7 October 1977, Volume 198, Number 4312 **SCIENCE**

Suid Evolution and Correlation of African Hominid Localities

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Abundant suid remains of known stratigraphic context have been recovered by intensive collecting at Plio-Pleistocene fossil localities in eastern Africa during the past 20 years. The potential value of the Suidae for biostratigraphic analysis and correlation was recognized by Leakey, Cooke, and others (*1*, *2*), and certain species such as *Mesochoerus limnetes* have proved useful by affording insight into stratigraphic and chronologic problems in eastern Africa (*2*). Former phylogenetic and systematic interpretations did not, however, fully recognize the similarity of southern and eastern African fossil suid species or the potential that these have for precise correlation of radiometrically dated East African sedimentary sequences with the important hominid-bearing cave breccias of South Africa.

Summary. Recently discovered Plio-Pleistocene vertebrate assemblages have allowed complete systematic revision of the sub-Saharan African Suidae. New phylogenies are proposed for the 7 genera and 16 species of fossil and extant representatives. Suids are common elements of African Plio-Pleistocene faunas, and their evolutionary trends, particularly in the species *Mesochoerus limnetes* and *Metridiochoerus andrewsi*, are of great correlative value. Suid data are employed in a refinement of stratigraphic correlations at Omo Shungura, Olduvai, and east of Lake Turkana (formerly East Rudolf) and in a correlation of East African and South African sites, with important implications for interpretation of hominid evolution. The suid record also bears significantly on questions of theoretical evolutionary biology.

Fossil suid skulls from Africa are relatively rare and show strong sexual dimorphism. In contrast, suid dentitions are plentiful, and the third molars (the most adaptively significant teeth) are usually well represented in paleontological collections. African suid dental evolution consists largely of phylogenetically gradual changes that permit reconstruction of continuous morphological evolutionary series. Several independently evolving lineages occur contemporaneously and provide internal cross-checks and safeguards against geographic or ecologic bias.

Use of the available fossil suid record allows refinement of stratigraphic interpretations at Omo Shungura, Olduvai, and east of Lake Turkana (formerly East Rudolf); in addition, these and other East African hominid-bearing localities can be correlated with the South African sites of Makapansgat and Swartkrans. In the analysis presented here, suid evolution has been used as a correlative device in the recognition of a relative temporal sequence. Because of unresolved controversy concerning radiometric age determinations at East African fossil sites (*3*, *4*), no attempt is made here to place precise chronometric determinations on any of the correlations. Refinement of both established and potentially useful but less well calibrated methods of absolute age determination should ultimately provide an internally consistent, rigorously tested, and adequately precise chronologic framework for the fossil material assessed below.

Suid Evolution

African fossil suid specimens collected from approximately 50 localities have, in this century alone, been assigned to a total of 77 species within 23 genera. Harris and White have recently undertaken a detailed systematic revision of Plio-Pleistocene suids from sub-Saharan Africa and recognize only 16 species from 7 genera (*5*). Four major groups are identified in the period under discussion (Fig. 1). Group 1 comprises the genera *Nyanzachoerus* and *Notochoerus*. Group 2 consists of *Mesochoerus* and *Hylochoerus* (the forest hog). Group 3 comprises *Metridiochoerus* and *Phacochoerus* (including the warthog). The fourth group consists only of *Potamochoerus* (the bushpig). Group 1 predominates in the Pliocene but is supplanted by groups 2 and 3 in the early Pleistocene. Group 4 has only an intermittent fossil record.

Group 1. *Nyanzachoerus* is the dominant suid genus at the earliest known Pliocene sites of East and South Africa (Lukeino, Lothagam, and Langebaanweg) (Fig. 2). The smallest, earliest, and most primitive species is *Ny. tulotos* (*6*) from Lothagam and Lukeino, a similar species being known from North Africa (*7*). *Nyanzachoerus tulotos* seems related to *Bunolistriodon* species from the Miocene (*8*), but determination of the precise relationships of *Nyanzachoerus* to earlier African and Asian suids must await results of current investigations on Siwalik faunas. *Nyanzachoerus kanamensis* is the common nyanzachoere from later Pliocene localities. It is probable, both temporally and morphologically, that *Ny. kanamensis* evolved from a form similar to *Ny. tulotos*. *Nyanzachoerus jaegeri* is represented by less complete material than *Ny. tulotos* or *Ny. kanamensis*, differing from the latter

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by increases in the length, height, and cusp complexity of the third molars and by a decrease in the size of the premolar row. There is evidence from Langebaanweg specimens to suggest that *Ny. jaegeri* evolved from *Ny. kanamensis*.

The ancestry of the genus *Notochoerus* lies with the progressive *Ny. jaegeri* of the Mursi, Chemeron, and Kanapoi Formations. *Notochoerus* is distinguished from *Nyanzachoerus* by relative and absolute premolar reduction, increased third molar size and complexity (Fig. 3a), and differences in cranial anatomy. Species of *Notochoerus* are common elements in the later Pliocene of East and South Africa, coexisting initially with *Potamochoerus* and *Ny. kanamensis* and later with *Mesochoerus* and *Metridiochoerus* species. Evolving members of the latter genera eclipse the *Nyanzachoerus*-*Notochoerus* radiation in the terminal Pliocene.

Group 2. The earliest African mesochoeres occur in the Laetolil Intermediate Beds and the Omo Shungura Formation (Figs. 1 and 2). No clear case can be made for the derivation of *Mesochoerus* from endemic African stock, and the fossil record suggests that *Mesochoerus*, like *Potamochoerus*, came to Africa from an extracontinental source. Upper and lower third molars of *Mes. limnetes* increase in height through time and become progressively longer through the addition of extra major pillars to the rear of the tooth (Fig. 3b and Table 1a). Observed evolutionary changes are gradual, the present total sample no longer substantiating earlier attempts to divide this unquestionably single lineage into more than one species (*2*). *Mesochoerus majus* is a conservative species whose teeth retain a primitive molar pattern but show convergence toward those of *Potamochoerus*. *Hylochoerus* is virtually without fossil record until the late Pleistocene but was undoubtedly endemically derived from *Mesochoerus*. It is unlikely that *Hylochoerus* originated before the early Pleistocene, but the timing of its subsequent radiation cannot presently be substantiated.

Group 3. The most primitive members of the genus *Metridiochoerus* occur in Shungura Member B, the initial appearance of the genus coinciding with that of *Mesochoerus* (Fig. 1). *Metridiochoerus* underwent a substantial adaptive radiation during the early Pleistocene, and at one point four distinct metridiochoere species existed contemporaneously. The most primitive specimens of *Met. andrewsi* (Fig. 3c) superficially resemble those of *Mes. limnetes* (Fig. 3b). Confusion by earlier workers of the more advanced specimens of *Met. andrewsi* with *Notochoerus*, *Phacochoerus*, and pro-

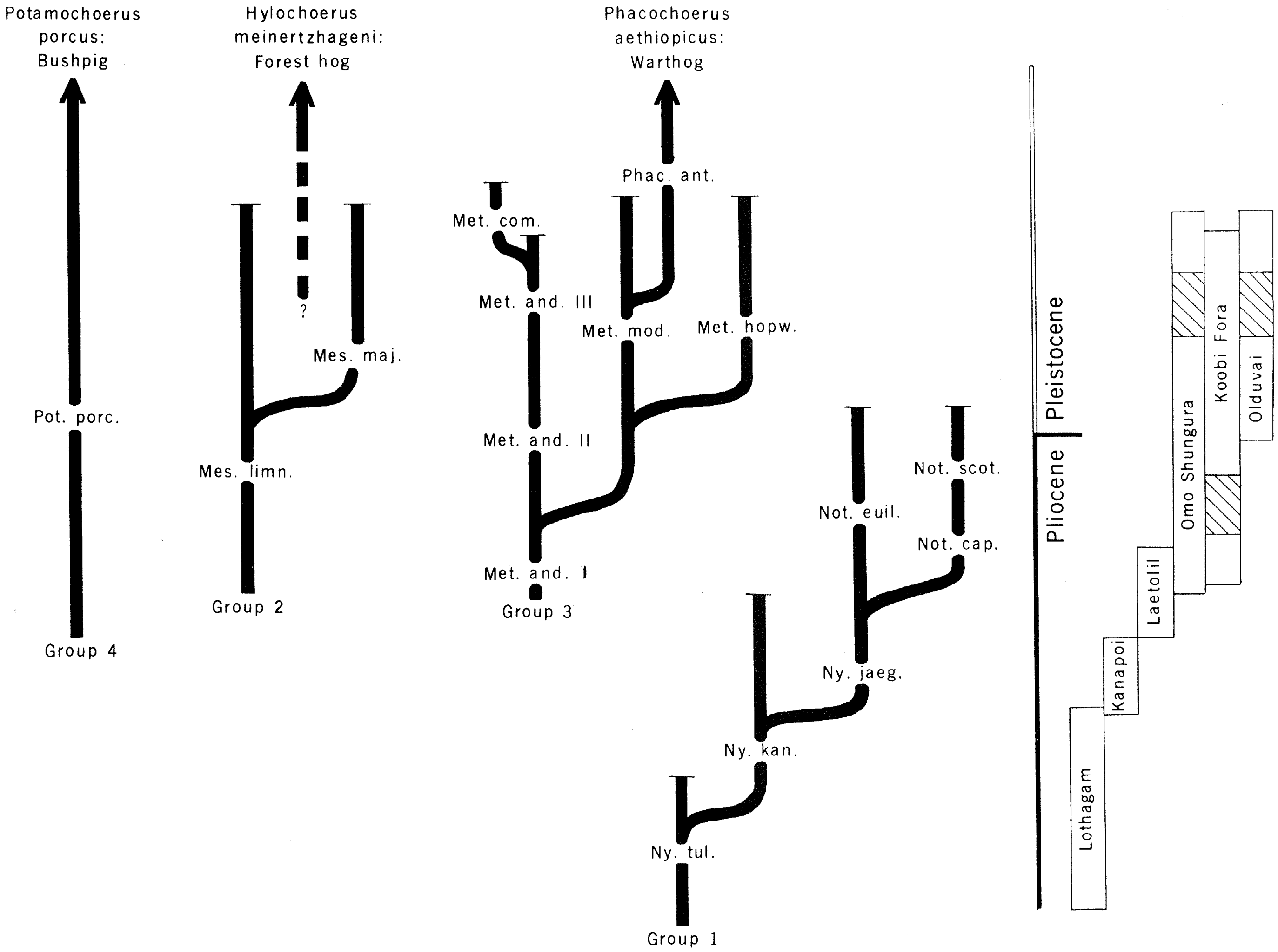


Fig. 1. Revised phylogeny of African Plio-Pleistocene Suidae. Group 1: *Nyanzachoerus* Leakey, 1958; *Ny. tulotos* Cooke & Ewer, 1972; *Ny. kanamensis* Leakey, 1958; *Ny. jaegeri* Coppens, 1971; *Notochoerus* Broom, 1925; *Not. euilus* (Hopwood), 1926; *Not. capensis* Broom, 1925; *Not. scotti* (Leakey), 1943. Group 2: *Mesochoerus* Shaw & Cooke, 1941; *Mes. limnetes* (Hopwood), 1926; *Mes. majus* (Hopwood), 1934; *Hylochoerus* Thomas, 1904; *H. meinertzhageni* Thomas, 1904. Group 3: *Metridiochoerus* Hopwood, 1926; *Met. andrewsi* Hopwood, 1926; *Met. modestus* (Van Hoepen & Van Hoepen), 1932; *Met. hopwoodi* (Leakey), 1958; *Met. compactus* (Van Hoepen & Van Hoepen), 1932; *Phacochoerus* Cuvier, 1817; *Phac. antiquus* Broom, 1948; *Phac. aethiopicus* (Pallas), 1766. Group 4: *Potamochoerus* Gray, 1854; *Pot. porcus* (Linn.), 1758. The *Met. andrewsi* lineage has, for convenience, been divided into three successive stages.

gressive examples of *Mesochoerus* [see (5)] has hindered understanding of evolution within the genus but serves to illustrate the effects of evolutionary convergence on African Plio-Pleistocene suid lineages. The morphologically most primitive specimens of warthog come from Kromdraai, Bolts Farm, and Swartkrans B in South Africa. Available evidence points to the derivation of *Phac. antiquus* from *Met. modestus* (Fig. 1), but both taxa are contemporaneous in Olduvai Bed IV.

Group 4. The first African representatives of *Potamochoerus* occur in the late Pliocene. The genus is unknown from the Pliocene of Europe (9), and, since there is currently no evidence to support derivation from endemic African stock, an Asian origin is plausible. *Potamochoerus* specimens are abundant in the Laetolil Beds and Hadar Formation. Their subsequent rarity in early and mid-Pleistocene faunas may be due to sampling and ecologic factors. It seems likely that the role of the late Pliocene bushpig was taken over by the early representatives of *Mesochoerus* and *Metridiochoerus*, with *Potamochoerus* being displaced into environments less favorable for the preservation of fossils.

The major suid radiations of groups 1 through 3 discussed above are all characterized by forms featuring increasing emphasis on the third molar as the prime functioning dental unit. The genera *Nyanzachoerus, Notochoerus, Mesochoerus*, and *Metridiochoerus* are characterized by one or more species which exhibit progressive and parallel increase in third molar height and length (Table 1, a and b). Dental convergence has led to considerable taxonomic confusion and is such that *Mes. limnetes*, a common low-crowned suid of the early Pleistocene, is by mid-Pleistocene times superficially identical in third molar morphology to the high-crowned Pliocene *Not. euilus* (Fig. 3, a and b). These and other species also feature strong multilineal cranial convergence (orbital elevation, maxillary deepening, and reduced insertion of the temporalis muscle). In groups 1 through 3 there is a tendency for conservative ancestral stocks to give rise to more progressive species but to exist alongside the daughter species after the presumably allopatric speciation event.

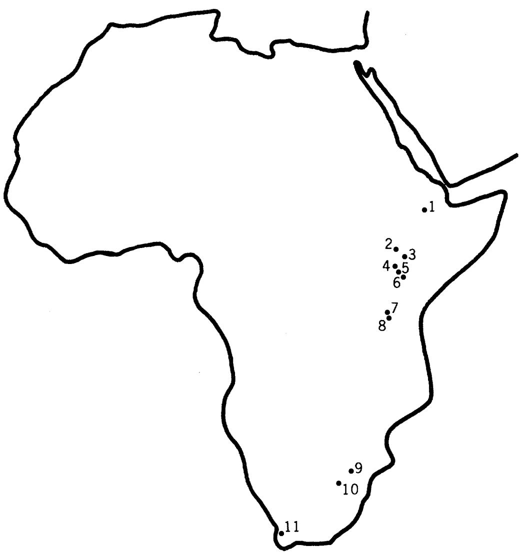
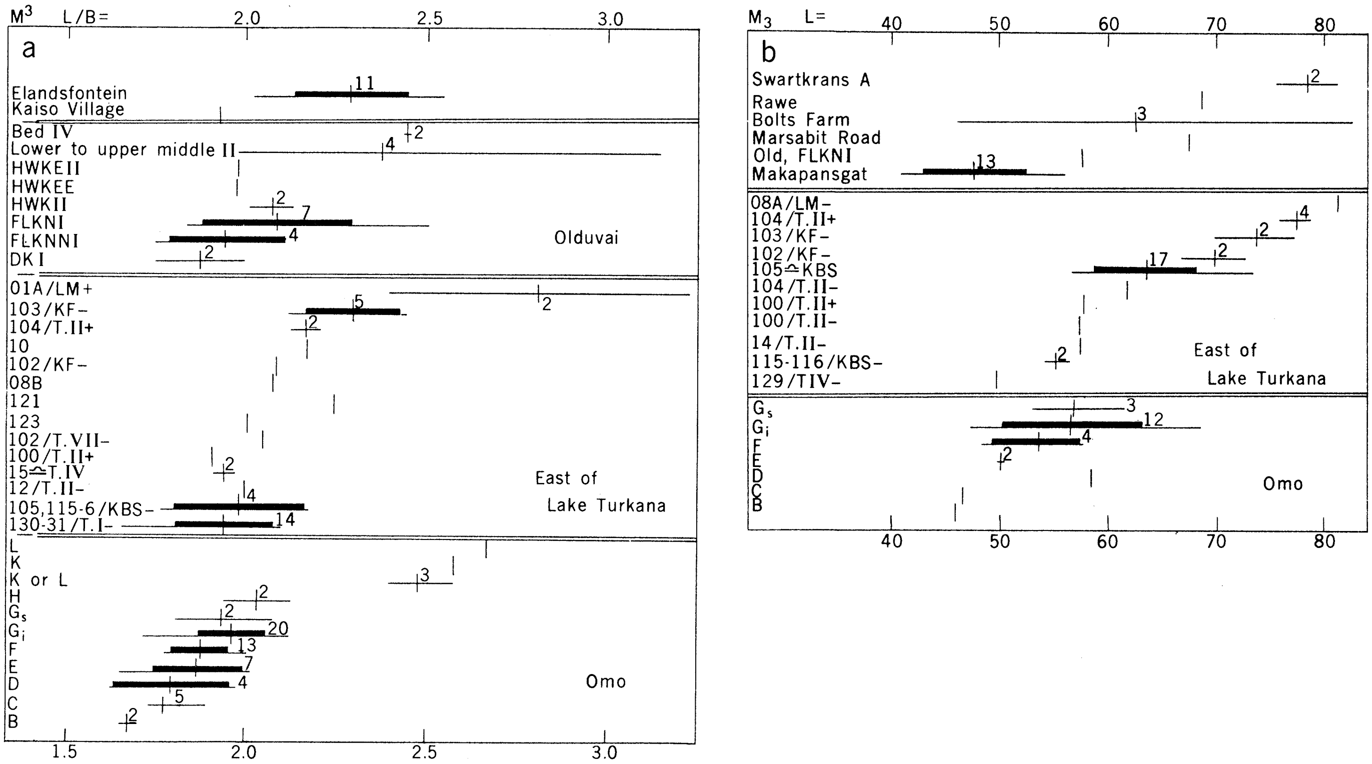
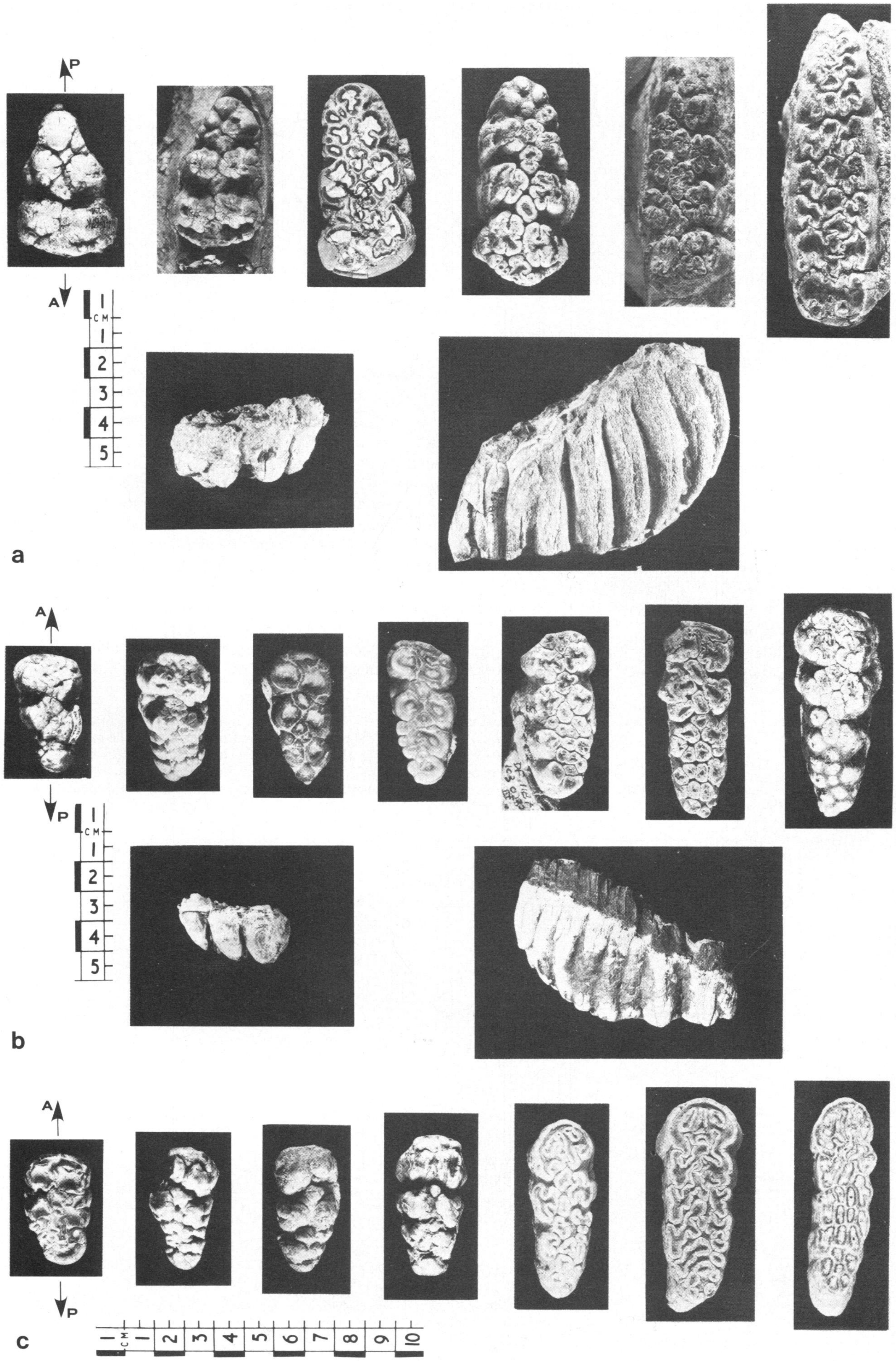


Fig. 2. Some important Plio-Pleistocene suid or hominid localities, or both, in sub-Saharan Africa: 1 = Hadar, Ethiopia (Pliocene); 2 = Omo, Ethiopia (Plio-Pleistocene); 3 = east of Lake Turkana (formerly East Rudolf), Kenya (Plio-Pleistocene); 4 = Lothagam, Kenya (Pliocene); 5 = Kanapoi, Kenya (Pliocene); 6 = Lukeino, Kenya (Mio-Pliocene); 7 = Olduvai Gorge, Tanzania (Pleistocene); 8 = Laetolil, Tanzania (Pliocene); 9 = Makapansgat, South Africa (Pliocene); 10 = Swartkrans, South Africa Pleistocene); and 11 = Langebaanweg, South Africa (Pliocene).

Table 1.(a) Ratio of the length to the breadth of the upper third molars (M^3) of *Mesochoerus limnetes* from various African sites. Vertical lines represent means and horizontal lines represent ranges; horizontal bars represent one standard deviation from the mean. The number of measured specimens appears to the right of the mean. These kinds of metric data are used in the present analysis only to supplement observations on morphology and thereby provide accurate assessment of the phylogenetic status of suid populations represented in paleontological samples. Comparison of these samples allows biostratigraphic correlations. (b) Maximum lengths (in millimeters) of the lower third molars (M_3) of *Metridiochoerus andrewsi* from various African sites.

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Biostratigraphic Analysis

The most meaningful biostratigraphic approach to correlation consists of a comparison of relative evolutionary status of representatives from several independently evolving lineages. For the Plio-Pleistocene of Africa the Suidae is the mammalian family that at present best satisfies these conditions. Ultimately other families (Equidae, Elephantidae, Bovidae, Hippopotamidae) may prove similarly useful in this respect. Correlations based on the presence or absence of taxa are liable to be less reliable, especially if faunal lists are prepared by different investigators, and may also be biased by ecologic factors. It is obvious that any attempted correlation requires an initial understanding of lengthy fossiliferous sequences in which temporal relationships of faunal elements can be demonstrated by absolute stratigraphic position. In East Africa such understanding has only been achieved during the past two decades.

An examination of the entire fossil suid record has resulted in the correlative conclusions presented in Figs. 4 and 5. The summary presented below applies only to certain hominid-bearing localities of the African Plio-Pleistocene (Fig. 5); a fuller account of all sites will appear elsewhere (*5*).

Omo group. The Omo Shungura Formation of southern Ethiopia has been subdivided into a number of members on the basis of the occurrence of a series of widespread volcanic ash horizons (tuffs), which are usually readily distinguishable. The members are designated A to M from the base upward (*10*). This succession has yielded a number of conventional K/Ar dates (*11*) and a complete magnetostratigraphic column (*12*). The fossiliferous sequences of the lower portion of the Omo Shungura Formation (Members B through G) provide a virtually unbroken documentation of the early evolutionary history of *Mes. limnetes* and *Met. andrewsi* and can be used as a standard for comparison with other sites. The suid evidence suggests, however, that sediments above Member H have yielded a somewhat interrupted and discontinuous faunal record. Moreover, it conflicts with published stratigraphic interpretations (*10*) in two respects. First, some of the Kalam localities examined by French participants in the International Omo Expeditions and recognized as Member K (for example, locality K.10) yield a clearly older fauna that best matches Member G in the type Shungura exposure. Second, a fault-bounded block of fossiliferous localities in the Shungura type area examined by American investigators (localities 401 through 415, 417, and 419), said to represent Member G, is clearly the time equivalent of Member K or above in the Kalam area. Kalam age (Member K or L) deposits can, on the basis of suid evidence, now be demonstrated to occur in the Shungura type area, and reevaluation of relevant parts of the stratigraphy in light of such faunal evidence would appear desirable.

East of Lake Turkana (formerly East Rudolf). Along the northeastern shores of Lake Turkana, sediments of late Pliocene and early Pleistocene age are exposed over an area approaching 1000 square miles (2600 square kilometers) in extent. A scheme of stratigraphic subdivisions and correlations has been proposed by Bowen and Vondra (*13*), and maps and further stratigraphic commentary have been presented by Findlater (*14*). In both of these published schemes beds of tuffaceous sediment have been used as local markers and a framework of lithostratigraphic correlations linking discontinuous tuff outcrops has been proposed. Since this geological work was done, we have collected numerous fossil suid specimens and have grouped these into samples by reference to the designated area subdivisions (Fig. 6) and to the intervals between the tuff beds which occur in any given area (Table 2). Comparison between these localized and stratigraphically restricted samples of fossils thus provided an independent cross-check on correlations between tuff outcrops that had been linked on the basis of field mapping considerations. Available suid evidence strongly supports most of the provisional lithostratigraphic correlations proposed for the Koobi Fora and Ileret regions, but in a number of instances the evolutionary status of the suid fossils represented in the samples appears to contradict the correlations (see Table 2b). In recognition of the need to engage in a critical review of the correlations of tuff outcrops in different areas, tuffs exposed in each area have been given independent index labels by the Koobi Fora Research Project (area number plus Roman numeral—see Table 2). The names for tuffs that have become widely known among scientists (for example, Tulu Bor, KBS, and others) should for the time being be used only in the type area and in immediately adjoining areas where correlation amounts to certainty.

The Koobi Fora Formation has yielded a large number of hominid fossils of great potential importance for the understanding of human evolution. It is thus imperative that horizons from which they have been retrieved can be related within the local sedimentary basin and equated with other hominid-bearing localities. Evidence from geophysical dating methods has so far proved controversial (*3, 4, 15*).

Suids from the lower part of the Lower Member of the Koobi Fora Formation (below the time-stratigraphic horizon of the Tulu Bor tuff) equate well with those from Shungura Member B (Fig. 4). Those from slightly higher in the section (below the time-stratigraphic horizon of the KBS tuff) equate with samples from Shungura Member G. The Koobi Fora Formation apparently lacks fossiliferous horizons equivalent in age to Shungura Members C through F, although there are indications that the Kubi Algi fauna may, in part, fill this hiatus. The bulk of the fauna from the upper part of the Lower Member of the Koobi Fora Formation correlates with Shungura Member G and Olduvai Bed I. The Koobi Fora Formation lacks faunas equivalent to those of Shungura Members C through F below the level at which the hominid cranium KNM-ER 1470 was found. These observations independently confirm Cooke's (*2*) earlier suggestions to a similar effect and serve to place these important sediments into a more meaningful perspective. The abundant local faunas collected from the lower part of the Upper Member of the Koobi Fora Formation (below the Koobi Fora or Middle tuffs) are evidently poor-

Fig. 3. (a) Upper third molars of the *Nyanzachoerus-Notochoerus* group (group 1). Occlusal view (left to right in approximate chronological sequence): *Ny. tulotos* (KNM-LT 286), *Ny. kanamensis* (KNM-KP 223), *Ny. jaegeri* (KNM-KP 234), *Not. euilus* (KNM-ER 430), *Not. capensis* (KNM-ER 448), *Not. scotti* (KNM-ER 3438). Lateral view (left to right): *Ny. tulotos* (KNM-LT 286), *Not. scotti* (KNM-ER 3319). Note the increases in tooth crown length and height from left to right. A = anterior, P = posterior. (b) Upper third molars of the *Mesochoerus limnetes* lineage (group 2). Occlusal view (left to right in chronological sequence): Omo 28-2099 (Shungura B), L.193-122 (Shungura C), Omo 33-329 (Shungura F), Old. 63 DK I (Olduvai Lower Bed I), KNM-ER 1139 (Koobi Fora, Upper Member), KNM-ER-1140 (Koobi Fora, Upper Member), Omo K-5-2139 (Shungura L). Lateral view (left to right): L. 367-2 (Shungura B), Omo K5-2139 (Shungura L). (c) Upper third molars of the *Metridiochoerus andrewsi* lineage (group 3). Occlusal view (left to right in approximate chronological sequence): L. 1-459 (Shungura B), L. 576-6 (Shungura C), L. 123-1A (Shungura D), L. 616-39 (Shungura G), KNM-ER 1162 (Koobi Fora, Upper Member), KNM-ER 3415 (Koobi Fora, Upper Member). Far right: *Metridiochoerus compactus* Old. 57-1027 (Olduvai Upper Bed II).

ly represented at other East African sites and are important for the correlative applications that they thus make possible.

The conventional K/Ar determination of Curtis *et al.* for the KBS tuff and other tuffs from the upper part of the Lower Member of the Koobi Fora Formation (*4*) agree with widely accepted conventional K/Ar dates for Shungura Member G and Olduvai Bed I. It is possible that ^{40}Ar/^{39}Ar step-heating methods and fission track determinations that provide an age of 2.4×10^6 years for the KBS tuff and lithostratigraphic correlates (*3*) are better chronometric measures; in this case suid evidence would suggest that accepted ages for Shungura Member G and Olduvai Bed I are too young by about 0.5×10^6 years. These alternative hypotheses require further research.

Olduvai Gorge. In terms of stratigraphic thickness, the Olduvai succession is condensed relative to either the Shungura or the Koobi Fora Formation (Fig. 4). Differences between the Olduvai Bed I plus Lower Bed II fauna and that from Middle and Upper Bed II were formerly assigned to a depositional hiatus (*16*) and to ecologic change resulting from tectonic disturbance of the Olduvai basin (*17*). It now seems probable that both factors were involved, contemporary tectonic deformation of the basin in Middle Bed II times being coincident with a proportional increase in savanna elements in known East African faunal assemblages. The current paucity of faunal elements from lower Middle Bed II is unfortunate, but from the few available (advanced *Met. andrewsi*) suid specimens it seems clear that lower Middle Bed II equates with the lower part (below the Koobi Fora or Middle tuffs) of the Upper Member of the Koobi Fora Formation.

The Acheulian stone tool industry is first represented at Olduvai archeological site EF-HR above the hiatus in Middle Bed II. The faunal correlation may thus have an important bearing on the evolution (or lack thereof) in biface industries from an Oldowan substrate (*17*). It is particularly significant that the artifact assemblages reported from the Upper Member of the Koobi Fora Formation (*18*), on present suid correlative evidence, seem to lie chronologically between Oldowan of Lower Bed II and the Acheulian of Middle and Upper Bed II. The results of the present analysis suggest the need for renewed focus of paleontologic investigation of Lower and Middle Bed II between the Lemuta Member and the MNK type site.

South African sites. Current radiometric methods have not been successfully used to independently date the hominid-bearing cave breccias of South Africa. Faunal correlation therefore assumes primary importance in the relative placement of these sites. One of the most recent attempts to use faunal evidence in such placement is that of Vrba on Bovidae (*19*). Problems previously encountered in the use of suid remains to obtain valid correlations have stemmed partly from difficulties in establishing phylogenetic relationships within the genera *Notochoerus* and *Metridiochoerus* and partly from the scarcity of pertinent fossiliferous horizons in Olduvai Bed II or the Omo Shungura sequence. These problems have been alleviated by improvement of the East African fossil rec-

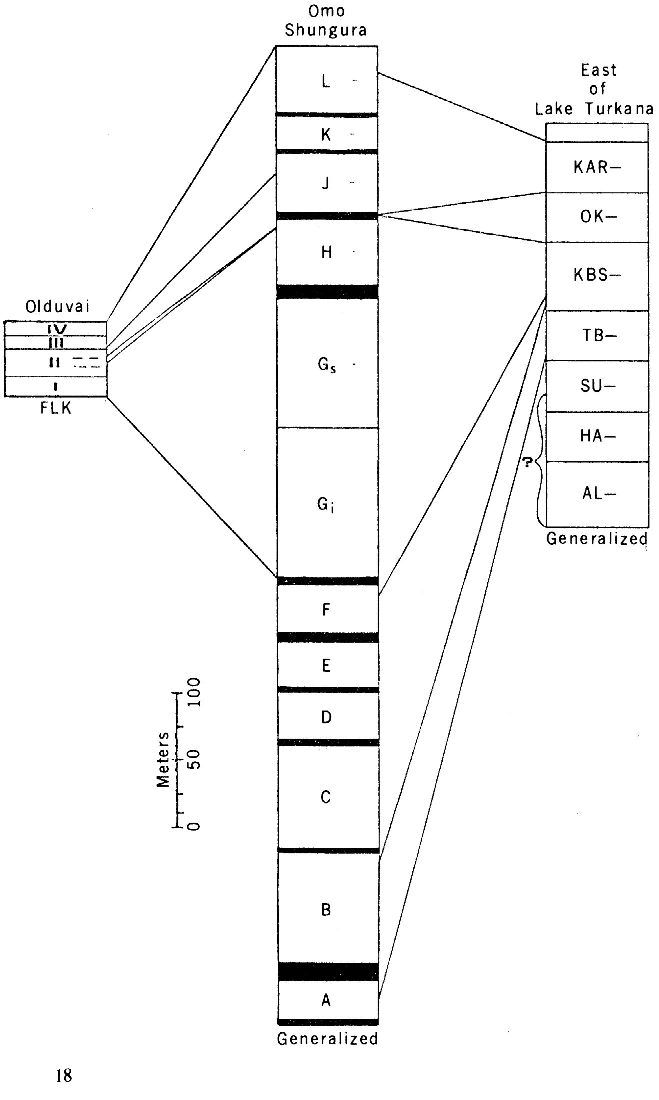

Fig. 4. Generalized stratigraphic sections for Olduvai Gorge [after Hay (*17*)], Omo Shungura Formation [after de Heinzelin *et al.* (*10*)], and east of Lake Turkana [after Findlater (*14*)]. Approximate correlations are based on available suid evidence. The Lake Turkana column is composed of biostratigraphic units based on paleontological samples representing equivalent evolutionary stages in the suid species studied. These units are made up of samples known to come from below the type outcrop of the indicated tuff as well as from below tuffs whose equivalence was hypothesized lithostratigraphically and then tested and verified on the basis of the suid evidence (see Table 2b for details). For example, the KAR-block (sub-Karari) refers to fauna from between the base of the Karari tuff and the base of the Okote tuff and other equivalent faunas as defined above. A revision of lithostratigraphic and biostratigraphic nomenclature for the east Lake Turkana area by the Koobi Fora Research Project is under way and will be published later. See text for details.

ord, particularly at localities of the Koobi Fora Formation.

Two suids are present in the Makapansgat Limeworks assemblage—*Not. capensis* and *Met. andrewsi*. *Notochoerus capensis* is a species intermediate between the better known East African species *Not. euilus* and *Not. scotti*. The presence of advanced specimens of *Not. euilus* in the upper part of Shungura Member B and primitive examples of *Not. scotti* in Shungura Member C suggests the Makapansgat fauna is equivalent in age to Members B and C of the Omo Shungura sequence. This observation gains independent support from the fact that *Met. andrewsi* is at an equivalent evolutionary position to examples from Shungura Member C (Table 1b). This suid-based correlation both supports and permits refinement of recent geomagnetic polarity determinations at Makapansgat (*20*). Only one suid species is known from the austra-

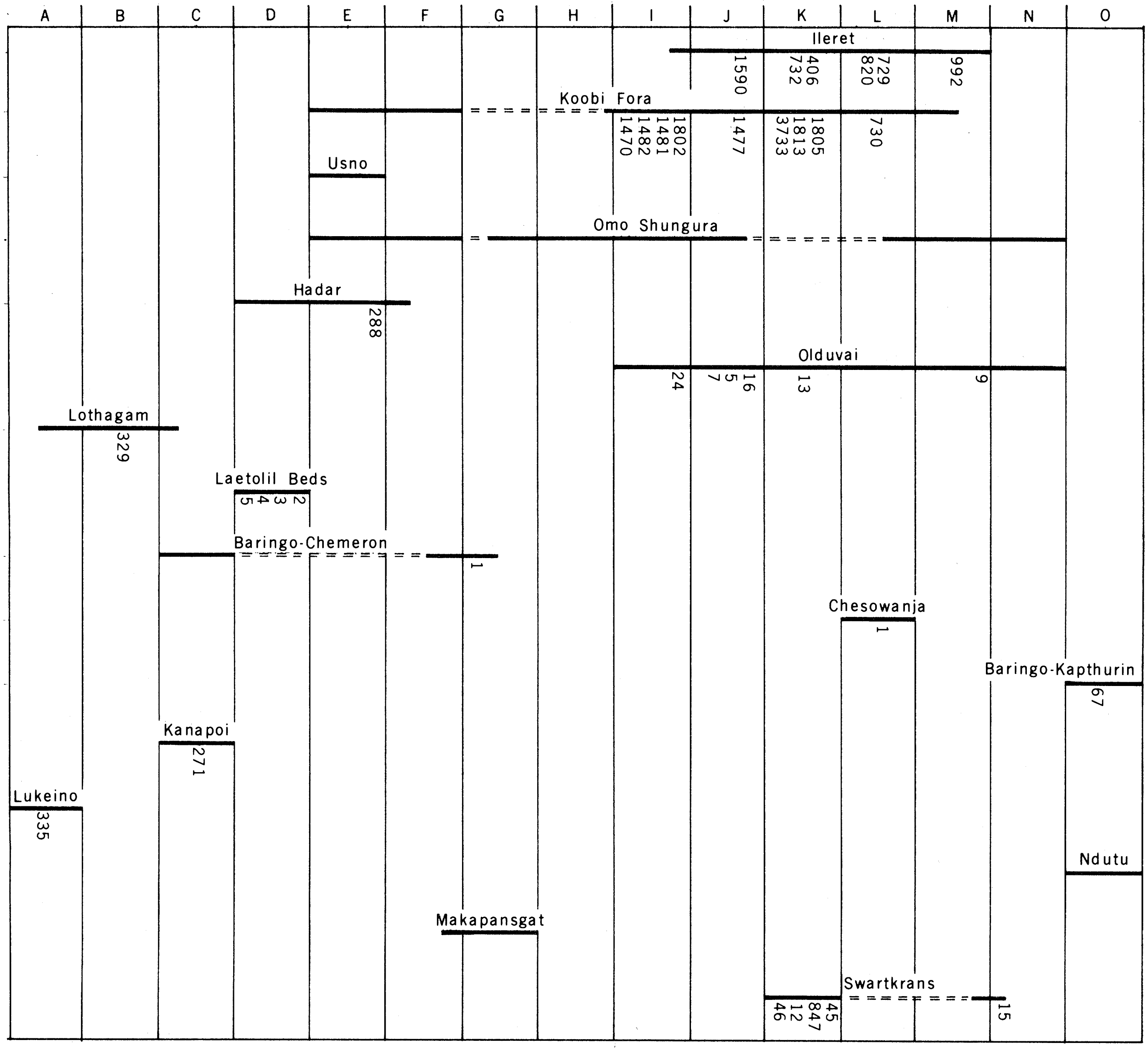

Fig. 5. Correlation of important hominid-bearing sites showing approximate relative temporal position of some significant hominid specimens. Time is plotted along the horizontal axis. Correlations are based on available suid evolutionary data; prior chronometric interpretations are not considered here. The heavy horizontal lines denote stratigraphic portions of each locality that bear diagnostic suid fossils. Dashed portions represent breaks in the fossil suid record at each locality. Fossil hominid specimen numbers are placed below each locality designation in the appropriate vertical column. These columns represent 15 arbitrary divisions (A to O) used for relative site placement; these divisions are defined on suid faunas from particular sites as detailed below. They represent convenient although not necessarily equal chronologic or evolutionary partitioning. The chart should be used only as a supplement to information provided in the text. Some correlations have necessarily been based on small samples and should be treated with caution (*5*). A = Lothagam Formation (Members 1B to 1C); B = Lothagam Formation (Member 3); C = Mursi and Kanapoi Formations, Chemeron Formation (part); D = Hadar Formation (Sidi Hakoma Member), Laetolil Beds; E = Usno Formation, Koobi Fora Formation (sub-117/T.III and 129/TB), Hadar Formation (Denen Dora Member); F = Shungura Formation (Member B Upper), Koobi Fora Formation (sub-117/T.VI); G = Shungura Formation (Member C), Kubi Algi Formation (sub-202/T.IV), Makapansgat (gray, hominid-bearing breccia); H = Shungura Formation (Members D to F); I = Shungura Formation (Member G), Koobi Fora Formation (sub-130+31/T.I.), Olduvai (Lower Bed I); J = Koobi Fora Formation (just above 105/KBS), Olduvai (Middle Bed I to Lower Bed II); K = Koobi Fora Formation (above 104/T. II), Olduvai (lower Middle Bed II), Swartkrans (A or "pink breccia"); L = Koobi Fora Formation (just below 103/Koobi Fora Tuff), Olduvai (upper Middle to Upper Bed II); M = Koobi Fora Formation (below Chari Tuff at Ileret), Shungura Formation (Member J); N = Olduvai (Bed IV), Shungura Formation (Members K and L); O = Olduvai (post-bed IV).

lopithecine breccia of Swartkrans A. This is an advanced stage of *Met. andrewsi* which is found also in the lower part of the Upper Member of the Koobi Fora Formation, Olduvai lower Middle Bed II, and Shungura Members H through J. Unfortunately, the limited suid sample from the critical Sterkfontein site is undiagnostic for purposes of correlation.

Implications for Hominid Paleontology

The results summarized above concerning the correlation of major African sites are significant in their bearing on the correlation of those hominid and artifactual levels that have also yielded diagnostic fossil suids. The most important implications are summarized below and in Fig. 5.

1) Although their absolute ages remain temporarily uncertain, those early hominids from the Lower Member of the Koobi Fora Formation that are generally attributed to the genus *Homo* [KNM-ER 1470 (*21*), 1590 (*22*), and 1802 (*22*)] are, from suid correlative evidence, essentially contemporaneous with similar (but more fragmentary) specimens from Olduvai Bed I and Lower Bed II [OH.7 (*23*) and OH.16 (*23*)] and not, as earlier radiometric estimates had suggested (*3*), substantially older.

2) The Makapansgat "gracile" australopithecines are approximately equivalent in age to Shungura Member C. They are therefore appreciably older than the "robust" australopithecine sample from Swartkrans A, which equates with Shungura Members H to J and Olduvai Middle Bed II.

3) Suid evidence demonstrates the essential contemporaneity of hominids OH.13 (*23*), KNM-ER 1805 (*22*), KNM-ER 1813 (*22*), and SK-847 (*24*) with the newly discovered *Homo erectus* KNM-ER 3733 (*25*) and the robust australopithecines KNM-ER 406 (*26*) and 732 (*27*). Thus the option of viewing these morphological variations in ancestral-descendant relationships is not supported by faunal evidence.

4) The demonstrated time relationships between such "hyper-robust" East African australopithecines as KNM-ER 406, 729 (*25*), 818 (*28*), and OH.5 (*29*) and the smaller South African forms from Swartkrans (*30*) also appear to remove the possibility that the observed differences can be attributed to hypothetical ancestor-descendant status (Fig. 5). The observed differences appear to be geographic instead of chronologic and may reflect phyletic separation, taphonomic bias, or morphological response to different prevailing ecologic conditions.

Theoretical Considerations

The suid material discussed has been collected from statigraphic sequences that in toto represent a geologically short period of time. It therefore has some bearing on questions and problems

Table 2. (a) List of known tuffs of the Koobi Fora and Kubi Algi formations, designated by area. Named tuff abbreviations: KAR: Karari; CH: Chari; L/M: Lower/Middle; KF: Koobi Fora; OK: Okote; KBS: KBS; TB: Tulu Bor; SU: Suregei; HA: Hasuma; AL: Allia. Roman numerals were assigned in a vertical sequence within each area and do not imply correlation between areas. Named tuffs (or letter abbreviations) indicate correlations which are direct and secure between the type and adjoining areas. The base of each tuff enclosed within a box has been used as a paleontologic marker horizon. (b) Seven major tuffs were formerly interpreted as traceable throughout the region investigated by members of the Koobi Fora Research Project. This assumption is no longer tenable. We indicate here which of the named and numbered local tuff outcrops were formerly assigned to one of the seven major tuffaceous units. These data should not be used as a guide to correlation until further geologic work has been completed. Circled tuff numbers indicate correlations that are definitely considered erroneous from faunal evidence.

a

	Ileret														
Areas	1A	01	02	03	04 06 6A	05	07 7A	08 8A	8B	09	10	11	12	14	15
	L/M	CH	CH	CH	CH	CH	CH	L/M		L/M		CH	II	III	IV
		L/M	L/M	L/M	L/M		L/M	I				L/M	I	II	III
														SU	II
															SU

Koobi Fora																			Kubi Algi				
Karari Ridge				KBS-Kokoi area				Koobi Fora Ridge								Bura Hasuma							
118	129	130	131	105	115	116	117	100	101	102	103	104	106	119	127	110	121	123	202	203	204	206	250
KAR	V	KAR	KAR	III	I	KBS	VI	II	KF	KF	KF	III	KF	KF	III	III	I		IV	V	IV	I	I
OK	IV	OK	OK	KBS		III	V	I	I	VII	IV	II	II		II	II			III	IV	III		
II	III	II	III	I		II	IV			VI	III	I	I		I	I			II	III	AL		
I	TB	I	II			I	III			V	II								HA	II	I		
	I		I				II			IV	I									I			
							I			III													
										II													
										I													

b

	Ileret														
Tuffs / Areas	1A	01	02	03	04 06 6A	05	07 7A	08 8A	8B	09	10	11	12	14	15
Karari		CH	CH	CH	CH	CH	CH					CH			
Okote	L/M	L/M	L/M	L/M	L/M		L/M	L/M		L/M		L/M			
KBS													II	III	IV
Tulu Bor															
Suregei														SU	SU
Hasuma															
Allia															

	Koobi Fora																			Kubi Algi				
	Karari Ridge				KBS-Kokoi area				Koobi Fora Ridge								Bura Hasuma							
Tuffs / Areas	118	129	130	131	105	115	116	117	100	101	102	103	104	106	119	127	110	121	123	202	203	204	206	250
Karari	KAR		KAR	KAR																				
Okote	OK	V	OK	OK						KF	KF	KF		KF	KF	III								
KBS	II	IV	I	I	KBS	I	KBS	VI			VI	II	II	II										
Tulu Bor		TB					II	III	III		IV													
Suregei								I			II									IV				
Hasuma																				HA	II	IV		
Allia																						AL	I	I

⬚ Type locality of named tuff

◯ Correlations considered erroneous from faunal evidence of theoretical evolutionary biology. Changes in tooth size and morphology in the various suid lineages apparently conform to simple Darwinian directional selective processes. Gradual changes in the populational means and ranges are observed through time. It has become evident that radiometric age determinations achieved by different methods are not always compatible, and it would seem wise to defer strict assessment of evolutionary rates until the important suid faunas from east of Lake Turkana, particularly those from the Upper Member of the Koobi Fora Formation, can be more firmly linked chronometrically with other East African assemblages. Nevertheless, the gradual nature of many observed morphological changes appears to contrast with the evolutionary model of punctated equilibria proposed by Eldredge and Gould (*31*). The identification and quantification of these gradualistic evolutionary tendencies are based on simple empirical observations in relatively complete stratigraphic contexts. It is difficult to believe that such gradual progressions as the increase in the third molar length of *Mes. limnetes* (Table 1a) reflect any preconceived notions of evolutionary process. The Omo Shungura, Olduvai, and Koobi Fora successions, at one time considered to represent virtually intact and continuous faunal sequences (see above), are instructive in this regard. Observed morphological discontinuities between related suids from these sites have sometimes been explained as ecologically based and would almost certainly have been ascribed to processes of punctated equilibria, were the relevant horizons yielding intermediate forms not preserved at other localities. In such cases, morphological discontinuities in a phyletic sequence are due to stratigraphically invisible imperfections in the geologic and fossil record.

Acceptance of the evolutionary model of phyletic gradualism rather than that of punctated equilibria is possible and appropriate only in a relative sense. Speciation among the Plio-Pleistocene suids occurred both by branching of a lineage (cladogenesis) and by change in a single lineage over time (anagenesis). Depending on the completeness of the fossil record and the continuity of the sedimentary sequences, available evidence may support either models of punctated equilibria or models of phyletic gradualism. The continued representation of these models as either/or alternatives could therefore be both unproductive and theoretically misleading. The documentation of phyletic speciation depends entirely on fortuitous preservation of relevant stratigraphic sequences, and the rates of this process can only be assessed in the light of independent, reliable geophysical chronology.

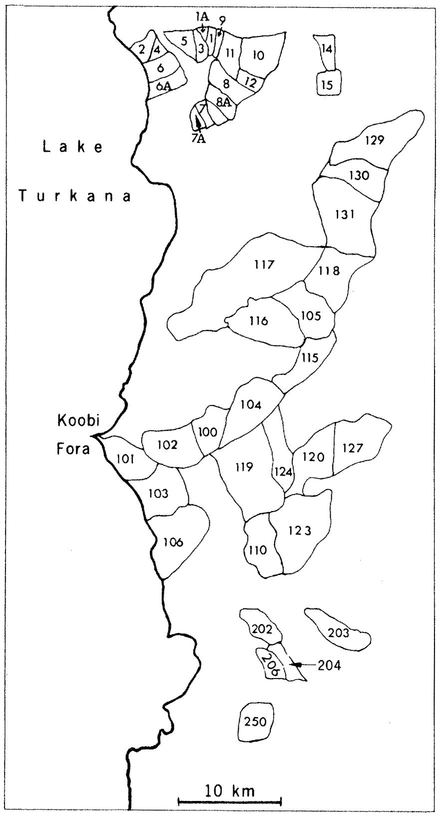

Fig. 6. Map of fossiliferous localities (areas) of the Koobi Fora and Kubi Algi Formations, east of Lake Turkana, northern Kenya.

The results of this study appear to have important applications for a number of different disciplines. Our interpretations of suid evolution in the African Plio-Pleistocene are based on evidence currently available and should be regarded as testable hypotheses when further material comes to light from continuing field work in Africa and Asia.

References and Notes

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32. This article is based on investigations of the fossil Suidae from east of Lake Turkana encouraged by the Koobi Fora Research Project and R. E. Leakey and undertaken by permission of the Museum Trustees of Kenya. Financial support for travel expenses was provided by the National Museum of Kenya, L. S. B. Leakey Foundation (J.M.H.), the National Science Foundation graduate fellowship program (T.D.W.), and the Scott Turner Fund of the Department of Geological Sciences, University of Michigan (T.D.W.). Field work was supported by grants to the Koobi Fora Research Project by the National Environmental Research Council (Great Britain), the National Science Foundation, the National Geographic Society, and the William H. Donner Foundation. The following institutions facilitated this study: National Museum of Kenya; British Museum (Natural History); Cleveland Museum of Natural History; Nasionale Museum (Bloemfontein); Musée de l'Homme, Institut de Paleontologie (Paris); National Museum of Ethiopia; Transvaal Museum; South African Museum; Louis Leakey Memorial Institute (Nairobi); Bernard Price Institute for Palaeontological Research (Johannesburg); Anatomy Department, University of the Witwatersrand; Geology Department, Dalhousie University; and Anthropology Department, University of California (Berkeley). Assistance from and discussions with many people from these institutions is gratefully acknowledged. Special thanks are due to H. B. S. Cooke, Y. Coppens, I. C. Findlater, F. C. Howell, D. C. Johanson, members of the Koobi Fora Research Project (particularly G. Ll. Isaac, K. Kimeu, and the paleontology team), M. D. Leakey, and R. E. Leakey.