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FURTHER REVISION OF THE FOSSIL ELEPHANTIDAE OF SOUTHERN AFRICA

By H. B. S. Cooke

Abstract

The South African fossil *Metarchidiskodon griqua* is regarded as indeterminable and hence as a *nomen vanum;* the generic name thus also falls away. A new method for representing graphically the main dimensional features of elephant molar teeth is applied to the fossil species from southern and East Africa. It is suggested that the genus *Palaeoloxodon* is not represented in these regions and that most of the extinct elephants must be placed in *Archidiskodon.* The species distinguished are *A. subplanifrons, A. broomi, A. exoptatus, A. recki* and *A. transvaalensis,* while *A. africanavus* and *A. archidiskodontoides* are of uncertain status. The North African *"Elephas" atlanticus* is placed in *Loxodonta* and the South African species *zulu* is regarded as a synonym. It is considered that the Pleistocene elephants of Africa have evolved within the continent itself.

Introduction

During the period from 1906 to 1939 there were described twenty-one supposedly extinct species of elephant from southern Africa. In 1947 the writer[1] attempted a revision of the material and reduced the number to eleven while, in the same year, Arambourg[2] rejected all the South African names. In 1955 Meiring[3] added a new species *Archidiskodon scotti* and in 1958 Singer and Hooijer[4] recorded, for the first time, a *Stegolophodon* which they wisely refrained from naming specifically. During 1956 the writer had the opportunity of examining large numbers of fossil proboscidean teeth at museums in Europe and in 1958 was able to study material in various institutions in the United States of America, the result of these studies being to invoke a far more critical attitude towards the multiplicity of species still recognised in southern Africa.

Status of Metarchidiskodon griqua

One of the most serious problems is the status and position of *"Metarchidiskodon griqua".* Haughton[5] described in 1922 a fragmentary lower molar which he named *Loxodonta griqua.* The generic reference was changed to *Archidiskodon* in 1928 by Osborn[6] and in 1934[7] he founded upon it the new genus *Metarchidiskodon.* In 1951 Dietrich[8] discussed the phylogeny and taxonomy of some of the African fossil elephants and applied the generic name *Metarchidiskodon* to the majority of the fossil elephants from East and South Africa, including the abundant East African *"Elephas" recki.* The present writer stated in 1947 "It is unfortunate that it (the type specimen) is of so fragmentary a nature as this fact renders specific deductions very difficult . . . and the differences hardly seem to be even of

sub-generic rank . . . It would seem that the specific distinction of *Mammuthus griqua* must be accepted more because the nature of the material prevents its rejection than because it is a clearly identifiable form". There is even doubt as to whether it is a lower molar (Haughton[5], Cooke[1]) or an upper molar (Osborn[6]). The simple fact is that the specimen is not adequate for the proper definition and identification of specific characters and far too much has been built upon a very tenuous foundation. It is here proposed that the species be regarded as practically indeterminable (see Simpson[9]) and hence as a *nomen vanum* to which other material should not be referred. The genus *Metarchidiskodon* also falls away.

Graphical Study

Method

In his paper on *Archidiskodon scotti,* Meiring[3] made a graphic comparison of the width and height of the teeth for the species named in South Africa and showed that a "width/height index $\frac{(\text{width} \times 100)}{\text{height}}$" is more useful than the traditional length/breadth index, which cannot be employed on fossil teeth lacking some of their plates through damage. As far back as 1938, Arambourg[10] used the converse ratio $\frac{\text{height}}{\text{breadth}}$ as a figure for "the hypsodonty". The present writer proposes that the ratio $\frac{\text{height} \times 100}{\text{breadth}}$ should be known as the "index of hypsodonty" and finds that it can be combined with the length/lamellae ratio to provide a useful method for representing graphically the main dimensional features of elephant molar teeth. In these diagrams the vertical axis represents the value of the index of hypsodonty (H/W) and the horizontal axis shows the value of the length-lamellae ratio (L/P). A single point thus serves to show for a particular molar the relationship between the maximum breadth of the widest lamella (W), the maximum height (H) of the tallest preserved plate (measured over the enamel) and the average thickness of a complete plate (which is also the complement of the lamellar frequency) derived from the length of the tooth (L) measured perpendicular to the plates, divided by the number of plates (P). Plots of this type for a number of specimens indicate the range of variation within a group. The index of hypsodonty is preferred to Meiring's index as high-crowned teeth are then shown in their most easily interpreted position towards the top of the diagram. Such plots are truly representative only when the real maximum height is known; in moderately worn teeth the height is usually measured on an unworn lamella (if one is present) and little error is introduced but it is clear that excessive wear will lead to displacement of the plotted position *down* the graph and an undue extension of the apparent range of variability.

Plots have been prepared for a number of species but the literature is somewhat defective and in some cases the writer has had to depend entirely on his own

measurements, with consequent reduction in the statistical quantity available. A few generalizations may be made. (a) Somewhat surprisingly, there is a considerable overlap between the plots for corresponding upper and lower molars, presumably because lower teeth are commonly a little narrower than uppers, thus tending to compensate to some extent for the higher crowns of upper molars; the difference between upper and lower teeth is most apparent in the very hypsodont species. (b) The lower teeth normally possess slightly thicker lamellae than the uppers and the limits for the lower teeth extend one or two units towards the right and those of upper teeth towards the left in the diagrams. (c) Second molars tend to have somewhat thinner lamellae than third molars and thus tend to lie a few units towards the left in the diagram; in the case of the most high crowned species they tend to lie below the mean values of the index of hypsodonty for the third molars.

Figures 18 and 19 represent data for 73 second molars and 30 third molars respectively of *Loxodonta africana* but only a proportion of the individual teeth are plotted so as to show the distribution without cluttering up the diagrams. Figure 20 is a plot for third molars of *Palaeoloxodon antiquus*, based on specimens from famous localities in Great Britain, Germany and Italy and covering the various "mutations". The differing averages for upper and lower teeth are well brought out. A few plots for *Archidiskodon meridionalis* from Italian localities are also shown in Figure 20 but, unfortunately, the writer posesses very limited numerical data on this species. Figure 21 shows plots for *Archidiskodon planifrons* and is based solely on material from the Upper Siwaliks in the collections of the British Museum (Natural History) and the American Museum of Natural History. Figure 22 represents Arambourg's data for *"Elephas" atlanticus* from North Africa[10] and shows also the plot for his *"Elephas" africanavus* from Ichkeul, Tunisia[11].

These five diagrams furnish comparative data of value in a reconsideration of the described material both from East Africa and from southern Africa. While the method is useful for metrical comparisons it does not, of course, indicate other characteristics of the teeth such as the form of the plates or their number and these considerations must also be taken into account in assessing specimens.

The Material from South Africa

The named species from southern Africa, excluding the fragmental *Gomphotherium* sp. (Fraas[12]) and the recently described *Stegolophodon*[4] are listed in Table I under their original names, together with some of the main measurements which are plotted in Figure 23. Inspection of the plots suggests the existence of four groups as indicated and these have been labelled A, B, C and D to facilitate discussion.

Table I

Main Measurements of Molars of Fossil Elephantidae from Southern Africa

(Used in constructing the diagram of Figure 23)

		Pos	P	L	H	W	L/P	$\frac{H \times 100}{W}$
1	Archidiskodon subplanifrons Osborn 1928	RM_3	+5⅜	153	64	101	27	63
2	A. cf subplanifrons Haughton 1932	RM_3	+6	179	63	104	30	60
3	A. proplanifrons Osborn 1934	LM^3	8¾	253	62	103	29	60
4	A. andrewsi Dart 1929	LM_3	2½+1½	100+	60+	c80	25	75
5	Loxodonta griqua Haughton 1922 .	LM^3?	+3+	97	81	86	32	94
6	Archidiskodon vanalpheni Dart 1924 .	RM^3	7½+	235	131	112	31	117
7	A. milletti Dart 1929	LM^3	+7½	222	118	108	28	109
8	A. loxodontoides Dart 1929	LM^2	+4¾	146	105	92	31	114
9	A. broomi Osborn 1928	LM^3	6+	168	145	109	28	133
10	A. transvaalensis Dart 1927 . . .	RM^3	9½	307	231	110	22	210
11	A. sheppardi Dart 1927	LM^2	10½	246	188	100	21	180
12A	Palaeoloxodon darti Cooke 1939 . .	LM^3	12½+	234	219	94	19	233
12B	„	LM_3	+8½	212	160	95	25	169
12C	„	RM^3	+3+	60	209	93	20	224
13	Archidiskodon hanekomi Dart 1929 .	RM^3	16+	312	220	102	19	216
14A	Elephas (Loxodon) zulu Scott 1907 .	LM_3	12+	265	c95	85	22	112
14B	„	RM_3	12+	c260	c90	c85	22	106
15	Pilgrimia yorki Dart 1929	RM_2	9	180	115	79	20	146
16	P. kuhni Dart 1929	LM_2	+4¾+	96	100	75	19	133
17	P. subantiqua Haughton 1932 .	RM_2	10¾+	243	105	84	22	125

18	P. wilmani Dart 1929	LM^2	7+	119	128	70	18	183
19A	P. archidiskodontoides Haughton 1932 .	LM_2	9+	148	145	94	16	154
19B	„	RM^2	7+	108	c120	94	15	128
20	Archidiskodon scotti Meiring 1955 . . .	LM_2	8½	196	67	91	23	74

Pos = Position in dental series
L = Greatest length of molar perpendicular to plates
W = Greatest width of widest lamella (excluding cement)
L/P = Length-Lamellae ratio

P = Number of plates preserved (+ indicates missing parts)
H = Greatest height of enamel on tallest plate
$\frac{H \times 100}{P}$ Index of hypsodonty

Group A incorporates the low-crowned, wide, thick-plated species the writer had already[1] merged under the single species *Archidiskodon subplanifrons* Osborn 1928. Meiring's *A. scotti* is most probably a second molar as it shows signs of a posterior indentation and there is no valid reason to separate it from Osborn's species; it has associated with it a fine tusk of Archidiskodont character and an ulna, both of which make Meiring's account of particular interest and value. Most of the teeth are well worn and it has been suggested by Hooijer[13] that Osborn's estimates of the heights are too low. This is probably true but it is still clear that the crown heights were never very great. In the type of "*proplanifrons*" the actual height of the almost intact fourth and fifth plates is 55 mm. (Haughton[14], Osborn[7]) and it is restored to a maximum of 62 mm. (Cooke[1]); it seems most unlikely that the anterior plates of this tooth could have been higher than 75 mm. In Meiring's *A. scotti* the eighth and ninth plates are barely worn and their height is 66 — 67 mm., with an estimated maximum height for the anterior plates of 80 mm. Arrows in Figure 23 indicate the adjusted positions for these teeth using estimated instead of measured heights. The South African specimens would then correspond fairly closely to those described by Hooijer from Bethlehem in Israel[13], and the group would lie at the bottom fringe of the range for *A. planifrons* from the Siwaliks, shown in Figure 21. However, the plots of lower hypsodonty for *A. planifrons* are also based on worn teeth and if estimated heights were used the index of hypsodonty for this species would not fall below about 90 — 95. It is thus clear that the South African material still lies below the normal range for *A. planifrons* from the type area and there seems to be a reasonable case for regarding *A. subplanifrons* as a distinct African species. It is possible that Hooijer's material from Israel belonged to an emigrant colony.

Group B embraces a number of very thick-plated teeth of moderate crown height. In 1947 the writer[1] merged three of these (6, 7 and 8) as *A. vanalpheni* with

signs of a median expansion resembling the loxodont sinus but retained *A. broomi* (9) as probably separate as there was little sign of median expansion. The type of *A. broomi* is the anterior portion of an upper third molar (not a lower as Osborn stated[6]), the type of *A. loxodontoides* is an almost unworn anterior fragment of a second or even a first molar, and both the other specimens are posterior portions of second or third molars. Great variation in the form of the plates and development of a sinus has been observed by the writer in teeth of *A. meridionalis* in Italy, as well as marked simplification in pattern with advancing wear, so that there is no longer considered to be any good reason to separate these forms. The specific name *A. broomi,* dating from 1928, has priority. The fragment of *"Metarchidiskodon griqua"* might fall metrically within this group but its peculiar characters make it impossible to merge *A. broomi* with it and, as suggested above, *M. griqua* is best regarded as a nomen vanum.

Group C includes the type lower third molar of *Palaeoloxodon zulu* and also the three species *"Pilgrimia" yorki, P. kuhni* and *P. subantiqua* which the writer has already indicated[1] should be regarded as lower second molars and placed within the range of *P. zulu.* Arambourg[2,10] suggested in 1938 that Scott's species fell within the range of the North African *"Elephas" atlanticus* and, having had the opportunity of examining material of this species in Paris as well as the South African specimens themselves, the present writer endorses the view that the two species cannot be distinguished one from the other.

Not at present assigned to this group are the rather peculiar upper molars of the type of *P. archidiskodontoides*[14] (19A and 19B). The plates in these teeth are thick and in close contact with little intervening cement — a feature not reported in other material. There is a general resemblance in the form of the teeth to those of *P. recki* from East Africa, but in the latter the crowns are more hypsodont and the plates thinner than in *P. archidiskodontoides.* The fragments of skull and humerus differ markedly from *Loxodonta africana* and resemble *P. recki* of East Africa but are somewhat smaller, all features which are consistent with a related but possibly different species. More material is required before the problem can be settled.

Group D embraces the high crowned forms, of which *Palaeoloxodon transvaalensis* was the first to be described. *P. sheppardi* was merged with *P. transvaalensis* by Osborn[7]. The present writer[1] retained *P. hanekomi* as a distinct species on account of its apparently peculiar enamel islands but has since observed similar variations in paired teeth of *P. antiquus* from Italy and there is no longer any reason to separate *P. hanekomi* from *P. transvaalensis.* The writer's own species *P. darti* from the Victoria Falls[15] must also be merged with *P. transvaalensis* but the material from Rhodesia is important in providing the only lower molar certainly belonging to this group. This lower tooth indicates a substantial gap between this species and the type of *P. zulu.* The specimen described under the name *P. wilmani*

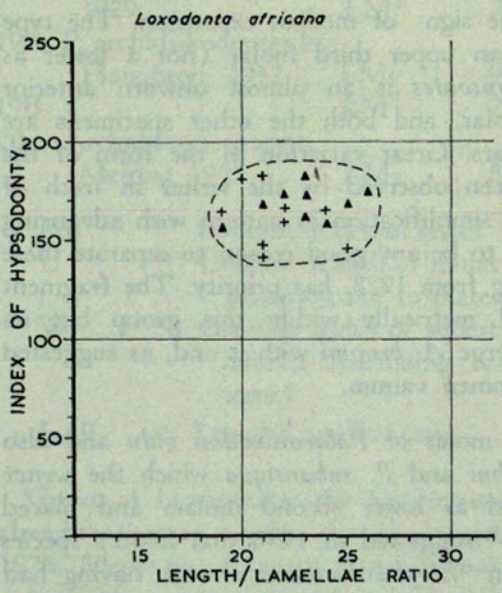


Figure 18

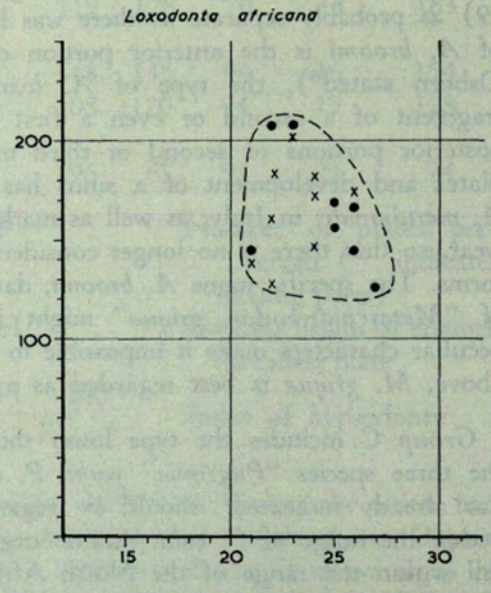


Figure 19

+ = M^2 x = M^3
▲ = M_2 ● = M_3

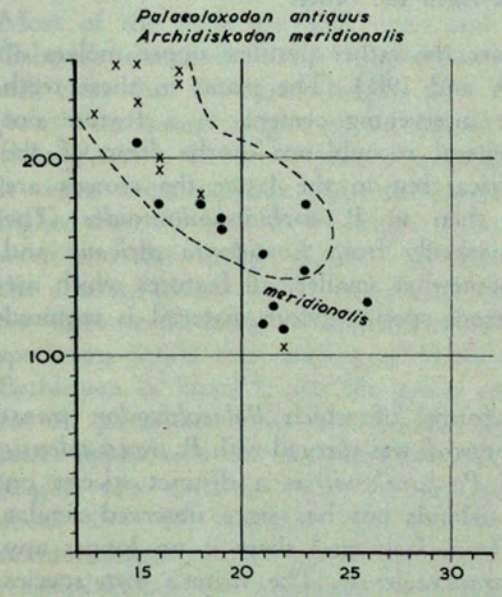


Figure 20

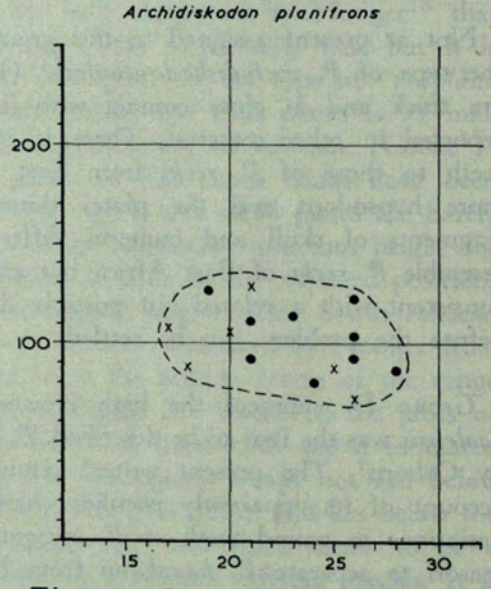


Figure 21

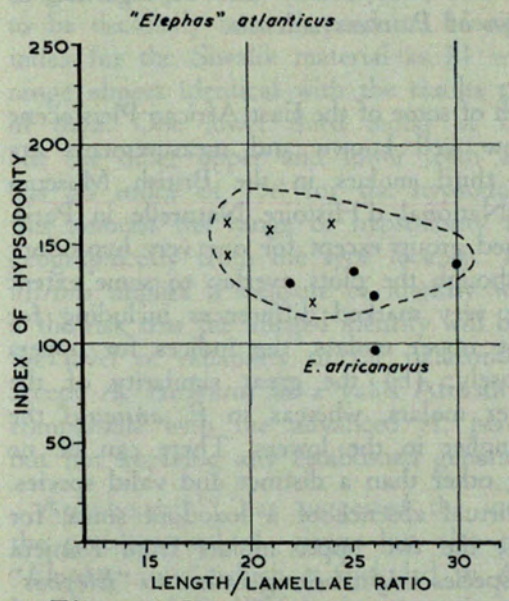


Figure 22

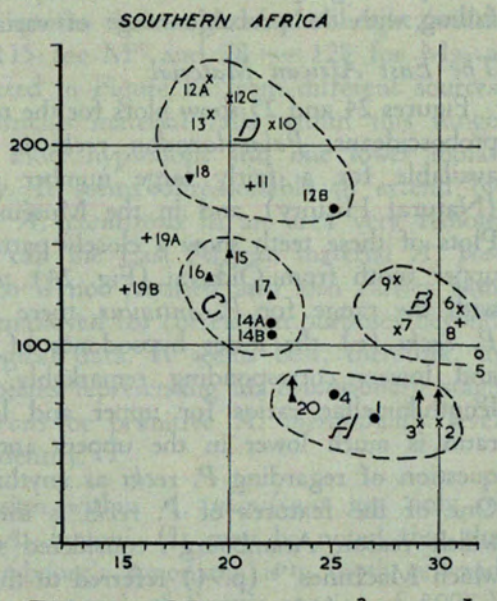


Figure 23

+ = M^2 x = M^3
▼ = M_1 ▲ = M_2 ● = M_3

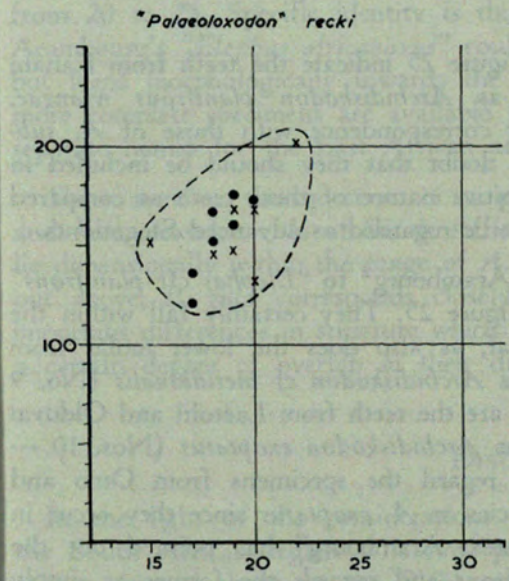


Figure 24

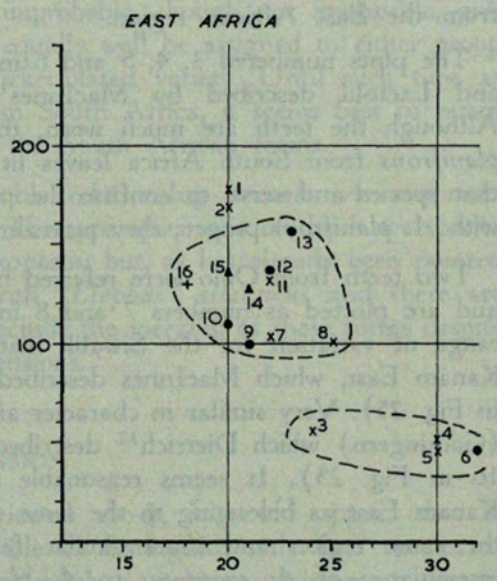


Figure 25

as a third lower molar is most probably a first molar and comparison with corresponding specimens of *P. antiquus* shows that it may also be regarded as falling with the probable range of variation of *P. transvaalensis*.

The East African Material

Figures 24 and 25 show plots for the teeth of some of the East African Pleistocene proboscideans. *Palaeoloxodon recki* is now well known and measurements are available for a fairly large number of third molars in the British Museum (Natural History) and in the Muséum National d'Histoire Naturelle in Paris. Plots of these teeth show a closely patterned group except for one very hypsodont upper tooth from Olduvai (Fig. 24). Although the plots overlap to some extent with the range for *P. antiquus*, there are very marked differences including for *P. recki* (a) the lesser hypsodonty of the upper molars, the indices for uppers and lowers corresponding remarkably closely; (b) the great similarity of the length-lamellae ratios for upper and lower molars, whereas in *P. antiquus* the ratio is much lower in the uppers and higher in the lowers. There can be no question of regarding *P. recki* as anything other than a distinct and valid species. One of the features of *P. recki* is the virtual absence of a loxodont sinus, for which reason Arambourg[2] considered that the two upper molars from Kanjera which MacInnes[16] (p.94) referred to this species might belong rather to *"Elephas" atlanticus* and there is much to support this view despite the fact that the Kanjera specimens are slightly higher crowned than the Moroccan material. These two molars are plotted in Figure 25 as numbers 1 and 2 together with other teeth from the East African region.

The plots numbered 3, 4, 5 and 6 in Figure 25 indicate the teeth from Kanam and Laetolil described by MacInnes[16] as *Archidiskodon planifrons nyanzae*. Although the teeth are much worn, their correspondence with those of *A. subplanifrons* from South Africa leaves little doubt that they should be included in that species and serve to confirm the primitive nature of these teeth as compared with *A. planifrons* proper; they may almost be regarded as advanced Stegodonts.

Two teeth from Omo were referred by Arambourg[2] to *"Elephas* cfr *planifrons"* and are plotted as numbers 7 and 8 in Figure 25. They certainly fall within the range of variation for the Siwalik material, as also does the lower molar from Kanam East, which MacInnes described as *Archidiskodon* cf *meridionalis* (No. 9 in Fig. 25). Very similar in character also are the teeth from Laetolil and Olduvai (Gadjingero) which Dietrich[17] described as *Archidiskodon exoptatus* (Nos. 10 — 16 in Fig. 25). It seems reasonable to regard the specimens from Omo and Kanam East as belonging to the same species as *A. exoptatus* since they occur in the same region and share similar features. Arambourg[2] has pointed out the resemblance of *A. exoptatus* to *A. planifrons* and regards the former as simply a synonym. Hooijer[18] similarly dismissed Arambourg's *Elephas africanavus*[11] as a synonym of *A. planifrons* because it falls within the range of variation of the latter species. However, when *A. exoptatus* and the other teeth here regarded

as belonging to the same group are considered as a whole, it is clear that the range overlaps that of *A. planifrons* but that the East African material tends to be decidedly more hypsodont. Hooijer quotes the range of the height/width index for the Siwalik material as 71 — 115 for M^3 and 78 — 125 for M_3, a range almost identical with the results plotted in Figure 21 from different sources of data. One lower third molar of Dietrich's material falls within this range but the other upper and lower teeth are more hypsodont and one lower molar has an index of 158 for the hypsodonty. It seems unreasonable to extend by this amount the range of hypsodonty for *A. planifrons* in an area very remote geographically from the type locality. To call the East African material *A. planifrons* implies a measure of identity which is not justified and also carries with it the risk that the alleged identity will be employed for correlation purposes beyond the level of reliability of the palaeontological data. It seems best, therefore, to accept *A. exoptatus* as a valid African species representing an evolutionary stage comparable with the advanced *A. planifrons* or primitive *A. meridionalis* level but not implying any established genetic identity.

Arambourg[2,10] has suggested the inclusion within *A. planifrons* not only of the problematical *A. griqua* but also of *A. broomi.* (It may be noted that the *"Elephas zulu"* which is included in Arambourg's synonymy is a tooth referred by Hopwood in 1926 and is not the type material of Scott's species of 1907.) The South African specimens of "Group B" in Figure 23 have length/lamellae ratios of 28 to 32 whereas *A. exoptatus* and its East African associates range from 20 to 25. Specific identity is thus improbable, though not impossible, and Arambourg's *"Elephas africanavus"* could equally well be assigned to either group but leans morphologically towards the thicker-plated variety. Until such time as more complete specimens are available from South Africa, it seems best to retain separate names for the East African and the South African forms.

There remains the question of a possible relationship between *A. exoptatus* and *Palaeoloxodon zulu* of South Africa. The type specimens of the latter species lie dimensionally within the range of *A. exoptatus* but, as has already been pointed out above, *P. zulu* corresponds closely with *"Elephas" atlanticus* and there are important differences in structure which preclude the merging of these forms despite a certain degree of overlap in their dimensions.

Discussion

In the light of the considerations reviewed above, it would appear that in the South African region it is now possible to distinguish only four species of extinct true elephant in the Pleistocene, though a unique specimen at present not adequately known occupies an isolated position as a fifth species *P. archidiskodontoides;* in addition there are two primitive mastodonts, *Trilophodon* (*Gomphotherium*) and *Stegolophodon.* The living African elephant is also present in the

fossil and semi-fossil state, usually in superficial deposits of later Pleistocene age. In East Africa four extinct elephants are also recognisable, as well as the living species and the archaic *Anancus kenyensis* and *Stegodon kaisensis*. From North Africa a large number of forms have been described but their present status is somewhat uncertain and it is not the purpose of this account to discuss them. The position is summarized in Table II.

TABLE II

South Africa	*East Africa*	*North Africa*
Loxodonta africana	L. africana	L. africana
"Elephas" atlanticus	E. atlanticus (?)	E. atlanticus
Palaeoloxodon transvaalensis	P. recki	E. aff. meridionalis
Archidiskodon broomi	A. exoptatus	E. africanavus
A. subplanifrons	A. subplanifrons	E. cf. planifrons
Stegolophodon sp.	Stegodon kaisensis	Stegolophodon sp.
Trilophodon sp.	Anancus kenyensis	Anancus osiris
		Mastodon sp.
also *incertae sedis*		
P. archidiskodontoides		E. jolensis
		E. pomeli

The striking parallelism of the occurrences in each region makes it tempting to suggest that the number of species could be still further reduced. From Figures 23 and 24 it might well be supposed that *P. recki* and *P. transvaalensis* had a considerable overlap in range. While the *relative* dimensions give such an impression, it is largely due to the greater height of the southern forms being compensated in the index of hypsodonty by a greater breadth. The upper molars in the East African collections have a maximum crown height of 165 mm. and the more usual figure is 115 — 120 mm., while the width ranges from 75 to 93 mm. as compared with heights of over 200 mm. for *P. transvaalensis* and widths of 93 to 110 mm. The lower molars of *P. recki* are 73 to 92 mm. wide and the maximum crown height is 150 mm., compared with a width of 95 mm. and a height of 160 mm. for the only lower molar of *P. transvaalensis;* the length/lamellae ratio of the latter is 25 compared with a maximum of 20 for *P. recki*. It would thus seem unwise at present to merge the two species. Similar arguments apply to the separation of *A. exoptatus* (80 to 91 mm. wide and with a length/lamellae ratio of 20 to 23) and *A. broomi* (92 to 112 mm. wide and with length/lamellae ratios of 28 to 31), though *E. africanavus* does occupy an intermediate position.

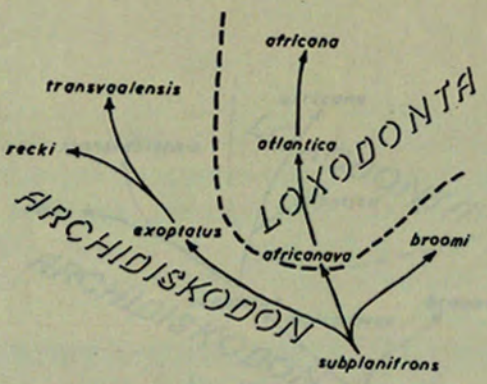


Figure 26

Arambourg has long employed the broad generic term *"Elephas"* for the African fossil elephants and this procedure has much to recommend it. The East African material was referred to *Palaeoloxodon* because of a supposed relationship of *P. antiquus* with *P. recki* which Arambourg has demonstrated[2] to be superficial and unreal. The resemblance of the skull structure to that of *Archidiskodon meridionalis* leaves little doubt as to its affinities. The South African *"P." transvaalensis* parallels the American *Archidiskodon imperator* rather than the European *Palaeoloxodon antiquus* in dental structure. *"Elephas" atlanticus* shows many of the characteristics of the living African elephant and may well be placed in the same genus. There is thus no good reason to regard *Palaeoloxodon* as being represented in Africa at all except, perhaps, in parts of the North African littoral. Incipient loxodont features are present in the teeth of *A. subplanifrons* and *A. exoptatus* and a possible phylogeny may be suggested in Figure 26. This does not differ fundamentally from that proposed by Dietrich[8], though it differs considerably in specific details. The presence of *Stegodon* and of *Stegolophodon* in the early Pleistocene indicates that the true elephants in Africa may well have evolved from a member of this stock quite independently of the Indian *Archidiskodon planifrons* and its descendants. It appears impossible, at this stage, to avoid using the generic name *Archidiskodon* for the African fossils but this should not be taken to imply too close an Asiatic connection. It seems very likely, as Arambourg[11] has suggested, that the Pleistocene elephants of Africa have evolved within the continent itself, paralleling the stages of progress observed elsewhere but not linked to Europe and Asia by periodic invasions as Osborn and others have suggested. The Oligocene and Miocene proboscidea suggest the existence of a basic stock in this continent from which "exports" to Europe and Asia may have been more significant than "imports".

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