIDEA

- †*Archidiskodon africanavus*(1)
- †*A. recki*(2)
- †*Anancus* sp.
- †*Stegodon* sp.

PERISSODACTYLA

- †*Stylohipparion* sp.
- *Ceratotherium simum*

ARTIODACTYLA

- †*Hippopotamus* cf. *protamphibius*
- †*Sivatherium*(3) sp.
- *Giraffa camelopardalis*
- *Alcelaphus* sp.

REPTILIA

- *Crocodilus niloticus*

(1) According to Cooke, 1960=*Elephas africanavus.*
(2) According to Cooke, 1960=*Palaeoloxodon recki.*
(3) See footnote to Langebaanweg fauna (p. 280).

Kaiso[1]

CARNIVORA

- † ? *Homotherium ethiopicum*

PROBOSCIDEA

- †*Stegodon kaisensis*
- †*Archidiskodon exoptatus*

PERISSODACTYLA

- †*Stylohipparion albertense*
- †*Metaschizotherium hennigi*
- *Ceratotherium simum*

ARTIODACTYLA

- †*Hippopotamus imaguncula*
- †*H. protamphibius*
- †*Notochoerus euilus*
- †*Mesochoerus limnetes*

Kanam[1]

CARNIVORA

- *Crocuta crocuta*

PROBOSCIDEA

- †*Anancus kenyensis*
- †*Stegodon kaisensis*
- †*Archidiskodon subplanifrons*
- †*A. exoptatus*
- †*Deinotherium bozasi*

PERISSODACTYLA

- †*Stylohipparion albertense*
- †*Equus oldowayensis*
- *Ceratotherium simum*
- *Diceros bicornis*

ARTIODACTYLA

- †*Hippopotamus imaguncula*
- †*Metridiochoerus pygmaeus*
- †*Nyanzachoerus kanamensis*
- *Giraffa camelopardalis*
- †*Libytherium olduvaiense*

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[1] Compiled from Hopwood, Leakey & McInnes *in* Leakey, 1951; Dietrich, 1950; McInnes, 1953; Cooke, 1963; Leakey, 1958.

Eyasi[1]

PRIMATES

- *Homo* sp.

RODENTIA

- †*Pedetes surdaster*
- *Thryonomys swinderianus*

CARNIVORA

- *Crocuta crocuta*
- *Caracal caracal*
- *Panthera leo*
- *Panthera pardus*

TUBULIDENTATA

- †*Orycteropus aethiopicus*

PERISSODACTYLA

- *Equus burchelli*
- †*Stylohipparion* sp.
- *Diceros bicornis*

ARTIODACTYLA

- *Hippopotamus amphibius*
- *Potamochoerus koiropotamus*
- *Giraffa camelopardalis*
- *Strepsiceros strepsiceros*
- *Taurotragus oryx*
- *Syncerus caffer*
- †*Homoioceras nilsoni*
- *Kobus ellipsirymnus*
- †*Adenota kob*
- †*Redunca redunca*
- *Pelea* sp.
- †*Oryx beisa*
- *Aepyceros melampus*
- †*Gazella granti*

Laetolil (South Serengeti)[1]

PRIMATES

- †*Simopithecus oswaldi*

RODENTIA

- †*Pedetes surdaster*
- †*Hystrix galeata*

CARNIVORA

- *Canis mesomelas*
- *C. mesomelas latirostris*
- †*Canis africanus*
- *Crocuta crocuta*
- *Caracal caracal*
- ? *Panthera pardus*

TUBULIDENTATA

- †*Orycteropus aethiopicus*

PROBOSCIDEA

- †*Anancus kenyensis*
- †*Archidiskodon subplanifrons*
- †*A. exoptatus*
- †*A. recki*
- †*Deinotherium bozasi*

PERISSODACTYLA

- †*Stylohipparion albertense*
- *Equus burchelli*
- †*Metaschizotherium hennigi*
- *Ceratotherium simum*
- †*Serengeticeros efficax*

ARTIODACTYLA

- *Hippopotamus amphibius*
- †*Notochoerus euilus*
- †*Okapia stillei*
- *Giraffa camelopardalis*
- †*Libytherium olduvaiense*
- †*Tragelaphus buxtoni*
- *Taurotragus oryx*
- *Syncerus caffer*
- ? *Kobus ellipsirymnus*
- †*Redunca redunca*
- †*Hippotragus equinus*
- †*Damaliscus angusticornis*
- *Aepyceros melampus*

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[1] See footnote p. 295.

Olduvai (After Leakey, 1958, and Cooke, 1963)
Numbers I, II, III and IV refer to the various beds

PRIMATES

†*Simopithecus oswaldi* (I, II, III, IV)
†*S. jonathani* (II, ? IV)
†*Paranthropus boisei* (I, II)
†*Homo sp.* (I, II)

CARNIVORA

Canis mesomelas (II, IV)
C. mesomelas latirostris (II, IV)
†*Canis africanus* (II, IV)
Aonyx capensis (II)
Crocuta crocuta (I)
Panthera leo (II, III)
P. pardus (? I)

PROBOSCIDEA

†*Anancus kenyensis* (I, II)
†*Archidiskodon exoptatus* (I)
†*A. recki* (I, II, III, IV)
†*Deinotherium bozasi* (I, II)

PERISSODACTYLA

†*Stylohipparion albertense* (I, II, III, IV)
Equus burchelli (II, III, IV)
†*E.* aff. *grevyi* (I, II, III, IV)
†*E. oldowayensis* (I, II, III, IV)
†*Metaschizotherium hennigi* (I, II)
Ceratotherium simum (I, II, III, IV)
†*Serengeticeros efficax* (II)
Diceros bicornis (I, II, III, IV)

ARTIODACTYLA

†*Hippopotamus gorgops* (I, II, III, IV)
†*Notochoerus hopwoodi* (III, IV)
†*N. compactus* (II)
†*Mesochoerus olduvaiensis* (I, II, III, IV)
†*Potamochoerus majus* (I, II, III, IV)
Phacochoerus africanus (II, III, IV)
†*P. altidens altidens* (II, III, IV)
†*P. altidens robustus* (I, II)
†*Tapinochoerus minutus* (IV)
†*T. meadowsi* (I, II, III, IV)
†*Afrochoerus nicoli* (II, III, IV)
†*Metridiochoerus andrewsi* (I)
Orthostyonyx brachiops (II)
†*Okapia stillei* (? I)
Giraffa camelopardalis (II, IV)
†*G. gracilis* (II)
†*Libytherium olduvaiense* (I, II, III, IV)
Strepsiceros strepsiceros (? I, II, IV)
†*Strepsiceros imberbis* (? I, II, IV)
†*Tragelaphus buxtoni* (II)
Taurotragus oryx (I, II, IV)
†*Homoioceras nilssoni* (IV)
†*Bularchus arok* (II, III, IV)
†*Adenota kob* (I, II, III)
†*Hippotragus equinus* (III, IV)
†*H. niro* (II, IV)
†*Oryx beisa* (I)
†*Damaliscus angusticornis* (II, IV)
†*D. teste* (I, II, IV)
†*Alcelaphus kattwinkeli* (II, III, IV)
†*Beatragus hunteri* (I, II, IV)
†*Gorgon taurinus semiticus* (I, II, III, IV)
†*Gazella gazella praecursor* (I, II, IV)
†*G. granti* (I, II, IV)
†*Phenacotragus recki* (IV)
†*Pultiphagonides africanus* (I, II)
†*Pelorovis oldowayensis* (II, IV)

Vaal River Younger Gravels (After Cooke and Wells, 1946; Cooke, 1949, 1963; Wells, 1964)

CARNIVORA

cf. *Crocuta crocuta*

PROBOSCIDEA

†*Gomphotherium* sp.

†'*Archidiskodon*' *subplanifrons*
†'*Archidiskodon*' *broomi*
†'*Archidiskodon*' *transvaalensis*
†'*Palaeoloxodon archidiskodontoides*' (=*P. recki* ?)
†'*Loxodonta*' cf. *atlantica*
cf. *Loxodonta africana*

PERISSODACTYLA

†*Stylohipparion steytleri*
†*Equus helmei*
†*Equus plicatus*
†'*Equus sandwithi*' (=*E. plicatus* ?)
Equus cf. *burchelli*
Equus cf. *quagga*
cf. *Diceros bicornis*

ARTIODACTYLA

†*Mesochoerus paiceae*
†*Notochoerus capensis*
†*Tapinochoerus modestus*
†'*Tapinochoerus*' *meadowsi*
†*Stylochoerus compactus*
†*Phacochoerus aethiopicus*
Phacochoerus africanus
Hippopotamus cf. *amphibius*
†*Sivatherium* (?) *cingulatum*(1)
†*Sivatherium olduvaiense haughtoni*(1)
cf. *Alcelaphus caama*
†'*Alcelaphus robustus*'
†cf. *Megalotragus eucornutus*
Connochaetes cf. *gnou*
cf. *Connochaetes* sp.
cf. *Damaliscus* sp.
cf. *Sylvicapra grimmia*
cf. *Aepyceros melampus*
cf. *Antidorcas marsupialis*
†*Gazella wellsi*
cf. *Hippotragus* sp.
cf. *Strepsiceros strepsiceros*
Taurotragus cf. *oryx*
Syncerus cf. *caffer*
†'*Homoioceras*' cf. *baini*

(1) See footnote to Langebaanweg fauna (p. 280).

Cornelia (Uitzoek) (After Cooke, 1963)

PERISSODACTYLA

†*Stylohipparion steytleri*
Equus burchelli
†*E. plicatus*
†*Eurygnathohippus cornelianus*

ARTIODACTYLA

†*Hippopotamus gorgops*
†*Notochoerus compactus*
Phacochoerus africanus
†*Orthostonyx* sp.
Giraffa camelopardalis
†*Libytherium olduvaiense*
Strepsiceros strepsiceros
Taurotragus oryx
†'*Homoioceras*' *baini*
†*Kobus venterae*
Damaliscus cf. *albifrons*
†*Damaliscus* sp.
Alcelaphus caama
†? *A. helmei*
†*Connochaetes laticornutus*
†*Megalotragus eucornutus*
†*Gazella wellsi*
†*G. helmoedi*
†*Gazella* sp.
†*Antidorcas marsupialis*

Kromdraai (After Cooke, 1963)

INSECTIVORA

†*Proamblysomus antiquus*
†*Elephantulus langi*
Crocidura cf. *bicolor*
Suncus cf. *etruscus*
†? *Myosorex robinsoni*

PRIMATES

†*Parapapio jonesi*
†*Papio robinsoni*
†*Paranthropus robustus*

LAGOMORPHA

Lepus capensis

RODENTIA

†*Mystromys antiquus*
Tatera cf. *brantsi*
?*Desmodillus auricularis*
Grammomys cf. *dolichurus*
†*Rhabdomys* cf. *pumilio*
Mastomys cf. *natalensis*
Malacothrix cf. *typica*
Steatomys cf. *pratensis*
†*Palaeotomys gracilis*
†*Cryptomys robertsi*

CARNIVORA

Canis mesomelas pappos
†*Canis atrox*
†*Canis terblanchei*
Vulpes pulcher
†*Herpestes mesotes*
†*Crossarchus transvaalensis*
†*Crocuta spelaea*
†*C. ultra*
†*Hyaena bellax*
†*Felix crassidens*
†*Therailurus piveteaui*
†*Panthera* aff. *leo*
†? *P. whitei*
†*P. shawi*
†*Megantereon eurynodon*

HYDRACOIDEA

†*Procavia antiqua*
†*P. transvaalensis*

PERISSODACTYLA

†*Stylohipparion steytleri*
? *Equus burchelli*
†*E. plicatus*
†*E. helmei*

ARTIODACTYLA

†*Potamochoerops antiquus*

Bolt's Farm (After Cooke, 1963)

INSECTIVORA

†*Proamblysomus antiquus*
†*Atelerix major*
†*Elephantulus langi*
†*Elephantulus antiquus*
E. cf. *brachyrhynchus*
Suncus cf. *etruscus*
†*Myosorex robinsoni*

CHIROPTERA

Rhinolophus cf. *capensis*
†cf. *Myotis* sp.

PRIMATES

† ?*Parapapio broomi*
†? *P. whitei*
†*Cercopithecoides williamsi*

RODENTIA

Pedetes cf. *caffer*
†*Mystromys hausleitneri*
Tatera cf. *brantsi*
†*Dasymys bolti*
†*Rhabdomys* cf. *pumilio*
†*Thallomys debruyni*
Leggada cf. *minutoides*
L. cf. *major*
Malacothrix cf. *typica*
†*Palaeotomys gracilis*
Hystrix africae-australis
†*Cryptomys robertsi*

CARNIVORA

Canis mesomelas
C. mesomelas pappos
Aonyx cf. *capensis*
Suricata suricatta
†*Crossarchus transvaalensis*
†*Hyaena bellax*
†*Leptailurus spelaeus*

†*Therailurus barlowi*
†*Panthera* aff. *leo*
†*Machairodus transvaalensis*

PROBOSCIDEA

†*Loxodonta atlantica*

HYDRACOIDEA

Procavia capensis

PERISSODACTYLA

†*Stylohipparion steytleri*
Equus burchelli
†*E. plicatus*

ARTIODACTYLA

†*Tapinochoerus meadowsi*
†*Potamochoeroides shawi*
†*P. antiquus*
Tragelaphus scriptus
Taurotragus oryx
Syncerus caffer
Damaliscus cf. *pyrgatus*
? *D.* cf. *lunatus*
†*Alcelaphus robustus*
†*A. helmei*
Connochaetes taurinus
†*Makapania broomi*
†? *Raphicerus campestris*
†*Gazella wellsi*
†? *Phenacotragus vanhoepeni*
† ?*Antidorcas marsupialis*

Makapansgat (After Cooke, 1963)

INSECTIVORA

†*Chrysotricha hamiltoni*
†*Elephantulus langi*
Suncus cf. *etruscus*
†*Myosorex robinsoni*

PRIMATES

†*Simopithecus darti*
†*Parapapio jonesi*
†*P. broomi*
†*P. whitei*
†*Papio robinsoni*
†*Australopithecus africanus*
†*Cercopithecoides williamsi*

LAGOMORPHA

Pronolagus randensis

RODENTIA

†*Mystromys hausleitneri*
†*M. darti*
? *Tatera* cf. *brantsi*
Grammomys cf. *dolichurus*
Pelomys cf. *fallax*
†*Rhabdomys* cf. *pumilio*
Aethomys cf. *namaquensis*
Mastomys cf. *natalensis*
Leggada cf. *minutoides*
Dendromus cf. *mesomelas*
† ?*Malacothrix makapani*
Steatomys cf. *pratensis*
†*Palaeotomys gracilis*
†*Hystrix major*
H. africae-australis
†*Xenohystrix crassidens*
†*Gypsorhychus makapani*
†*Cryptomys robertsi*

CARNIVORA

? *Canis mesomelas pappos*
†*Cynictis penicillata brachyodon*
†*Crocuta* cf. *brevirostris*
†*Hyaena makapani*
†*Therailurus barlowi*
†*Megantereon* sp. nov.

HYRACOIDEA

†*Procavia antiqua*
†*P. transvaalensis*
†*Procavia* sp.

PERISSODACTYLA

†? *Stylohipparion steytleri*
†*Equus helmei*
†*Metaschizotherium* (?) *transvaalensis*
Ceratotherium simum
Diceros bicornis

ARTIODACTYLA

Hippopotamus amphibius
†*Notochoerus euilus*
†*Potamochoeroides hypsodon*
†*P. shawi*
Giraffa camelopardalis
†*Libytherium* cf. *olduvaiense*
Strepsiceros strepsiceros
Tragelaphus angasi
Taurotragus oryx
Syncerus caffer
†*S.* cf. *makapani*
†*Cephalophus pricei*
C. caerulus
†*Redunca darti*
Redunca arundinum
R. fulvorufula
Oryx gazella
†*Alcelaphus robustus*
†*A. helmei*
Connochaetes taurinus
†*Oreotragus major*
†*Makapania broomi*
Aepyceros melampus
†*Gazella gracilior*
†*Phenacotragus vanhoepeni*

'ELANDSFONTEIN', HOPEFIELD (SOUTH AFRICA)

(Modified from Singer, 1957)

PHOLIDOTA

Manis sp.

PRIMATES

†*Simopithecus oswaldi hopefieldensis*
†*Homo sapiens rhodesiensis* ('Saldanha Man')

LAGOMORPHA

Lepus sp. (cf. *capensis*)

RODENTIA

Bathyergus sp. (cf. *suillus*)
Georychus sp. (cf. *capensis*)
Hystrix sp. (cf. *africae-australis*)
Otomys sp. (cf. *saundersiae*)
Parotomys sp. (cf. *brantsi*)

CARNIVORA

Canis mesomelas
Canis adustus
†*Lycaon pictus magnus*
Mellivora capensis
Herpestes sp. (cf. *ichneumon*)
Herpestes eogale
Hyaena brunnea
†*Crocuta spelaea*
Lynx caracal
Leptailurus serval
†*Panthera leo spelaea*
†*Megantereon gracile*

PROBOSCIDEA

†*Loxodonta* (*Palaeoloxodon*) cf. *antiquus recki*
† ? *Archidiskodon* sp.

PERISSODACTYLA

†*Equus* (*Hippotigris*) *plicatus*
†*E. helmei*
†*E.* cf. *sandwithi*
Ceratotherium simum
Diceros bicornis

ARTIODACTYLA

†*Mesochoerus lategani*
†*M. paiceae*
†*Tapinochoerus meadowsi*
Hippopotamus amphibius
†*Sivatherium olduvaiense*(1)
†*Giraffa* cf. *gracilis*
†*Homoioceras* sp.
Taurotragus oryx
Redunca arundinum
Raphicerus campestris
Antidorcas marsupialis
†*Antidorcas* sp.
Tragelaphus(2) sp.

cf. *Hippotragus niger*
†cf. *H. leucophaeus*
†*Hippotragus* sp.
†*Damaliscus* cf. *dorcas*
†*Damaliscus* sp.
Connochaetes sp.
†*Lunatoceras* sp.
†*Pelea* sp.
†cf. *Gazella wellsi*
†*Gazella* sp. nov.

(1) See footnote to Langebaanweg fauna (p. 280).

(2) In the other faunal lists *Tragelaphus* has not been substituted for the earlier labelling *Strepsiceros*.

Refer now to table 1 on pages 303 to 313.

COMMENTARY ON THE PUBLISHED FAUNAL ASSOCIATIONS AT HIPPARIONID SITES IN AFRICA

MIOCENE

Oued el Hammam and Marceau

Arambourg (1959) has clearly demonstrated that these two sites contain fundamentally the same fauna: both include *Hipparion africanum*, *Samotherium* sp. and *Hyaena algeriensis*, and cannot but be contemporaneous, as is confirmed by their stratigraphy.

It seems clear that these assemblages correspond to a very special and, so far, little-known stage of development of the fauna of Africa, posterior to the Burdigalian and anterior to the 'classical Pontian'. The fauna from these sites are very different from the well-represented assemblage of the Lower Miocene in East Africa (Losodok, west of Lake Rudolph; Rusinga and Moboko Islands in the Kavirondo Gulf of Lake Victoria) and South West Africa. The typical Burdigalian assemblages contain, *inter alia*, *Mastodon* cf. *longirostris*, *Deinotherium hobleyi*, *Aceratherium*, *Teleoceras*, and *Anthracotheriidae*, *Propalaeochoerus*, *Bunolistriodon*, *Dorcatherium*, *Creodonta*, none of which are found at Oued el Hammam, nor are the anthropomorpha which constitute the typical African 'touch' of this Burdigalian fauna. The only similarity between the sites and a Burdigalian fauna is the presence at Oued el Hammam of an orycterope, namely, *Orycteropus mauritanicus* which is comparable with *Myorycteropus* McInnes of East Africa. The separation between Oued el Hammam and the Lower Miocene fauna of East and South West Africa is emphasized by the presence (at Oued el Hammam) of Giraffidae (*Samotherium* and *Palaeotragus*), the development of Bovidae (*Damalavus*, *Gazella*, *Tragocerus*, *Cephalophus*) and the appearance of *Hyaena* and especially of the equids with *Hipparion africanum*.

On the other hand, the assemblages from the two North African localities are at first sight characteristic of the so-called 'classical Pontian' of Eurasia (Eppelsheim, Pikermi, Mont Luberon). However, on detailed study and comparison of the several groups involved, Arambourg has shown that Eurasian 'Pontain' assemblages and the material from Oued el Hammam may belong to the same ensemble, but they are not identical: specific and generic differences exist and there is not even a single species in common (table 2).

TABLE I

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gambian'
INSECTIVORA																																
**Proamblysomus antiquus*					X	X																										
**Chrysotricha hamiltoni*			X																													
**Chlorotalpa spelea*		X		X																												
**Atelerix major*						X																										
**Elephantulus langi*		X	X	X	X	X						X																				
**Elephantulus antiquus*						X																										
E. cf. *brachyrhynchus*	X			X		X																										
**Mylomygale spiersi*	X	X																														
**Crocidura taungsensis*	X																															
C. cf. *bicolor*		X			X							X					?															
Suncus cf. *etruscus*		X	X	X	X	X																										
**Myosorex robinsoni*		X	X	X	?	X																										
CHIROPTERA																																
Rhinolophus cf. *capensis*	X		X			X																										
R. cf. *geoffroyi*												X																				
*cf. *Myotis* sp.						X																										
Miniopteris cf. *schreibersi*												X																				
PRIMATES																																
**Simopithecus oswaldi*[a]									X													X	X	X	X	X	X		X			
**S. jonathani*[a]																									X		?					
**S. darti*[a]			X																													
**S. danieli*[a]				X																												
**Simopithecus* sp.																	?															

[a] See also Singer (1962).

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gamblian'
**Gorgopithecus major*				X																												
**Dinopithecus ingens*				X																												
**Parapapio antiquus*	X																															
**P. jonesi*	X	X	X	X	X																											
**P. broomi*		X	X			?																										
**P. whitei*	X	X	X			?																										
**Papio neumanni*																																X
**P. izodi*	X																															
**P. wellsi*	X																															
**P. angusticeps*				X																												
**P. robinsoni*			X	X	X																											
P. ursinus												X	X																			
**Paranthropus boisei*																								X	X							
**P. robustus*				X	X																											
**Australopithecus africanus*	X	X	X																													
**Telanthropus capensis*				X																												
**Homo rhodesiensis*									X								X															
**H.* cf. *sapiens*										X		X																				
**Homo* sp.																					X			X	X						X	X
**Cercopithecoides williamsi*	X	X	X	X		X																										
LAGOMORPHA																																
Pronolagus randensis			X									X																				
Lepus capensis	X			X	X				X																							
Lepus saxatilis												X																				
PHOLIDOTA																																
Manis sp.									X																							

RODENTIA																															
Xerus capensis										X																					
**Pedetes hagenstadi*										*X*																					
**P. surdaster*																							*X*								*X*
**P. gracile*	*X*																														
P. cf. *caffer*						X																									
Mystromys antiquus	*X*																														
**M. hausleitneri*		*X*	*X*		*X*	*X*																									
**M. darti*			*X*																												
Tatera cf. *brantsi*	X	X	?		X	X																									
Desmodillus auricularis	X				?																										
Grammomys cf. *dolichurus*			X		X																										
**Dasymys bolti*				*X*		*X*																									
Pelomys cf. *fallax*		?	X																												
**Rhabdomys* cf. *pumilio*	*X*	*X*	*X*		*X*	*X*																									
Aethomys cf. *namaquensis*		X	X																												
Aethomys cf. *chrysophilus*												X																			
**Thallomys debruyni*	*X*					*X*																									
T. cf. *paedulcus*												X																			
Mastomys cf. *natalensis*	X	X	X		X																										
Leggada cf. *minutoides*		X	X			X																									
L. cf. *major*		X				X																									
Saccostomus campestris												X					?														
**Dendromus antiquus*	*X*																														
D. cf. *mesomelas*		X	X									X																			
Malacothrix cf. *typica*	X				X	X																									
*? *M. makapani*			*X*																												
Steatomys cf. *pratensis*			X		X							X																			
Otomys cf. *irroratus*										X							X														
**O.* cf. *saundersiae*									*X*																						
Myotomis cf. *turneri*										X																					
M. cf. *unisulcatus*										X																					
Parotomis cf. *brantsi*									X																						
**Palaeotomys gracilis*	*X*	*X*	*X*	*X*	*X*	*X*						?																			
**Prototomys campbelli*	*X*																														
**Hystrix major*			*X*																												

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	'Olorgesailie'	Eyasi	Gamblian
Hystrix cf. *cristata*		X																														
H. africae-australis			X			X			X			X	X				X	X														
**H. galeata*																							X									X
**Xenohystrix crassidens*			X																													
Thryonomys swinderianus												X						X													X	X
**Petromus minor*	X																															
**Gypsorhychus darti*	X																															
**G. minor*	X																															
**G. makapani*			X																													
Georychus cf. *capensis*									X																							
**Cryptomys robertsi*	X	X	X	X	X	X																										
Bathyergus cf. *suillus*									X																							
FISSIPEDA																																
Canis mesomelas	X					X			X			X											X		X		X					
C. mesomelas latirostris																							X		X		X					
C. mesomelas pappos		X	?	X	X	X																										
**C. africanus* (? *Lycaon*)																							X		X		X					
**C. atrox*					X																											
**C. brevirostris*		X																														
**C. terblanchei*					X																											
C. adustus									X								X	X														
Vulpes pulcher				?	X																											
V. chama											X	X																				
Lycaon pictus											X	X																				
**L. pictus magnus*										X																						
Otocyon megalotis												X																				
Mellivora capensis									X				X																			

Aonyx capensis																								X							X
A. cf. *capensis*						X				X																					
Suricata suricatta						X						X																			
**Herpestes mesotes*					X																										
H. cauui										X																					
H. ichneumon									X			X					X														
**Atilax paludinosus*										X																					
**Crossarchus transvaalensis*					X	X																									
Cynictis penicillata				X																											
**C. penicillata brachyodon*			X																												
**Leecyaena forfex*				X																											
**Lycyaena silberbergi*		X		X																											
**L. nitidula*		?		X																											
Crocuta crocuta							X				X	X						X			X		X	X						X	
**C. crocuta angella*				X																											
**C. spelaea*					X				X																						
**C. venustula*				X																											
**C. ultra*					X																										
**C.* cf. *brevirostris*			X																												
Hyaena brunnea				X					X	X			X				X	X													
**H. dispar*				X																											
**H. makapani*			X																												
**H. bellax*					X	X																									
**Felis crassidens*					X																										
Lynx caracal									X																						
Caracal caracal												X											X							X	
**Leptairulus spelaeus*						X																									
**L. hintoni*																	X														
L. serval									X																						
**Therailurus barlowi*		X	X	?		X																									
**T. piveteaui*					X																										
Panthera leo									X								X								X	X					X	X
**P.* aff. *leo*				X	X	X			X																						
P. pardus											X						X						?	?							X	
**P. pardus incurva*				X																											
**P. whitei*				?	?																										
**P. shawi*				?	X																										

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG	Chelmer	Broken Hill	Mumbwa	Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gamblian'
**Megantereon gracile*		*X*							*X*																					
**M. eurynodon*				*X*	*X*																									
**M.* sp. nov.			*X*																											
**Machairodus transvaalensis*						*X*																								
**M.* sp.																*X*														
**Homotherium ethiopicum*																		?		*X*										
PINNIPEDIA																														
cf. *Arctocephalus*														X																
TUBULIDENTATA																														
**Orycteropus aethiopicus*																					*X*						*X*		*X*	*X*
**O.* sp.																	*X*													
PROBOSCIDEA																														
**Gomphotherium* sp.							*X*																							
**Anancus kenyensis*																			*X*		*X*	*X*	*X*							
**Stegodon* sp.														*X*																
**Stegodon kaisensis*																		*X*	*X*											
**Stegolophodon* sp.														*X*																
**Loxodonta atlantica*						*X*	*X*																				*X*			
L. africana																*X*														*X*
**Archdiskodon subplanifrons*							*X*												*X*		*X*									
**A. exoptatus*																		*X*	*X*	*X*	*X*	*X*								
**A. recki*									*X*											*X*	*X*	*X*	*X*	*X*	*X*		*X*	*X*		
**A. broomi*							*X*																							
**A. transvaalensis*							*X*																							
**A.* sp.									*X*					*X*																
**Palaeoloxodon*														*X*																
**Deinotherium bozasi*																			*X*	*X*	*X*	*X*	*X*							

HYRACOIDEA																																
Procavia capensis						X						X						X														
*P. antiqua	X	X	X	X	X																											
*P. transvaalensis	X	X	X	X	X	X																										
*P. sp.			X																													
PERISSODACTYLA																																
*Hippariinae sp.[a]														X																		
*Stylohipparion albertense[a]																				X	X	X	X	X	X	X	X		X	X		
*S. steytleri[a]			?		X	X	X	X																								
Equus burchelli					?	X	X	X		X	X	X	X			X	X						X		X	X	X				X	X
*E. aff. grevyi																						?		X	X	X	X		X			
*E. oldowayensis																					X	X		X	X	X	X		X	X		
*E. plicatus				?	X	X	X	X	X	X	X		X			X		X														
*E. helmei			X		X		X		X	X	X	X	X	X		X																
*E. quagga							?			X			X																			
*E. sandwithi									X																							
*Eurygnathohippus cornelianus[a]								X																								
*Metaschizotherium hennigi																				X			X	X	X							
*M. (?) transvaalensis			X																													
Ceratotherium simum			X						X				X	X			?			X	X	X	X	X	X	X	X	X	X	X		
*Serengeticeros efficax																							X		X							
Diceros bicornis			X				X		X	X		X	X				X				X			X	X	X	X				X	
ANCODONTA																																
*Hippopotamus gorgops								X																?	X	X	X	X	X	X		
*H. imaguncula																				X	X							X				
*H. protamphibius																						X										
H. amphibius			X				X		X	X	X					X				X		X	X						X		X	X
ARTIODACTYLA																																
SUIDAE																																
*Notochoerus capensis							X																									
*N. hopwoodi																										X	X	X				
*Notochoerus euilus			X																	X			X									
*Notochoerus compactus							X	X		X	X														X							
*Notochoerus sp.																						X										

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gambian'
**Mesochoerus paiceae*							X		X																							
**M. olduvaiensis*																								X	X	X	X					
**M. heseloni*																						X										
**M. lategani*									X																							
**M. limnetes*																				X												
Potamochoerus koiropotamus																		X													X	
**P. majus*																								X	X	X	X					
Phacochoerus africanus							X	X		X			X												X	X	X					
**P. altidens altidens*							X																		X	X	X					
**P. altidens robustus*																								X	X							
**Tapinochoerus minutus*																											X		X			
**T. meadowsi*		X		X		X	X		X															X	X	X	X			X		
**Afrochoerus nicoli*																									X	X	X					
**Metridiochoerus andrewsi*																								X					X			
**M. pygmaeus*																					X											
**Pronotochoerus nyanzae*																												X				
**P. jacksoni*																						X										
**Hylochoerus meinertzhageni*																																X
**Hylochoerus antiquus*																													X			
**Nyanzachoerus kanamensis*																					X											
**Orthostonyx brachiops*																									X							
**O.* sp.								X																								
**Potamochoeroides hypsodon*			X																													
**P. shawi*	X		X			X																										
**Potamochoerops antiquus*		?		X	X	X																										
GIRAFFIDAE																																
**Okapia stillei*																							X	?								

Giraffa camelopardalis			X					X		X		X					X				X	X	X		X		X	X	X	X	X	
*_G. gracilis_									_X_													_X_			_X_							
*_Libytherium olduvaiense_							_X_	_X_	_X_								_X_				_X_	_X_	_X_	_X_	_X_	_X_	_X_	_X_		_X_		
*_L._ cf. _olduvaiense_			_X_																													
BOVIDAE																																
Strepsiceros strepsiceros			X				?	X	X								X	X						?	X		X				X	
*_S. imberbis_																						_X_		?	_X_		_X_					
*_Tragelaphus buxtoni_																							_X_		_X_							
T. scriptus						X																										
T. angasi	X		X										X				X															
Taurotragus oryx			X			X	X	X	X	X	X	X	X			X	X	X					X	X	X		X				X	
Syncerus caffer			X			X	X					X	X					X				X	X								X	
*_S._ cf. _makapani_			_X_																													
*_Homoioceras nilssoni_																											_X_				_X_	_X_
*'_Homoioceras_' _baini_							_X_	_X_	_X_	_X_	_X_	_X_	_X_			_X_	_X_															
*_Homoioceras_ sp.														_X_																		
*_Bularchas arok_																									_X_	_X_	_X_		_X_			
*_Cephalophus parvus_	_X_																															
*_C. pricei_			_X_																													
C. caerullus			X															?														
Sylvicapra grimmia							X			X	X		X					X														
Kobus ellipsirymnus												X	X									?	?								X	
*_K. venterae_								_X_		_X_	_X_																					
*_Adenota kob_																								_X_	_X_	_X_					_X_	
Onotragus leche												X																				
*_Redunca redunca_																							_X_								_X_	
*_R. darti_			_X_																													
R. arundinum			X						X			X						X														
R. fulvorufula			X															?														
_R._ sp.														X																		
Pelea capreolus												X																				
_P._ sp.									X																							
Hippotragus equinus													_X_					_X_					_X_			_X_	_X_		_X_		_X_	
*_H. niro_																									_X_		_X_					
*_H. broomi_		_X_																														
H. niger							X																									

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	‘Gamblian’
*_H._ sp.									X																							
*_Oryx beisa_																								X							X	
O. gazella			X										X				X															
*_Damaliscus angusticornis_																							X		X		X					
_D._ cf. _pygargus_						X	?		X				X																			
*_D. teste_																								X	X		X					
_D._ cf. _lunatus_						?	X					X					X	X														
_D._ cf. _albifrons_							X	X		X	X						X															
*_D._ sp.									X																							
*_D._ sp.								X		X	X	X																				
*_D._ sp.														X																		
*_Alcelaphus kattwinkeli_																									X	X	X		X			
A. caama							X	X				X	X			X		X														
*_A. robustus_			X			X	X					X																				
*_A. helmei_			X			X	X	?		X	X	X	X			X																
A. lichtensteini																		?														
*_Beatragus hunteri_ (?)																								X	X		X					
Connochaetes taurinus			X			X	X					X	X			X	X	X														
*_C. antiquus_										X																						
C. gnou							X																									
*_C. laticornutus_								X		?																						
*_C. grandis_																X																
*_Gorgon taurinus semiticus_																								X	X	X	X					
Oreotragus oreotragus												X																				
*_Oreotragus major_			X																													
*_O. longiceps_	X																															
_O._ sp.														X																		
*_Makapania broomi_		X	X			X																										

*Raphicerus campestris						?			X			X	X																		
*Lunatoceras mirum									X	?																					
*Megalotragus eucornutus								X																							
Aepyceros melampus			X				X					X										X	X								X
Litocranius walleri																	X														
*Gazella gazella praecursor																								X	X		X				
*G. granti																								X	X		X				X
*G. gracilior			X																												
*G. wellsi		X				X	X	X	X																						
*G. bondi										X	X	X				X															
*G. helmoedi								X																							
*G. sp.								X																							
*Phenacotragus recki																											X		X		
*P. vanhoepeni			X			?																									
*Antidorcas marsupialis		?				?	X	X	X	X	X	X	X																		
*A. (?) sp.									X																						
*Pultiphagonides africanus																								X	X						
*Pelorovis oldowayensis																									X		X				

Table 1. Synopsis of the Pleistocene faunal assemblages at sites in East and South Africa (according to Cooke, 1963, tables 4, 6 and 7, but the list for Hopefield is replaced by Singer, personal data. The Suidae are corrected after Leakey, 1958).
[*=extinct; *X*=extinct]

EURASIA	*OUED EL HAMMAM*
Dicerorhinus schleiermacheri	*D. primaevus*
Dicerorhinus orientalis	
Hipparion gracile	*H. africanum*
H. mediterraneum	
Orycteropus gaudryi	*O. mauritanicus*
Hyaena salonicae	*H. algeriensis*
Palaeotragus roueni	*P. germaini*

Table 2. Comparison between the 'classical Pontian' fauna of Eurasia and that from Oued el Hammam.

These differences indicate that the fauna of Oued el Hammam is more primitive than that of the Eurasian 'Pontian', thereby suggesting an ancient biogeographical autonomy of Africa. The presence of a fauna more primitive than the 'classical Pontian' does not necessarily mean that it antedates the Pontian. However, as is indicated in the section on the geological aspects of the sites (*vide supra* p. 283), the Oued el Hammam deposit lies under lacustrine or marine deposits. These contain clearly recognized Upper Miocene fauna of the Sarmatian or of the Tortono-Sahelian age, which were formed by the marine transgression at the end of the Miocene. As indicated by Arambourg, there is no possible correlation between Oued el Hammam and the 'classical Pontian' which is formed posteriorly to the Sarmatian.

PLIOCENE

The Hipparion-bearing sites in North Africa and in the Nile Valley, which are usually considered to be Pliocene, cannot be satisfactorily dated on the basis of the fauna alone. The faunal assemblages at Tozeur, Aïn el Bey and Mascara are rather poor. Their antiquity is suggested by the presence of *Merycopotamus*, *Helladotherium* and *Rhinoceros pachygnathus*. The Pliocene nature of these sites can only be determined from their geology.

At Wadi Natrun, none of the rare fossils recovered is characteristic of a particular period. Determination of stratigraphical relationships is necessary for the assessment of the Pliocene date of the fossiliferous beds.

PLEISTOCENE

The simple comparison of lists of fauna from numerous sites often results in misleading or incorrect conclusions for the following reasons:

1. The assemblages may represent a sampling of fauna from different biotopes, and furthermore, the sampling (i.e. collecting) may have been made by means of different methods and for differing requirements. For example, in the case of small rodents, they may be an incidental part of a general collection recovered during a thorough investigation, or they may have been sought for exclusively from, say, breccia by a specialist. However, they may have been overlooked in the field when the investigator was merely collecting the larger bones. Thus they would be absent from the collected assemblage, but this would not reflect the fact that they may have been present in situ. Thus someone studying or re-studying a particular collection, and being unaware of the conditions of recovery of the material, may accurately record frequencies but these may yet be misleading.

2. Different palaeontologists may use criteria and terminology at variance with others, often because of a familiarity with material from particular areas or countries. In addition the fragmentary nature of certain specimens may be responsible for differing interpretations.

3. Just as different biotopes may express slight differences in similar forms, so climatic differences may influence similar forms even in adjacent

regions. These differences may be interpreted on a specific rather than on a subspecific level, thus influencing statistical analyses.

Consequently, a practical method of comparing sites within a geographical region is by studying the results obtained by either a single palaeontologist or by a particular institute. This requirement is partially met for the 'Villafranchian' sites of North Africa, for the australopithecine breccias in South Africa, for Olduvai Gorge, and possibly for Laetolil and Rawi in East Africa. It is to be remembered that the success of the investigation within each of these three geographical units varies.

The North African 'Villafranchian' fauna is characterized by the association of the latest mastodonts with primitive elephants, of the Sivatheriinae with *Giraffa*, and of the hipparionids with the modern Equidae.

However, there is sufficient evidence available to suggest that such associations, found in several places in Africa, are not necessarily contemporaneous. Unfortunately, the term 'Villafranchian fauna' is loosely used with a different interpretation in different areas, but it may only be applied, sensu stricto, in a chronological sense to the Mediterranean basin.

Arambourg (1947) proposed a relationship between the fossil-bearing sites of Africa according to the presence or absence of archaic elements, such as *Archidiskodon planifrons*, *Anancus*, *Stegodon* and *Chalicotheriidae*. During the Lower Pleistocene some of these forms seem to have disappeared, being replaced by *A. recki*, while other primitive groups with tertiary affinities like *Stylohipparion*, *Deinotherium* and *Libytherium* persisted.

By means of the Proboscidea sequence, a subdivision of the 'Villafranchian' can be formulated:

A. Lower 'Villafranchian'

Characterized by the PRESENCE of *Anancus*, *Stegodon*, *Stegolophodon* (?), and the appearance (in a stratified deposit) of *Archidiskodon* (or *Elephas subplanifrons*, *planifrons*, *africanavus*, and *exoptatus*): Kanam, Kaiso, Garet Ichkeul.

B. Middle 'Villafranchian'

Characterized by the extinction of *Stegodon*, the persistence of *Anancus*, *Mastodon*, *Archidiskodon* (or *Elephas*) *planifrons* or *subplanifrons* and *exoptatus* and the first appearance of *Palaeoloxodon recki* (or *E. meridionalis*): Koro Toro, Laetolil, Aïn Hanech, Olduvai I.

C. Upper 'Villafranchian'

Characterized by the presence of *Anancus*, *Stegodon*, *Mastodon*, and the continued presence of *A. exoptatus*, *E. africanavus* and even *Deinotherium*: Omo.

The post-'Villafranchian' horizon commences when *Anancus*, *Stegodon*, and *Mastodon* as well as primitive forms of *Archidiskodon* (*exoptatus*) and *Elephas* (*planifrons*, *africanavus*) become totally extinct, coincidental with the appearance of *Loxodonta africana* and *atlantica* as well as the further development of *P. recki*.

North Africa

In a comparison of Garet Ichkeul with Aïn Hanech, the fauna of which are substantially the same, Arambourg (1949) concluded that Garet Ichkeul was the more ancient (Lower 'Villafranchian') because of the more abundant *E. planifrons* and *Stylohipparion* at the former site, while the latter had remains of *P. recki.*

There is good evidence that there is close identity between Aïn Hanech (and Bel Hacel) on the one hand, and Garet Ichkeul, Aïn Boucherit (i.e. Beni Foudda of Pomel) and Oued el Akrech (Arambourg and Choubert, 1957), on the other. On the basis of the fauna alone, it does not seem possible to compare these in any great detail with the other North African Pleistocene *Hipparion*-bearing sites.

	Total number of identified species	*Extinct species*	*Extant species*	*Extinct / Total*	*Extant / Extinct*
				%	%
SOUTH AFRICA					
Taung	34	25	9	73·5	36·0
Sterkfontein	37	26	11	70·4	42·3
Makapansgat	70	43	27	61·4	62·7
Swartkrans	39	32	7	82	21·9
Kromdraai	41	29	12	70·7	41·4
Bolt's Farm	56	35	21	62·6	60·0
Vaal River	35	20	15	57	75·1
Cornelia	23	17	6	74	35·3
Hopefield	45	23	22	51·2	95·6
Florisbad	32	15	17	46·9	113·4
Vlakkraal	18	9	9	50	100
Cave of Hearths	45	10	35	22·2	350·0
Wonderwerk	25	8	17	32	213·0
RHODESIA					
Chelmer	11	6	5	—	—
Broken Hill	31	7	24	22·6	342
Mumbwa	18	3	15	16·6	500
EAST AFRICA					
Kaiso	10	8	2	80	25
Kanam	16	12	4	75·0	33·3
Omo	21	15	6	71·4	40
Laetolil	33	20	13	60·6	65·0
Olduvai I	34	28	6	82·2	21·4
Olduvai II	49	38	11	77·4	29·0
Olduvai III	23	18	5	78·4	27·8
Olduvai IV	39	30	9	76·9	30·0
Rawi	7	4	3	—	—
Kanjera	17	14	3	82·3	21·4
Olorgesailie	9	7	2	—	—
Eyasi	24	9	15	37·5	166·0
'Gamblian'	12	7	5	58·4	71·4

TABLE 3. The relationships between identified extinct and extant fauna from African Pleistocene sites.

East and Central Africa

The OLDUVAI GORGE has been extensively studied. From the four Beds, 55 species have been identified (table 1), Bed II and IV containing respectively 49 and 39 of them (table 3). However, recent discoveries and more detailed analyses will considerably alter these figures. Dietrich (1942), Arambourg (1947), Hopwood (1951) stressed the general Middle Pleistocene character of the Olduvai faunal assemblage. It has been pointed out that no available faunal evidence suggests that the lower part of Olduvai is of Lower Pleistocene age. This view will probably be considerably modified when descriptions and analyses of recent discoveries are published shortly. In this paper, only the available published data are assessed. Leakey (1963) emphasizes the point that 'Bed I covers a very long period of time with a gradual change from a very wet climate at the beginning to savanna conditions and then subdesert ones'. It is no longer possible to speak simply of 'the fauna of Bed I'. He also points out that the fauna from Bed I, although 'Villafranchian' and older than Omo, does not conform with the Lower 'Villafanchian' fauna as represented in East Africa at Kanam East and West. Furthermore, it is no longer certain whether Bed I contains *Hippopotamus gorgops*, *Taurotragus oryx*, *Tragelaphus strepsiceros*, and even *Palaeoloxodon recki* which is super-abundant in Bed II and Bed IV.

Olduvai I	21·4
Swartkrans	21·9
Olduvai III	27·8
Olduvai II	29·0
Olduvai IV	30·0
Cornelia	35·3
Taung	36·0
Omo	40·0
Kromdraai	41·4
Sterkfontein	42·3
Bolt's Farm	60·0
Makapansgat	62·7
Laetolil	65·0
Vaal River	75·1
Hopefield	95·6
Florisbad	113·4
Eyasi	166·0
Wonderwerk	213·0
Broken Hill	342·0
Cave of Hearths	350·0

TABLE 4. List of sites in the order of increasing proportions of extant species. Ratios (extant/extinct) are determined only for those sites where more than 20 species have been identified.

Cave of Hearths	22·2
Broken Hill	22·6
Wonderwerk	32·0
Eyasi	37·5
Florisbad	46·9
Hopefield	51·2
Vaal River	57·0
Laetolil	60·6
Makapansgat	61·4
Bolt's Farm	62·6
Sterkfontein	70·4
Kromdraai	70·7
Omo	71·4
Taung	73·5
Cornelia	74·0
Olduvai IV	76·9
Olduvai II	77·4
Olduvai III	78·4
Swartkrans	82·0
Olduvai I	82·2

TABLE 5. List of sites in the order of increasing proportions of extinct species. Ratios (extinct/total) are determined only for those sites where more than 20 species have been identified.

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Cornelia	Hopefield	Vaal River	Cave of Hearths	Wonderwerk	Broken Hill	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Eyasi	Florisbad
Taung		*10* 41	*10* 58	*6* 51	*6* 48	*8* 52	42	48	45	*1* 34	33	32	40	45	53	63	43	55	34	40
Sterkfontein	24·4		*15* 54	*14* 44	*10* 45	*16* 45	*2* 41	*3* 46	*3* 43	*3* 33	*1* 33	33	41	46	*1* 53	*1* 63	*1* 43	*1* 55	35	*1* 40
Makapansgat	17·2	27·8		*10* 65	*12* 60	*17* 61	*2* 58	*1* 65	*4* 59	*5* 48	*1* 50	50	58	*1* 62	71	81	61	73	52	*2* 56
Swartkrans	11·8	31·8	15·4		*15* 46	*12* 55	*1* 48	*3* 52	*2* 50	*2* 40	40	39	47	52	*1* 59	*1* 69	*1* 49	*1* 61	41	*1* 46
Kromdraai	12·5	22·2	20	32·6		*13* 51	*2* 44	*4* 48	*3* 46	*1* 38	37	36	44	49	57	67	47	59	38	*2* 42
Bolt's Farm	15·4	35·6	27·8	21·8	25·4		*5* 47	*5* 53	*8* 47	*6* 39	*3* 40	42	50	55	*1* 62	*1* 72	*1* 52	*1* 65	44	*3* 47
Cornelia		4·9	3·4	2·1	4·5	10·6		*4* 36	*8* 29	*4* 23	*3* 22	*2* 22	*1* 31	*1* 36	*2* 43	*3* 52	*2* 33	*2* 45	26	*8* 24
Hopefield		6·5	1·5	5·7	8·3	9·4	11·1		*7* 36	*3* 30	*3* 28	*3* 27	*4* 34	*3* 40	*4* 47	*5* 56	*4* 37	*4* 49	32	*5* 33
Vaal River		7·0	6·8	4	6·5	17·0	27·6	19·4		*4* 26	*3* 25	*2* 25	*1* 34	*2* 38	*3* 45	*4* 54	*3* 35	*3* 47	29	*7* 28
C. of Hearths	2·9	9·1	10·4	5	2·6	15·4	17·4	10·0	15·4		*4* 14	*1* 16	25	30	38	48	28	40	19	*6* 19
Wonderwerk		3·0	2·0			7·5	13·6	10·7	12·0	28·6		*1* 14	23	*1* 27	36	46	*1* 25	*1* 37	*1* 16	*3* 20
Broken Hill							9·1	11·1	8·0	6·3	7·1		*1* 21	*1* 26	*1* 34	*1* 44	*1* 24	*1* 36	16	*1* 21
Omo							3·2	11·8	2·9			4·8		*6* 29	*10* 33	*9* 44	*6* 27	*7* 38	24	30
Laetolil			1·6				3·0	7·5	5·3		3·7	3·9	20·6		*9* 39	*11* 47	*5* 33	*7* 43	*4* 25	35
Olduvai I		1·9		1·7		1·6	4·6	8·5	6·7			2·9	30·3	23·1		*23* 43	*13* 33	*16* 42	*4* 33	43
Olduvai II		1·6		1·4		1·4	5·8	8·9	7·4			2·3	20·4	23·4	53·4		*17* 39	*25* 43	*3* 44	*1* 52
Olduvai III		2·3		2·0		1·9	6·1	10·8	8·6		4·0	4·2	22·2	15·1	39·4	43·5		*17* 41	*2* 25	33
Olduvai IV		1·8		1·6		1·5	4·4	8·1	6·4		2·7	2·8	18·4	16·3	38·1	58·0	41·5		*3* 36	45
Eyasi											6·3			16·0	12·1	6·8	8·0	8·3		24
Florisbad		2·5	3·6	2·2	4·8	6·4	33·3	15·1	25·0	3·2	15·0	4·8				1·9				

TABLE 6. Statistical interpretation of the extinct fauna represented at any two Pleistocene sites. Above the oblique line the italicized figures constitute the absolute number of extinct species *common* to two sites, while the non-italicized figures are the total number of different extinct species identified at any two sites.

Below the oblique line the number of extinct species common to two sites are expressed as a percentage of the total number of different extinct species, i.e. $\left(\frac{\text{italicized}}{\text{non-italicized}}\%\right)$

OMO has classically been equated with Olduvai I and II but recently a proposal has been made that it is more similar to the base of Olduvai II (tables 4, 5). The extinct fauna common to Omo and Beds I and II are 30·3% and 20·4% of the total respectively (table 6). There is no substantial difference between the faunal assemblages except for the presence of *Anancus* and hominids at Olduvai. The absence of *Zinjanthropus* and '*Homo habilis*' at Omo, does not *per se* imply that Omo is younger than Bed I, because the Olduvai Lake shores, permitting the possible development of living sites, favoured a concentration of hominids.

The SERENGETI (Laetolil) fauna is closely related to both Olduvai and Omo. The extinct species at Serengeti in common with Olduvai I are 23·1% with Olduvai II are 23·4%; and with Omo are 20·6% (table 6). The essential difference seems to be the presence at Laetolil of *Anancus* and *Archidiskodon subplanifrons*, both of which are absent at Omo, and also the presence of *Metaschizotherium hennigi* (which is also present at Kaiso). Leakey (1958) believes that the differences between the Laetolil and Bed I faunas do not imply a temporal separation but rather illustrate a difference in ecological conditions existing contemporaneously. He indicates that it has not been proved that Laetolil is older than Olduvai I. Furthermore, it should be pointed out that Laetolil probably contains a mixed assemblage of different faunal stages, as was already suggested by Dietrich.

KAISO and KANAM are badly represented from a faunal viewpoint: 10 (8 of which are extinct) and 16 (12 of which are extinct) species respectively have been identified. In spite of the fact that information about their recovery is unsatisfactory, there is no doubt that a real archaic character is attached to these sites, from which *Chalicotherium*, *Stegodon*, *Anancus*, *Stegolophodon* and *Hippopotamus imaguncula* have been recovered. These forms are considered by most authorities to represent the most ancient East African Pleistocene fauna known at present.

KORO TORO consists of five 'apparently equally old' deposits which contain about 30 identified species of mammals. Abadie, Barbeau and Coppens (1959) and Coppens (1960), studying the fauna of the lowest level, conclude that it belongs to the Lower 'Villafranchian' because of the contemporaneity of *Mastodon*, *Stegodon* and *Elephas*. However, the rarity of both stegodont and mastodont (more typical of the base of the Lower Villafranchian and the Pliocene) and of *P. recki* (more typical of the Kamasian), and at the same time the abundance of *E. africanavus* suggest that we are dealing with an intermediate stage between the very base (e.g. as at Kaiso where *africanavus* is present without *recki*) and the top (e.g. as at Omo where *recki* and *africanavus* are abundant but stegodont and mastodont are absent).

Kent (1942) and Arambourg (1943, 1947) emphasized the great similarity between the Olduvai and the Omo faunal assemblages, and indicated that they considered the Omo fauna to be slightly older. Arambourg suggested that the various East African deposits may be considered to correspond to different phases of the transition between the Upper Pliocene and the Lower Pleistocene: the Serengeti, Kaiso and Kanam tuffs being the most ancient and being the equivalent of the 'Villafranchian' horizons in North Africa and Europe, while Omo and Olduvai I should be considered as being younger and corresponding to the first true Pleistocene deposits. This view has been partially modified because of the recent discoveries at Olduvai. Leakey (1963) describes a major climatic, faunal and geological 'break' near the base of Bed II, the lowest part of which (overlying the 'marker bed' at the top of Bed I) he considers to be of Upper 'Villafranchian' age and comparing very closely with that of Omo. According to Howell (1959), 'the faunas (from the Villafranchian sites of Central and East Africa) differ somewhat in composition, that from 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.'

South Africa

The fauna of the TRANSVAAL cave breccias (Taung, Sterkfontein, Makapansgat, Kromdraai and Swartkrans) has been extensively studied. The fauna of these sites show a very high degree of similarity: 11·8—32·6% of the total number of extinct species are common to the different sites (table 6). A similar range (15·4—35·6%) has been calculated for the BOLT'S FARM faunal assemblage found in the vicinity of Sterkfontein. The six sites show an extinct/total ratio of species of 61–74% (table 4) and an extant/extinct ratio lower than 63% (table 5), which indicates a considerable antiquity. The conditions of accumulation at and the geology of these sites are also similar. On the basis of the fauna (Ewer, 1957), as well as of mineralogical and climatological studies of the breccia (Brain, 1958; Robinson, 1961), a relative age sequence has been derived, namely, Sterkfontein–Taung, Makapansgat, Swartkrans and Kromdraai, extending from the Lower to the early Middle Pleistocene.

HOPEFIELD and FLORISBAD faunas seem to have rather similar frequencies: not only are 15·1% of the total of extinct species common to both sites, but their close faunal relationship is expressed by a similar ratio of extinct/total species (51% and 47% respectively). However, the extant/extinct ratio (viz. 96% and 113% respectively) suggests a greater antiquity for Hopefield. Furthermore, there are considerable differences in the types of hominids and artefacts recovered from these two sites. Although *Hipparion* has not been recovered from these two sites, they are included as important Middle–Upper Pleistocene sites.

From purely a consideration of the fauna, the YOUNGER VAAL RIVER GRAVELS and CORNELIA could fit satisfactorily in the chronological sequence between the Transvaal cave breccias and Hopefield–Florisbad with the following intermediate ratios (tables 4, 5): 57–74% of extinct species; 35–75% of extant/extinct species; and 27·6% of all the extinct species being common to both sites (table 6). According to Cooke and Wells (1946) 'while it is possible that some of the living species may post-date the Younger Gravels phase of deposition, it appears most probable that the bulk of their material forms a fairly coherent whole, representative of the fauna of the later part of the first wet phase'. The fauna from the Younger Vaal River Gravels and Cornelia deposits could be broadly considered as a Middle Pleistocene fauna, especially in the light of the recent reinvestigation by Cooke and Wells who indicated that the Cornelia fauna is comparable with the Younger Vaal River Gravel material (unpublished; quoted by Cooke, 1963, page 96; see also Wells, 1964).

Although the Lower Pleistocene sites of East and of South Africa have ratios of extinct species higher than 60% and an extant/extinct ratio lower than 70%, direct comparisons between East and South Africa have severe limitations. From an analysis of the fauna (table 1), based on the lists drawn up by Cooke (1963), it appears that not a single species as recorded is common to both East and South African Lower Pleistocene sites. We believe that this lack of relationship is really less marked than indicated because different names have been given to the same species in East and in South Africa. This is mainly because the taxonomy in the two regions has been developed by independent investigations, e.g. the species of *Simopithecus* (Freedman, 1957; Leakey and Whitworth, 1958; Singer, 1962). To some extent this shows the poor state of our knowledge of the African fauna as a whole. Furthermore, Pickering (1960) warned that a critical approach will always be required when comparing a plains fauna, such as that found at Olduvai, with an assemblage obtained from a cave deposit which is usually the case in the Lower and early Middle Pleistocene of South Africa.

There is some affinity between the Younger Vaal River Gravels, Cornelia and Hopefield assemblages on the one hand, and the East African early Middle Pleistocene collections on the other, ranging from 2·9–11·8% of the total number of extinct species for any two particular sites among these groups (table 6).

CONCLUSIONS BASED UPON THE FAUNAL AND GEOLOGICAL EVIDENCE IN THE LITERATURE

The large amount of data discussed in previous chapters may be utilized for the construction of a tentative illustration of the relationships between the sites at which *Hipparion* has been discovered in Africa (fig. 8). By and large this supports the views expressed by Cooke (1963) and Bishop (1963).

CHRONOLOGICAL RANGE OF *Hipparion*

Apart from the actual dating of the geological deposits from which *Hipparion* has been recovered in Africa, there is the general question of its first appearance and its ultimate disappearance on the continent.

It seems that Africa was not the area of origin of hipparionids, as the

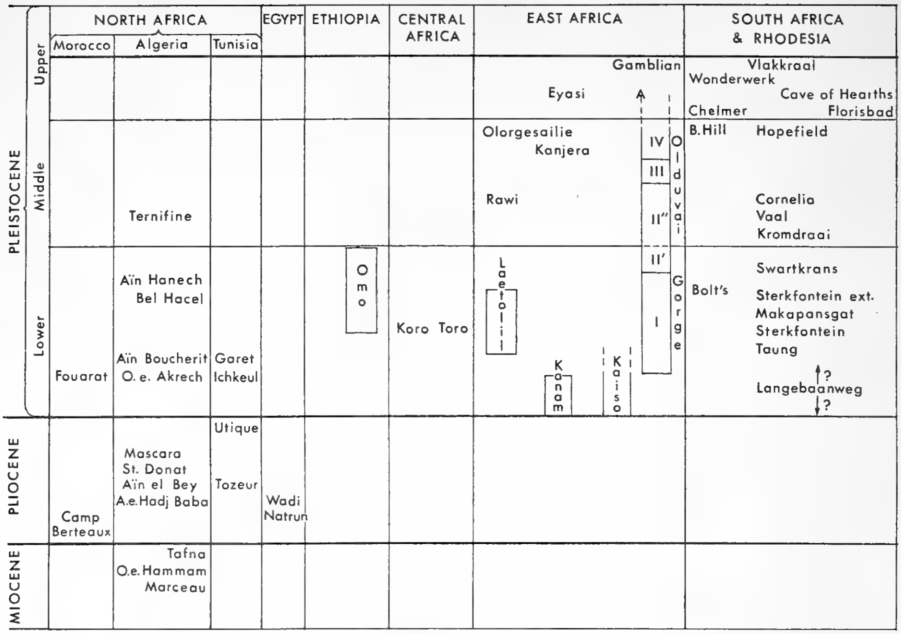

Fig. 8. Tentative correlation between *Hipparion* sites in Africa. A few other sites have been incorporated for reference. B. Hill = Broken Hill; O.e. = Oued el; A.e. = Aïn el; Gamblian = Gamble's Cave; Bolt's = Bolt's Farm.

evidence points to probable migrations from Eurasia. Nevertheless, it is sometimes claimed that Africa contains the evidence of the early, if not the earliest, existence of *Hipparion* in the Old World.

At the other end of the chronological range, the hipparionids survived much longer in Africa than in any other area known at present. With very few exceptions, most of the sites where African *Hipparion* have been located are of Pleistocene origin, i.e. a period when they no longer existed in Eurasia and in America.

Consequently it is considered necessary to compare the geological range of occurrence inside with that outside Africa.

UPPER LIMIT

According to available information, the upper limit of *Hipparion* outside Africa seems to correspond roughly to the Upper Pliocene. It is generally accepted that the Villafranchian is defined by the appearance of some modern genera, among which is *Equus*. However, there is no reason to deny, *a priori*, a coexistence of *Hipparion* with modern *Equus* which developed on a parallel line from *Pliohippus*. Such co-existence has actually been demonstrated for Africa. Outside Africa, *Equus* not only heralds the Pleistocene, but it practically replaces the more primitive *Hipparion* in its habitats.

	AMERICA	CHINA	INDIA	USSR	MIDDLE-EAST	S.E. EUROPE	CENTRAL & W. EUROPE	AFRICA
PLEISTOCENE								Kanjera Cornelia Vaal Olduvai Koro Toro Aïn Hanech Omo Laetolil Fouarat, Garet Ichkeul, Aïn Boucherit Kanam, Kaiso
PLIOCENE	Blanco Hemphill Upper-Clarendon	Nihowan Pao-Te (Red Clays)	Pinjor Patrot Dhok Patan	Azov Sea (Khopry) Taraclia		Pikermi Samos	Val d'Arno, Sénèze Roussillon Gödöllö, Berechti Malouchteni Maragha Polgardi, Véllès Mont Lubéron	Wadi Natrun A.e. Hadj Baba Mascara
UPPER-MIOCENE	Clarendon		Chinji Nagri	Sebastopol Odessa	Istanbul		Vallès - Pénédès Rhône - Valley Teruel Eppelsheim	Oued el Hammam Marceau

FIG. 9. A diagrammatic representation of the probable chronological range of *Hipparion* in different continents.

The youngest formation bearing *Hipparion* remains in America is the Blanco formation (Upper Pliocene), where its presence is even questioned by some palaeontologists. Even if accepted, remains are very scarce.

In China, the latest occurrence is in the Nihowan deposits of the Sang Kan Ho Valley, east of Pekin (fig. 9); in India, in the Tatrot and the Pinjor zones of the Siwaliks, while the records are still very insufficient for Mongolia. In the U.S.S.R. (including its Asian portion), the most recent occurrence is to be found in the Azov Sea shore deposit at Khopry; in South and Central Europe at Berechti and Malouchteni in Rumania, and Gödöllö in Hungary. In western Europe, *Hipparion* has not been found in the Villafranchian deposits of the Val d'Arno and Senèze; and it is rather uncommon in the Roussillon, although it is still found in Perrier where it is rather exceptionally associated with *Equus*.

Without going into details which are irrelevant in the framework of this paper, it may be stated that outside Africa, *Hipparion* does not seem to have extended into the Pleistocene. In many instances, it was already becoming rather scarce during the Middle Pliocene and definitely more rare in the Upper Pliocene.

LOWER LIMIT

The lower limit of *Hipparion*, or the time of its first appearance, presents a more difficult problem, as it is not at all easy to correlate the chronological interpretations of all the localities. In addition, a different faunal basis (marine or continental) is applied to various areas, and a direct comparison of the fossil associations is not always possible. Furthermore, some geological terms, like 'Pontian', have been used in a different context and with a different meaning by various authors, e.g. as a facies, or a stratigraphical or a faunal horizon. Consequently it is especially difficult to appreciate the meaning of a particular statement, factual though it may be, without danger of misinterpretation. Therefore, the soundest approach may be, first, to locate the earliest occurrence of *Hipparion*, within a region, and then, to correlate as far as possible the interregional data.

In America, *Hipparion* is not found in the Barstov formation, appearing first in the Clarendon formation (fig. 9). It is also found right at the base of the Mint Canyon formation, and in the Hemphill formation. The upper Clarendon and the Hemphill formations are unanimously considered as 'Lower Pliocene' and correlated with the European 'Pontian'. But for more than thirty years, the Mint Canyon has been a major topic of discussion and argumentation. While most scholars follow Stirton's opinion (1939) and locate the continental basal horizon of Mint Canyon in the Pliocene, Maxson (1930), among others, basing his opinion on the debatable malacological fauna of the overlying marine Cierbo beds, considers it to be middle Upper Miocene age.

In China, *Hipparion* appear in the red clays of Chan-si, Chen-si and Kansou. These Pao-Te formations have not been properly subdivided. At different times, investigators have pushed them back to the Upper Miocene (Teilhard and Young, 1931), or restricted them to the Lower Pliocene (Teilhard and Leroy, 1942).

In India, the first *Hipparion* are recovered in the Chinji zone of the Siwaliks, which is referred either to the Middle (Pilgrim, 1938) or to the Upper (Lewis, 1937) Miocene, or even to the Lower Pliocene (Colbert, 1935).

In the U.S.S.R., the earliest occurrences are those of Moldavia and Odessa and the Sebastopol fauna (Borissiak, 1914). Russian geologists refer the former deposit to the Middle Sarmatian, and the latter two to the Upper Sarmatian, i.e. the Upper Miocene. Similar information was recently obtained from the Upper Sarmatian in the Istanbul vicinity (Chaput and Gillet, 1938; Yalçinlar, 1952).

In central and southern Europe, because of the exceptional associations of *H. primigenium* with the typical Miocene *Anchitherium*, Eppelsheim might be considered as one of the first known areas of occurrence of the genus. But in the Rhone Valley (Denizot, 1939), at Vallès-Pénédès in Catalogne (Villalta and Crusafont-Pairo, 1946, 1947, 1948) and in the Teruel Basin (Sondaar, 1961), abundant remains of *Hipparion* have been recovered in deposits which are dated as Tortonian. Maragha, Pikermi, Samos, Polgardi, Baltavar, Vélès and Mont Luberon, referred to as typical 'Pontian' sites, are probably somewhat younger, and should be placed in the Lower Pliocene.

In spite of many unsolved problems in correlating these sites, it seems difficult to deny that there is in North America, in Asia and in Europe constant and repeated indications of the appearance of *Hipparion* in the Upper Miocene (fig. 9).

GENERAL DESCRIPTION OF *Hipparion* TEETH

UPPER DENTITION

The pattern of horse teeth has been described many times and detailed structures have been extensively discussed in previous publications. The distinctive characters of horse teeth that have been described are based on the original description proposed by Osborn (1907). In 1918, he successfully applied this description in his study of the North American Equidae. Subsequent

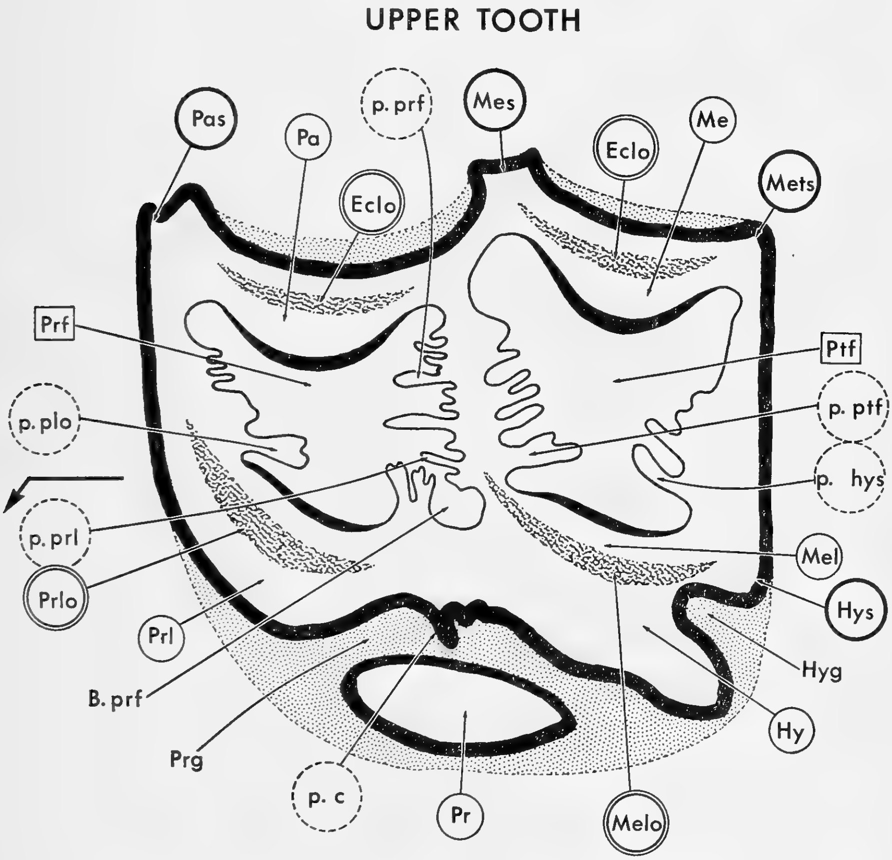

Fig. 10. Features of the occlusal surface of an upper molar tooth of hipparionids. Abbreviations: B. prf—bouclé prefossette; Eclo—ectoloph; Hy—hypocone; Hyg—hypoglyph or hypoconal groove; Hys—hypostyle; Me—metacone; Mel—metaconule; Melo—metaloph; Mes—mesostyle; Mets—metastyle; Pa—paracone; Pas—parastyle; p. c—pli caballin; p. hys—pli hypostyle; p. plo—pli protoloph; p. prf—pli prefossette; p. prl—pli protoconule; p. ptf—pli postpossette; Pr—protocone; Prf—prefossette; Prg—preprotoconal groove; Prl—protoconule; Prlo—protoloph; Ptf—postfossette.

alterations and additions have been proposed by, among others, Stirton (1941), Arambourg (1947, 1959), Gromova (1952), Hopwood (1937) and Cooke (1950). It is not proposed to make any further modifications here, but it is necessary to comment on the dental nomenclature, without any phyletic implications, so as to outline the basis adopted in this monograph.

Typically three crests are recognized. A mesiodistal ectoloph, joining paracone and metacone on the buccal surface, an anterior protoloph and a posterior metaloph. The latter two are more or less transverse in the primitive condition but in advanced Equids they are half-moon-shaped. Being lophodontic specializations of the protoconule and the metaconule, they build the protoselene and the metaselene, and they meet the ectoloph at parastyle and mesostyle, respectively (fig. 10).

Lingually deflected from the main selenic lophs, but more or less attached to them there is a protocone and a hypocone. Their rather deep bordering grooves, filled with cement, tend to isolate them from the crests. These grooves are the pre- and post-protoconal grooves (valleys, sinuses) which lie anteriorly and posteriorly to the protocone, respectively, and the hypoconal groove (sinus) or hypoglyph which is related to the hypocone (the posterior being usually very well marked, and the only one noticeable). Sometimes the protocone shows a 'spur': the 'protoconal spur'.

When the pre- and post-protoconal grooves are maximally deepened, they become confluent in a medivallum or internal depression. Thereby they produce complete isolation of the protocone. This is one of the major and characteristic features of the upper molars of *Hipparion*.

Elevations of the cingulum have also been described: parastyle, mesostyle and metastyle along the ectoloph; hypostyle on the posterior surface which ultimately develops a cusp, seemingly independent of the cingulum.

The protoloph and the metaloph crests enclose, more or less completely, the pre- and postfossettes. The more constant and deeper plications in the enamel wall of the fossettes ('marks') and also isolated 'horns' have been assigned special names: anteriorly, the pli protoloph and the pli postfossette, respectively; posteriorly in the anterior mark, the pli prefossette and the pli protoconule which isolates a 'boucle préfossette' or 'prefossette loop' (Stirton, 1955), while posteriorly in the posterior mark is the pli hypostyle (fig. 10).

Furthermore, a pli caballin appears constantly in the post-protoconal groove or in the internal depression. It is a lingual extension from the outer border of the selene, and eventually, after wear, it displays a two- or threefold division.

LOWER DENTITION

A distinction is commonly drawn between a mesial trigonid, with buccal protoconid and lingual metaconid, and a distal talonid, with hypoconid, entoconid and hypoconulid, separated on the buccal aspect at the level of a fairly constant external depression (fig. 11).

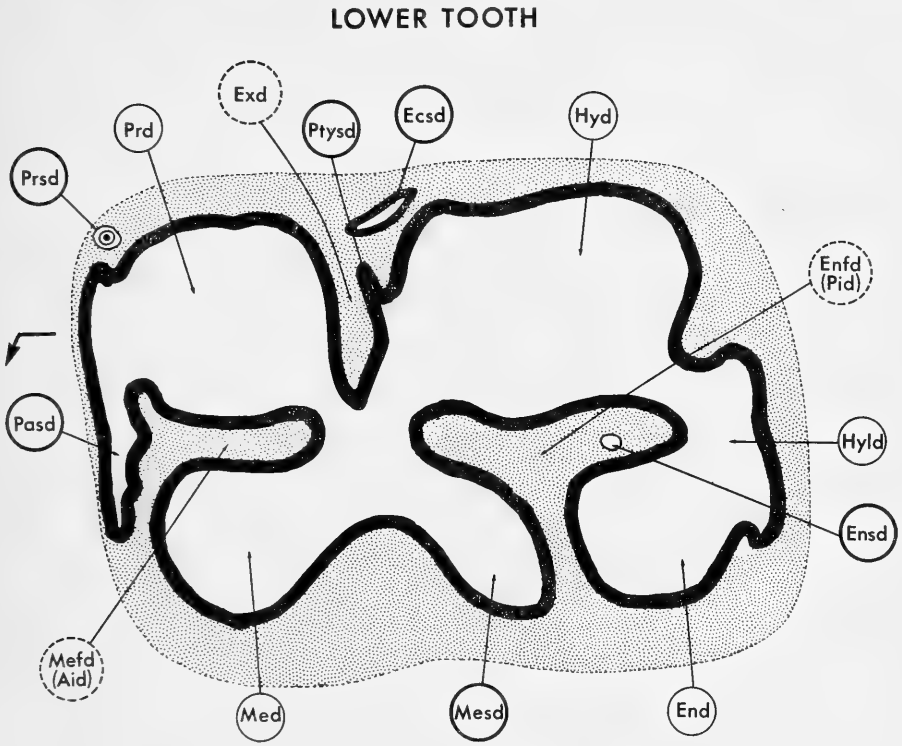

Fig. 11. Features of the occlusal surface of a lower molar tooth of hipparionids. Abbreviations: Ecsd—ectostylid; End—entoconid; Ensd—entostylid; Enfd (Pid)—entoflexid (Post. int. depression); Exd—external depression; Hyd—hypoconid; Hyld—hypoconulid; Med—metaconid; Mefd (Aid)—metaflexid (Anter. int. depression); Mesd—mesostylid; Pasd—parastylid; Prd—protoconid; Prsd—protostylid; Ptysd—ptychostylid.

The stylids on the buccal side are protostylid, an inconstant ectostylid and a ptychostylid, while on the lingual aspect there are the metastylid and the entostylid.

On unworn teeth, a crest, the paralophid, can be distinguished extending from the protoconid to the protostylid in the anterolingual corner.

On the lingual aspect there are two prominent internal depressions or invaginations, the metaflexid anteriorly and the entoflexid posteriorly.

The metastylid and the metaconid are two rounded formations joined by a narrow isthmus, giving the appearance of a bow tie and forming the so-called 'double knot'.

SUMMARY OF THE CHARACTERISTICS OF HIPPARION TEETH

Based on Gromova's detailed description (1952, pp. 70–6), the following characteristic features are noted.

Upper dentition

1. Less hypsodont. But note that the more recent (African and American) *Hipparion* are hypsodont.
2. Pli protocone is present.
3. Enamel plications are usually more developed.
4. There is a rather high percentage of open marks.

Lower dentition

1. Relatively less hypsodont.
2. Double knot:
   - (*a*) '*caballus*' type in African *Hipparion.*
   - (*b*) '*stenonis*' type in American *Hipparion*, and also in some Chinese.
   - (*c*) '*Hipparion*' type in Europe and Asia.
3. External depression: this is rather profound in the Miocene forms.
4. Posterior internal depression: this is elongated, curved anteriorly and lingually. Hence its oblique and 'broken' appearance.
5. Anterior internal depression: not only does this have an antero-external angulation (like in *Equus*), but it also has a postero-external angulation, with long sharp 'horns' directed towards the buccal aspect.
   At the posterior extremity there is a deep invaginated plication.
6. Talonid is bifid on M_3.
7. Anterior depression often shows plications at both extremities.
8. There is a tendency to build stylids (proto-, ecto-, hypostylids) in milk and permanent molars.

REVIEW OF ADDITIONAL ENAMEL ELEMENTS (STYLIDS) OF THE LOWER TEETH

DESCRIPTION

Ectostylid=Ectostylid of Gromova (1952), Arambourg (1959), Hopwood (1937), Sondaar (1961).
=Protostylid of Osborn (1907), Stirton (1941).
=Buitestyltjie of Van Hoepen (1930).
≠Ectostylid of Osborn (1918), Sefve (1912, 1927).

This stylid arises from the basal cingulum. It is an accessory external column or pillar that is always independent and located on the buccal side, close to the mesio-vestibular border of the hypoconid and in the external groove between hypoconid and protoconid, i.e. between talonid and trigonid. In early wear it is seldom apparent on the occlusal surface because it rarely reaches more than a short distance above the crown-root junction and it is usually embedded in very thick cement. It can usually be observed better on the buccal aspect where the cement is thinner.

Ptychostylid =Ptychostylid of Arambourg (1947).
=Pli caballinid of Stirton (1941).
=Ectostylid of Osborn (1918).

This is not an independent pillar, but a fold on the mesial border of the hypoconid, in the interlobar angle on the buccal side. It may be present when the ectostylid is present, but there does not seem to be any relationship between these two formations.

Protostylid =Parastylid of Gromova (1952), Van Hoepen (1932), Stirton (1941).
=Protoconid fold of Cooke (1950).
≠Protostylid of Osborn (1907), Stirton (1941).

This is a broad laminated pillar, compressed mesiodistally, found close to the protocone where it is located on its antero-buccal side. With increasing wear it fuses fairly rapidly with the protocone. This stylid also arises from the cingulum and it may develop into an independent element on the antero-labial angle of a tooth.

Hypostylid

This is a postero-external plication, appearing as a raised element on the talonid. Sometimes it may develop into an independent pillar facing the talonid.

Entostylid

This is a rare and inconstant enamel formation in the entoflexid. It may be completely isolated in the cement (pl. 8, A) or connected to the mesio-lingual corner of the entoconid.

FREQUENCY

Independent of the degree of attrition, which may tend to hide the presence or the development of these formations, the stylids are very differently developed in various genera, species and even in individuals. The stylids may only be observed on some of the teeth of a particular jaw, and occasionally they are found to be present only on one tooth in a complete dentition. Observations have been made by various authors since the time when these stylids were first described by Gaudry (1862) and Weithofer (1888) on the milk and permanent teeth of *Hipparion mediterraneum* from Pikermi.

According to Gromova (1952), these additional elements are usually poorly developed in the non-hipparionid equids. The stylids are best developed in the *Hipparion* group in which they are always present on the milk teeth, but to a varying degree on the permanent teeth. In this respect the African *Hipparion* are the most progressive.

Ectostylid

Statistical analysis of *Hipparion elegans* provides a frequency of 12% ectostylids on the premolars and 1% on the molars, and in *H. moldavicum* frequencies of 7·5% and 6·7% respectively. Sondaar (1961) presents the following data on the presence of ectostylids:

H. periafricanum: 0
H. concudense aguirrei: 0
H. gromovae: 1 in 200 specimens
H. concudense: 5 in 84 specimens
H. koenigswaldi: 20 in 150 specimens
H. primigenium: 23 in 80 specimens

Therefore it can be concluded that the ectostylid is not quite a rarity in Eurasiatic *Hipparion* permanent teeth, especially on the premolars. Nevertheless, the ectostylids appear to be much more frequent in the later forms of *Hipparion*, i.e. in Africa, where it has often been stated to be 'a constant feature' (Arambourg, 1956, 1959). Comments on this will be given below. Furthermore, it can be stated without dubiety that the ectostylids have been commonly observed in most of the specimens from Pleistocene deposits: not only are these stylids very frequent, but they are occasionally strongly developed when they reach along the whole length of the crowns of the teeth.

Ptychostylid

This is the external hypolophid fold which is quite common among all hipparionids, reaching a maximum development in *Neohipparion eurystyle* Cope found in America, in which as many as four may occur. These stylids do not arise from the cingulum and cannot be considered as true stylid cusps. There does not seem to be any direct association between these stylids and ectostylids.

Protostylid

According to Sondaar (1961), this stylid is almost a diagnostic feature of the genus *Hipparion* even though it varies quite considerably in its extent. It is often a fold attached to the protoconid, but it may develop into an isolated pillar. Here again, the African *Hipparion* seem to present the most progressive features: it is found in them as early as the Upper Miocene (i.e. *H. africanum*) and as late as *Notohipparian namaquense*, in which it is a very tall and isolated pillar.

A high frequency is also found in some Eurasiatic forms, namely, in *H. elegans* 75·5% is noted in P_3–P_4 and 80% in M_1–M_2; in *H. moldavicum* 88% is noted in P_3–P_4 and 96% in M_1–M_2

Sondaar (1961) states that it is a common, although not constant, feature in all the Spanish species of *Hipparion*, except *H. truyolsi.* Sometimes a double protostylid has been observed, and this has been especialy noted in *H. koenigswaldi*, in which there is a high frequency of ectostylids (*vide supra*).

In connection with the American material, Stirton (1942), who used 'parastylids' for 'protostylids', points out that 'the statement that the parastylid does not appear in the American *Hipparion* is not supported by the evidence. Though the isolation is not as persistent nor as complete in the New World forms as in some Eurasiatic *Hipparion* (*H. platyodus* Sefve), it does appear in early stages of wear in some teeth. This is true not only in *Neohipparion*, but in *Nannippus* and *Pliohippus*, though extremely rare in the latter.'

Hypostylid

This is very frequently observed in *Equus stenonis* and in *zebra* but it is very rarely seen in *Hipparion*. However, it is sometimes found in the African forms, the most typical example of which is a M_3 from Omo (Joleaud, 1933).

EVOLUTIONARY HISTORY OF THE STYLIDS

The development of these stylids seems to be influenced by a common factor: a higher frequency of ectostylids in a particular group is correlated with a more precocious appearance of the protostylid (i.e. a higher protostylid) in the same population, and vice versa.

In a particular group it is noted that the protostylid seems to be more frequently, more strongly and more permanently developed than the ectostylid.

There seems to be an evolutionary pattern in the tendency to build stylids, from *Merychippus* (possibly from *Parahippus* which already shows a weak protostylid) through Miocene times up to *Hipparion*. Arambourg (1959) notices that this 'tendency to develop cingular formations' is already present in the Upper Miocene *H. africanum* from Oued el Hammam. The tendency seems to have developed further during Pliocene and early Pleistocene times, being most obvious in the African *Hipparion*, in which the most recent forms show the strongest development.

Protostylids and ectostylids appear on the milk teeth of *Merychippus* in which they show slight development. They are constantly present and show a fair degree of development on the milk teeth of all *Hipparion*, and they appear on the permanent dentition of the African Pleistocene *Hipparion*.

Along another evolutionary line of the Equidae, the *Pliohippus–Equus* sequence, it has been shown that protostylids and ectostylids remain weakly developed, the hypostylid being temporarily more developed, as, for example, in *Equus stenonis*. With the appearance of *E. caballus*, all the stylids have practically disappeared.

EVOLUTIONARY SIGNIFICANCE OF THE CONES AND STYLIDS

In a phyletic perspective, it has been established that the additional stylids have originated from enamel buds on the basal cingulum of brachyodont teeth. They developed first on the milk dentition and only later in the evolutionary sequence, and in particular groups, did they become permanent features of the adult dentition, appearing initially on M_1 and M_2 and eventually on the premolars. For example, it is known that the parastylid was present in *Parahippus*, but only on the milk teeth as an ill-developed feature. Later it became a constant and developed characteristic, even of permanent teeth, in *Merychippus* and later equids of the same phylum. The ectostylid is present in *Merychippus*, but only on the milk teeth, and then only occasionally. It becomes an element of the permanent dentition in *Hipparion*, where it appears to be constant in some of the latest representatives of the group, i.e. in the Pleistocene forms of Africa.

The tendency to raise enamel buds and isolate them is thus an early ontogenetic trend, which in evolution has progressively influenced the later (adult) stages of individual development.

Later in this paper it is suggested that this trend was necessitated by the special architecture of the lower dentition with its characteristic development of highly individualized conids.

The same trend, both ontogenetic and phylogenetic, seems to be recognizable in the formation and the isolation of the major cones in the upper dentition. It is really remarkable that the separation of the protocone and the hypocone from the main lophs is a gradual process, both ontogenetic and phylogenetic. The isolation of the protocone is rather ancient, and in the permanent teeth of *Hipparion* it has extended right down to the base of the crown. Contrariwise, the isolation of the hypocone is hardly noticeable on the permanent teeth, but in very early stages of wear it has been observed (*vide infra* p. 373). However in milk teeth the isolation of the hypocone reaches a much more characteristic degree in similar hipparionid groups, e.g. in the South Serengeti *Hypsohipparion* and in the Langebaanweg specimens (see p. 368).

The difference between the expression of cones and stylids in milk and permanent dentitions on the one hand, and the more explicit individualization of these features among later representatives in some phyletic lines, on the other hand, seem to be linked with the increasing hypsodonty of the Equidae teeth in Upper Cenozoic times.

ECOLOGICAL CONSIDERATIONS

Gromova (1952) outlined the ecological significance of the development of the styles (stylids). She promoted the idea that they played a role in strengthening the tooth so as to meet the heavier requirements of coarser food in a dry country where the grass was becoming very tough. The presence of additional pillars and folds probably increases the trituration power of the teeth and their resistance to pressure forces. Thus their appearance on the milk teeth would prevent or decrease rapid wear.

Furthermore, Gromova developed a very suggestive correlation between elongation of the protocone, development of the stylids, thickening of the enamel, reduction of the external groove and higher hypsodonty. These functional features are different methods of improving the efficiency of a tooth with increased power of trituration. Consequently it was suggested that the styles were developed as an adaptation for improving the grinding of coarser food in drier climates.

Sondaar (1961), in turn, described a similar correlation among the Spanish *Hipparion* which have the highest frequency of stylids. In *H. koenigswaldi* the maximal development of plications in the upper molars increased the enamel surface with a double hypoconal groove, while the lower teeth display wavy internal depressions—entoflexid and metaflexid. However, *H. elegans*, with the same functional features, only displayed a very high frequency of protostylids. Most of the African *Hipparion* developed the stylids and a maximal hypsodonty, but not the extreme plications. There seems to be a balanced compensatory effect between stylids, plications and other elements so that, dependent on the specific region, one or other of these elements would develop to a varying degree. In America, *Hipparion* adapted to a hard and tough grass by an increased hypsodonty and a thickening of the enamel. There can be no doubt that numerous plications and deep invaginations of the enamel pattern, as well as elevations of folds and stylids, provide the teeth with a more efficient trituration surface, and are very suitable for herbivorous animals in an area of increasing aridity (Stirton, 1941).

TAXONOMY BASED ON STYLIDS

The observation of the presence of stylids, both proto- and ectostylids, provided a new basis for generically differentiating the various African hipparionids. Haughton (1932) decided to create the genus *Notohipparion* because of the appearance of these stylids. Van Hoepen (1932) followed the same line of reasoning and erected the genus *Stylohipparion*, a distinction supported by Joleaud's publications of *S. libycum* from Omo (1933).

To some extent Dietrich (1942) followed the same tendency and, on the basis of the presence or absence of ectostylids, he divided the Serengeti LOWER cheek teeth into two groups. The group without stylids he termed *Hypsohipparion* and he referred those with stylids to *Stylohipparion*. However, Dietrich did not attach a true taxonomic value to this separation because he found it impossible to distinguish between the UPPER teeth of the two groups. He indicated that the frequency and development of styles (-ids) can be influenced by environment or selective pressure. Consequently he suggested that *Stylohipparion* might not represent a true genus, but only a variety formed under a strong developmental pressure ('Entwicklungswucht').

However, outside Africa, the variation in the development of stylids did not lead to such taxonomic differentiation. Arambourg (1947) questioned the validity of a generic difference (*Stylohipparion*) based upon the presence of a feature which did not seem to separate clearly the Eurasiatic Pliocene forms. Nevertheless, he opined that the very high frequency and the strong development of the ectostylid in African forms supported the validity of the generic differentiation.

Gromova also discussed this matter. She did not consider a true generic differentiation of African hipparionids valid. Ectostylids are not an entirely new characteristic in them exclusively but only represent a further development (either in frequency or structure) of a feature not at all exceptional (albeit irregular and even rare) in Eurasiatic *Hipparion*. Gromova proposed a subgeneric rank *Hipparion* (*Stylohipparion*) for the African group on the basis of obvious peculiarities of this geographical unit. However, she writes of these ectostylids: 'the importance as a diagnostic feature and generic character has been somewhat exaggerated'.

This criticism can be expanded (see pp. 387–92) and even the sub-generic status of *Stylohipparion* can be questioned. In spite of the 'air de famille' (Arambourg, 1959) of all African hipparionids, the major reason for placing the Pleistocene African hipparionids in a special genus or sub-genus is precisely the presence and constancy of a very high frequency (which the present authors doubt) of the ectostylids. Although this is generally accepted, it is a highly debatable basis of separation. As mentioned above, Dietrich (1942) described a very large collection of lower teeth without ectostylids and placed them in the 'genus' *Hypsohipparion*. However, Arambourg (1947) suggested that these teeth had 'erroneously' been attributed to a hipparionid and that, in fact, they belong to *E. zebra*. This suggestion tends to remove *Hypsohipparion* from the hipparionid scene so that the 'frequency' of the ectostylids among African hipparionids still remains artificially high. Arambourg's suggestion and his deletion of this group seem to have been largely accepted. Gromova's monograph does not include the Serengeti material and does not refer to this paper of Dietrich (1942). Arambourg (1956) has maintained his viewpoint and speaks of 'the typically African genus *Stylohipparion* characterized by the presence of a broad ectostylid'. Naturally this does not positively exclude *Hypsohipparion*, but in 1959, in a revision of the 'few' fossil African hipparionids, Arambourg explicitly limits the Pleistocene material to *Stylohipparion*, 'characterized by a *permanent* ectostylid'.

However, it can now be stated that the Serengeti *Hypsohipparion* material can no longer be excluded because of the assumption that it belongs to *zebra*. More than 90% of the small series of Langebaanweg equid upper teeth unquestionably belong to *Hipparion* so that it cannot be asserted that all the lower teeth belong to *zebra* merely because they do not possess an ectostylid. Not only is this statistically highly unlikely but also the morphological features, for example, the division of the talonid in M_3 (on L938, the only M_3 available at Langebaanweg) would definitely exclude this group from belonging to *zebra*. Consequently, as the Langebaanweg material, in which the ectostylid is constantly absent, belongs to *Hipparion*, there are no longer sufficient grounds to exclude *a priori* the Serengeti *Hypsohipparion* teeth from the hipparionid group only on the basis that they do not possess an ectostylid.

Furthermore, it can now also be stated that the concept that African *Hipparion* possess a very high frequency or permanent presence of ectostylid is no longer applicable. Consequently the validity of the generic status of *Stylohipparion* becomes highly questionable. Later in this paper this will be discussed more fully in the light of the evidence presented. At present it suffices to state that in Africa the Pleistocene *Hipparion* may be found with and without ectostylids.

REVIEW OF PUBLISHED AFRICAN *Hipparion* CRANIAL MATERIAL

MIOCENE

Oued el Hammam and Marceau

The presence of *Hipparion* in the Miocene of the Maghreb has been known since 1932 when Suess discovered a mammalian fossiliferous deposit upstream from Bou Hanifia (Oran) during the construction of the Oued el Hammam dam. On several occasions brief comments have been made about this material by, among others, Arambourg (1947, 1951, 1954). A rather rich collection of cranial and postcranial material, with fairly complete milk and permanent dentitions, as well as isolated teeth (table 7), have now been recovered from two Upper Miocene sites in Algeria (figs. 3 & 4): Oued el Hammam (Oran) and Marceau (Algiers). A detailed description was given by Arambourg (1959): he discussed their relationships to and differences from Eurasiatic forms of similar age, and other African forms of the Plio-Pleistocene period. He suggested that this material should constitute a new specific form, namely *Hipparion africanum* for which he proposed the following diagnosis:

> *Hipparion* with a large skull, medium-sized limbs and heavily built extremities. Face and snout are elongated; nasal aparture is long and broad; orbits are situated far back; pre-orbital fossae are long, simple and distant from the orbit. Dentition of medium size: P^2–$M^3 = 141 - 154$ mm. Upper molars with strongly plicated enamel; compressed elliptical or lenticular protocone. Cingular formations developed on lower milk teeth but a laminated protostylid sometimes persists on permanent molars. The limbs are rather short, with robust metapodials that have well-developed lateral digits.

Arambourg emphasizes the 'African character' (*vide infra*) of the dentition of this new species: enamel plications and narrow elongated protocone, as well as a tendency to develop cingular formations. Because of these features which distinguish it from all Eurasiatic forms, and because of its stratigraphical location in the Upper Miocene, he suggested that this species should belong to an independent African stock, isolated on the continent of Africa since the end of the Miocene.

Camp Berteaux

Bourcart (1937) mentioned the discovery of *Hipparion* at Camp Berteaux (Taourirt, Eastern Morocco). This material and additional specimens, described by Ennouchi and Jeannette (1954), are now considered to belong to *Hipparion africanum.*

Other sites

It is not possible to comment on the *Hipparion* material that was merely mentioned by Dalloni (1915) and Solignac (1927), which was derived from

UPPER	*Specimen*	P^2	P^3	P^4	M^1	M^2	M^3
A–P length	141	33·0	26·0	25·0	23·0	23·0	20·0
	Mar.*		27·0		24·0		
Transv. breadth	122	22·0	24·0	23·0			16·0
	141	22·5	24·5	25·3	23·0	20·5	18·5
	Mar.*		26·0		25·7		
Height	122	48·0	58·0	60·0			47·0
Protocone length	141	7·8	9·2	10·2	7·3	7·5	7·6
	Mar.*		8·4		8		
Protocone breadth	141	5·0	4·0	3·5	3·7	3·5	2·5
	Mar.*		5·0		4·0		

LOWER	*Specimen*	P_2	P_3	P_4	M_1	M_2	M_3	DM_2	DM_3	DM_4
A–P Length	143	30·0	23·6	25·0	25·3	26·0	23·4			
	89	27·0	27·0	25·0	23·0	23·0	25·0			
	3	29·0	24·0	23·5	20·7	21·0	27·0			
	Mar.*	31·5								
	6							30·5	24·2	26·0
	105							31·6	29·0	30·4
Transv. breadth	Mar.*	18·0								
	6							14·0	14·4	13·5
	105							12·0	12·0	9

*=Marceau: no number given.

TABLE 7. Measurements (mm.) of the teeth of *Hipparion africanum* (from Arambourg, 1959).

the Upper Miocene layers of the lower Tafna Valley (near Guiard, Oran), and the Djebel M'Dilla 'Pontian' horizons (of Tunisia) respectively.

Discussion on the 'African character' of Hipparion africanum Arambourg, 1959

The relationships of *H. africanum*, of the Upper Miocene of the Maghreb, to other African hipparionids have been discussed by Arambourg. He distinguishes three species, stratigraphically separated: *H. africanum* of the Upper Miocene, *H. sitifense* of the Pliocene of the Constantine and Oran area, and *Stylohipparion libycum* of the 'Villafranchian' of North, East and South Africa. Despite the great temporal span, Arambourg believes that there is a 'family air' or unity common to these three forms, which distinguishes them from the Eurasiatic material, and which stresses the common origin of the African hipparionids, isolated since the end of the Miocene.

From the description given of the skeletal material of *H. africanum*, it seems obvious that there is a marked difference between it and the Eurasiatic forms. Until the present, only teeth have been available for comparison, so that the lack of adequate comparative postcranial material has made it impossible to determine to what extent *H. africanum* shares common skeletal features with the African hipparionids of the Pliocene and Pleistocene. Dr. Leakey indicates (personal communication) that considerable postcranial material has now been recovered from Olduvai. These are to be described by Dr. R. H. Stirton of Berkeley, California, who will elucidate the skeletal relationships.*

On the basis of the teeth alone, it is difficult to acknowledge a close resemblance between the three African species. As there is a long span of time separating *H. africanum* from *Stylohipparion libycum*, one expects to find some differences, but it is first necessary to assess and appreciate the importance of the resemblances stressed by Arambourg before it is possible to evaluate the phyletic implications.

Of the 'family air' features linking *H. africanum* and the later African species, Arambourg considers two as most typical: (i) In the upper cheek teeth, the enamel plications and the shape of the protocone of the molars; (ii) In the lower molars, there is a tendency to develop additional cingular stylids. Two other classical features which will be discussed are the hypsodonty of the cheek teeth and the shape of the double knot in the lower molars.

Enamel Plications: It is commonly believed that the enamel plications have little phylogenetic significance. The plications are very variable, being much influenced by functional and ecological conditions. In any event, because of the vast temporal and spatial differences, and especially climatic and biotopical environments, this feature cannot be used as a basis of comparison. This is just an *a priori* consideration.

However, Arambourg writes (p. 93) that *H. africanum* is characterized by the complex pattern of enamel plications, which are more numerous than on most of the European forms. Although there is quite considerable variation in the complexity of the enamel at a particular period and in a particular area (compare *H. crassum* and *concudense;* Greek and Samos Pliocene forms), it cannot be denied that the Eurasiatic forms normally possess a rather plicated enamel mark-wall pattern. Furthermore it is certainly far more developed than that of the African Pliocene and Pleistocene species, which are actually characterized by their small number of plications.

The multiple pli caballin seen in many teeth does not seem to be typically African either: it is observed in many other groups on both sides of the Mediterranean Sea, and also elsewhere—compare *H. sitifense* (Mascara), *H. gracile* (Pikermi), *H. koenigswaldi*, *H. concudense* (South Aragon), *Hypsohipparion albertense* (Serengeti), and even in America in *Neohipparion eurystyle* Cope, in which as many as four may occur on the anterolabial border of the hypoloph.

Protocone: The elongated and narrow protocone is undoubtedly a typical and constant feature of all the African hipparionids so far known from the Pliocene and Pleistocene deposits. It also seems to be a distinct, strongly expressed evolutionary trend in the whole group (see pp. 354–5; table 14;

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* See *Olduvia Gorge 1951–1961*, 1 by L. S. B. Leakey (1965) which was published while this paper was in press.

figs. 12, 13). A satisfactory comparison of individual teeth at different stages of wear is difficult, and published sketches of this feature may be deceptive. Nevertheless, it is obvious that a comparison of the indices of the length and shape of those protocones available for study definitely confirms this 'African feature' of *H. africanum*. For all teeth, it shows a constant greater 'African' index than any of the European species considered (except for the breadth/length index of P^2, which in any event, is a rather atypical tooth). It is important to note that such a progressive feature, characteristic of the African phyletic line, can be traced back as far as the Upper Miocene.

The double knot: Gromova (1952), in a recent review of all the available evidence, indicates that the original type of knot is the '*stenonis*' one: it presents a very different metaconid and metastylid, the latter being strongly angulated, and separated from the metaconid by a narrow deep valley. This original type, found in the *Merychippus* ancestor, has been retained mostly in the American *Hipparion*. However, there seems to be a constant modification amongst Old World *Hipparion:* towards a '*Hipparion*' type of knot in Eurasiatic forms, characterized by a symmetrical and rounded metastylid and metaconid separated by a wide and shallow valley; and towards a more '*caballus*' type in Africa, where the metastylid is sub-triangular. The description and drawings of *H. africanum* indicate clearly that it has a '*Hipparion*' type of knot, more typical of the Eurasiatic form and bearing no resemblance to the African forms. As *H. africanum* is the oldest species of *Hipparion* known in Africa, it needs to be decided whether it has acquired this 'progressive' feature very rapidly or whether the '*Hipparion*' type of knot is not as progressive as was previously considered, having already been present in some Merychippine ancestor, and developed in parallel with the '*stenonis*' type.

Stylids: The tendency to develop stylids is quite marked in many, but not all, African forms. It is said to be expressed in *H. africanum* by a small laminated or rounded, rather isolated protostylid on the permanent P_3–M_2 of specimen no. 2, and by a small ectostylid on the vestibular aspect of most of the milk teeth. The tendency is found to be constant among all *Hipparion.* The stated degree of development of these structures does not seem to be particularly 'African': it is certainly surpassed by some Eurasiatic species, for example, *H. koenigswaldi* from Teruel. Of course, it should not be overlooked that the feature seems to have been expressed rather weakly in *Merychippus* times. The minor development that it shows in the Upper Miocene of Algeria may hardly be considered 'African' when compared with the *Stylohipparion* of the 'Villafranchian'. However, the feature suggests a rather strong and precise evolutionary trend at work.

Hypsodonty: H. africanum is stated to be poorly hypsodont. The indices are by no means comparable to the 'African' specimens of the Pliocene and Pleistocene times, and they are of the same magnitude as the other *Hipparion* groups of the Mediterranean basin. *H. africanum* is even less hypsodont than *H. sitifense* which is stated to have low teeth.

PLIOCENE

Mascara

A palate with an almost complete dentition and a symphysial region with incisors, probably belonging to the same skull, have recently been described by Arambourg (1956).

This Pliocene form is characterized by very small dimensions of the teeth (table 8), which also show few and simple plications and little hypsodonty. The protocone, completely independent of the protoloph right to the base of the crown, is relatively compressed.

The specimens have been referred to *H. sitifense* Pomel with which they are stated to share 'almost identical morphological features and size'.

	P^2	P^3	P^4	M^1	M^2		M^3	P^2–M^3
1. MASCARA								
A–P length	30	20·5	20	19·5	19		18·8	129
Transv. breadth	17 (?)	19	20	19·5	18		18·6	
Crown height	7·4	6·6	10·5	10·7	15		13	
Protocone length	6·6	7	8·3	6·7	7·4		8·8	
Protocone breadth	3·8	4·2	4·4	3·7	3·2		3	
Protocone shape	57	60	55	55	46		34	
Protocone length/Tooth length	22	34	41	33	38		46	
2. ST. ARNAUD CEMETERY								
H. sitifense (type specimen)								
A–P length				23				
Transv. breadth				22·5				
3. AÏN EL HADJ BABA								
					R	L		
A–P length			22·5	20·2	20	20·2		
Transv. breadth			21	20·5	21	20·3		
Protocone length			6·2	6	6·7	6·3		
Protocone breadth			3·2	4	3·5	3		
Protocone shape			51·6	66·6	52·2	47·5		
Protocone length/Tooth length			27·6	29·7	33·5	31·2		

TABLE 8. Summary of measurements (mm.) of teeth of North African Pliocene *Hipparion.*

St. Arnaud Cemetery

The type specimens of *H. sitifensis* (*sic*) Pomel 1897 were recovered from the St. Arnaud Cemetery. These two upper teeth, figured by Pomel (see also Arambourg, 1956) are little hypsodont and rather small (although not quite as small as the Mascara teeth). A broken calcaneum is also mentioned.

Lower teeth of a correspondingly small size and medium hypsodonty, collected by Arambourg but as yet undescribed, have no ectostylid.

Aïn el Hadj Baba

Upper isolated, but partially serial right (?) P^4–M^2, a left M^2, lower teeth, and limb bones were described by Thomas (1884) who referred them to *H. gracile* (Kaup).

However, according to Arambourg (1956), the narrow and small number of plications of the enamel, the double pli caballin, features of the protocone, dimensions of the upper teeth and absence of the ectostylid on the lower teeth, make the Aïn el Hadj Baba specimens very similar to *H. sitifense* types and co-types, as well as to the Mascara specimens. Therefore he considered them to be *H. sitifense.*

From the metapodial, it may be observed that the lateral digits were still very strongly developed.

Utique (Northern Tunisia)

This area also includes the continental sands of the Ferryville region near Bizerta (fig. 4).

Solignac (1927) indicated that the fragmented remains had been assigned by Depéret to *H. crassum* Gervais, but Arambourg (1956) is inclined to refer them to *Stylohipparion.*

St. Donat (Algeria)

Teeth of two maxillae, which Arambourg (1956) interprets as being possibly referable to *H. sitifense*, were found at this site. Joly (1909) recognized further teeth from this site and hastily referred them to *H. gracile*, but they should probably be compared with Arambourg's 1956 material and pooled with *H. sitifense.*

PLEISTOCENE

North Africa

Oran: The teeth recovered by Pomel in the Oran area are among the first discoveries of *Hipparion* in Africa and formed the basis of the first description. Two sites were mentioned:

(i) 'St. Pierre sandstone quarry, on the property of Mr. Brunie, in the St. Charles district, in the east quarter of Oran, which is also the type locality of *Libytherium maurusium.*'

Two lower teeth were described by Pomel (1897) as the type specimens of *Hipparion* (?) *libycum.* The one, a left P_3 or P_4, has an ectostylid while the other is without an ectostylid, but the antero-external region is broken. The specimens were successively referred, first by Van Hoepen (1932) to *Stylohipparion steytleri* because of its similarity to P_3 (Nas. Mus. C795) from Cornelia (*vide infra*, p. 347); then by Joleaud (1933) to *Libyhipparion libycum* because of its fundamental similarity to the du Bourg de Bozas Mission material from Omo, although it is more elongated and somewhat larger; and later by Arambourg (1947, 1956) to *Stylohipparion libycum* (or *albertense*).

A distal portion of a third metatarsal was also recovered from this deposit.

(ii) Puits Kharouby.

Five upper molars were described by Pomel (1897) and referred to *H. massoesylium*. However, Pomel himself was not too sure whether or not these upper teeth belonged to those lower teeth which he had described under the name *Hipparion* (?) *libycum*. Their reciprocal kinship was ascertained by Joleaud (1933) who consequently referred *H. massoesylium* to his *Libyhipparion libycum*, and by Arambourg (1947, 1956), who for the same reason, placed them in *Stylohipparion libycum* (or *albertense*).

Aïn Jourdel (Constantine): The material consists of a M_3 and a lower premolar, the additional stylids of which seem to have been overlooked by Thomas (1884) who referred them to *Hipparion gracile*.

Joleaud (1933) emphasized their similarity to Pomel's Oran specimens and to the material discovered in the Orange Free State of South Africa. He proposed that the Aïn Jourdel material should be placed in a new species *Stylohipparion* (?) *thomasi*.

Arambourg (1947) can see no reason for not pooling Aïn Jourdel (one of the two teeth at least) and '*H. massoesylium*' (= Joleaud's *Libyhipparion libycum*) with *Stylohipparion libycum*.

Beni Foudda (Constantine): This site has been referred to as Aïn Boucherit by Arambourg.

A molar recovered here was attributed by Pomel (1897) to *Hipparion ambiguum* but was referred by Arambourg (1947, 1956) to *Stylohipparion libycum* (or *albertense*).

Wadi Natrun (Gart el Moluk Hill): Andrews (1902) described a left upper premolar (?P^4) of large dimensions (A–P 29 mm.; transv. breadth 28 mm.), but apparently it is little hypsodont (height 38 mm.). However, it is a rather worn specimen.

When the specimen was discovered, very few African *Hipparion* had been recovered, and the typical features of the few that had been recovered were still largely unknown or as such unrecognized. The best comparative material at that time was that from Oran: the enamel pattern of the specimen from Wadi Natrun appeared definitely more complex and it differed in the absence of isolation of its hypostyle. Therefore, in spite of its transversely more compressed protocone, which explicitly suggested some close resemblance to *Hipparion theobaldi* (from the Siwaliks), the specimen was referred to the more widespread *H. gracile*.

After the discovery of further material from Omo and Kaiso, Joleaud (1933) emphasized the difference in the parastyle and mesostyle features from *Libyhipparion ethiopicum*, and he stressed the resemblance with the Kaiso specimen, referring to it the Wadi Natrun premolar, which he called *Hipparion* cf. *albertensis* (*sic*).

Central Africa

Koro Toro: The *Hipparion* material recovered from the 'Villafranchian' horizon of the Tchad has been provisionally referred by Coppens (1960) to *Stylohipparion.* He is preparing a detailed description of these specimens, together with the associated fauna. Therefore, it is not possible to comment on this material at this stage.

East Africa

Omo: The first specimens were recovered by the du Bourg de Bozas Mission (1903) and were described by Joleaud (1933). They consist of a few isolated teeth, namely:

1 incisor;
5 lower cheek teeth (1 right premolar, one left M_3, two left molars and one right molar);
1 fragmented upper right molar.

To this group Arambourg (1947) added a left M^1 or M^2, first interpreted by Joleaud as *Hippotigris.*

A second series of specimens was recovered by Arambourg (1947) during his 1932–33 expedition, and comprises 1 right P^2; 1 left M^3; 1 fragmented right upper molar and 1 right M_1 or M_2.

The first of these groups was described by Joleaud (1933) who erected the new genus and species *Libyhipparion ethiopicum,*[1] generically distinct from the South African specimens from Namaqualand and Cornelia on the one hand, as well as from the Constantine material of Thomas, on the other, and specifically separated from Pomel's St. Charles teeth.

In a later reconsideration of these Omo specimens, to which the second series of teeth from the same area was added, Arambourg (1947) rather emphasized (*a*) the close relationships between all the Ethiopian hipparionids; and (*b*) their profound similarity to the East African (Kaiso, Serengeti *pro parte,* and probably Olduvai) material and the Orange Free State discoveries. Furthermore, Arambourg considered it reasonable to refer most of Pomel's and Thomas' North African (St. Charles, Puits Kharouby and the Constantine) material to *S. albertense* or possibly to *S. libycum.*

The characteristic features common to these specimens are:

(i) pronounced hypsodonty reaching 80 mm. in unworn teeth;
(ii) upper molars with very complicated enamel pattern and laterally compressed and strongly elliptical protocone;
(iii) lower teeth with strongly developed additional stylids, rather large oval or flattened and pointed ectostylid;
(iv) the presence of a ptychostylid; and
(v) ridged or pillar-like protostylid and well-built entostylid.

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(1) With exception of left upper molar, considered by Joleaud as belonging to *Equus* (*Hippotigris*).

Therefore, there are no reasons for proposing any generic or specific distinctions between these Pleistocene African *Hipparion*, which according to the priority rules have been referred to *Stylohipparion albertense*.

Olduvai: Some of the first fossils identified in the Olduvai Gorge, when it was first discovered by Kattwinkel in 1911, were the distal ends of 3 metatarsals of hipparionids, which Hopwood (1937) referred to *Stylohipparion* cf. *albertense* (Hopwood).

The dimensions of the lower articulations of metatarsal III were 40 × 30 mm. The broken metatarsal II and metatarsal IV are stated to have had 'originally' almost the same lengths as metatarsal III, and to have had the appearance of broadening distally.

Further specimens of teeth, recovered by Kattwinkel and Reck in 1913, as well as an upper dental series collected by the British expedition, were referred to the same genus and species. The diagnosis proposed by Hopwood (1937) for this *Stylohipparion* cf. *albertense* is:

> Three-toed equid, with high-crowned molars of the *Hipparion* group. Lower teeth are laterally compressed and display a strong, often laminated ectostylid. Genotype: *Stylohipparion hipkini* Van Hoepen (1932).

Unpublished data

In recent years a large collection of equid material has been recovered from the Olduvai Gorge by Dr. L. S. B. Leakey. All the specimens from Bed II (and a few from Marsabit Road, Olorgesailie and Omo) are now being studied by Dr. R. A. Stirton in California. Dr. Leakey kindly permitted the authors to make a brief survey of this material. In order not to encroach on the final description, only a few features relevant to this paper are mentioned:

(i) In this mixed sample there are 471 *Equus* teeth, of which 224 are from the upper dentition. Of the 186 teeth of hipparionids, 100 are upper. The vast majority of these are from Bed II, only a few deriving from other sites.

(ii) This is then a reasonable sampling to ascertain the expected proportions of upper and lower teeth. It will be indicated below that at Langebaanweg there are approximately equivalent proportions of uppers and lowers, but at the latter site there are almost no *Equus* specimens.

(iii) The data is also useful to assess the situation at South Serengeti (*vide infra*). In this respect it is interesting to note that in the Olduvai collection, among the lower teeth, those of hipparionids have elonggated, strongly marked ectostylids, typical of *Stylohipparion*, while those without ectostylids lack the typical features of *Hipparion* as well as the protostylids of the Langebaanweg specimens. They are typically *Equus* in type.

(iv) There is a great range of variation in the size of these *Hipparion* teeth, and also in the length and shape of the protocone. On the whole, the range seems smaller than that of the Langebaanweg teeth, but the protocone is more elongated. In the *Hipparion* lower (as well as in these *Equus*) teeth, there is a complete absence of protostylids and hypostylids.

South Serengeti: A large collection of *Hipparion* has been made from various localities in the South Serengeti, and was described by Dietrich (1942). A complete list has never been published. However, from the available data, it is possible to ascertain that the collection consists mostly of isolated and fragmented specimens, a few maxillary and mandibular fragments (among which are symphysial portions with incisors), many loose upper and lower teeth, both milk and permanent. There are also some rare postcranial specimens, namely, a proximal fragment of a femur, a distal fragment of a tibia, two third metatarsals, one third metacarpal and tarsals. Dietrich artificially reassembled the isolated teeth into series, and most of the dental series figured in his publication are reconstructed. From the scattered data and illustrations, it is possible to establish an incomplete list of the South Serengeti dental material (table 9).

Description	Origin and Coll. Number	Plate Number in Dietrich (1942)
Milk Dentition		
Upper r dP2–dP4 ..	Vo 330	XIII 96
r dP2–dP3 ..	Gadj 10	XIII 97
l dP2–dP4 ..	Gadj 2.39	XX 162
Lower r dP2–dP4 ..	Vo 313	XIII 93b
r dP3–dP4 ..	Marambu	XIII 93a
r dP4	Gadj 10–13.3.39	XIII 94
Permanent		
Upper l P2–M3 ..	Vo, Gar.	XIII 87
l M2–M3	Vo 670	XIV 102
l P2–M3	Vo 330, Vo 670	XV 107, 108
l P2–P4	Vo 670	XX 160
r P2–M3	Vo, Gar.	XIII 88
r M2–M3	Vo 670 and Marumba	XIV 103
Lower l M3–P2	Vo 313, 670	XV 106
l P2–M3	Der., Gadj., Gar., Vo	XV 105
l P2–M3	Vo, Gar.	XIV 101
l P2–M3	Vo 330, Vo 670	XIII 90
l M1	Garussi 2.39	XIV 99
l M	Gar. River 200	XIII 95
r M3–P2	Vo 670, Gar., Olduvai Hill	XVI 109
r P2–M3	Vogel River	XIII 89
r P2–M3	Vo 670, Gar., Vo	XIII 91
r P3–M3	Gadj 10	XIII 92
Symphysial region with incisors	Vogel River 9–10–38	XVI 112

TABLE 9. *Hipparion* material mentioned by Dietrich (1942) and derived from South Serengeti region

In contrast to the relatively unchanged nature of the postcranial skeleton (*vide infra*) since Pliocene times, the advanced and progressive features of the dentition of the South Serengeti hipparionids have been emphasized by Dietrich. The teeth, both upper and lower, are strongly hypsodont (crown length: 9 cm.). The upper molars show numerous enamel plications, and an elongated, ungrooved protocone, completely isolated right down to the base of the crown, and embedded in a thick cement layer. The incisors (see p. 350) are longitudinally grooved on their anterior surface (in one case I_3 is missing).

It does not seem possible to distinguish different forms of hipparionids at Serengeti on the basis of the upper teeth. On the contrary the lower teeth show some constant features whereby it seems possible to distinguish two groups.[1] A large group of teeth, all apparently recovered from the gray tuffs, does not show any additional stylids while another group of some 50 (40 isolated teeth and 2 incomplete dentitions) displays the ectostylids characteristic of most of the African hipparionids then described. In these teeth the ectostylids are sometimes very strongly developed, pillar-shaped or flattened and ridged. Protostylids and hypostylids are also regularly present, and a very peculiar entostylid (see p. 360) may be observed on one tooth (Garussi River 200, fig. 95 of Dietrich, 1942). These teeth derive from deposits that seem to span over a longer period of time than do those from which the teeth without stylids were recovered: some of them probably occur in the gray tuffs, contemporaneously with the first group, while others belong to a probably younger horizon. However, as has been stated previously, the stratigraphy of the South Serengeti is very poorly documented. Other than the presence of the stylids and the average shorter total length of the dental series at a comparable stage of wear (156 mm. *v.* 170 mm.), there seem to be no appreciable differences between the two groups. However, the value that can be attached to the assessment of the total length of the dental series in these specimens is doubtful because (*a*) of the 'reconstruction' of most of Dietrich's series, and (*b*) of the variation of the total length due to wear.

In spite of the above distinction, Dietrich does not consider it necessary to separate generically the South Serengeti material. This attitude is reasonable because

(1) lack of knowledge of a stratigraphical sequence rules out a clear chronological sequence;

(2) too little was known of the skeleton, both cranial and postcranial;

(3) the upper teeth showed no features whereby they could be separated into two groups, and yet it is a statistical probability that, if there were two species at the site, all the uppers could not have belonged only to one of these species; and furthermore,

(4) the development of the ectostylids, ranging from absence through mild formation to strong development, is an expression of dental adaptation to environmental factors (*vide infra*, p. 352).

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[1] See also discussion on Arambourg's concept of the non-validity of *Hypsohipparion*, p. 333.

On the basis of the data available then,[1] Dietrich considered that within the Serengeti material there was an original and conservative African stock of hipparionids for which he erected a new genus *Hypsohipparion* Dietrich, 1942, with *Hipparion albertense* (Hopwood) from the Lake Albert Kaiso bone beds as the type specimen. Into this genus and species he placed the Serengeti material without stylids, as well as all the upper teeth and the postcranial remains. The diagnosis that he proposed was:

> An advanced three-toed, short-snouted *Hipparion* of the dimensions of a small *caballus*, the M^3 of which reaches a crown height of 9 cm. The protocone shows a tendency to become laminated, non-grooved and completely isolated from the protoconule. Teeth show no reduction of the main cusps and styles. Plications are more marked than in all Pliocene species. Lower teeth (deciduous premolars, permanent premolars and molars) are (?)[2] all without ectostylids.

Dietrich believed that the group manifesting the stylids was displaying the developmental trend of a selective pattern. He provisionally placed this group in *Stylohipparion* as a practical measure, partially comparable to *Stylohipparion libycum*, *Stylohipparion ethiopicum*, and *Stylohipparion steytleri*. However, he maintained that the generic labelling had no strict taxonomic value because of the scarcity of the material on which this was based. He did not see the value of assigning his material to a new species.

Arambourg (1947) questioned the validity of the generic status of *Hypsohipparion* on the basis of a possible incorrect determination of what he considered to be lower zebrine teeth (see p. 333). In later publications (especially 1956 and 1959) he seems to have definitely adopted this view permanently. In his opinion the Serengeti material belongs partly to *Stylohipparion* and partly to *E. zebra*. This opinion is discussed and considered unacceptable elsewhere in this paper.

Lake Eyasi: The few isolated teeth recovered from the Lake Eyasi shore (west and north of Mumba Hill) are very much rolled and unsuitable for any detailed study (*vide supra*, p. 287). They were referred to *Hipparion* sp. (Reck and Kohl-Larsen, 1936).

Lake Albert (Uganda): From the east shore of the Lake, one incomplete upper molar (B.M.N.H. M12615) was described by Hopwood (1926) as the holotype of *Hipparion albertensis* (*sic*). The tooth is rather hypsodont, with a complicated enamel pattern. Its antero-posterior diameter is 24·5 mm.

Dietrich (1942) used it as the genotype of his new genus *Hypsohipparion albertense*, the proposed diagnosis of which is noted above.

South Africa

Namaqualand (Cape Province): Nine isolated mandibular teeth of the same jaw, left P_2–M_1 and M_3 and right P_4–M_2 and M_3 (fragmentary) were

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[1] Through the kind collaboration of Dr. K. H. Fischer, Berlin, measurements of some of the '*Hypsohipparion*' teeth were made available to the authors: see table 20.

[2] Dietrich includes this 'query' in his original diagnosis in German (p. 97).

described by Haughton (1932), who erected a new genus and species *Notohipparion namaquense*. The type specimen is S.A.M. 9982. Unfortunately a diagnosis was not provided.

A small ectostylid and a protostylid are occasionally present. It is difficult to comment on the height and relative hypsodonty of these teeth because the crown is rather low, as the specimens are in a very advanced stage of wear (table 10). The teeth possess a thick cement.

Cooke (1950) proposed a diagnosis for the genus *Notohipparion* Haughton: 'rather low-crowned, heavily cemented hypsodont lower cheek teeth with an extra antero-external cingulum fold or column, either isolated or fused with the parastylid, present in all the permanent cheek teeth except the second pre-molar, and a deep groove separating the strongly developed metaconid and metastylid. The upper dentition is unknown'.

Because of the moderate hypsodonty and the weak development of additional stylids, Dietrich (1942) considers *Notohipparion* to be more primitive than *Stylohipparion*. This opinion had also been held by Van Hoepen (1932).

Arambourg (1947) compared these lower molars with the 'single' African Pleistocene genus *Stylohipparion* but, probably because of the poor stratigraphy, he did not revise its taxonomic status. In later comments on the African *Hipparion*, he (1959) makes no further mention of these specimens.

	P_2	P_3	P_4	M_1	M_2	M_3
A–P Length	29·5	27·0	26·0	23·0	24·0	29·0
Transv. breadth	16·0	17·0	17·0	16·0	14·5	12·5
Height	14·5	17·5	25·0	23·0	30·0	34·0
Transv. breadth/A–P length ..	54·2	63	65·4	69·6	60·4	43
Height/A–P length	49·2	64·8	96·1	100	125	117
Hypsodonty Index	110	97	67·9	69·5	48·2	36·8

TABLE 10. Measurements (mm.) of teeth of '*Notohipparion namaquense*' Haughton

Christiana (Cape Province): From this site an upper second (? third) left molar (Archaeol. Surv. 113), considerably worn, undescribed and not illustrated, has been referred to *Stylohipparion steytleri* by Cooke (1950).

Transvaal australopithecine cave breccias: Two lower teeth, recovered by Broom in the breccia filling the Kromdraai Cave, have been referred to *Stylohipparion steytleri* (Cooke, 1950). *Hipparion* teeth recovered from Bolt's Farm and Makapansgat Limeworks have been similarly referred (Cooke, 1963). These specimens have not been described.

Cornelia (Uitzoek): Eleven isolated upper and lower teeth include a group of five and another group of two teeth belonging to single individuals (table 11):

(i) one right M^1 or M^2 (Nas. Mus. C558), one left M^3 (C555), one left M_1–M_2 (C556),[1] described by Van Hoepen (1930) as a new species

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[1] In the original publication (1930), C556 was stated to be composed of lower milk teeth (DM_3 and DM_4), and only in 1932 were they correctly acknowledged as permanent teeth.

Hipparion steytleri, the type being C558 and the paratypes being C555–556.

(ii) A series of five left lower teeth P_3–M_3 (C795), recovered from the type locality, were referred by Van Hoepen (1932) to the same species.

(iii) A right M_2 (C797), in very early wear and therefore displaying a completely uncharacteristic pattern, was used by Van Hoepen (1932) to erect a new genus, namely, *Stylohipparion*, and a new species *hipkini*, to which a left P_2 (C796), recovered from the same locality and formation, was provisionally referred.

Van Hoepen (1932) subsequently referred *steytleri* to the new genus *Stylohipparion*. He considered *Stylohipparion* to be 'obviously the terminal stage of the evolutionary line which originated from *Hipparion* with *Notohipparion*.'

Joleaud (1933), who compared *steytleri*, with *Libyhipparion ethiopicum*, and *hipkini* with the Aïn Jourdel specimen of Thomas, accepted the specific distinction between *steytleri* and *hipkini*. Cooke (1950) considered this distinction to be invalid. This opinion is strongly supported here, for both *a priori* and *a posteriori* reasons: first of all, no upper teeth of *hipkini* have been recovered, and Van Hoepen's species is based on one single lower tooth (C797), which constitutes a very inadequate basis for creating a new taxonomic unit. Furthermore, the tooth is in a very early stage of wear, which is the case of the obviously atypical, peculiar pattern of its occlusal surface. Thus the 'difference' between it and the *Stylohipparion steytleri* is not at a species level.

Van Hoepen provisionally referred specimen C796 to the new species, but it is even less different from the known *steytleri* specimen. In any event, being a P_2, it does not show the typical features of a species.

On the other hand, and quite apart from this question of a specific distinction, the genus *Stylohipparion* Van Hoepen has been generally accepted by all subsequent authors. Hopwood (1932), Dietrich (1942), Arambourg (1947, 1956, 1959), Cooke (1950) and Gromova (1952), among others, have considered *Stylohipparion* as a valid unit (at least at a subgenus level), which expresses the 'African' trend of Pleistocene hipparionids. The following diagnoses have been proposed:

> *Arambourg* (1947): 'Tridactyl equid, with very hypsodont dentition. Upper molars with compressed protocone of very elliptical section, wavy parastyle; especially complicated enamel pattern, particularly around the prefossette. Lower molars with broadly developed ectostylid, laterally compressed, and close to the antero-external hypoconid pillar.' (Direct translation from the French.)

> *Cooke* (1950): 'High-crowned rather hypsodont lower cheek teeth with a strongly developed isolated pillar external to the ectostylid, possessing no external groove between hypoconid and hypoconulid, having no protoconid and hypoconid and small rather widely separated metaconid

and metastylid. High-crowned upper cheek teeth with isolated oval protocone and possessing a small flange on the antero-internal side of the parastyle.'

We wish to point out that the 'ectostylid' referred to by Cooke is actually the *ptychostylid*, while the 'strongly developed isolated pillar' is the *ectostylid.*

UPPER TEETH	*St. steytleri* (van Hoepen)	
	M^1 or M^2	M^3
	(C558)	(C555)
A–P length	22·0	21·0
Transv. breadth	22·0	18·0
Height	54·0	66·0

	St. steytleri				*St. steytleri*		*St. hipkini*	
LOWER TEETH	P_3	P_4	M_1	M_2	M_1	M_2	M_2	P_2
	(C795)				(C556)		(C797)	(C796)
A–P length	25·0	28·0	22·0	24·5	—	21·0	28·5	31·0
Transv. breadth	15·0	12·0	12·0	11·5	12·0	12·5	15·0	14·5
Height	64·0	74·0	69·0	73·0	32·0	41·0	81·0	46·0

TABLE 11. Dimensions (mm.) of teeth of '*Stylohipparion*' from the Orange Free State, South Africa.

From Uitzoek also comes an anterior portion of a lower jaw (Nas. Mus. C679), containing four large first and second incisors, which are flattened anteriorly and arranged almost in a straight line. Each incisor shows the 'mark' or the cement-filled depression in the enamel. The third incisor is small and lies behind and in contact with the second incisor.

The above description (Cooke, 1950) is a slightly modified interpretation (also suggested by L. H. Wells) of the original description by Van Hoepen (1930), made, according to Cooke, so as to avoid the 'startling supposition' of the complete absence of the third incisor. However, it should be pointed out that specimen GADJ. 10 from South Serengeti shows complete absence of not only I_3, but also of the canines (Dietrich, 1942).

One of the special features of this specimen C679, besides the reduction (? complete, i.e. absence) of I_3, is that the lingual aspect of I_1 and of I_2 has two surfaces, meeting at an angulated thick ridge. Each surface also has longitudinal parallel 'costae'.

A new genus and species *Eurygnathohippus cornelianus* van Hoepen (1930) was created to include the above material. No measurements were published, but from the illustrations and the cast it is clear that the jaw fragment belongs to a very large skull.

Dietrich (1942)(1) made the suggestion that this mandibular symphysial

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[1] Dietrich incorrectly describes the specimen as belonging to a milk dentition ('Milchvordergebiss', p. 97).

region (for which no cheek teeth are known), should belong to *Stylohipparion*, or at least to the advanced *Hipparion* of the Cornelia layers.

Ewer (1963) refers to *Eurygnathohippus* as a chalicothere. The basis for this opinion is not clear to the authors.

NOTE ON *Hipparion* INCISORS

Hipparion incisors have rarely been discovered in Africa. In a recent, comprehensive study of a large assemblage of *Hipparion* material from South Aragon, Sondaar (1961) indicates a similar shortage there. The small number of recorded specimens from Africa are:

(i) *Upper incisors:* the *H. africanum* type specimen (no. 141) from Oued el Hammam presents a complete snout, and, from the same site, there are also three maxillae with incisors. They have been described by Arambourg (1959) without comment, because there is no comparative material.

(ii) *Lower incisors:*

- (*a*) The *Libyhipparion ethiopicum* (Joleaud, 1933) collection from the Omo Valley contained one incisor (*vide supra*, p. 342).
- (*b*) Dietrich (1942) mentions some incisors from the South Serengeti without going into any detailed description (*vide supra*, p. 344).
- (*c*) *Eurygnathohippus cornelianus* (Van Hoepen, 1930): an anterior portion of a lower jaw. This may belong to an individual of the genus *Hipparion* or *Stylohipparion*, as has been suggested already by Dietrich (1942) and in a personal communication (1964) from Dr. L. S. B. Leakey (who bases his view on material recently discovered at Olduvai).[1]

Each of these specimens raises difficult problems, which cannot be solved until more complete material becomes available. A few of these problems are:

1. The '*Libyhipparion*' incisor does not show the sub-elliptical section of *Hipparion*. It is completely subdivided into two clearly separated 'marks', no other example of which is known among *Hipparion* in the literature. It has been suggested that this feature is an extreme manifestation of the enamel plications, typical of the African hipparionids. It is impossible to state whether or not the feature is really exceptional. It is not demonstrable in the other few available incisors.
2. *Eurygnathohippus:* The 'costae' and the blunt ridge on each specimen are unique in this small series. A possible explanation for these features is that they are adaptations to browsing and strengthen the teeth, set practically parallel to the horizontal symphysis.
3. The occasional reduction (? absence) of the third incisor is referred to above.

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[1] Confirmed while in press. See Leakey, L.S.B.: *Olduvai Gorge 1951–1961*, **1**. p. 26.

A SUMMARY OF PUBLISHED POSTCRANIAL REMAINS OF AFRICAN *Hipparion*

The postcranial skeleton of African hipparionids is very poorly known. The only described specimens are:

Camp Berteaux: A femur fragment with the proximal epiphysis.

Oued el Hammam: Distal fragment of humerus (no. 159); radio-ulna (no. 123) and fragments 13, 22 and 27; femur without epiphysis and a distal fragment; distal fragment of tibia; pelvic fragment; two astragali; one calcaneum; five metacarpals and five metatarsals, many with lateral digits.

Aïn el Hadj Baba: Metapodials with lateral digits.

Oran: One fragmentary calcaneum and one third metatarsal.

Omo: Right humerus.

Olduvai: Distal end of three metatarsals. There are also quite a number of undescribed specimens. The authors examined a number of such specimens recently collected at Olduvai Gorge. Data on the metapodials is provided below.

South Serengeti: Proximal fragment of a femur; distal fragment of tibia; two metatarsals III; one metacarpal III; tarsals.

Arambourg (1949) has probably described the largest collection known from one site: it consists mainly of numerous complete metapodials (many of them with lateral digits) which have been referred to *Hipparion africanum.* From the description and the measurements, this North African Upper Miocene *Hipparion* seems to have been about the same size as the smallest *H. mediterraneum* of Pikermi. The extremities indicate that *africanum* was rather short and heavily built. The lateral digits were more robust and strongly developed than those of most other hipparionids, and they certainly were still functional.

From the Pliocene, only a few metapodials with very well developed lateral digits are known from Aïn el Hadj Baba. They have not been adequately studied. It has been assumed that they belong to *H. sitifense.*

From the Pleistocene of East Africa a right humerus is known from Omo, and a few fragmentary long bones and metapodials have been recovered at Olduvai and South Serengeti. The material has not been described. Size and morphology of the metatarsals do not seem to differ noticeably from *H. gracile.* Dietrich (1942, p. 101) states that the South Serengeti metatarsal III 'must

	Breadth, distal end	*A–P diameter, distal end*
Olduvai (Hopwood 1937)	40	30
South Serengeti (Dietrich 1942)	37	35
H. elegans	29·6	25·1
H. moldavicum	33·9	26·8
H. mediterraneum	32·8	

TABLE 12. Dimensions (mm.) of metatarsal III of *Hipparion*

have a length similar to *H. gracile*, i.e. 23–24 cm.' The lower articulating surface is 37 mm. broad and 35 mm. A–P, so that it is only possible to state that the distal end is broader and thicker than in most of the European *Hipparion* (table 12). The lateral metapodials reach almost to the distal articulating facet and are rather strongly developed, but it is not possible to state firmly whether or not they possessed three phalanges. Nothing is known about the front extremities at present.

The only species with similar dimensions of the lower end of metatarsal III is *H. longipes* with 40 and 33 mm. for the breadth and A–P dimensions respectively. *H. africanum* has a distal breadth of 34·7 mm. It is difficult to assess whether these greater dimensions of the East African Pleistocene forms are indicative of larger overall dimensions of the animal, or whether they only refer to more massive metapodials. Although there is no direct correllation between the different structures, it may be mentioned that the larger size of some of the South Serengeti molars may suggest that the first possibility is not excluded. In general, too, Pleistocene mammals tend toward giantism.

On the basis of published material, it was not known whether or not the African Pleistocene hipparionids were three-toed horses. There is some information concerning the existence of metatarsal II and metatarsal IV at Olduvai, of which it is stated that 'they originally had practically the same length as metatarsal III and that they are broadening distally' (Hopwood, 1937). However, no phalanges are mentioned.

Unpublished data

Examination of the *Hipparion* third metapodials from Olduvai Bed II, now in Berkeley, California, reveals conclusively that the lateral digits were robust, reached the distal ends of the metapodials, and were as well developed as those of *Hipparion* from Pikermi. The metapodials II and IV are not represented by complete specimens or by the distal articular end. Measurements of the fragments are considered to be of no value. Despite the lack of complete lateral digits, the evidence of the articular grooves formed by them on the third metapodials convincingly indicates that the East African *Hipparion* were three-toed. Furthermore the data suggests that they possessed slightly longer, but more massive, limbs than the Pikermi *Hipparion* (see also p. 363).

Table 13 indicates the dimensions of the available third metapodials from Bed II, compared with two specimens from Pikermi.

It appears that the African hipparionids have hardly modified their locomotor apparatus since the Pliocene.

THE ECOLOGICAL ADAPTATIONS OF *Hipparion*

Considerable plasticity exists in biological organisms. Factors such as climate (with such variations as in temperature and humidity) considerably affect water supply, food, animal and plant associations and the actual nature of the environment, e.g. savanna, sand dunes, forests. The range of an intra-

Metacarpal III	*Total length*	*Proximal A–P*	*Proximal breadth (max.)*	*Distal A–P*	*Distal breadth (max.)*
1957. SHK II 935* ..	217	36	46	33	42
F. 345† ..	206	37	44	34	?45
1955. BK II 45 ..	223	37	>45	36	48
MEAN ..	215	37	45	34	45
Pikermi UC63402**	206	31	40	29	38
Metatarsal III					
1957. SHK II 557*	253	38	48	35	45
1957. SHK II 729/730	260	37	47	36	45
1955. BK II 68 ..	257	40	46	35	45
1953. BK II ..	242	37	45	34	44
1957. SHK II 1177 ..	254	—	—	33	>42
1957. BK II 663 ..	—	41	46	—	—
1955. BK II 135 ..	—	—	—	38	48
1941. S I F 797 ..	—	—	—	32	43
MEAN ..	253	38·6	46·4	36	44·7
Pikermi UC63415** ..	241	37	45	33	40

* These appear to belong to one individual.

** University of California, Berkeley (Dept. of Paleontology).

† There is a unilateral pathological growth at the distal end.

TABLE 13. Dimensions (mm.) of third metapodials of *Hipparion* from Olduvai Bed II. All the specimens, except the two labelled 'Pikermi', are from Olduvai.

species variation may be considerable and will allow extensive pliability in adaptation to changing environmental conditions. Such modifications may not change the genetic background or consequently, the taxonomic status. In comparing different anatomical patterns, this concept must be borne in mind.

On the other hand, it is also obvious that the environment may favour, either the greater adaptive potential of some individuals in a particular population or mutations, so that selective forces may operate to promote different races and eventually a new species. Therefore, in a survey of a biological group which extends over a vast continent, it is essential to appreciate the plasticity of the organism.

Such a study has been successfully developed for the family Equidae, and the hipparionids in particular, because of the vast amount of available fossil material, both in America and in Eurasia. Following other scholars, Gromova (1952), in her revision of the genus *Hipparion*, has emphasized its variability and evolutionary trends in relation to ecological factors.

The aims of this section are

(*a*) to summarize the main conclusions about the ecological and functional significance of *Hipparion* characteristics;

(*b*) to summarize the available information concerning the African biotopes occupied by *Hipparion* from Upper Miocene to Pleistocene times; and

(*c*) to draw possible conclusions about the migrations and evolution of African *Hipparion* under the influence of these bionomical circumstances, and thereby to contribute to the appreciation of the taxonomic status of the African groups.

ECOLOGICAL AND FUNCTIONAL SIGNIFICANCE OF HIPPARION FEATURES

The *overall dimensions of the Hipparion skeleton* do not allow definite conclusions about the biotope. It is known that the smallest races of extant Equidae are to be found in the driest areas characterized by drier food and, in the northern part of their dispersion, in areas of poor economic conditions. It is probable that similar factors have influenced the *Hipparion*-associated fauna, and that their general dimensions illustrate in some way the nature of the biotope. However, larger and smaller forms (? species) have repeatedly been recovered from the same deposit so that it appears that they co-existed in the same climate, but they may have occupied, within the same area, slightly different ecological niches. On the other hand, this is not a general rule because exceptions have been documented. For example, at Pavlodar (on the right bank of the Yrtych, Moldavia, U.S.S.R.) where it was possible to make independent studies of the nature of the biotope at different ecological stations, a species characterized by longer and more slender extremities and reduced lateral digits, viz. *H. longipes*, lived in a drier habitat than the shorter-limbed *H. elegans* did. Therefore, it is not possible to make any direct inferences about the biotope from a mere consideration of the overall dimensions of the animal. Various factors are probably involved which cannot be adequately isolated.

Relative dimensions of cheek teeth and incisors seem to be largely influenced by the quality of the food: a drier, more steppe-type grass usually develops larger teeth. However, the incisors and the cheek teeth may show differing reactions and adaptability to this ecological feature. This has been demonstrated by comparing species presenting large cheek teeth with species having small cheek teeth, e.g. *H. gratum* and *H. longipes*, which show comparable incisors. The relative size of the teeth in proportion to the overall dimensions of the animal must also be considered, a smaller animal normally having relatively larger teeth.

The development of the preorbital fossa, which has become an important taxonomic consideration, is in the present state of our knowledge not related to any ecological feature. Animals with large and with small preorbital fossae are found together in the same xerophytic (*H. proboscideum* and *H. matthewi*, at Samos) and moist habitats (*H. moldavicum* at Taraklia, or *H. theobaldi* in the Siwaliks). Preorbital fossae may even be missing (*H. platygenys* at Taraklia) without any apparent ecological reason.

The isolated protocone, completely detached from the protoloph and the protoconule right down to the base of the crown, is a constant feature of the hipparionids. It obviously weakens the structure of the tooth. This has to be compensated for, especially in the case of a hard and dry grass diet, by a greater development of the cement in the anterior and the posterior valleys so as to bind and strengthen these individual elements (Stirton, 1931).

Two elements are involved in shaping the protocone: antero-posterior length and transverse breadth. It is known that, relative to the total dimension of the tooth, the A–P length of the protocone is more constant than its transverse breadth. Therefore, a protocone may look elongated, but this is only a reflection of its narrowness. Thus it is advisable to express the functioning structure of the protocone by means of two indices:

(*a*) the protocone length is expressed relative to the general mesiodistal measurement of the tooth, i.e. the 'length index'.

(*b*) The so-called 'shape index' expresses the length of the protocone relative to its breadth (table 14; figs. 12, 13).

These indices highlight the differences in adaptation between the African and Eurasiatic *Hipparion*.

The two indices for the African forms are compared to those for 7 Eurasiatic *Hipparion* species. Available measurements of the total dental series have been utilized. It may be noted from figure 12 that the length index of the African *Hipparion* is constantly higher for each tooth than that of the corresponding tooth of any of the Eurasiatic species. However, in both groups the length index tends to increase in a mesiodistal direction. On the contrary, the shape index (fig. 13) is constantly lower for the African forms, decreasing for both African and Eurasiatic groups in a mesiodistal direction. Thus it may be concluded from the two indices that the protocone of the African *Hipparion* is both relatively longer (elongated) and narrower than in the Eurasiatic forms.

The shape of the protocone varies with progressive wear, the section tending to become more oval and less elongated. But independently of these modifications, for particular locations in the dental series at comparable levels of attrition, there seems to be also an adaptive elongation or broadening of the protocone which is linked with the type of food it has to deal with. It is suggested that the efficiency of the protocone's function in trituration lies in the action of its buccal and lingual enamel crests, developed perpendicularly to the lateral chewing movements of the mandible. It is obvious that the efficiency is maximal for a narrow and elongated protocone, for here the crests are at one and the same time the longest and the most perpendicular. Thus they would favour a dry and harder bunch grass. This suggestion is strengthened by the contemporaneity of the lengthening of the protocone and the development of a typical xerophytic vegetation in America.

Enamel plications

It has been successfully demonstrated that the complexity of the enamel pattern on the occlusal surface of *Hipparion* molars has developed synchronously with the drier environment in Upper Miocene and Pliocene times. Like the elongated protocone, the numerous enamel plications are oriented perpendicularly to the movement of the jaws, and are increasing the triturating power of the teeth for coping with harder grass. Although there seems to be a parallel increase in the degree of plications with increasing toughness of food, there

	H. africanum[b]		*H. sitifense*[c]		*H. elegans*[d]		*H. moldavicum*[d]		*H. platygenys*[d]		*H. periafricanum*[e]		*H. gromovae*[e]		*H. concudense*[e]		*H. koenigswaldi*[e]		*Langebaanweg*	
	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.
P^2	23·6	64·2	22	57	22·8	59·3	21	65·2	21·9	58·5	20·7	62.6	22·3	60·5	20·1	70	22·9	57·2		
P^3	35·3	43·2	34	60					24·8	64·8										
P^4	40·8	34·3	41	55					28	62·2										
P^3 or P^4					28·4	59·3	25·7	60·6			24·2	68·9	26·2	64·6	26	64·5	30·2	51·1	34·7	49·9
M^1	31·7	50·5	33	55																
M^2	32·6	46·6	38	46					31·6	61.9										
M^1 or M^2					32·3	57	30	60·1			28·2	64·7	27·7	58	28·6	57·2	31·1	47·9	36	47·9
M^3	38	32·9	46	34	35	50·8	34·8	47·1	30·2	53·8	27·7	63·5	31	54·6	29·1	52·4	32·2	47·9		
P^3, P^4 M^1 or M^2:																				
a. range of variation:																			26·5–45·6	36·4–58·9
b. mean for little or moderately worn teeth:																			35·2	48·6
c. General mean:	35·1	43·4	36·5	54	30·3	58·1	27·9	60·3	28·1	62·9	26·2	66·8	26·9	61·3	27·3	60·8	30·7	49·5	35·1	48·9

[a] Length Index (L.I.) = protocone length relative to tooth length.
Shape Index (S.I.) = protocone breadth relative to protocone length.

[b] According to, or calculated from Arambourg, 1959.

[c] According to, or calculated from Arambourg, 1956.

[d] According to, or calculated from Gromova, 1952.

[e] According to, or calculated from Sondaar, 1961, for 'little or moderately worn teeth'.

TABLE 14. Protocone Length Index and Shape Index.[a]

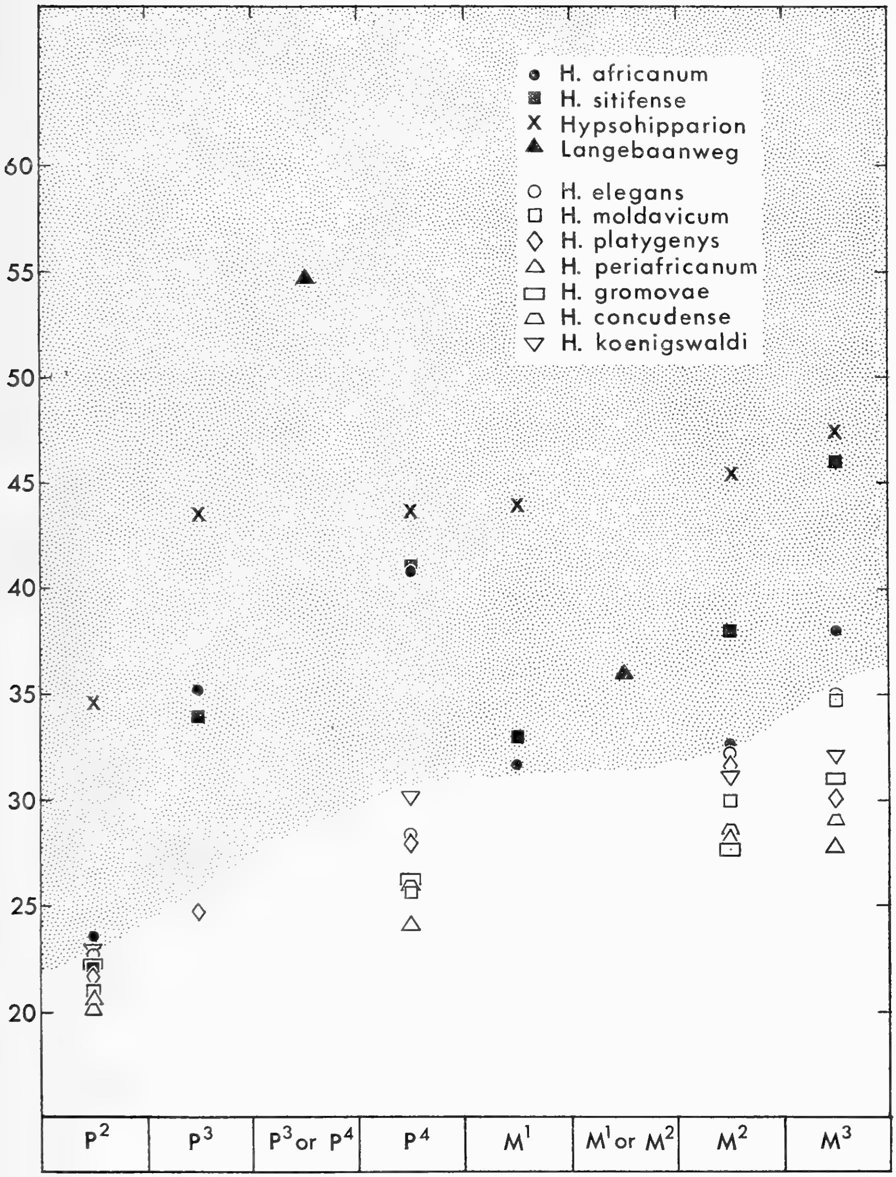

FIG. 12. Protocone length index in the various teeth of African and non-African *Hipparion* species.

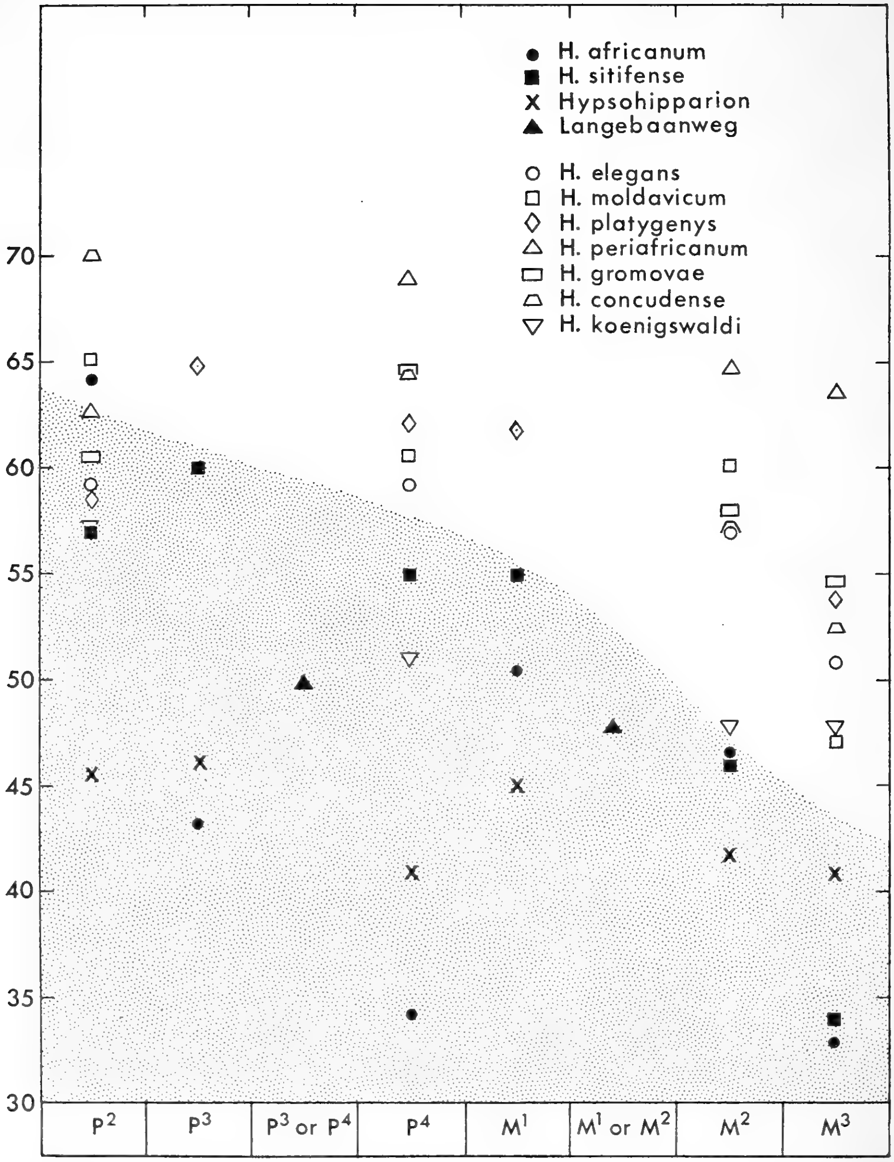

FIG. 13. Protocone shape index in the various teeth of African and non-African *Hipparion* species.

must be a limit to the former. The quantity of available enamel is fairly constant and probably limited, so that an increase in the complex pattern of the enamel will result in a thinning out of the plications. Eventually this would produce too weak a support for the triturating pressure required for hard grass. When this point is reached, the plications again reduce in number and the protocone lengthens as a compensatory mechanism.

Therefore, it is not always possible to ascertain from the small number of plications whether they represent a primitive condition corresponding to a humid environment, or whether they are secondary, resulting from a reduction under the influence of a hard grass food. Then other factors must be considered, e.g. the shape of the protocone, to solve the problem.

A directly comparable situation is encountered in the development of proboscidean teeth. Here an increase in the available grinding surface of the enamel ridges (lamellae) could represent the increasing plications in the teeth of the Equidae, especially as they are also oriented perpendicular to the grinding movement. This parallelism is also demonstrated in the hypsodonty of these two groups.

Hypsodonty

In the evolution of the Equidae most lines show a constant increase in the crown height of the cheek teeth. However, from *Merychippus*, in Miocene times, the progressive hypsodonty has advanced along two phyletic lines (*Hipparion* and *Pliohippus*) at a faster tempo, again under the influence of a general increase in aridity. The same observation has been made among Bovidae. It seems obvious that it is once more an adaptive response of the organism to the xerophytization of the diet.

The dietary changes involved in the evolution of Cenozoic hypsodont horses probably corresponded to a shift from browsing on softer herbaceous plants to grazing on harsh, siliceous grasses, which acted as abrasive agents on the teeth. These changes are, in turn, a consequence of an increasing aridity as has been clearly demonstrated for the Great Plains of America (Stirton, 1947). The association of widespread sandy deposits and of bunch grass of the *Stipidium* type, with the increasing aridity of this area is actually known to be contemporary with the development of hypsodonty from Lower Miocene times onward. This increased height of the crown has played an important role as a protective modification in the dentition. It is supposed, although impossible to prove from the fossil record, that a mutation or other factors, favoured an increase in activity of the odontoblasts and ameloblasts to lay down more dentine and enamel when the tooth was still in the formative stage. The root closure (fusion) may have been considerably retarded as well. Furthermore, it may be suggested that dry climate has influenced the teeth by necessitating some protective mechanism not only because of the harsh conditions of the grass, but also because of the sand mixed with it as a foreign substance. Stirton (1947) states that in the Great Plains area, a close inspection reveals much sand adhering to grass or lodged in between blades and stems, where it is blown by wind or splashed after thunder showers.

The double knot in the lower cheek teeth of the hipparionids displays three typical features:

(*a*) a primitive '*stenonis*' type, inherited from *Merychippus* and generally retained throughout the evolutionary sequence among American species;

(*b*) a more progressive, typical '*Hipparion*' type has been developed by most European forms; and

(*c*) the '*caballus*' type which was lately acquired, particularly in African representatives.

It has been suggested that the double knot of the lower teeth was shaped and typified under the influence of the protocone structure in the upper teeth, with which it is functionally linked in occlusion. There is good reason for developing a long, narrow metastylid parallel to an elongated, elliptical protocone, as is found in most African *Hipparion*. Here, the shape of the metastylid in particular, and consequently of the whole knot, conveys useful information about diet and climate. However, the correlation is probably not a simple one, because American *Hipparion* display an elongated protocone and a rounded '*stenonis*' type of metastylid simultaneously.

Total tooth structure

Upper teeth are rather compact. The outer enamel forms a fairly continuous and parallelipipedic structure, only grooved slightly by a small hypoglyph. The only weak structure which can be broken away from the tooth under excessive strain is the protocone, separated from the rest of the tooth by the internal depression. In the Langebaanweg material, this plane of fracture is noted in L935, L942, L945, L956, S.A.M.11722 and S.A.M.11724 (pls. 1, 7, 8, 9). It has been noted above that, with increasing dryness of the food, this weakness is largely corrected by the development of a narrow protocone closely adherent to the protoloph.

Lower teeth, on the other hand, are built on a very different pattern. The many conids and stylids are much more individualized: they are contiguous but are separated from each other by rather deep depressions right down to the base of the crown. These intervals are filled with cement, but it is softer than the enamel and does not always supply sufficient compensatory protection, as can be seen in many fossil teeth where the cement has disappeared. In drier environments, the hard food influences this structure of the lower teeth, demanding additional strengthening of the enamel-dentine pillars which are embedded in their cement coating to prevent both fracturing and excessive wear of the tooth. Support can be provided in two ways, either

(i) by reducing the depth of the internal and external depressions separating protoconid from hypoconid, metaconid from metastylid, and metastylid from entoconid, or

(ii) by additional stylids.

Reduction of the depth of the depressions is commonly observed. As has been stated previously, this occurs on the lingual surface by the development of a '*caballus*' type of double knot, while on the buccal surface it is secured by a broader connection between the two halves of the ectolophid.

The alternate solution lies in the construction of additional pillars: ectostylid and ptychostylid in particular, just in front of the external depression, and protostylid and hypostylid on the antero- and postero-external corners. Entostylids are occasionally developed in the postero-internal depression. In one particular case (a '*Stylohipparion*' Gar. Fluss no. 200, figured by Dietrich, 1942, pl. XIII, fig. 95), a strong additional pillar is seen between metastylid and metaconid.

The higher frequency of these additional pillars in milk teeth seems to have been necessitated by the lowness of the crown of these teeth and their softer construction. This is the obvious way to prevent too rapid attrition which cannot be compensated as there is no continuous growth of the tooth.

As suggested previously, enamel plications, shape and size of protocone, structure of the double knot, increased hypsodonty and additional pillars are many different methods of meeting the mechanical requirements of a tougher diet. They do not all necessarily develop together at a parallel tempo. Some of them are functionally linked but other elements develop compensatory roles so that all need not be present at one time. Therefore, no single element can give reliable information about climate, biotope and the quality of food, but an assessment of the whole picture and of the reciprocal values of the different features must be considered.

The extremities

Duerst (1926) has successfully demonstrated how a humid climate and a soft grass develop a heavier type of equid with broader extremities (eurysome type), while a leptosome type of a smaller, more slender animal with more gracile extremities tends to be built in drier biotopes characterized by a xerophyte vegetation. This seems to apply especially to metapodials which become relatively longer.

The progressive reduction in size and the disappearance of the lateral digits in equids, with the concentration of the whole body weight on the third metapodial, has always been interpreted as an adaptation to increasing speed in steppe surroundings. It has been repeatedly suggested that the high tempo of evolution of *Pliohippus* towards monodactyly is an expression of its drier habitats, while the lateral digits of African *Hipparion* are kept more or less functional right into the Pleistocene, probably because of a more humid environment.

THE UPPER MIOCENE AND PLEISTOCENE BIOTOPES OCCUPIED BY AFRICAN HIPPARIONIDS

Our knowledge concerning past climates and biotopical conditions in those areas where African hipparionids have been recovered is still inadequate.

The fragmentary information spans over a very long period of time (probably 10–12 million years) and is derived from a large continent where the climates have certainly been variable. Consequently it is not always possible to draw accurate conclusions from the collected data, nor is it possible often to correlate data from one site with those of another.

Furthermore, this information is deduced from fossil assemblages of which some are listed on the basis of debatable fragments, while others are wrongly identified. For example, at Olduvai Gorge, recent and more extensive collections will permit a better analysis.

Even where there is sufficient and accurately identified material, it should be remembered that a fossil specimen is not necessarily found in the typical habitat of the living form. It is well known that in periods of drought or volcanic eruptions (which have played such an important role in the Cenozoic sedimentation of East Africa, from Omo to Eyasi), animals have concentrated around swamps, temporary pools and tuffs, possibly fairly distant from their normal biotope.

This biotope is often less restricted than one imagines, and the adaptation of some organisms is quite fantastic. So, it seems futile to draw definite conclusions from the presence of one or even a few animals. Real associations must be considered to avoid misinterpretation of the presence of a species at a particular site.

(*a*) In the Upper Miocene, the Oued el Hammam faunal assemblage contained *Palaeotragus*, *Samotherium*, *Damalavus*, *Gazella*, *Dicerorhinus*, *Hippopotamus* and *Hyaena*. With slight generic differences, it corresponds very closely to the fauna of the East African plateau of today, and indicates the typical savanna with mimosa biotope of the tropics. According to Arambourg (1959), the presence of *Macaca* and *Cephalophus* in the contemporaneous deposit at Marceau suggests the proximity of forests. This is supported by the location of the deposit in a higher and already tilted portion of the Tellian Atlas, and by the lignite abundant in the deposit.

(*b*) The Lower and Middle Pleistocene faunal assemblages of the East African *Hipparion*-bearing sites clearly indicate the same type of steppe or plain and highland (mimosa) savanna environment, very similar to that of the present day, 'with a marked bias toward somewhat moister conditions in most cases' (Cooke, 1963). The main feature at Omo, Kaiso, Kanam, Olduvai I–IV and Eyasi is undoubtedly that of an open savanna. No true forest association is to be found in these areas, although forest strips and moist woodland occurred occasionally, as is indicated, for example, by the presence of *Nesotragus moschatus*. The cyclical and seasonal variation of the rainfall has provided more humid conditions at times, and consequently the development of swamps and (or) lakes in the lowlands, with very luxurious vegetation, are responsible for the abundant Suidae, Bovidae, Giraffidae, Elephantidae and Equidae. A swampy environment is explicitly suggested at Olduvai by *Aonyx*, and at Omo by *Kobus*. A lake shore or grassland adjacent to water is evident both at

Omo and Olduvai (e.g. *Hippopotamus*, *Omochoerus*) where this is also reflected by the nature of the deposit.

The presence of *Oryx* and *Beatragus hunteri* would suggest arid conditions prevailing in the locality.

Although most of the fauna are suggestive of plains or a plateau, *Tragelaphus nakuae* and *Dinopithecus brumpti* indicate that a mountainous biotope was probably part of the picture at Omo.

(*c*) In South Africa, forest and desert associations are similarly absent, and the prevailing feature remains that of a steppe or a savanna fauna. The Vaal River Gravels suggest a fauna of thornbush and grassland. The cave breccia—probably less representative of a true biocoenose—contains both open plains and dense bush-dwelling forms. It is believed that the rainfall varied considerably during the Pleistocene, with oscillations from 20% to 40% annually (Brain, 1958). The fossil forms represented there would have tolerated such changes. In any case, even in the driest conditions (Taung) well-watered bush valleys could be located at not great distances.

In conclusion, it may be stated in broad terms, that African Upper Miocene and Pleistocene *Hipparion* sites seem to have been areas of (dry to) moist savanna and grass steppe, or of open woodland with mixed savanna. It is not possible to define with any more precision the environment proper to *Hipparion* in this general biotope which extended over half of Africa for several million years. It is probable that local circumstances and features have directed the relationships and balance of the various species in particular areas: but as a whole, and in spite of replacement of species, the African fauna has maintained an essentially constant composition throughout late Cenozoic times, which indicates that the broad ecological pattern did not vary greatly from the Upper Miocene onwards. The main ecological feature, viz., the savanna, may at times have been extensively altered by moister climates producing swampy conditions and even patches of forest. Then later, it would be altered again by a rather low rainfall. Nevertheless, drastic changes probably never occurred. There seems little evidence of a true forest fauna or of conditions too dry to sustain a normal steppe biocoenose (Cooke, 1963).

EFFECTS OF BIONOMICAL CONDITIONS ON THE EVOLUTION AND THE MIGRATION OF AFRICAN HIPPARIONIDS

It has been generally accepted that the three-toed hypsodont *Hipparion* were typical steppe forms. The savanna biotope is commonly emphasized as an important equid environment of the late Tertiary in the Great Basin of the United States, and the vast reduction of this habitat is strongly suggested as a suitable explanation for the extinction of *Hipparion* by the end of the Hemphillian (Shotwell, 1961). The life span of *Hipparion* in North America, namely, Clarendonian-Hemphillian, corresponds rather precisely to the extension of the savanna or steppe biotopes in this area. The recent observations of Sondaar (1961) strengthen this view: at Nombrevilla, in Spain, where *Decennatherium*, *Aceratherium* and *Mastodon* were recovered together with *Hipparion,* there is good evidence for a steppe environment. However, it has become clear that *Hipparion* is not restricted to such narrow ecological conditions. Thenius (1950) interprets *H. gracile* as a forest-dwelling form, and Kurtén (1952), on the basis of the Chinese 'Pontian' fauna, enforced the necessity of a reconsideration of this hypothesis. Because of the almost identical frequency (13%) of *Hipparion* in both the *gaudryi* and *dorcadoides* faunas, characteristic, respectively, of the 'forested' or 'southern', and of the 'steppe' or 'northern' provinces (the classical distinction of Schlosser, 1903), it was suggested that the Chinese *Hipparion* thrived in various surroundings, or at least that the genus as such was not exclusively a steppe form. Furthermore, it is not possible to make a direct correlation between the geographical distribution of a particular species and its biotope. Of the eleven different species recorded by Sefve (1927), some are confined to one locality and others turn up in widely different areas; in some instances, up to four different species have been recorded from the same fossil pocket.

The adaptability of hipparionids explains their extraordinary diffusion both in North America and in the ancient world, from Upper Miocene times onwards. Ecological conditions influenced structural features in different and varying ways, often difficult to explain. A similar geographical distribution and even the simultaneous presence of different fossil forms in one particular pocket are compatible with slightly different ecological niches or habitats in a small vicinity.

Under favourable conditions, observations have often been made of the association of more massive animals (with larger skull, shorter limbs, longer lateral digits and strongly plicated enamel) with open forested areas, characterized by soft and wet ground and tender vegetation. Lighter forms (with slender and elongated limbs, reduced lateral digits and simpler enamel pattern, elongated and narrow protocone and increasing hypsodonty) are found in a more xerophytic environment. Outside Africa, *H. primigenium, theobaldi, crassum* are representatives of the former group; *H. elegans, longipes, moldavicum, proboscideum, matthewi* are typical of the latter.

In general, the various characteristics observed in the African *Hipparion* are clearly indicative of animals adapted to a rather xerophytic steppe environment, although this never seems to have been very severe, and was certainly not constant everywhere. It has been stated above that nowhere in Africa are *Hipparion*-bearing sites located in true desert areas, and none of the forms recovered shows the extreme leptosome type displayed by some North American forms, e.g. *H. whitneyi.*

Hipparion africanum, with its large skull, short and massive limbs with lateral digits well developed, and rather less hypsodont teeth, is probably, from the inadequate data available, the least adapted to a steppe environment. However, the enamel plications and the narrow protocone show an orientation in that direction. It is difficult to assess whether this moderate expression of the steppe features corresponds to the precocity (in time) of *H. africanum* or reflects a humid and even partially forested environment.

The moderate transverse flattening of the protocone, the few and simple plications, the absence of additional stylids, the reduced hypsodonty and the small dimensions of the teeth of *Hipparion sitifense*, as well as the development of the lateral digits, are to be interpreted in the same way, although the absence of skeletal remains does not permit evaluation of the degree of massiveness.

The postcranial skeleton of the African Pleistocene forms is practically unknown. However, quite a few metapodials have been recovered in the Olduvai Gorge (Tanganyika). They are not particularly slender, and the lateral digits are still well developed, but the absolute length of the third metapodial is quite remarkable (metacarpal: 217–223 mm.; metatarsal: 242–260 mm.), being 5–9% longer than the corresponding elements from Pikermi (table 13).

The typical features of the dentition are strongly marked hypsodonty, the fairly complicated enamel pattern of the 'mark' walls, and the elongation of the protocone, which may become very flattened. The extreme flattening corresponds to a spectacular development of the additional stylids. It seems clear that these features must be interpreted as a positive pattern of adaptation to a steppe environment throughout Africa. However, the absence of any extreme slenderness of the metapodials and the complicated enamel pattern seem to strengthen the conclusion drawn from the faunal assemblages, viz. that the xerophytic environments of the African *Hipparion* were never very severe.

In the absence of sufficient cranial and postcranial remains, and because of the vicarious role played by the different tooth structures in their adaptation, it is unnecessary to comment any further on the special features of every single group so as to define more precisely the particular environment of each. Discussion is further limited by the fact that climate and biotope seem to have been rather uniform over a great part of Africa, and have certainly not undergone drastic changes. Throughout the continent, African *Hipparion* reflect in their known morphology the vastly extended steppe or savanna environment with an absence of much aridity.

UNPUBLISHED MATERIAL FROM THE VAAL RIVER DEPOSITS, SOUTH AFRICA

Sydney-on-Vaal and Pniel

The exact location of these two specimens is not known (fig. 6). Cooke (1949) describes other material from these sites which are in the northern Cape Province.

Material:

MMK 431 —left M^3
MMK 5225—left M_1 or M_2

These specimens were diagnosed by the authors as belonging to *Hipparion* in the collection of equid material which was kindly sent on loan by the Director of the McGregor Memorial Museum, Kimberley, South Africa.

MMK 431 (pl. 1)

This is a left M^3 with fairly high crown, in an early stage of wear.

Half of the ectoloph: fairly deep, flattened arc, being angulated at the parastyle and slightly angulated at the mesostyle.

The *parastyle*: the lateral angle is chipped away at the occlusal surface but near the base it is seen to be prominent. It is rounded and projecting, and is separated by a fairly deep groove from the ridged anterior angle. The surface is very oblique, almost in the same plane as the anterior surface.

The *mesostyle* is partly broken. It is fairly large and rounded, and it has a deep groove.

The *metastyle* tends to be broad with a ridged lateral angle, a smaller ridged posterior angle and a slightly concave surface, which is oblique.

The *protocone* is isolated. It is very long, being about half the length of the tooth. Anteriorly and posteriorly, it is sharply angulated. Its inner surface is flattened, and the lateral, outer surface is wavy, presenting an elongated cigar shape.

The *protoconule* is short and has a flattened arc. Posteriorly it becomes markedly angulated and turns laterally to join the base of the pli caballin.

The *hypocone* is elongated and flattened. Its two sides are almost touching.

The *hypoglyph* is deep and circular, demarcating an angulated hypostyle.

The *hypostyle* is joined to the metastyle by a concave arc of enamel.

The *pli caballin* is long, with unequal sides almost touching the protocone.

The *prefossette*: the anterior wall has a small plication and a very deep, narrow pli protoloph which tends to separate the medial part of the prefossette. The posterior wall has shallow plications and a deep narrow pli protoconule which tends to separate the medial part of the fossette.

The *postfossette*: the anterior wall has an irregular shape, with one plication and a very deep and narrow pli postfossette, which tends to separate off a flattened portion of the medial part of the postfossette. The pli hypostyle is duplicated. It is fairly deep, tending to isolate the medial part of the postfossette. The anterolateral angle of the postfossette tends to form a rounded, almost isolated pillar.

MMK 5225 (pl. 1)

A left M_1 or M_2, probably M_1.

The tooth is partly fragmented, especially on its inner aspect.

The *protoconid* is partly broken mesially. It appears that the other wall is flattened. The protoconid is shorter than the hypoconid. The metaflexid is elongated, flattened and biconcave with rounded anterior and posterior ends.

The *metaconid* is broken away. Its outer wall appears to be a flattened arc.

The *parastylid* is partly broken but its posterior wall turns sharply inwards and almost touches the outer wall of the metaconid.

The *metastylid:* the outer wall is flattened in a mesiodistal direction. The entoflexid is elongated, flattened and anvil-shaped.

The *entoconid* is rounded and pillar-like, being almost completely separated.

The *hypoprotonocid groove* is deep and wide, being rounded internally. It has a narrow mouth laterally and a bulge posteriorly.

The *ptychostylid* is finger-like, projecting anterolaterally. The sides are almost parallel and it has a narrow base.

The *ectostylid groove* is a marked indentation, broad and shallow.

The *hypoconid* has a flattened, elongated outer surface with posterior parts tapering sharply inwards.

The *ectostylid* is an isolated triangular pillar, the outer wall being chipped at the occlusal surface, but it can be seen to be flattened near the root. The inner wall is flattened and meets the outer wall at a sharper angle. The two walls are separated anteriorly by a somewhat irregularly concave base. The inner wall of the enamel joins the metaconid.

The *metastylid* forms a distinctive broad arc near the base of the tooth where it is intact.

MMK 5225	
A–P length	*ca* 23·5
Breadth	—
Max. A–P length protoconid	8·1
Max. A–P length hypoconid	12
Max. A–P length metastylid	6·2
Max. A–P length entoconid	4·6
Max. A–P length entoflexid	11·8
Max. A–P length metaflexid	6·8
Breadth hypoconid	5·6
Breadth entoconid	4·1
Crown height	*ca* 40

MMK 431	
A–P length	22·3
Breadth	21·1
Breadth/A–P	94·7
Protocone length A–P	12·5
Prefossette A–P length	10·8
Prefossette breadth	8·3
Postfossette A–P length	10·8
Postfossette breadth	7·0
Protocone A–P/total A–P length	56·2
Crown height	*ca* 70

TABLE 15. Dimensions (mm.) of MMK 431 and MMK 5225 from the Vaal River Deposits.

Taxonomic status

The above two teeth are referred to *Hipparion* (*Stylohipparion*) *libycum* (see p. 387–92 for diagnosis).

MATERIAL FROM LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

DESCRIPTION OF HIPPARION TEETH

Milk dentition

Material:

S.A.M. 11717—right DM^3
S.A.M. 11718—right DM^2

*S.A.M.*11717 (pl. 2)

A right DM^3 in medium stage of wear with a thick layer of cement particularly on the inner side.

Half of the ectoloph: it is shallow and has a slight arc. It is sharply angulated at the mesostyle and slopes up into the parastyle.

Parastyle: the lateral angle is chipped but it is seen to project markedly in a lateral direction near the base of the tooth. The surface is oblique and not quite in the same plane as the anterior surface of the tooth. There is a marked groove. The anterior angle is rounded and forms a ridge.

The *mesostyle* is stumpy, projecting, and flanging at the surface. A fairly marked overlap exists anteriorly. The surface is rounded, not grooved. The sides tend to be parallel.

The *metastyle* is slight and rounded.

The *posterior ectoloph* has a vertical bulge at the centre of its surface.

The *protocone* is oval in a mesiodistal direction, with the medial side slightly more flattened than the other side. It is distinctly separated from the other cones by a thick layer of cement.

The *protoconule* is an elongated, flattened arc with a fringed effect.

The *protoglyph* is deep and wide with an irregular base.

The *hypocone* is elongated, with a rounded medial side and a flattened lateral side, tending to come to a point posteriorly. Anteriorly it is almost completely isolated by a very deep indentation of the hypoglyph. Opposite, there is an indentation tending to separate it from the metaconule. The metaconule also has a fringed appearance.

The *hypoglyph* has a broad mouth. Lateral to the mouth of the hypoglyph, the enamel shows a V-shaped indentation.

The *pli caballin* is long, narrow and arched, tending to touch the protocone. At the base of the pli anteriorly, there is a trace of a duplication of the pli.

The *prefossette:* the anterior wall shows two deep plications and a deeper, narrow pli protoloph which tends to isolate the medial part of the prefossette. The posterior wall of the prefossette shows numerous plications which are markedly complex. One of the plications adjacent to the pli protoconule is large and has become isolated, forming the typical island lateral to the base of the pli caballin, and wedged between the medial portion of the pre- and postfossette. The pli protoconule is deep and narrow, almost touching the medial wall of the paracone. The pli prefossette is deep and complicated with a bifid base, tending to isolate the posterolateral angle of the prefossette.

The *postfossette:* the anterior wall has numerous plications that are not as complicated as the posterior wall of the prefossette. The pli postfossette is deep and narrow, tending to isolate the medial part of the postfossette. The posterior wall of the postfossette shows numerous plications, the most lateral one being rather deep. The pli hypostyle is deep and angulated, tending to isolate the medial wall of the postfossette.

*S.A.M.*11718 (pl. 2)

This is a right DM^2 of the same individual as 11717.

The anterior portion of the tooth is broken away but the remainder of the tooth shows the same features as 11717 with the following differences:

(*a*) Protocone is more elongated and more oval.
(*b*) Hypocone is more oval.
(*c*) Pli caballin is bifid medially.
(*d*) Pli protoconule is more complicated, and is duplicated.

Dimensions	*S.A.M.*11717 (DM^3)	*Hypsohipparion* (DP^3–DP^4)
A–P	31·9	28–34
Transv. breadth ..	26·2	23–26
Height	21	28–34
	(medium wear)	(early wear)

TABLE 16. Dimensions (mm.) of Langebaanweg milk molar compared with '*Hypsohipparion*'.

The features which are observable on the two Langebaanweg milk molars are identical to the description given by Dietrich (1942) for the *Hypsohipparion* material (19 individual teeth and 2 maxillary fragments). The isolation of the hypocone and the shape of the protocone of Dietrich's (1942) specimen illustrated in his figure 162 is typical of the Langebaanweg milk teeth. The dimensions of the latter fall into the range of Dietrich's specimens (table 15).

Lower permanent dentition

Material:

P_2:	Left: L947, L1465D (pl. 6). Right: L939 (pl. 5).
P_3 or P_4:	Left: L937, L943 (pl. 6). Right: L941, L946, L956, L1451A, L1465A (pls. 5, 6, 8, 9).
M_1 or M_2:	Left: L944, L952, L959, L1448 (pls. 6, 8). Right: L948, L954 (pl. 7).
M_3:	Left: L938, L949, L1465B (pls. 8, 9). Right: L1465F (pl. 2).

One specimen, L1465C, a M_1 or M_2, is excluded because of its size and its fragmented appearance which does not permit recognition of any typical hipparionid features.

The following specimens seem to belong to single individuals:

1. L937, L939.
2. L941, L943, L944, L948.
3. L954, L957.
4. L938, L959.

Classification of specimens according to wear:

A. *Unworn or slight wear:* L949.

B. *Early to medium wear:* L947, L1465D, L939, L937, L943, L941, L946, L1451A, L1465A, L944, L952, L959, L1448, L948, L938, L1465B, L1465F.

C. *Late wear:* L954, L957.

General description

All the Langebaanweg specimens obviously belong to one group, viz. *Hipparion* (*Hipparion*) *albertense baardi* subsp. nov. The dimensions are presented in table 17. The following features are distinctive:

1. *Entoconid:* Usually in P_2 it is more or less flattened in a bucco-lingual direction. It tends to be more rounded or quadrangular in shape in P_3, P_4, M_1 and M_2. However, in early wear a slight indentation of the enamel produces a ridged effect on its lingual surface mesially.

2. *Metaconid:* It has a slight tendency to a bilobed formation due to a fairly marked indentation on the mesiolingual aspect, which is only recognizable in a very early stage of wear.

3. *Double knot:* This is of the '*caballus*' type which is usually found in African *Hipparion*.

4. *Metastylid:* It has a triangular shape with the right angle found distally on the lingual side of the entoflexid.

5. *Metaflexid:* It constantly shows unique invagination on both its anterior and its posterior walls.

6. *Entoflexid:* The buccal wall shows varying degrees of waviness (plications).

7. *Internal depression:* This valley, lying between the metaconid and metastylid, is very broad, shallow and irregular in P_2, while in P_3–P_4 it is broad but slightly deeper giving it a U-shaped appearance.

8. *Ectostylid:* This is constantly absent, but on L952 there is a small elongated thickening of the enamel at the crown-root junction. However this 'bud' does not arise from the cingulum but extends from the posterior root onto the crown just above the junction (pl. 8).

9. *Ptychostylid:* Present on P_2, and occasionally it is very well-developed. In P_3–P_4 there are irregular indentations on the bucco-distal aspect of the protoconid, i.e. in the valley (external depression) opposite the ptychostylid. Inconstantly, slight indentations are seen on the wall of the hypoconid in the depression.

In M_1–M_2 the ptychostylid and the indentations are not constantly present. In M_3 these features are both absent.

10. *Protostylid:* It may appear as a laminated ridge or as an isolated pillar. Usually, when present, it extends along the whole height of the crown.

Specimens	Crown height	Length	Breadth	Breadth / Length	Length, ant. int. depression	Length, post. int. depression	Length, ant. depression / Length post. depression	Length, post. depression / Tooth length	Max. breadth of entoconid (projection)	Entoconid length (incl. talonid)	Entoconid breadth / Entoconid length	Hypsodonty Index	Height / Length
P_2 L 947	41·1	33·5	17	50·7	9·2	16·2	56·8	48·4	5·4	10·1	53·3	41·3	123
L 939			14·9			16·8							
L 1465D ..	50		18·2			15·8			5·1	10·1	50·5	36·4	
P_3 or P_4: L 937													
L 941	62·3	29·9	16·2	54·2	10·1	12·9	78·5	43·1	6·6	9·7	68·2	26	208
L 943	65	28·3	18·2	64·4	10·5	12	87·5	42·3	4·7	9·6	49	28	230
L 946	53·3	29·1	17·8	61·2	8·9	13·2	67·4	45·3	6·1	9	67·7	33·4	183
L 957			18·7										
L 1451A ..	69	32	18·6	58·2	11·6	13·9	83·4	43·4	5·4	8·5	63·5	26·9	216
L 1465A ..	70	30	16·3	54·3	8·8	14·2	62·1	47	5	9·3	53·7	23·3	233
M_1 or M_2:													
L 944	64·4	28·4	15	52·8	10·1	11·1	91·1	39·1	4·2	10·7	39·2	23·3	226
L 948	62·7	29·3	15·7	53·7	9·9	11·8	84	40·2	4·5	11·2	40·3	25	214
L 952	48·5	26·5	16·7	63·1	7·8	9·7	80·3	36·6	5	9·2	54·3	34·5	183
L 954	47·2	28·6	18·5	64·7	8	11·3	71	39·5	5·7	8·4	68	30·3	165
L 959	50·5	26·5	15·1	56·9	7·3	10·6	68·9	39·9	4·9	8·3	59·2	29·9	190
L 1448	62·6	28·9	16·1	55·7	8·6	11·4	75·6	38·7	4·6	11·4	40·4	25·7	216
M_3 L 938		31·2	11·5	36·9		9·3		29·9	4	14·6	27·4		
L 949	67	24·3	13	53·4								19·3	276
L 1465B ..	53												
L 1465F ..	53	25·3	13·5	52·7	7·7	10·6	72·7	41·8	6	6·8	88	24·5	209
Abs. mean	57·6	28·8	16·4	56·4	9	12·3	76·1	41·0	5·2	9·8	54·8	28·8	236
Mean of indiv. teeth, P_3–M_2	60·7	28·9	17·1	58·9	9·1	11·7	78·0	41·3	5·2	9·5	54·8	28·2	205
Mean of teeth in slight to med. wear: P_3–M_2	65·7	29·6	16·6	56·2	10·1	12·6	81·0	44·1	5·1	9·8	52·3	25·4	221

TABLE 17. Dimensions (mm.) of Langebaanweg lower permanent dentition

It can always be observed as a prominent ridge along the mesio-buccal border of the tooth. It is constantly present on P_3–P_4, and always present on M_1–M_2.

11. *Entostylid:* One entostylid has been observed (L946) *in* the entoflexid on the bucco-mesial aspect of the entoconid. It presents as a distinct flattened enamel island (pl. 8).

12. *Talonid:* Bilobed.

Upper permanent dentition

Material:

P^3 or P^4:	Left: L934, L936, L942, L1463, L1467E, S.A.M.11716 (pls. 1, 2, 5, 7). Right: L955, L1467C, S.A.M.11722, S.A.M.11724 (pls. 1, 3, 7, 9).
M^1 or M^2:	Left: L945, L953, L958, L1467B, L1467D, L1467H, S.A.M.11719 (pls. 3, 4, 9). Right: L940/950, L951, L956, L1459 (pls. 1, 2, 4).
M^3:	Right: L935 (pl. 9).
? premolar:	Left: S.A.M.11723 (embedded in plaster for sectioning).
Cheek teeth:	?: L1785 (fragment).

The following specimens probably belong to single individuals:

1. L935, S.A.M.11722, S.A.M.11724.
2. L1473, S.A.M.11719.
3. L942, L945, L956.
4. L940/L950, L951.
5. L934, L953, L955, L1459.
6. L1467B, L1467C, L1467D, L1467E.

A completely unworn tooth, L1467A, recovered from the same site as L1467B–E and H (viz. Baard's Quarry), does not present the typical features of hipparionids. It shows the same type of fossilization as the other L1467 specimens, but, because of its exceptional dimensions (*ca.* 32 × 28 mm.), it is provisionally excluded.

The teeth are classified according to their degree of wear as follows:

(*a*) *completely unworn or just erupting:* S.A.M.11716.

(*b*) *early wear:* L1463, S.A.M.11719.

(*c*) *moderate wear:* L935, L940/950, L942, L945, L951, L956, L1467B–E, S.A.M.11722, S.A.M.11724.

(*d*) *advanced wear:* L934, L936, L953, L955, L958, L1459, L1467H.

General dimensions (mm.) of P^3*–*M^2*:*

1. A–P length: range of variation: 21·8–30·5
   Mean: 26·6
2. Transverse breadth: range of variation: 23·5–30·3
   Mean: 26·9
3. Breadth/length index: range of variation: 90·7–111·4
   Mean: 99·1
4. Hypsodonty:

Means	*Absolute crown height* (mm)	*Hypsodonty Index** (%)	*Height/length Index* (%)
All P^3–M^2	49·7	49·6	193
Unworn teeth	70	36·4	249
Early wear	63–69·2	42·3	233
Moderate wear	51·8	51·6	201

* The ratio between crown height and breadth.

To indicate the relationships between the Langebaanweg dimensions and those of other African *Hipparion*, the following data has been extracted from table 18 and summarized (table 19):

	H. africanum	*H. sitifense*	'*Hypsohipparion*' *albertense* (South Serengeti)	Langebaanweg
A–P length	23–27	19–23	25–31	26·6
Transv. breadth	20·5–26	18–22·5	24·5–29·5	26·9
Breadth/length	97·2		95·1	99·1
Height (unworn and early wear)	48–60		70	67·4
Hypsodonty index (unworn and early wear)	38·3–41·3			39·3
Height/length index (unworn and early wear) ..	223–240		249	238

TABLE 19. Comparison of dimensions (mm.) of Langebaanweg upper teeth with summary of data of other African *Hipparion*.

From these figures, it is clear that the Langebaanweg *Hipparion* has hypsodont upper teeth, but this hypsodonty has not reached the same degree as it has in the South Serengeti specimens.

Description of selected individual teeth:

Two specimens, an unworn left premolar (S.A.M.11716) and a left M^1 or M^2 (S.A.M.11719) in early wear, have been selected for detailed

	Height	Length	Breadth	Breadth / length	Protocone length	Protocone breadth	Protocone breadth/length (=Shape index)	Protocone length / Tooth length (=Length index)	Hypsodonty Index	Height / Length
L 934	42	27·5	28	102	10·8	5·2	48·2	39·3	66·7	
L 935	40·1	23·6								
L 936	27				7·8	4·6	58·9			
L 940/50	51				8·4	4	47·7			
L 942	54	29·2								
L 945	53	25·7								
L 951	56	25·5	27·2	107	9	4·8	53·3	35·3	48·6	220
L 953	43	24·1	26·8	111·4	11	5·2	47·3	45·6	62·3	
L 955	40	27·8	27·3	98·2	10	5	50	36	68·3	
L 956	45	24·2								186
L 958	23	21·8	23·5	107·8					102	106
L 1459	48·6	24·1	24·3	101	7·6	3·8	50	31·5	50	143
L 1463	69·2	28·9			8·3	4·2	50·5	28·7		239
L 1467B	54·2	24	26·1	108·9	9	4·4	48·9	37·5	48·3	226
L 1467C	56·8	30	28·8	96·1	9	5	55·6	30	50·8	190
L 1467D	54·2	26·5	28·2	106·4	8·3	4·8	57·8	31·3	52·1	204
L 1467E	52	28·9	30·3	104·9	9·4	4·2	44·7	32·5	58·2	180
L 1467H	45·9	30·5			9·3	4·8	51·7	26·5		151
S.A.M. 11716	70	28·1	25·5	90·7	12	5	41·7	42·7	36·4	249
L 11719	63	27·8	26·6	95·7	11	4	36·4	39·6	42·3	227
S.A.M. 11722	54	28·1								
General Mean	49·7	26·6	26·9	99·1	9·3	4·6	48·9	35·1	49·6	193
Mean of Individual Teeth, P_3 to P_4 ..	51·6	28·7	27·9	98·3	9·6	4·7	49·9	34·8	56·0	214
Mean of Individual Teeth, M_1 to M_2 ..	48·8	25·4	26·1	106·2	9·2	4·4	49·1	35·4	57·9	183

TABLE 18. Dimensions (mm.) of Langebaanweg upper permanent teeth.

description. They display the characteristic features of the other Langebaanweg specimens. The typical features of the whole group will be outlined below (see p. 376).

*S.A.M.*11716 (pl. 5)

A left P^4, unworn.

Occlusal surface: Paracone and metacone are V-shaped and they are curved towards the medial side. The protoconule and metaconule are less angulated than the lateral cone and tend to curve less towards the medial side. The paracone and the metacone tend to overhang the fossettes.

Protocone: The cement is split off near the apex of the tooth. It is lozenge-shaped, completely isolated and the apex tends to curve in a buccal direction.

Shape: The tooth has medium hypsodonty. It has a gentle convexity from root to apex in a lingual direction. The styles stand out as clear costae, forming deep hollows between them. One-third of the distance from the occlusal surface, the hypoglyph becomes increasingly deep so that in the upper half of the tooth the hypocone becomes well demarcated.

Appearance of the tooth, sectioned just above the middle:

The *halves of the ectoloph* are deep and arc-shaped with a slight angularity at the mesostyle.

The *parastyle* is prominent. Most of the prominence is taken up by the lateral angle which is rounded. The surface, flattened but with a slight groove, is markedly oblique and almost in the same plane as the anterior (mesial) surface of the tooth.

The *mesostyle* is prominent, and, because its rounded surface is flanged, it overlaps the buccal depressions on both sides.

The *metastyle* is very slight (almost negligible), its rounded ridge decreasing in prominence from the occlusal surface to the root.

The *protocone* is slightly elongated and oval. Completely separated from the protoconule.

The *protoconule* is a flattened arc, angulating fairly sharply toward the pli caballin.

The *hypocone* is elongated posteriorly, rather flattened. There is no tendency to isolation. There is a deep V-shaped hypoglyph, and the hypostyle is angulated.

The *pli caballin* is bifid, the posterior process just touching the protocone.

The *prefossette:* There are plications which are so deep and complex that the centre of the prefossette is very narrowed and reduced. The anterior wall is plicated and the antero-lateral angle is knob-shaped, tending to be separated from the prefossette. The pli protoloph is deep and narrow, touching the very deep and narrow pli protoconule so that the medial portion of the prefossette is an almost isolated triangle. The plications on the posterior part of the prefossette are very deep and complex. One of the more medial ones tends to flange out to form an almost isolated irregular pillar just lateral to the base of the pli caballin and wedged between the most medial part of the prefossette and postfossette.

The *postfossette:* The plications on the anterior wall are also deep and complicated but not as numerous as on the posterior wall of the prefossette. The pli postfossette is deep and irregular-shaped, almost touching the base of the pli hypostyle, thus tending to isolate an oval portion of the medial part of the postfossette. Just lateral to the pli postfossette, the plications tend to isolate a small rounded pillar.

*S.A.M.*11719 (pl. 3)

A left M^1 or M^2.

It is slightly higher crowned than S.A.M.11716, and slightly less curved.

Half of the ectoloph: The paracone is deep and quadrangular-shaped, angulated at the mesostyle and parastyle.

The *parastyle* is prominent and narrow. The sides tend to be parallel, slightly widening at the base.

The *metastyle* is partly broken. It forms a slight ridge.

The *protocone* is elongated, oval and angulated anteriorly and posteriorly. It is completely isolated.

The *protoconule* forms a broad flattened arc, slightly angulated toward the pli caballin.

The *pli caballin* tends to be duplicated with the anterior tongue longer and almost touching the protocone.

The *hypocone* is rather short, tending to be separated from the metaconule. There is a very deep hypoglyph that is very broad-mouthed.

The *prefossette:* There are a few anterior plications, continuous with a deep narrow pli protoloph which tends to isolate the medial wall of the fossette. The pli protoconule is shallow. The plications tend to be absent. However, the original plications have become isolated to form an irregular circular island (prefossette loop) just lateral to the pli caballin and wedged between medial parts of the pre- and postfossette.

The *postfossette:* The plications tend to be worn away but it can be seen that they were complex anteriorly. The pli postfossette is very deep and touching the medial wall of the metacone. The pli hypostyle is deep, angulated and wide, and it has almost isolated the medial part of the postfossette.

Typical features of the upper teeth:

1. *Protocone:* The characteristic isolated protocone of *Hipparion* is observed in all the complete molars mentioned above. On L935, L942, L945, L956, S.A.M.11722 and S.A.M.11724, as well as on L1785, the lingual portion of the tooth has been broken away along the pre- and postprotoconal grooves and

does not allow any observations of the protocone. However, there is no reason to suppose that the protocone in these teeth displayed different features, and it is as umed that the description proposed for the other teeth applies to these specimens as well.

The protocone is elongated in a mesiodistal direction, and clearly shows angulation in those teeth not worn or in early stages of wear. It becomes more elliptical or oval in the later stages of attrition. Thus the shape index (breadth/length) varies from 36·4 to 58·9, with an absolute mean of 48·9 for all the teeth and an average of 48·3 for those teeth which have not reached an advanced stage of wear (table 14).

The length index ranges from 42·7 to 28·7, with a mean of 35·1 for all the teeth, of 34·7 for teeth in early wear, and of 35·7 for those in advanced wear. This smaller range of variation indicates that the actual length of the protocone does not change as much with wear as does the breadth, and that the apparent elongation of the protocone of the unworn teeth is more due to its narrowness than to its actual length.

Thus it is clear that the Langebaanweg specimens display this typical feature of African hipparionids (see p. 355). In so far as the few available specimens in varying stages of attrition from other African sites permit comparison, there seems to be a great similarity in the shape and dimensions of the protocone between *H. africanum* and the Langebaanweg *Hipparion*. The 'African' character is even more strongly expressed in '*Hypsohipparion*' *albertense* (tables 14, 20; figs. 12, 13).

2. The *hypocone* is commonly angulated, tending to isolate in early wear. Later it becomes more rounded, and the isolation from the metaloph is no longer discernible, the anterior groove tending to disappear. Parallel variations in the shape of the hypoglyph are observed with progressive attrition.

3. The *marks* are constantly closed.

4. The *plications* are numerous, profound and often bifurcated, especially in early or moderate stages of wear (e.g. S.A.M.11716, L940/950, L951). The enamel pattern is most complex on the posterior wall of the prefossette and on the anterior wall of the postfossette. The plications have been counted according to the method suggested by Gromova (1952), and the average plication formula for the Langebaanweg specimens has been established:

$$\frac{(0\text{–}3)-(1{\cdot}5\text{–}6{\cdot}5)-(0{\cdot}5\text{–}5)-(0\text{–}1)}{(1\text{–}2)}$$

There is a constant isolation of a prefossette loop in the lingual-distal angle of the prefossette, being bilobed and large in early stages of wear, and rather triangular and arrow-shaped in advanced wear (e.g. specimens L934, L951, S.A.M.11716; best example is the latter on pl. 5).

The pli caballin is constant, often double, in early and moderate stages of wear. It is not observed in very advanced wear.

In all these features there is not a clear basis of distinction between the

UPPER TEETH	Length	Breadth	$\frac{\text{Breadth}}{\text{Length}}$	Protocone length	Protocone breadth	$\frac{\text{Protocone length}}{\text{Tooth length}}$ (=length index)	$\frac{\text{Protocone breadth}}{\text{Protocone length}}$ (=shape index)
P^2	39	29	74·4	13·6	6·2	34·7	45·5
P^3	31	27·5	88·6	13·2	6·1	43·5	46·2
P^4	31	29·5	95	13·7	5·6	43·6	40·9
M^1	27·3	27	99	12	5·4	43·9	45
M^2	25	24·5	98·1	11·3	4·7	45·4	41·7
M^3	24·2	24	99	11·5	4·7	47·4	40·9
LOWER TEETH							
P_2	33	15·5	47				
P_3	29·5	17·5	59·3				
P_4	28·5	21·5	75·3				
M_1	27	18·5	68·6				
M_2	27	16	59·2				
M_3	26·5	15	56·6				

TABLE 20. Dimensions (mm.) of random teeth of '*Hypsohipparion*' *albertense* Dietrich (1942, table XIII, figs. 88–89) from South Serengeti. Measurements communicated by Dr. K. H. Fischer, 1964.

Langebaanweg material and the '*Hypsohipparion*' upper teeth from Serengeti, the plication formula of which is found to be very similar:

$$\frac{(0\text{–}4{\cdot}5)-(2\text{–}5)-(0{\cdot}3)-(0\text{–}2)}{(0\text{–}3)}$$

POSTCRANIAL EQUID REMAINS

At Langebaanweg seven phalanges have been recovered. Because of their equid structure it could not be excluded *a priori* that they belonged to *Hipparion* represented by the dental remains at the sites. It must be pointed out that a few teeth of *Equus* (to be described in another publication) have been recovered at these sites. However, they only constitute 10% of the total number of equid remains collected thus far. Consequently, because of the lack of comparable *Hipparion* remains from Africa, the Langebaanweg specimens are hesitantly included in this paper, more as a documentation for comparison by others than a positive contribution to the reconstruction of the *Hipparion* limb.

Material:

First phalanges: L1456, L1462A, L1462B, L1462C (pls. 10, 11).
Second phalanges: L1449, L1462D (pl. 12).
Third phalanges: L1444 (pl. 13).

All the absolute dimensions namely, length, diameter of the proximal and distal ends and of the median shaft are usually considerably larger than those (after Gromova, 1952) of the three species of *Hipparion* compared, i.e. *elegans*, *moldavicum* and *longipes* (table 21). There is virtually no overlap between the two series, although the highest figures for *H. longipes* (the largest of the three species) are sometimes very close to the lowest figures for Langebaanweg (table 22). Sondaar (1961) mentions one first phalanx of the forelimb third digit with an exceptional length of 69·8 mm. In Europe the highest *mean* is known from Eppelsheim, *H. primigenium*, with a length of 64·3 mm. and a proximal extremity breadth of 41·3 mm.

A comparison of the dimensions of the proximal end of the first phalanges from Langebaanweg with the breadth of the distal extremity of metatarsal III from Olduvai and South Serengeti (tables 12, 13) makes it obvious that the Langebaanweg specimens require a much broader metatarsal for articulation. For *H. longipes* the respective breadths of the distal end of metatarsal III and the proximal end of the first phalanx are 40 mm. and 42 mm. The mean distal breadth of the known specimens of metatarsal III from East Africa is 44·7, the maximum being 48 mm., the widths of the proximal end of the first phalanx at Langebaanweg are 50–56 mm. Therefore, either the Langebaanweg specimens belong to a slightly more massive limb of an *Hipparion* or else they belong to *Equus*.

Compared with *Equus zebra* and *burchelli*, the Langebaanweg specimens are larger in a number of dimensions, but there is a greater amount of overlapping

PHALANX I, THIRD DIGIT	Langebaanweg				*H. elegans*[a]		*H. longipes*[a]		*H. moldavicum*[a]		*E. zebra*[b]		*E. burchelli*[b] (ZIN 18411) (female)	
	L1462A	L1462B	L1462C	L1456	Fore	Hind	Fore	Hind	Fore	Hind	Fore	Hind	Fore	Hind
A. Total length	70·2	79·0	77	75·5	58·2	55·5	67·5	69·5	59·6	59·3	74	70	75	70
B. Breadth prox. end	56	55·5	54·0	50	30·6	30·8	41·7	42	32·9	34·6	44	44	48	50
B/A Index	79·8	70·4	70·2	66·2	52·3	55·4	63·2	60·4	55·4	60·1	60	60·5	64	71·3
C. A–P diam. prox. end	44	37·4	36·8	40	24·1	26·2	31·7		25·9	28	31	32	32·5	35
C/A Index	62·7	47·4	47·7	52·9	41·2	47	47·1	48·9	43·5	49·7	41·9	45·7	43·4	50
C/B Index	78·6	67·4	68	80	78·7	85·5	76	80·9	78·6	81·4	70·5	72·7	67·7	70
D. A–P diam. prox. artic. surf.	32	27·3	27	27	20·8	21·7	28·2		22·6	23·8				
E. Breadth distal end	43·3		41·4	41·2	25·9	26·2	34·8	34·5	27·7	28·9	37	37	40	40
E/A Index	61·7		53·7	54·5	44·4	47·4	53·5	49·6	46·4	50·3	49·1	50·8	53·4	57
F. A–P diam. distal end	27·4	25·9	23·2	25·1	15·5	16	21·5	21	17	17·3	22	21	22	22
G. Breadth shaft, median	41·9		34·1	36·6	12·3	22·2	28·7	30·3	22·8	24	27·5	27·5	32	32
G/A Index	59·7		44·3	48·5	35·6	39·1	42·6	43·6	38·2	42·1	37·2	36	42·7	45·7
PHALANX II, THIRD DIGIT														
			L1462D	L1449										
A. Maximum length			48·9	47·2	33·7	34·4	39·9	42	35·7	34·4	37	37	40	40
B. Length ant. surf. (median)			38·1	34·1	27·8	27·8	33·2	34·5	29·8	29·7	29·5	30	32·5	34
C. Breadth prox. end			51·6	47·8	30·2	30·6	39·1	39·5	32·8	33·1	42·5	41	46	46
C/A Index			105·6	101	89·3	89·3	98	94·0	92·2	96·6	114·7	111	115	115
D. A–P diam. prox. end			31·0	31·8	21·5	22·5	28·3		22·8	24·4	25·7	26·5	29	29
E. Breadth distal end				41·7	29·4	27·2	39·4	35	31·2	28·8	38·5	35	43	40
E/A Index				88·3	87·2	70·5	98·5	83·3	87·4	84·4	104	94·6	107	100
F. A–P diam. distal end			25·4	24·1	16·3	16·7	21·5	23	17·7	17·9	27	27	28	29
F/E Index				57·8	53·6	61	54·4	65·7	56·6	62·9	70·2	77·2	65·2	72·5
G. Min. breadth shaft			42	38·4	25·2	24·6	32·9	32·5	26·7	26·6	37	34·5	41·5	39
G/A Index			85·9	81·3	77·5	73·5	82·7	77·4	77·2	76·8	100	93·2	104	97·5

TABLE 21. Dimensions (mm) of the Langebaanweg limb bones compared with Eurasiatic *Hipparion* (means) and modern African *Equus* (*zebra* and *burchelli*).

[a] According to, or calculated from Gromova (1952).
[b] According to, or calculated from Gromova (1949).

and the dimensions are closer together than in the comparisons with the *Hipparion* above (figs. 14, 15; tables 22, 23, 24). The difference between the Langebaanweg and the *Equus* proximal phalanges average 6%.

The situation is less clear for the relative dimensions. The lowest index for Langebaanweg is constantly smaller than the highest for *burchelli*, and very often even overlaps *H. longipes*. The relatively smaller indices indicate that in the Langebaanweg specimens the length versus the breadth and the breadth versus the A–P diameter are somewhat greater than in *Hipparion* and *burchelli*. In these limited comparisons it seems that, to some extent, the Langebaanweg architecture differs from these groups.

It cannot be denied that the Langebaanweg measurements fit more satisfactorily within the range of *Equus*, but more material and comparisons are needed before this discussion can be taken further.

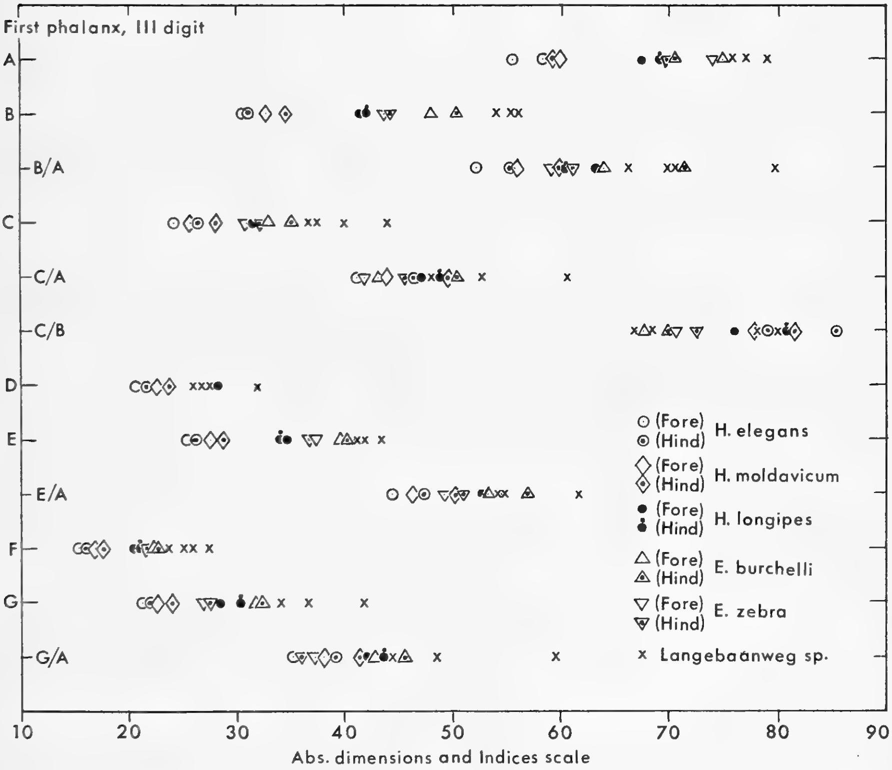

FIG. 14. Absolute dimensions and indices scale for the first phalanx of the third digit in various species of *Hipparion* and *Equus* compared with the Langebaanweg specimens.

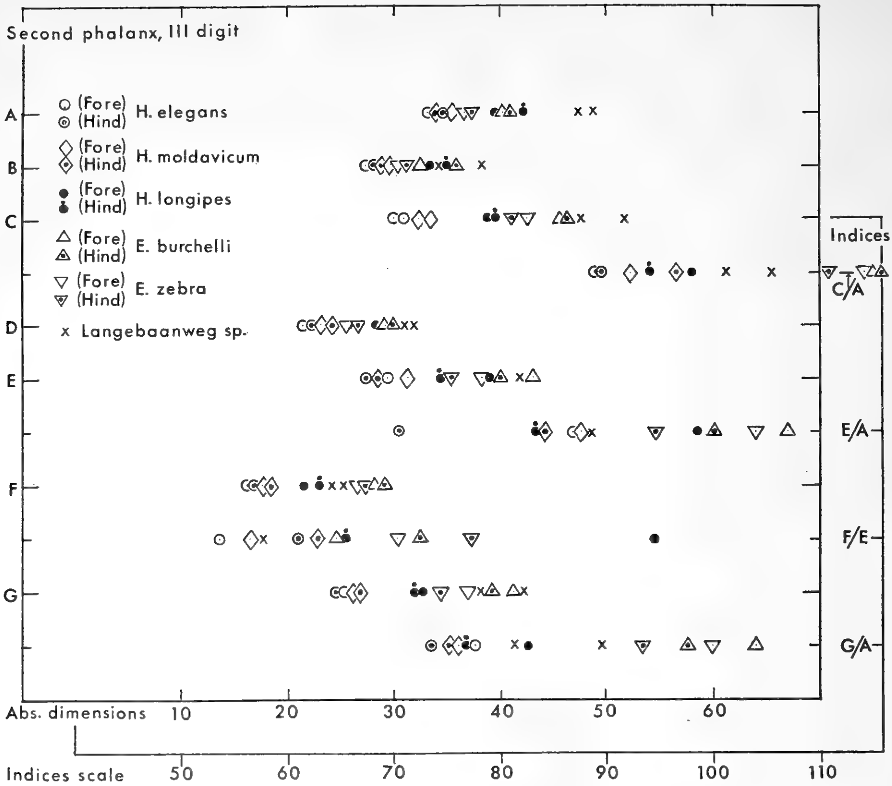

FIG. 15. Absolute dimensions and indices scale for the second phalanx of the third digit in various species of *Hipparion* and *Equus* compared with the Langebaanweg specimens.

ORIGIN AND DIFFERENTIATION OF AFRICAN HIPPARIONIDS

In recent years, it has become evident that Africa was more a true and independent centre of evolution and dispersion than a refuge for 'Pontian' Eurasiatic animal forms. Discoveries at different levels of the history of the mammals and in different regions have supported this concept proposed originally by Pilgrim (1941), and later vindicated by, *inter alios*, Arambourg (1959) and Cooke (1963).

Several independent observations have definitely established the original role played by Africa in the development of late Tertiary mammals in general, and have illustrated its contribution to the establishment of the 'Pontian' fauna in particular:

(i) The endemic evolutionary differentiation of the Proboscidea and Hyracoidea from the Oligocene onwards;

A. ABSOLUTE DIMENSIONS

	H. longipes (largest)	*Equus burchelli* (largest)	Langebaanweg (smallest)
PHALANX I			
Total length	69·5	*75·0*	70·2
Breadth prox. end	42	50	50
Diameter prox. end	31·7	35	36·8
Diameter prox. artic. surf. ..	*28·2*		27·3
Breadth distal end	34·8	40	41·2
Diameter distal end	21·5	22	23·2
Breadth median shaft	30·3	32	34·1
PHALANX II			
Maximum length	42	40	47·2
Length median ant. surface ..	*34·5*	34	34·1
Breadth prox. end	39·5	46	47·8
Diameter prox. end	28·3	29	31
Breadth distal end	39·4	*43*	41·7
Diameter distal end	23	*29*	24·1
Minim. breadth shaft	32·9	*41·5*	38·4
PHALANX III	*H. moldavicum*		
Anterior length	54·1	47·5	61
Maximum breadth	54	59	72

B. INDICES

PHALANX I	*H. longipes*		
Prox. breadth/length	63·2	*71·3*	66·2
Prox. diam./length	*48·9*	*50*	47·4
Prox. diam./breadth	*80·9*	*70*	68
Distal breadth/length	53·5	*57*	53·7
Breadth med. shaft/length ..	43·6	*45·7*	44·3
PHALANX II			
Prox. breadth/length	98	*115*	101
Distal breadth/length	*98·5*	*107*	86·3
Distal diam./breadth	*65·7*	*72·5*	57·8
Minim. breadth shaft/length ..	*82·7*	*104*	81·3

TABLE 22. Comparison of dimensions (mm.) and indices of Langebaanweg smallest phalanges with the largest of *H. longipes* and *E. burchelli*. The italicized figures indicate those dimensions in which the Langebaanweg specimens are smaller.

PHALANX III	Langebaanweg	*H. medit.* (Pikermi)	*H. elegans*		*H. moldav.*		*E. burchelli*	
			ant	*post*	*ant*	*post*	*ant*	*post*
Length ant. surface ..	61	50	45·8	47·2	51·8	54·1	46	47·5
Maximal breadth ..	72	55	46·3	44·2	54	43·4	59	58·5
Index B/L ..	118	110	101·1	93·6	103	78·9	128	123

TABLE 23. Dimensions (mm.) of phalanx III of Langebaanweg and of some Eurasiatic species and *E. burchelli*.

	Hipparion		*Equus*		Langebaanweg			
	elegans	*moldav.*	*cab* s.l.	*zebra*	L 1444 L 1449	L 1444 L1462D		
Index of length Phal. III, 3d digit/Phal. II	ant. 135·9 post. 140·1	145·1 157·3	116·4 118·8	110 116·9	127	123		
Index of length III/I	ant. 78·7	86·9	64·2	57·6	L1444	L1444	L1444	L1444
	post. 85	91·2	66·4	61·3	L1462A	L1462B	L1462E	L1456
					85·3	75·8	77·7	79·3

Table 24. Comparison of relative lengths of phalanges.
(In the case of Langebaanweg indices have been calculated from the possible associations.)

(ii) the presence in the Lower Miocene of East Africa and in the Upper Miocene deposits of North Africa of a complete specialized faunal assemblage with typical African characteristics before parallel diversification took place in Europe;

(iii) the constant specific differences between comparable Pontian Eurasiatic and African forms; and

(iv) the African pre-Pleistocene differentiation of Bovidae with the evidence of the local origin of Cephalophini, Neotragini and probably the Alcelaphini (Wells, 1957).

It is suggested that, because of the stability of its climate, its geography and its vegetation, Africa has provided a suitable habitat throughout the Tertiary. Furthermore, groups have evolved and later have developed parallel forms. Elsewhere, these have become extinct, but survival was favoured in Africa. Even in modern times this seems to be the case, e.g. the Proboscidea, Giraffidae, Artiodactyla, and Anthropomorpha. The surviving species, far from being newcomers and refugees from outside, are local representatives of a fauna which has disappeared elsewhere.

Arambourg (1952) and Cooke (1960), *inter alios*, demonstrated that the Plio-Pleistocene forms of elephants may have differentiated within the continent of Africa, paralleling the steps of progress observed elsewhere, but not necessarily linked to Eurasia by periodic invasions as was previously thought.

Analogous circumstances may have influenced the origin and the differentiation of the hipparionids. There is abundant evidence that *Hipparion* evolved in North America from some *Merychippus* stock in Miocene times. Migration probably took place at a rather rapid pace, *Hipparion* being found on both sides of the Mediterranean basin before the end of the Miocene. *Hipparion* has been recovered from brackish water deposits dating from the Sarmatian in the area of Sebastopol (Borissiak, 1914) and Istanbul (Chaput and Nafiz, 1934; Chaput and Gillet, 1938). It is also known from the Upper

Tortonian Beds in the Rhone Valley (Denizot, 1939). Villalta and Crusafont-Pairo (1946a, b, c; 1947; 1948) have described *Hipparion* from the Vallés–Penedès area in Catalonia, in continental and brackish water deposits intercalated in sediments ranging from the Burdigalian to the Tortonian, with *Hipparion* appearing in the Upper horizon (Vallesian, parallel to the Meotian of Eastern Europe, i.e. Upper Sarmatian). In the basin of Teruel, *Hipparion* was recently found to appear in Los Algezares in some gypsum intercalation of the middle light-red clayish deposit overlying the Los Monotos series, dated as the Vindobonian (Sondaar, 1961).

Parallel to these occurrences, and probably very close to the last one in the chronological sequence, hipparionids have been recorded in the Upper Miocene of the Maghreb, i.e. *H. africanum* (Arambourg, 1959) from Oued el Hammam and Marceau.

It is still not known which Atlantic or Pacific bridge the hipparionids used to invade the Old World. The only reasonable assumption which has been proposed is that the migration route probably lay very much to the north. The absence of any important migration of Camelidae and Antilocapridae from America, or of hyaenas, antelopes and giraffes to America, provide good evidence in support of this high latitude of the migratory passage (Simpson, 1947). On the other hand, and as a confirmation, the most ancient Old World *Hipparion* seem to have been much better adapted to a humid and forested biotope of temperate, or even cold, climates than most of the American forms, which evidence a drier and steppe environment. Rather than indulging in some fantasy that a direct connection between America and Africa existed by way of a hypothetical chain of islands across the North Atlantic (Joleaud, 1919a, b), it seems more reasonable to accept the normal Bering route which certainly meets the climatic requirements of the migrants.

Furthermore, in the present state of our knowledge, it is neither possible to formulate any conclusion about those species of *Hipparion* responsible for the origin of the African group, nor to reconstruct the phyletic sequence of African *Hipparion*. The fact that *H. africanum* is found contemporaneous with, or possibly prior to, every other European form and that it already shows typical African differentiation, refutes a European origin of the group from any of the known 'Pontian' species. On the other hand, and for the same reasons, there seems at present to be no possible way of establishing an African origin for the European hipparionids. However, the metapodials of *H. africanum* are rather strong and the lateral digits are well-developed, which must be interpreted as 'primitive' features, less specialized than in most of the early Eurasiatic forms. But other characters, e.g. the articulation of the external cuneiform with the second metatarsal only, a typical mechanical adaptation to tridactyly, show more primitiveness in the relatively contemporaneous *H. catalaunicum* (Pirlot, 1956). It seems that here there is evident some expression of an independent mosiac pattern of evolution in different (Eurasiatic and African) groups. Although they obviously descend from a common ancestral stock, they have been precociously isolated on different continents and have developed their independent stages of evolution.

For several reasons it is not possible to depict accurately the actual evolutionary development of the African *Hipparion*. As has been stated previously, the fossil record is rather poor. At more than thirty sites where Pleistocene hipparionids have been recovered, the available material consists almost exclusively of isolated teeth, and virtually nothing is known of the skeleton. Furthermore, because of the plasticity of the group, and of the fluctuating character of many features, which seem to be highly adaptive to ecological requirements, it would appear hazardous to reconstruct artificially an orthogenetic series. Gromova (1952) states that the diversity among Old World hipparionids usually remains at the level of a particular genus and does not exceed specific differences. On the basis of our present knowledge, this typifies the African representatives of the group: overall dimensions, proportions, size of the teeth, plications of the enamel, development of stylids, elongation of the protocone, preorbital fossae and development of lateral digits. Most of these features are readily adaptive and susceptible to functional interpretation under climatic and ecological circumstances.

On the other hand, it cannot be denied that parallel to the ecological adaptation which has been emphasized previously, some general and fairly continuous trends have characterized the evolution of the hipparionids throughout the world. From *Merychippus* onwards, in late Cenozoic times, the various groups have shown a permanent tendency to

(*a*) increased hypsodont dentition;
(*b*) lengthening and flattening of the protocone;
(*c*) reduction of the external depression in the lower teeth;
(*d*) development of additional stylids; and
(*e*) evolution of the double knot in three different but constant directions, i.e. towards a '*stenonis*' type in America, towards a '*Hipparion*' type in Eurasia, and towards a '*caballus*' type in Pleistocene Africa.

There is insufficient evidence to state that the reduction of lateral digits and the elongation of the third metapodials have obeyed a clearly directed evolutionary trend. The enamel pattern has not been controlled by any constant progressive influence, but it has only responded to the changing ecological conditions.

There is little doubt that these trends have been developing on more or less parallel and independent pathways and at different and varying speeds along the several lines, with the resulting mosaic type of differential radiating evolution.

For the reasons stated earlier in this paper, the degree of relationship between *Hipparion africanum* and the Pleistocene stock of African *Hipparion* is not obvious. There is a great gap in our record, and this is not sufficiently bridged by the fragmentary remains of *H. sitifense*. Therefore it is difficult to appreciate to what extent the distance between *H. africanum*, *H. sitifense* and the Pleistocene forms illustrates the chronological or the phyletic separation.

All Pleistocene African *Hipparion* show a marked progression in the expression of trends (*a*), (*b*) and (*d*) above; and together with the special orientation of trend (*e*), this vindicates their common origin and their genetic homogeneity.

It is suggested that the 'African features' and the more stable biotope are responsible for the prolonged presence of *Hipparion* in Africa during the Pleistocene. However, the differential expression of these trends along various lines of evolution allowed for some differentiation during this period.

A basic group, represented by '*Hypsohipparion*' and the Langebaanweg specimens, is characterized by a greater conservatism in the building of additional stylids: the ectostylid is constantly absent. The flattening of the protocone and the hypsodonty are strongly manifested in '*Hypsohipparion*', but are less marked at Langebaanweg. This basic group seems to be restricted to the Lower Pleistocene (the basal grey tuffs of Serengeti and the archaic forms at Langebaanweg).

'*Stylohipparion*' is more advanced in the expression of additional stylids: the constancy of the ectostylid indicates a group subjected to a particularly clear trend of evolution ('*Entwicklungswucht*' of Dietrich, 1942) in the process of building a new *Hipparion* form. This successful group has rapidly extended throughout the continent, being found in Lower and Middle Pleistocene deposits from the Maghreb to the northern Cape Province, and possibly differentiated on a geographical basis. The oldest record derives from North Africa. It is not impossible that the group migrated eastward and then southward, and, after being widespread throughout Africa, became extinct first in North Africa during the Lower Pleistocene, then in East Africa where it is still found in the Middle Pleistocene deposits.

TAXONOMIC STATUS OF THE AFRICAN HIPPARIONIDS

Family **Equidae** Gray 1821

Sub-family **Equinae** Steinmann & Döderlein 1890

Elongated face with completely closed orbits. Molar teeth, at first moderately, then later strongly hypsodont, with closed valleys, the external portions of which become isolated in the shape of pits, called fossettes or marks. Abundant cement layer on the outer surface and in all the hollows of the tooth. Complete homeodonty, the largest tooth being P_2 of a triangular prismatic shape, pointed forwards. Ulna is first fused with the radius; however, later in the development, it is reduced to its proximal portion (olecranon process), which has the appearance of a mere apophysis of the radius. Limbs are tridactyl in primitive forms, with complete lateral digits although they no longer reach the ground, except during galloping, when they become functional. In advanced forms, however, limbs are monodactyl, and the lateral metapodials are reduced to small splints, eventually only persisting in their proximal portion. Unguligrade.

HIPPARION de Christol 1832

Face is relatively short, with profound lacrimal fossa. Prismatic hypsodont molars, of moderate height, slightly curved, with more strongly plicated enamel pattern than in *Equus*. The protocone pedicle has narrowed, isolating the protocone, giving the appearance of a column which is attached to the protoconule only at its base. On its occlusal surface, the protocone shows an island of dentine, circled with enamel, of a rounded or oval shape. The enamel of the fossettes is rather strongly plicated. Upper and lower incisors show a typical mark. Metapodial moderate to long. Persistent tridactyly; the lateral digits are strongly developed and more closely related to the third metapodial than in *Merychippus*.

Pomel (1897) included in his definition that the lateral metapodials are not very different from those of *Equus*, but they broaden distally into an articular head; there are three phalanges, the most distal not reaching the ground.

Hipparion africanum Arambourg 1959

Hipparion sp. Arambourg, 1951: 2464, Arambourg, 1954: 295.
Hipparion africanum Arambourg, 1959: 75, Pl. 10, 11, 12, 13, 16, fig. 7.

'Hipparion with skull of great dimensions, but with limbs of moderate size and heavy extremities. Face and snout elongated; nasal aperture long and broad; orbits far back; preorbital fossae long, simple, distant from orbit. Dental series of moderate size: P^2–M^3 = 141 to 154 mm. Upper cheek teeth with strongly plicated enamel; compressed protocone, elliptical or lenticular. Cingular formations developed on lower milk teeth. Limbs are relatively short, with strong metapodials, in which the lateral digits are still well-developed.' (Translated from Arambourg, 1959, p. 95.)

Hipparion sitifense Pomel 1897

Hipparion sitifensis (sic.) Pomel, 1897: 14, Pl. 1, figs. 11–15, pl. 2, figs. 9–10.
Hipparion sitifense Pomel, Arambourg, 1956: 817, pl. 26, figs. 1–5a.
Hipparion gracile [*Non*] Kaup, Thomas, 1884: 10, pl. 2, figs. 1–3.
Hipparion crassum [*Non*] Gervais, Thomas, 1884: 10.

Hipparion characterized by its small teeth (A–P and transverse dimensions of P^3–M^2, *ca.* 19 mm.), little hypsodont and markedly curved in the median plane. The upper teeth have a flattened protocone, completely independent from the protoloph right down to the base of the tooth. The enamel plications are few and simple. The lower teeth possess no ectostylid. The lateral digits are well-developed.

Hipparion (*Stylohipparion*) *libycum* Pomel 1897

Hipparion ? *libycum* Pomel, 1897: 8, pl. I, figs. 1–7, pl. 2, figs. 11–12.
Hipparion massoesylium Pomel, 1897: 11, pl. 1, figs. 8–9.
Hipparium[1] (sic) *ambiguum* Pomel, 1897: 15, pl. 2, figs. 2–4.
Hipparion crassum Gervais, Solignac, 1927: 756.
Hipparion steytleri van Hoepen, 1930: 21, figs. 14–19.
Eurygnathohippus cornelianus van Hoepen,[2] 1930: 23, figs. 20–22.
Stylohipparion hipkini van Hoepen, 1932: 31, figs. 14–20.
Stylohipparion steytleri (van Hoepen), van Hoepen, 1932: 33, figs. 21–23.
Notohipparion namaquense Haughton,[3] 1932: 421, text-fig. 5.
Libyhipparion ethiopicum Joleaud, 1933: 7, pl. 1, figs. 1–4, 6–8, 10–12.
Equus (*Hippotigris*) sp., (*pro parte*)—Joleaud, 1933: 25, pl. 1, figs. 9 and 13.
Libyhipparion steytleri (van Hoepen), Joleaud, 1933: 12.
Stylohipparion cf. *albertense* (Hopwood), Hopwood, 1937: 130.
Stylohipparion, *Notohipparion*, *Libyhipparion*, Dietrich, 1942: 98, pl. 13, figs. 91–95, pl. 14, fig. 99 *pro parte*, pl. 15, fig. 105, pl. 16, fig. 109.
Stylohipparion albertense (Hopwood), Arambourg, 1947: 303, pl. 10, fig. 3, pl. 11, figs. 3–5.

Diagnosis:

Three-toed equid with rather hypsodont cheek teeth with a strongly developed ectostylid, particularly constant on P_4 and M_1. Typically the ectostylid is broad in the centre and narrowed at each end, the greater length being mesiodistally and antero-lingually orientated. The upper teeth show the typical 'African' features, namely, complex enamel plications of the 'mark' walls, and the narrow elongated protocone.

Hipparion (*Hipparion*) *albertense serengetense*, subsp. nov.

Hipparion albertensis (sic) Hopwood, 1926: 17, fig. 4.
Hypsohipparion albertense (Hopwood), Dietrich, 1942: 97, pl. 4, fig. 39, pl. 13, figs. 87–90, 93b, 96, 97; pl. 14, figs. 101–104, pl. 15, figs. 106–108, pl. 16, figs. 110, 112; pl. 20, fig. 160.
Equus (*Hippotigris*), Arambourg, 1947: 306.
Stylohipparion albertense (Hopwood) (*pro parte*) Arambourg, 1947: 306.

Diagnosis:

Three-toed equid with very hypsodont teeth (the M^3 of which reaches a crown height of 80–90 mm.). The lower teeth are characterized by the constant absence of the ectostylid. The protocone is very elongated, the cement is very thick, the enamel plications being complex. The dental series is short, average length being 156 mm.

Hipparion (*Hipparion*) *albertense baardi*, subsp. nov.

Type specimen: L946 (pl. 8) in the S.A. Museum, Cape Town.
Paratypes: L951, S.A.M.11717 (pls. 4, 2) in the S.A. Museum, Cape Town.
Type site: Baard's Quarry, Langebaanweg, C.P.

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[1] It must be a misprint. Everywhere else, except in the title, Pomel writes *Hipparion ambiguum*.

[2] This is tentatively included here on the basis of our belief that this symphysial fragment is referable to other *Stylohipparion* specimens from this area.

[3] This may prove to be a transitional form between the typical *Hipparion* and the more progressive *Hipparion* (*Stylohipparion*).

Diagnosis:

Three-toed equid with rather hypsodont teeth, about 70 mm. crown height. The lower teeth are characterized by the constant absence of the ectostylid and by a tendency to form other additional stylids, especially protostylid extending along the total height of the crown. The protocone is elliptical but less elongated than in *serengetense*, enamel is thin and plications are complex.

DISCUSSION

1. THE AFRICAN NON-PLEISTOCENE HIPPARIONIDS constitute one genus (*Hipparion*) and two species (*africanum* and *sitifense*). The lack of marked affinity to any of the Pleistocene forms which constitute a homogeneous unity precludes any consideration of this group in terms of the subgenera proposed for the Pleistocene forms.

2. THE AFRICAN PLEISTOCENE HIPPARIONIDS constitute a certain unity marked by the characteristics of the genus *Hipparion*. Furthermore they have in common a number of 'African features' which distinguish them from the non-African forms. Nevertheless these different features do not necessitate generic distinction.

Within the group there exist variables of differing degrees of importance.

The most obvious differentiating characteristic is the presence or absence of ectostylids. The evolutionary trend and ecological adaptation of this feature have been discussed (pp. 331, 332, 333) and it is considered that it constitutes a differentiation at the subgeneric but not generic level. The statistical constancy of absence or presence of this feature within groups otherwise identical indicates that consideration must be accorded on both a non-generic and a non-specific basis. Consequently the African Pleistocene *Hipparion* are subdivided into two subgenera, viz.

Hipparion (*Hipparion*) de Christol 1832, and
Hipparion (*Stylohipparion*) van Hoepen 1932.

3. THE CONSIDERATION OF THE SPECIES of *Hipparion* (*Stylohipparion*) is beset with the obvious difficulty of the paucity of the material available. Previous workers, faced with the same problem, have either cautiously avoided speciation or unjustifiably proposed species that are void, e.g. Van Hoepen, 1932—*steytleri*, *hipkini*. Arambourg (1947, 1956, 1959) refers to *libycum* only when he is discussing the North African Pleistocene material; otherwise he generalizes to the extent of using the generic (subgeneric) name *Stylohipparion* without species determination. We concur with this cautious attitude. We recognize that material referable to this subgenus has been recovered from three different geographical areas, namely, the Maghreb, East Africa (incl. Omo) and South Africa. Joleaud (1933), also aware of the geographical distribution, recognized in his new genus *Libyhipparion* three

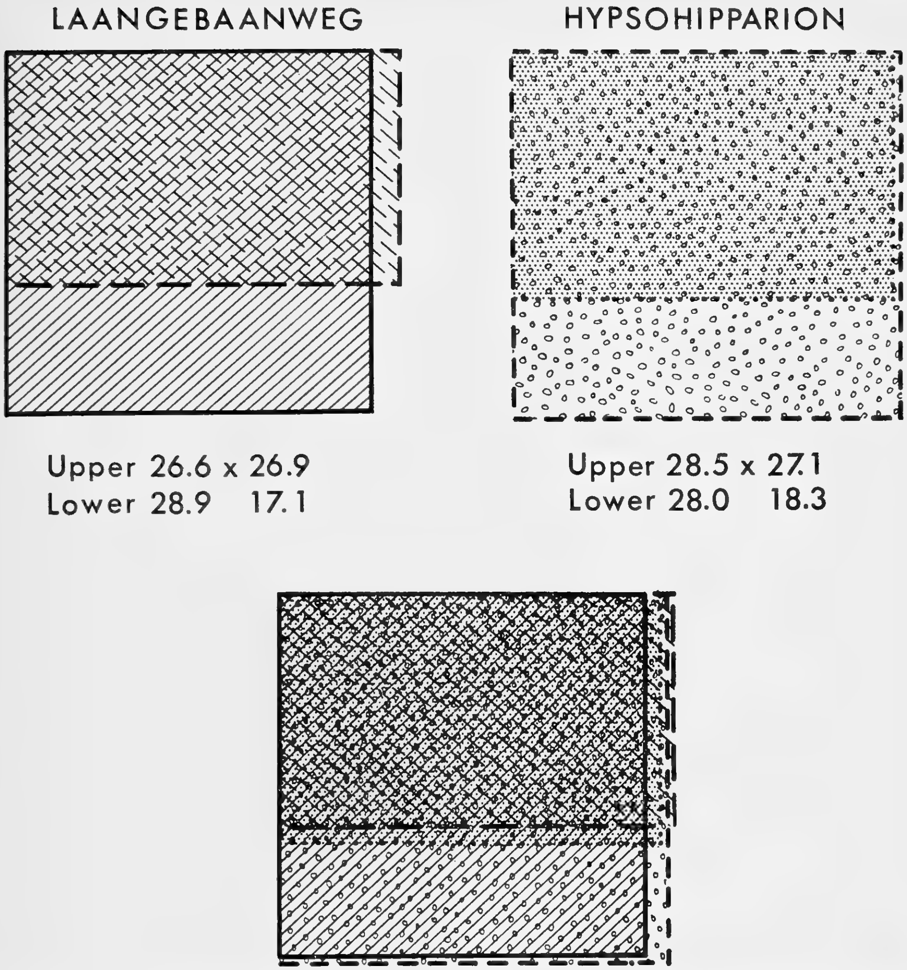

Fig. 16. Diagrammatic superimposition of an upper and a lower molar tooth of the South Serengeti '*Hypsohipparion*', and the Langebaanweg *Hipparion*.

species, viz. *libycum*, *ethiopicum* and *steytleri*. However, despite the differences of the localities, the wide range of variation within the small amount of available material does not provide the evidence for species separation.

Comparison of the various 'diagnoses' provided by Hopwood (1937), Arambourg (1947), and Cooke (1950), and reference to descriptions by Pomel (1897) and Joleaud (1933) indicate quite clearly that no true, clear-cut diagnosis is possible. Therefore, it is proposed to extend Arambourg's generalized usage of *libycum* to cover all the material included in this subgenus, but with the awareness that subsequent discoveries may bring to light information to highlight the differences of locality on a subspecies level.

4. A better situation exists with reference to *Hipparion* (*Hipparion*) which includes a portion of the material from South Serengeti (i.e. '*Hypsohipparion*' Dietrich) and the Langebaanweg specimens.

The dimensions and the main features (fig. 16) of the teeth from both areas are almost identical. However, there are differences in those features which emphasize the 'African' character of the dentition; namely, the hypsodonty, the elongation and narrowing of the protocone (tables, 16, 19, 20; figs. 12, 13). For both of these characters the Serengeti material displays a more progressive stage. Furthermore the latter also exhibits a thicker cement. These differences, although constant, do not constitute sufficient grounds for species separation. Therefore the species *albertense* is retained for both groups. Taking into consideration the ecological adaptation of these features, it is proposed to distinguish these two groups on a subspecies level. The Serengeti '*Hypsohipparion*' group, erected by Dietrich, is now considered to be *Hipparion* (*Hipparion*) *albertense serengetense*, subsp. nov. The reason for dropping the genus *Hypsohipparion* has been discussed above. The Langebaanweg group constitutes the subspecies *Hipparion* (*Hipparion*) *albertense baardi*, subsp. nov. The name *baardi* is chosen because the first specimens were recovered from Baard's Quarry, owned by Mr. J. Baard.

It seems that these two subspecies constitute the earliest Pleistocene forms. The material (to be described by Dr. Stirton) from the base of Olduvai Bed I should confirm or correct this suggestion.

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Dr. K. H. Fischer, Institut für Paläontologie und Museum der Math.-Naturwissenschaftlichen Fakultät der Humboldt-Universität zu Berlin kindly took some measurements (at the authors' request) on the original Serengeti material.

Mrs. M. A. Norris patiently typed the manuscript.

SUMMARY

The recent discoveries of hipparionid material at the Langebaanweg fossil sites (Cape Province, South Africa) necessitated a revision and interpretation of similar material recovered elsewhere in Africa. At the same time new data on material from the Vaal River Gravels, Olduvai Gorge and South Serengeti are added. A review of the geological and faunal data described from approximately 40 sites in Africa leads to a tentative chronological correlation. Consideration of the anatomical features (mostly of the dentition) provides opportunity for a discussion of the ecological adaptation and evolutionary trends. The problems of the origins and migrations of African hipparionids are dealt with.

It is concluded that the African hipparionids belong to a single genus, *Hipparion*. The Miocene forms remain limited to *H. africanum*. The Pliocene is represented by *H. sitifense*, while the Pleistocene forms are referable to two subgenera, viz. *Stylohipparion* and *Hipparion*.

The Serengeti '*Hypsohipparion*' group, is referred to *Hipparion* (*Hipparion*) *albertense serengetense* subsp. nov.

The Langebaanweg material forms a unified group and is referred to *Hipparion* (*Hipparion*) *albertense baardi* subsp. nov.

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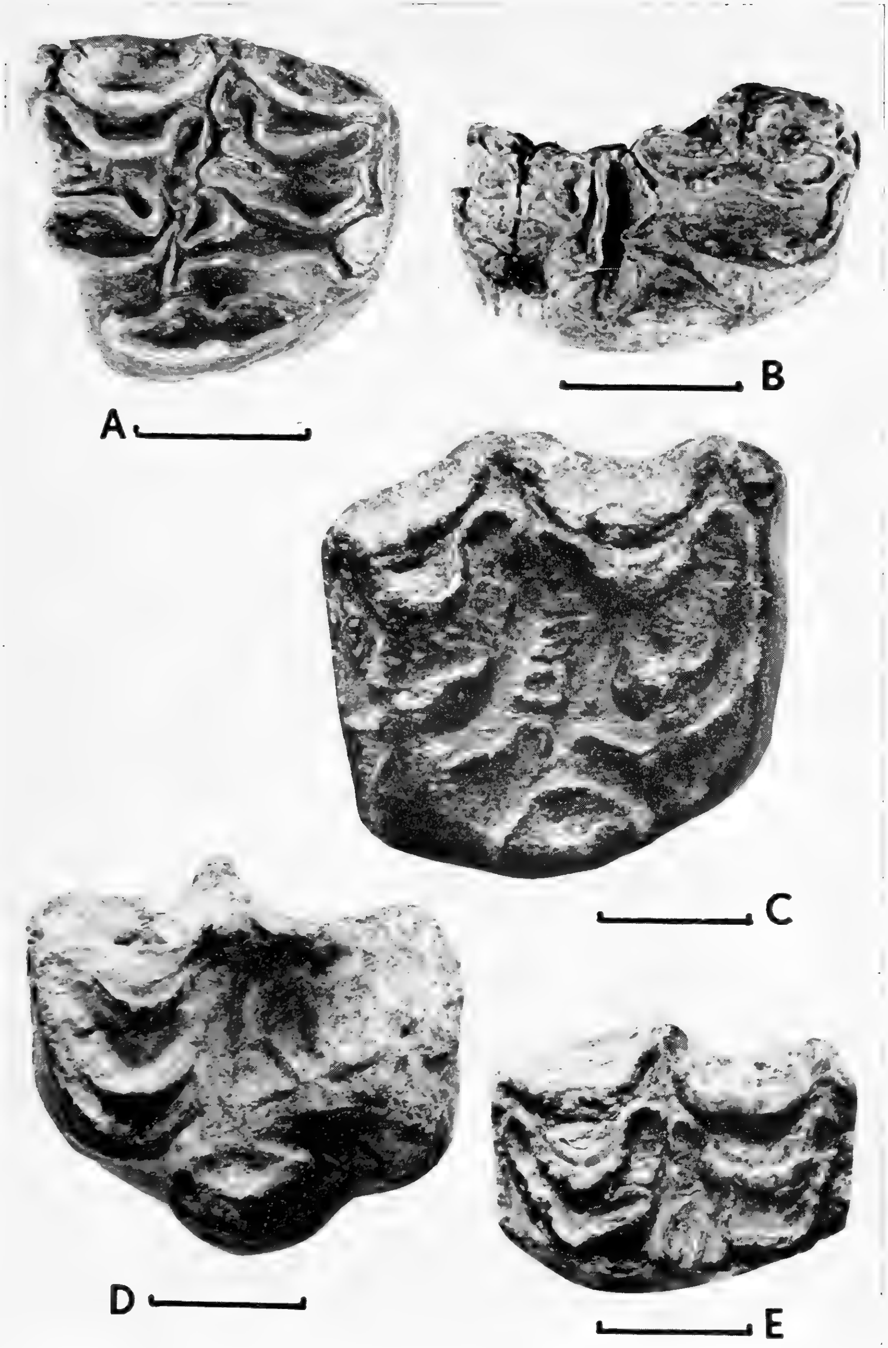
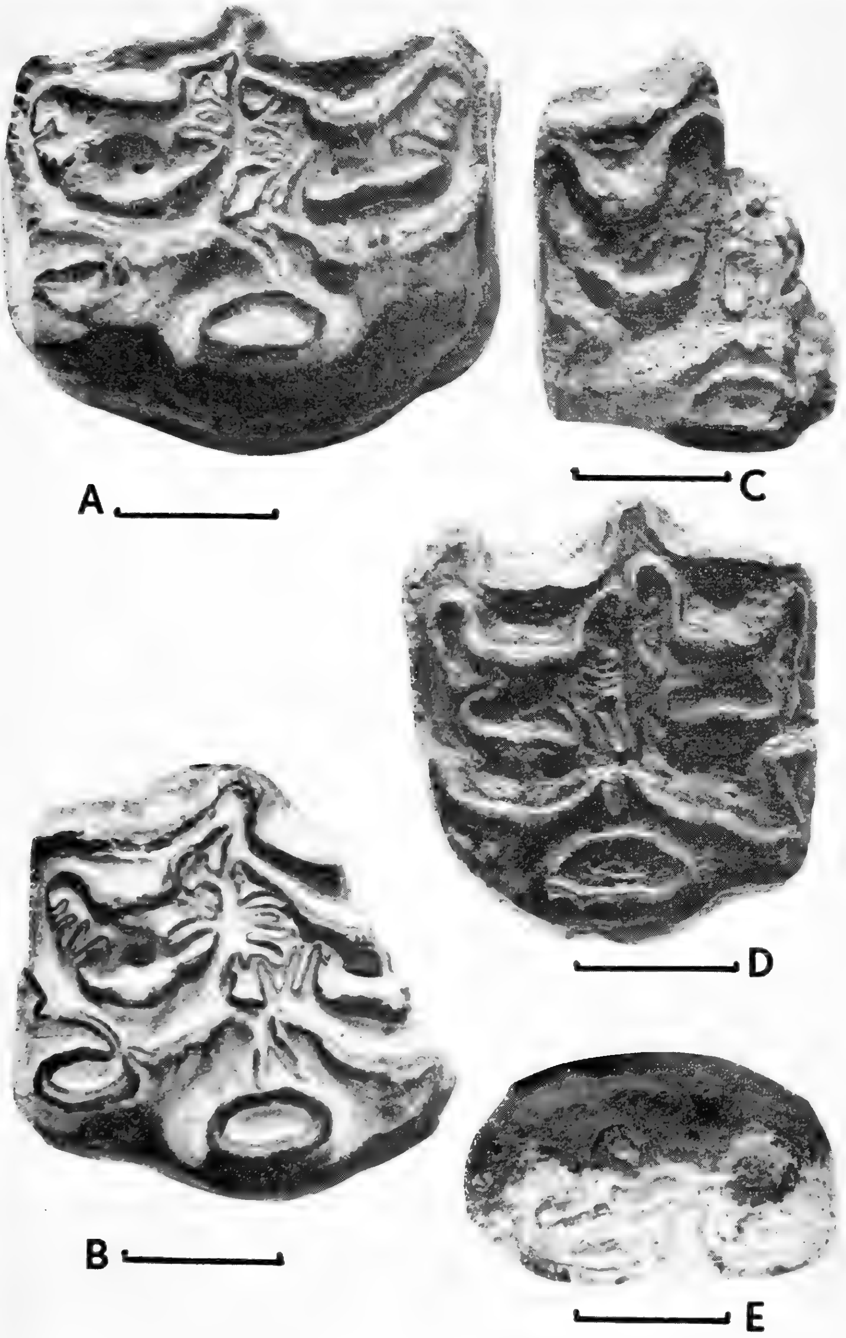
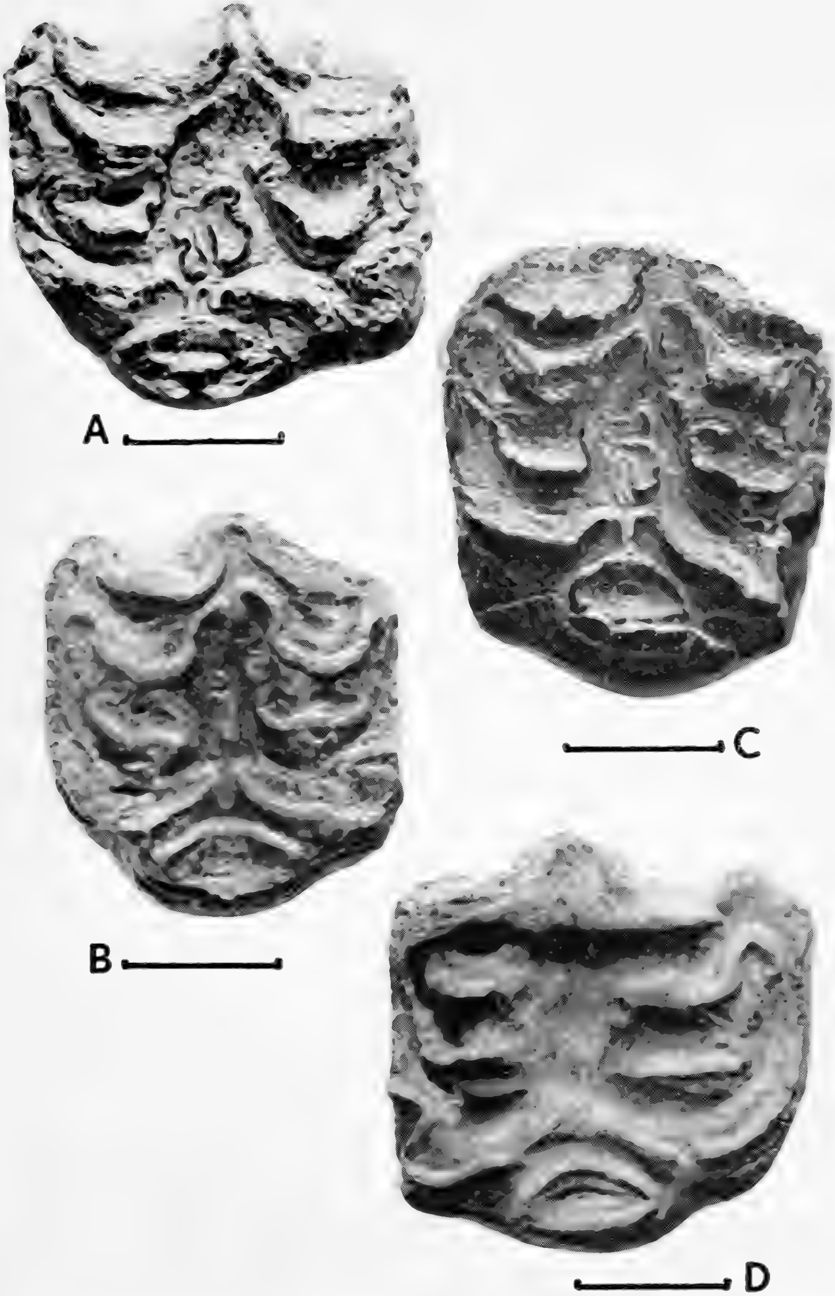


Occlusal aspect. Scale: 1 cm. **A**—MMK 431. **B**—MMK 5225. **C**—L1467c. **D**—L1463. **E**—L956.



Occlusal aspect. Scale: 1 cm. **A**—S.A.M. 11717. **B**—S.A.M. 11718. **C**—L940 / 950. **D**—L934. **E**—L1465F.



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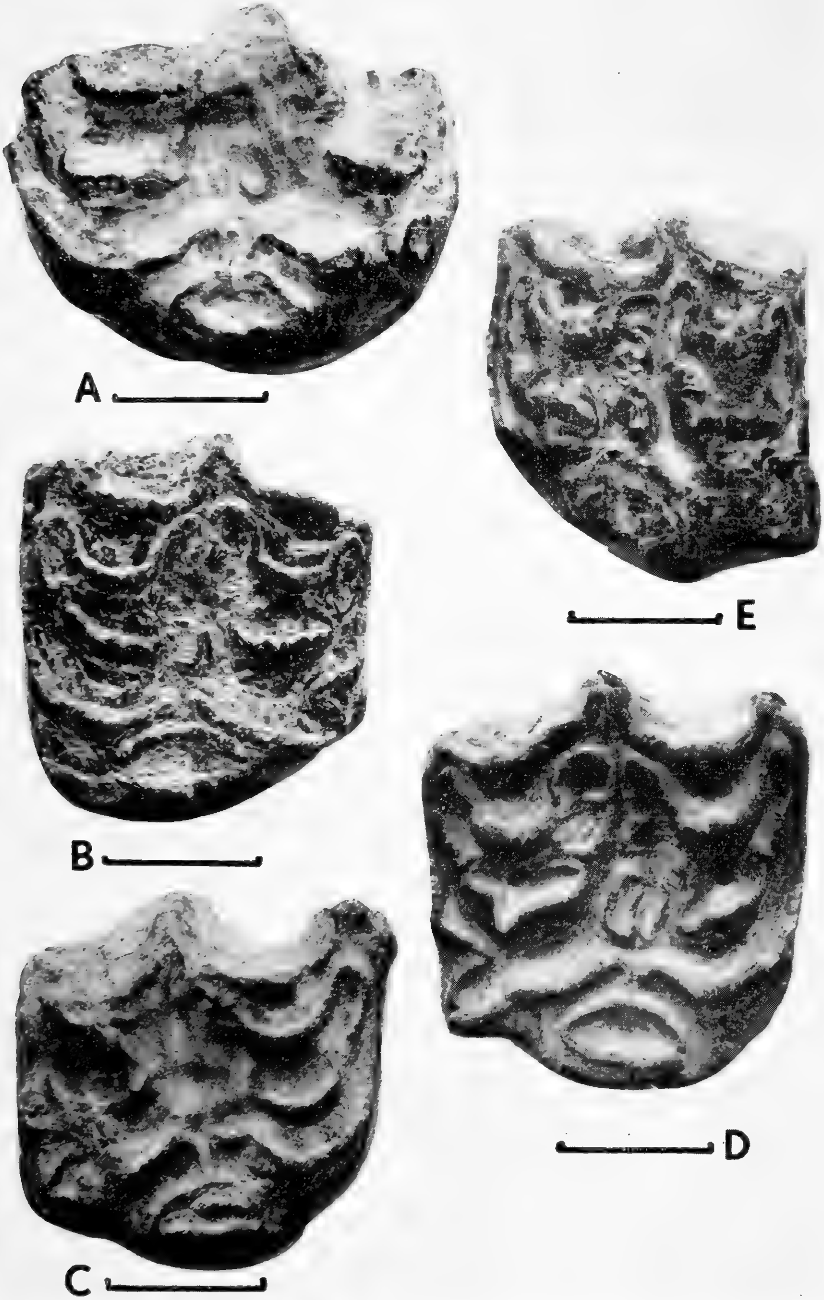

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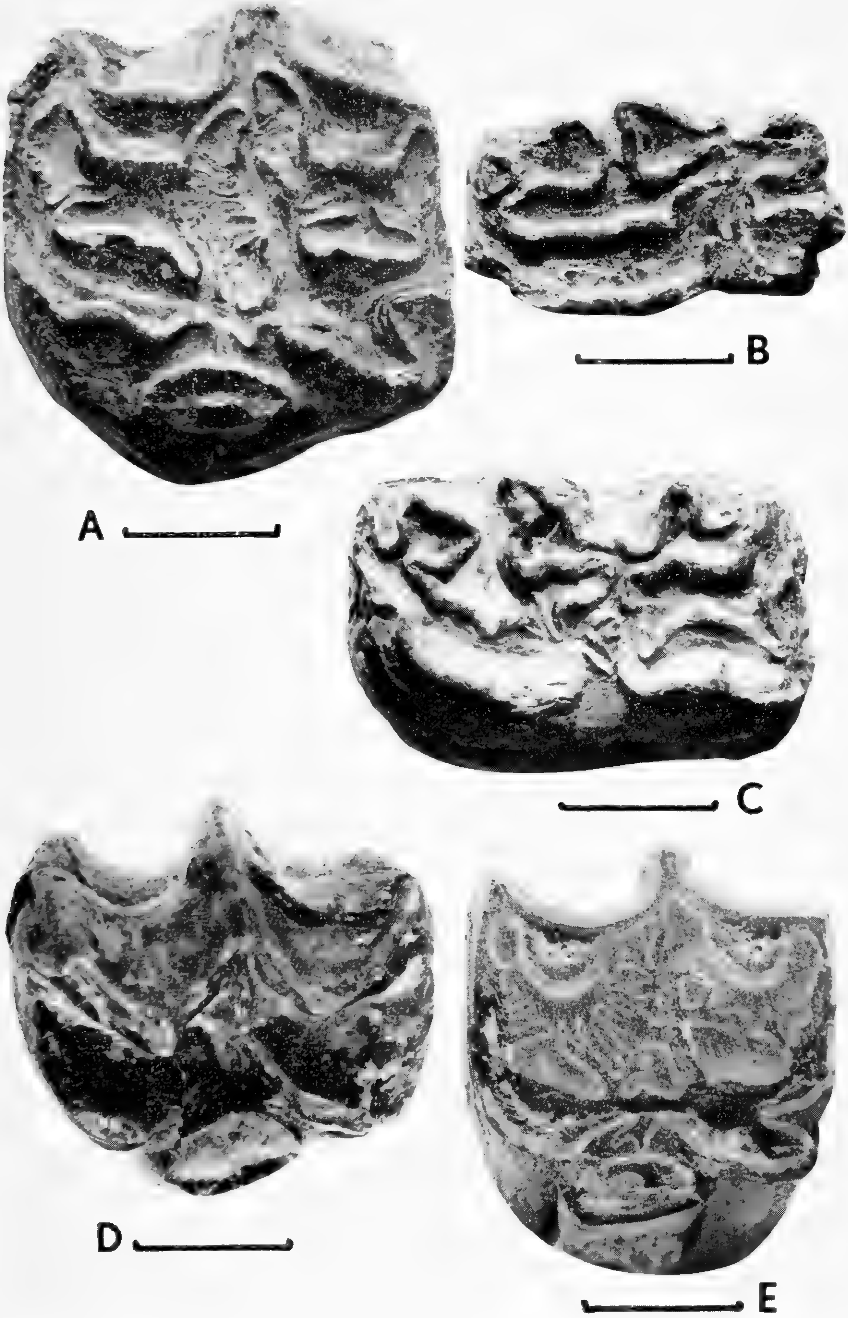
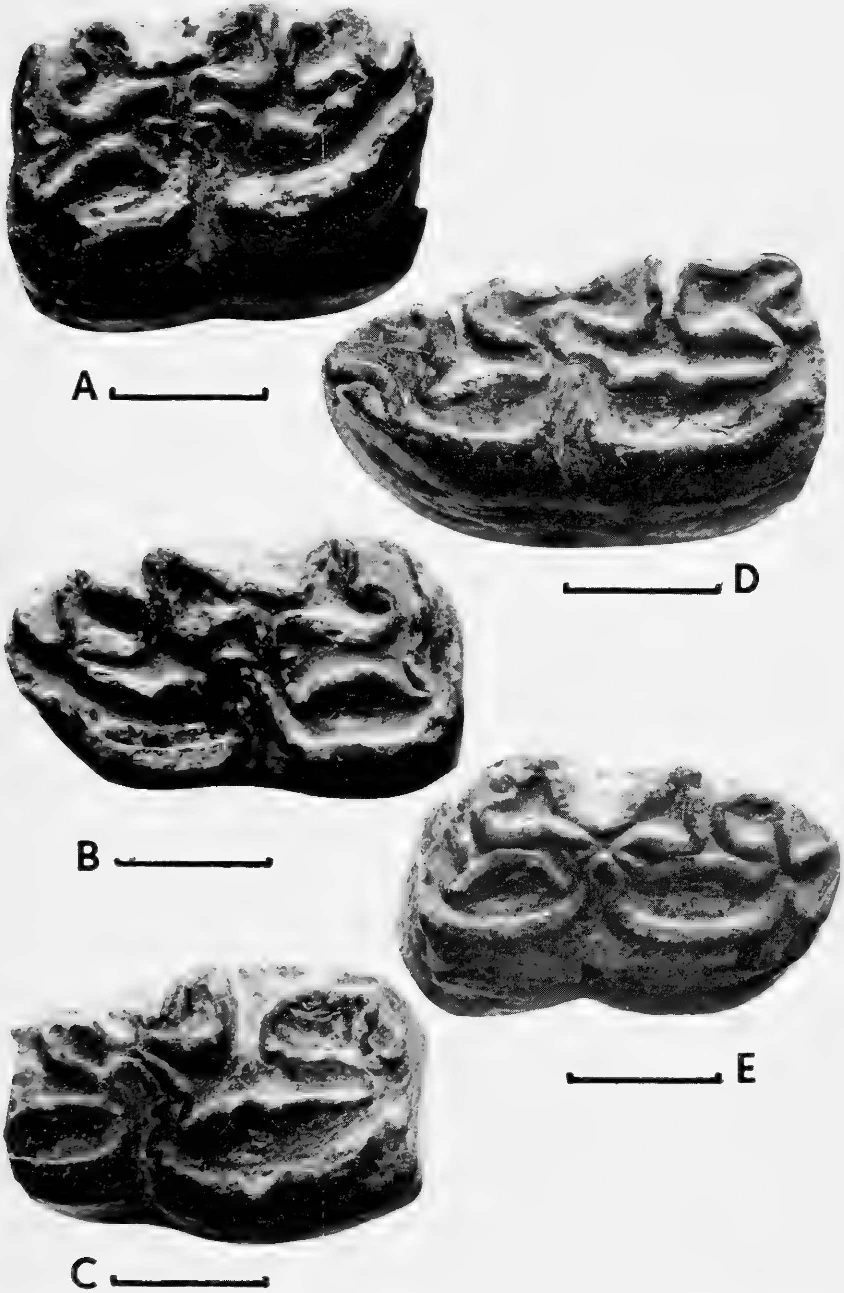


A—D: occlusal aspect. Scale: 1 cm. **A**—L1467E. **B**—L939. **C**—L1451A. **D**—S.A.M. 11716.
E—S.A.M. 11716: section across middle of crown.



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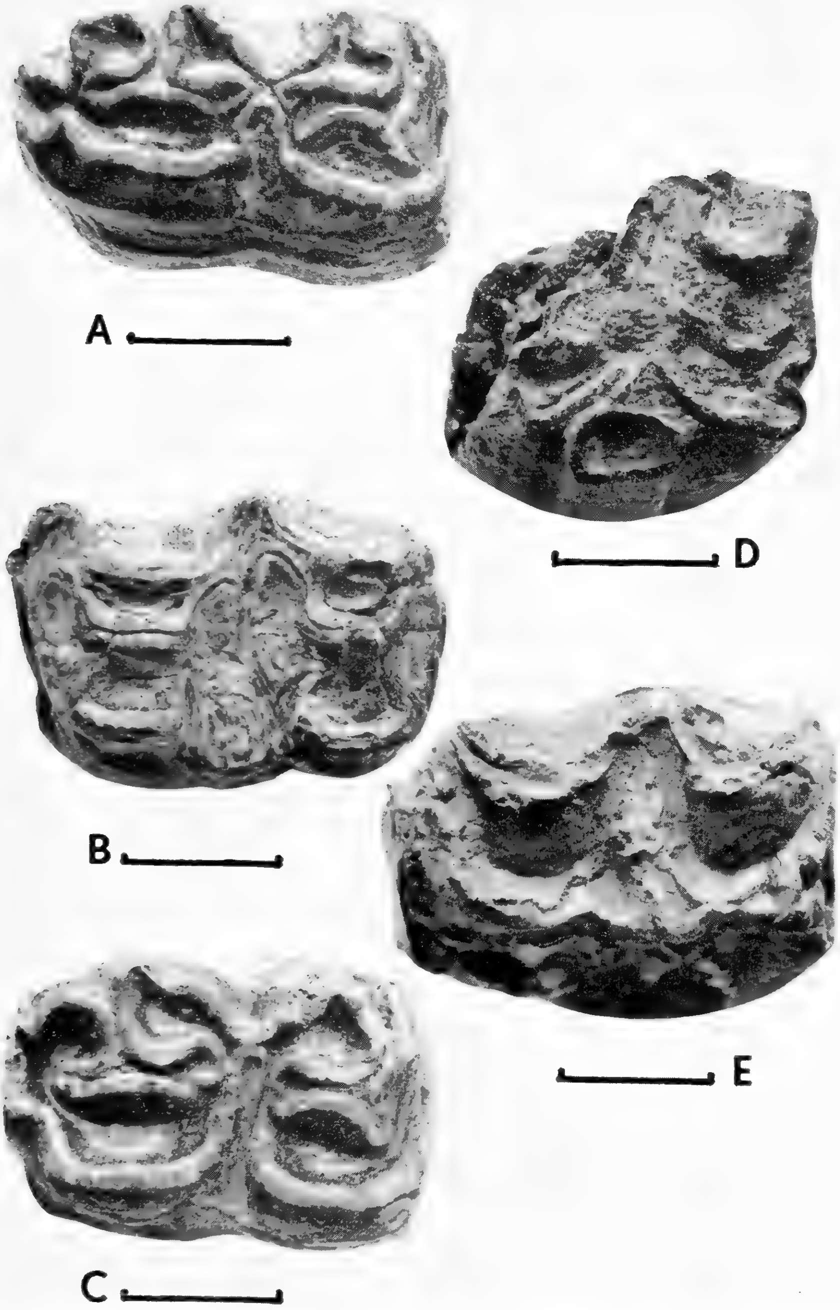

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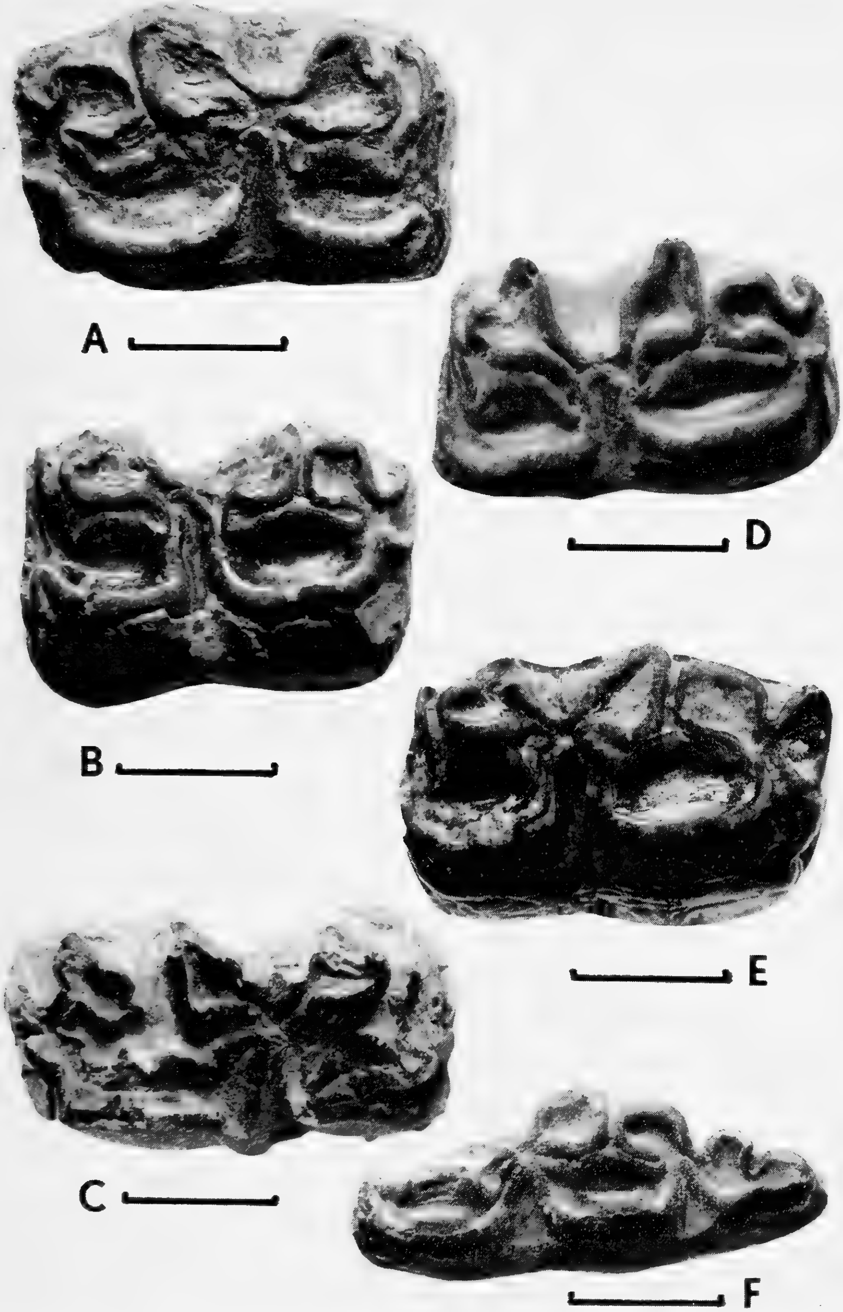

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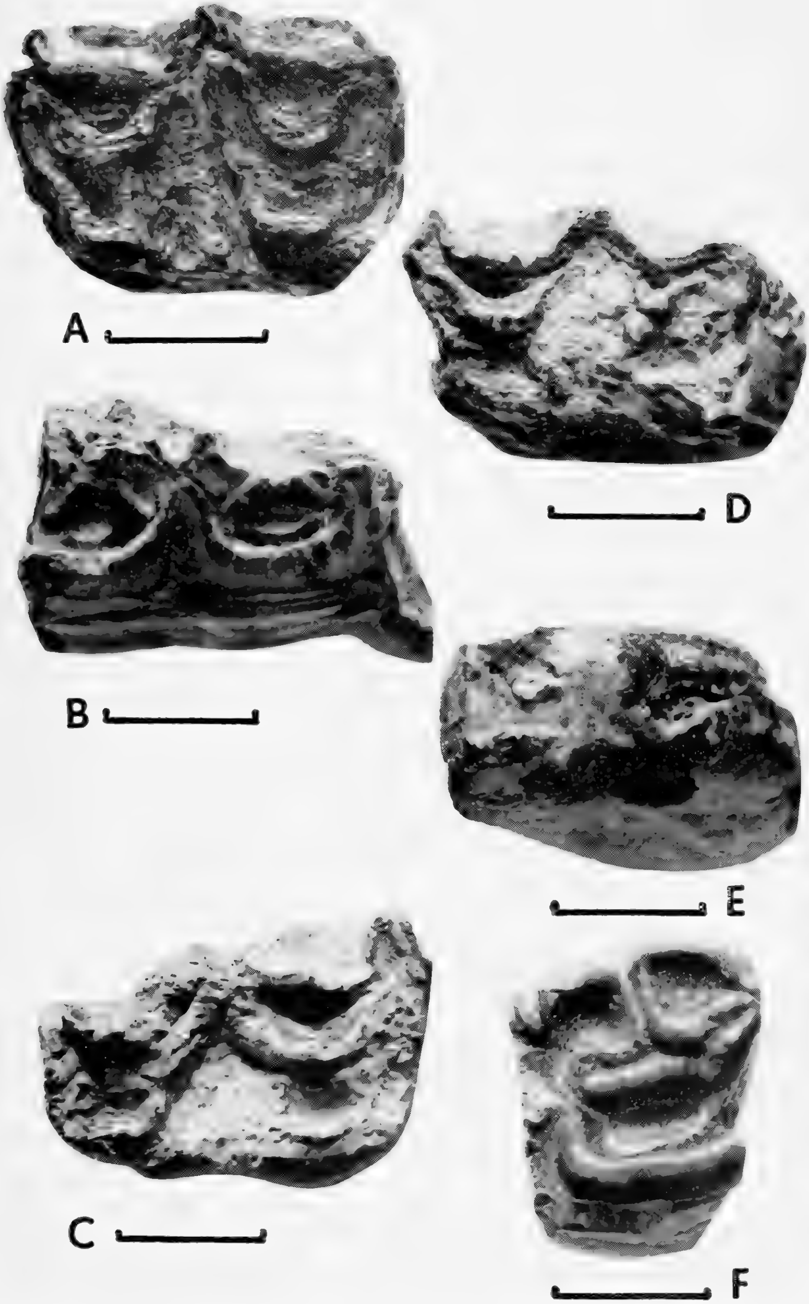

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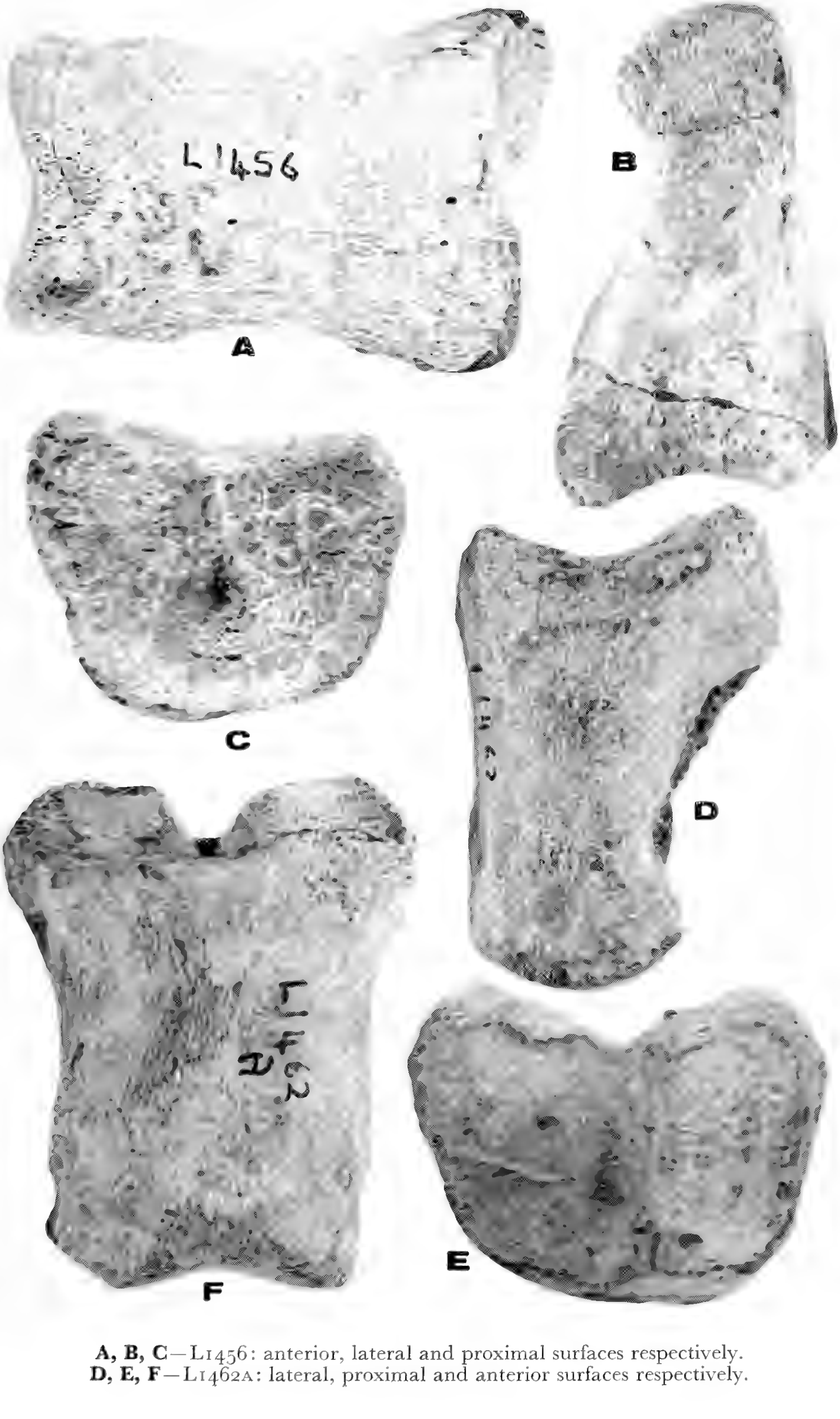

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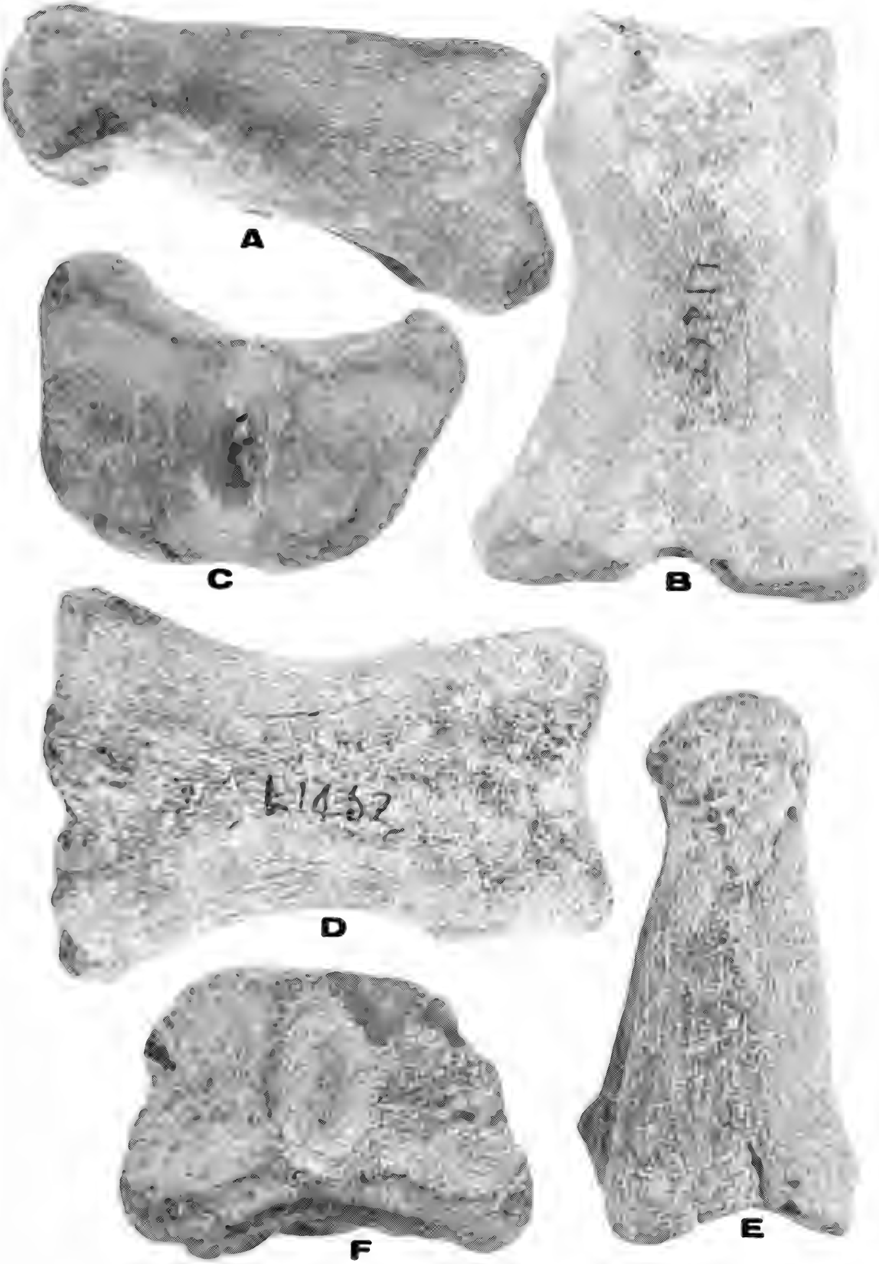
D, E, F—L1462A: lateral, proximal and anterior surfaces respectively.



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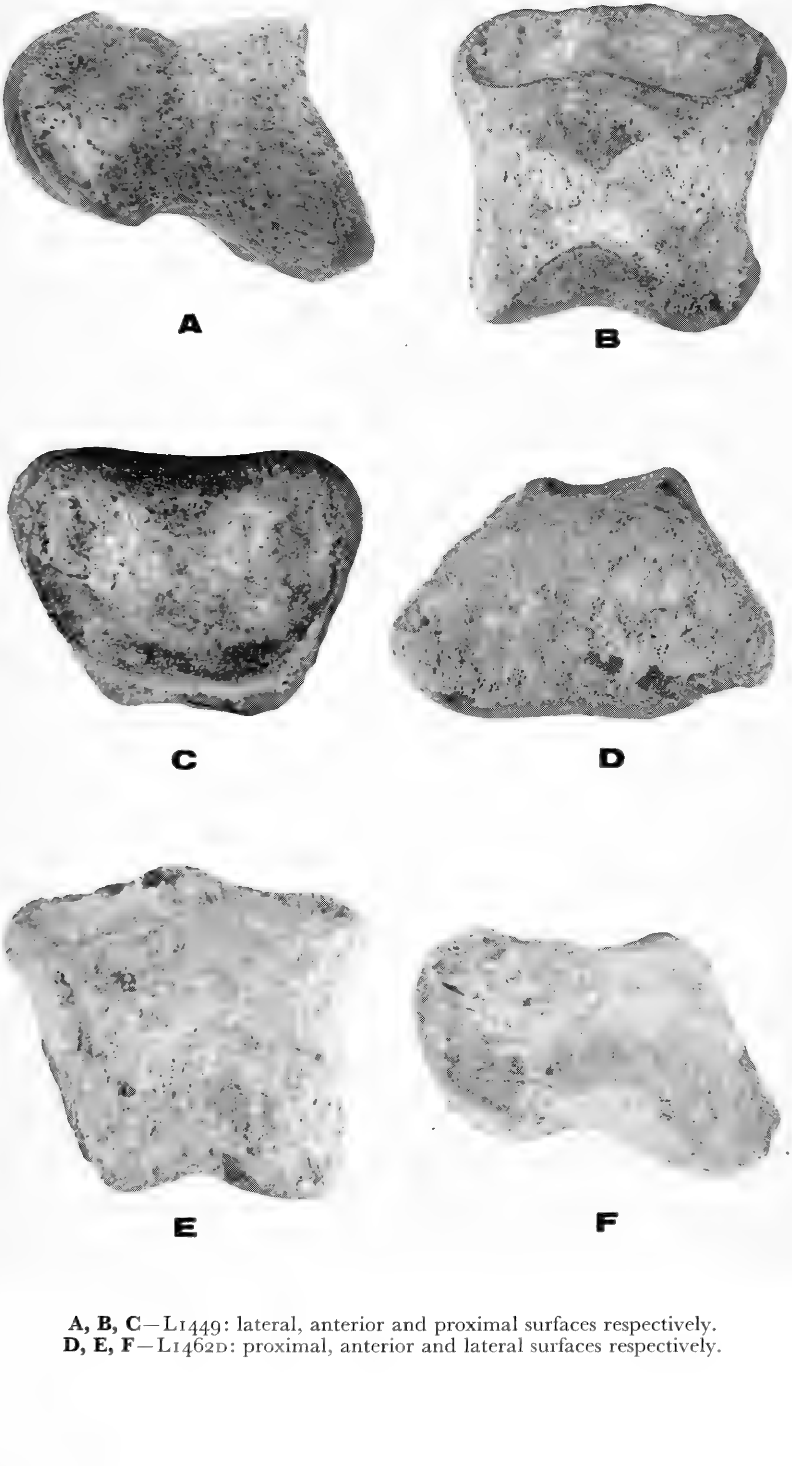
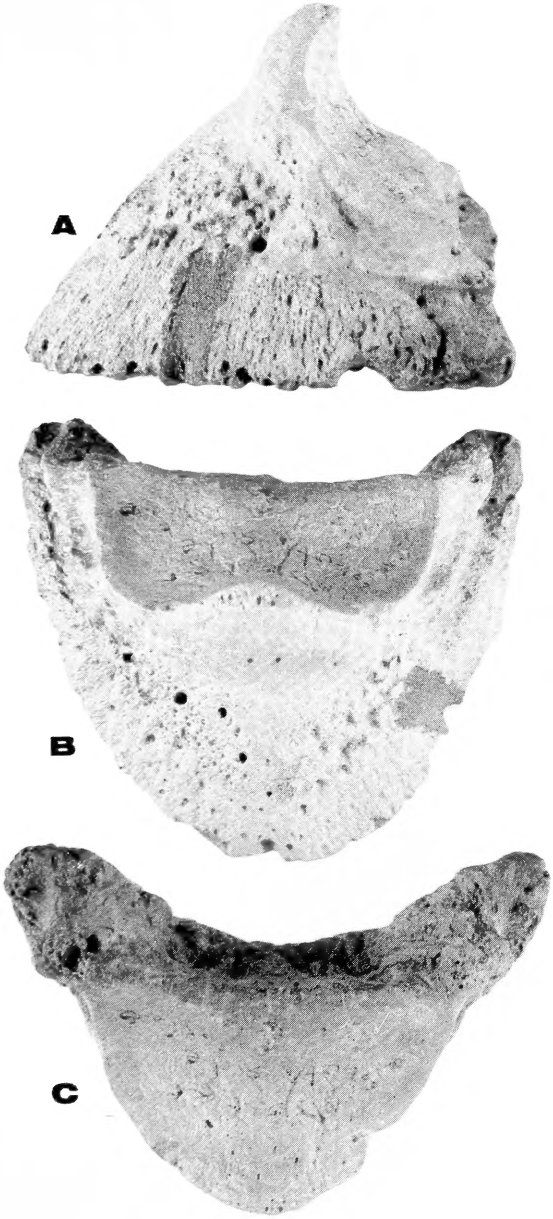


A, B, C—L1449: lateral, anterior and proximal surfaces respectively.
D, E, F—L1462D: proximal, anterior and lateral surfaces respectively.



A, B, C—L1444: lateral, anterior and inferior surfaces respectively.

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MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including Table of Contents and Summary. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than 4¾ in. × 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

Smith, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937–945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

Brown, X. Y. 1953. *Marine faunas.* 2nd ed. **2**. London: Green.

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Smith, C. D. 1954. South African Plonias. *In* Brown, X. Y. *Marine faunas.* 2nd ed. **3**: 63–95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July* 1958, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:
Euplonia capensis (Smith) Brown, 1955: 259.
When misidentified as another species:
Plonia natalensis (*non* West), Jones, 1956: 18.
When another species has been called by the same name:
[*non*] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).