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PRIMITIVE *ARCHIDISKODON* AND *PALAEOLOXODON* OF SOUTH AFRICA[1]

By Henry Fairfield Osborn

Every year brings fresh proof that Africa was the center of the origin and adaptive radiation of the Proboscidea. Since 1907 numerous more or less primitive superior and inferior grinding teeth have been discovered from the Vaal River terraces and other localities of the Transvaal, South Africa. The geologic level and localities are chiefly on the (1) higher and most ancient terrace (200–300 feet) of the Vaal River; (2) middle terrace (60–80 feet) of the Vaal River; (3) lowest and most recent terrace (40 feet) of the Vaal River. Theoretically the lowest terrace may be as old as the lower levels of the middle terrace. Flint implements occur in the middle and lower terraces only (Dart, 1929). In Osborn's opinion the *Archidiskodon subplanifrons*, and **Archidiskodon proplanifrons**, new species, types found in the middle terrace were washed in from an older Pliocene horizon.

Certain of the Transvaal grinding teeth surely belong to very primitive stages of *Archidiskodon;* others probably belong to primitive stages of *Palaeoloxodon* and were originally referred to *Loxodonta,* to *Archidiskodon* and to *Pilgrimia.*[2] Only by careful comparison and analysis is it possible to separate the species belonging to these several genera from each other.

Up to the present time the nineteen species described by W. B. Scott (1907), Raymond A. Dart (1927, 1929), S. H. Haughton (1922, 1932) and H. F. Osborn (1928) are provisionally referred as follows:

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[1]This is the thirty-third contribution by the author on the evolution and classification of the Proboscidea.
[2]*Pilgrimia* Osborn (December 20, 1924) is antedated by *Palaeoloxodon* Matsumoto (September 20, 1924).

Locality	Original Reference	Present Generic Reference
Zululand	*Loxodon zulu* Scott, 1907	= *Loxodonta*
?Middle terrace, Vaal River	*Loxodonta griqua* Haughton, 1922	= **Metarchidiskodon,** n. g.
Lowest terrace, Vaal River	*Archidiskodon transvaalensis* Dart, 1927	= *Palaeoloxodon*
Lowest terrace, Vaal River	*Archidiskodon sheppardi* Dart, 1927	= *Palaeoloxodon*
?Middle terrace (lower), Vaal River	*Archidiskodon subplanifrons* Osborn, 1928	= *Archidiskodon*
Lowest terrace, Vaal River	*Archidiskodon broomi* Osborn, 1928	= *Archidiskodon*
Middle terrace (lower), Sydney-on-Vaal	*Archidiskodon vanalpheni* Dart, 1929	= *Archidiskodon*
Middle terrace (lower), Sydney-on-Vaal	*Archidiskodon loxodontoides* Dart, 1929	= *Archidiskodon*
Middle terrace (lower), Sydney-on-Vaal	*Archidiskodon milletti* Dart, 1929	= *Archidiskodon*
?Middle terrace, Vaal River	*Archidiskodon andrewsi* Dart, 1929	= ?*Palaeoloxodon*
Lowest terrace, Vaal River	*Archidiskodon hanekomi* Dart, 1929	= *Palaeoloxodon*
Middle terrace, Vaal River	*Archidiskodon yorki* Dart, 1929	= *Archidiskodon*
Lowest terrace, Vaal River	*Pilgrimia yorki* Dart, 1929	= *Palaeoloxodon*
Lowest terrace, Vaal River	*Pilgrimia wilmani* Dart, 1929	= *Palaeoloxodon*
Pniel Estate, ? River	*Pilgrimia kuhni* Dart, 1929	= *Palaeoloxodon*
?Recent, Limpopo River	*Loxodonta prima* Dart, 1929	= *Loxodonta*
?Recent, Steelpoort River	*Loxodonta africana* var. *obliqua* Dart, 1932	= *Loxodonta*
?Middle Terrace, Vaal River	*Pilgrimia archidiskodontoides* Haughton, 1932	= *Palaeoloxodon*
Higher terrace, Vaal River	*Pilgrimia subantiqua* Haughton, 1932	= *Loxodonta*

Summing up these species, the ascending geologic level records (Dart, Haughton) are as follows (Table I):

TABLE I.—FAUNAL DISTRIBUTION ON THE RIVER TERRACES OF THE TRANSVAAL

Middle Terrace	Middle terrace, 60–80 feet. Sydney-on-Vaal. ?Lower Pleistocene	Lowest terrace, 40 feet. With flint implements. ?Middle Pleistocene. Bloemhof	Recent—4 feet. Pleistocene
	Upper levels:	Upper levels:	Levels unknown:
?*A. subplanifrons**	*A. yorki*	*Bubalis baini*	?*P. hanekomi*
?*A. proplanifrons***	*A. broomi*	*Equus capensis*	?*L. subantiqua*
Older than the Upper Pliocene *A. planifrons* of the Siwaliks, India	*M. griqua*		?*P. archidiskodontoides*
	Lower levels:	Lowest levels:	Recent:
*actually recorded from a depth of 50–60 feet, middle terrace (60–80 ft.)	*P. andrewsi*	*P. transvaalensis*	*L. prima*
	A. vanalpheni	*P. sheppardi*	*L. africana* var. *obliqua*
	A. milletti	*P. yorki*	
**at a depth of 56 feet, middle terrace, Vaal River	*A. loxodontoides*	*P. wilmani*	
	Bunolophodon ?gen. ?sp.	*P. kuhni*	

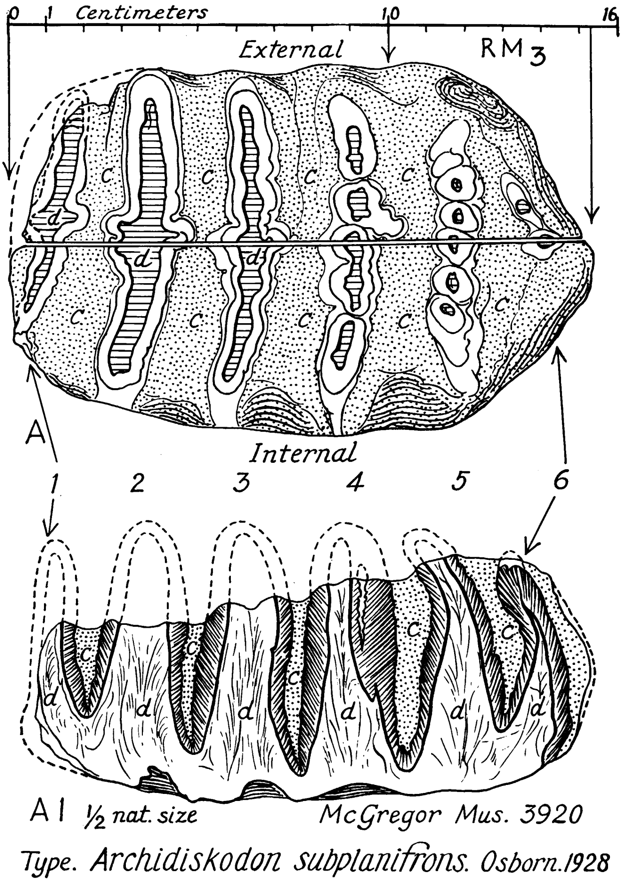

Fig. 1. Type, right third inferior molar, RM_3, of *Archidiskodon subplanifrons* Osborn, 1928, from the middle terrace, Sydney-on-Vaal, South Africa. McGregor Museum 3920, Kimberley, South Africa; cast Amer. Mus. 29124. One-half natural size.

A, crown view. *c*—cement. *d*—dentine. Line of midsection. A1, the same in midsection, exhibiting six ridge plates.

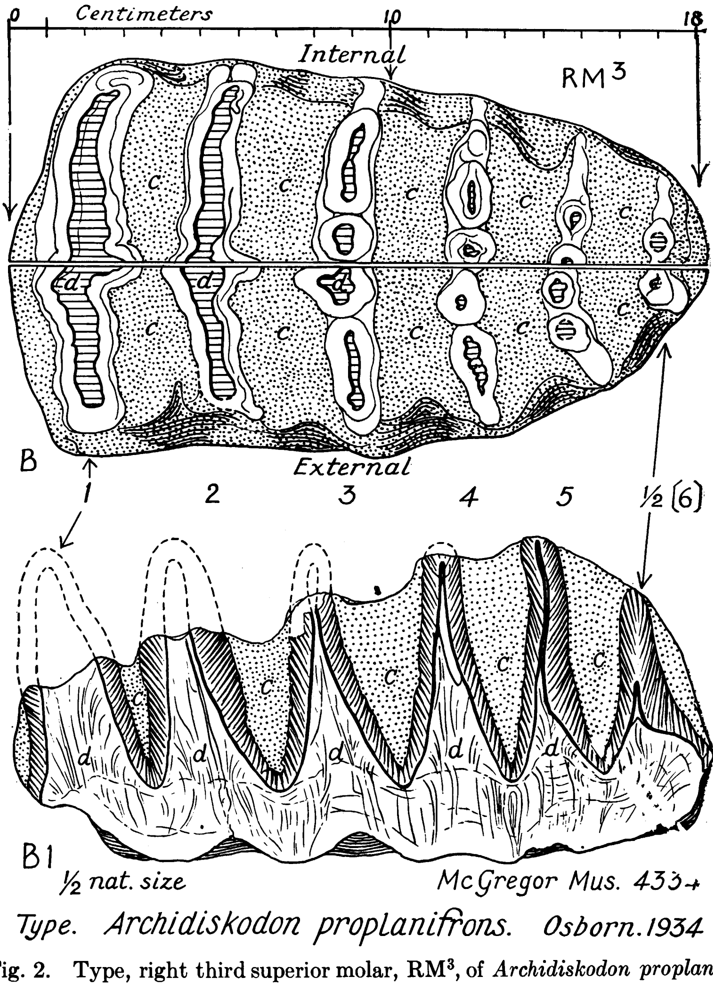

Fig. 2. Type, right third superior molar, RM³, of *Archidiskodon proplanifrons*, new species, after original. McGregor Museum 4334, Kimberley, South Africa; cast Amer. Mus. 26969. One-half natural size.

B, crown view showing 5½ ridge plates, very broad cement areas—*c, c, c;* six plates represented by two conelets. B1, section of the same showing cement-filled ridge plates more widely open than in *A. subplanifrons*.

By their outstanding characters these species divide into four groups as follows (Table II):

TABLE II.—PROVISIONAL GROUPING OF SPECIES REFERRED TO FOUR TRANSVAAL GENERA

A. subplanifrons group	*M. griqua* group	*P. transvaalensis* group	*Loxodonta prima* group
Crowns very broad, 101 to 114 mm. Enamel very thick. Transverse conelets 4–6 (*A. proplanifrons*) to 22–24 (*A. broomi*). Cement enveloping crown. V-shaped cemented valleys at summits broader than dentinal areas. Loxodont sinus foldings double, less prominent, irregular. The mass of cement exceeds the mass of dentine. Cf. paratype of *A. meridionalis* Nesti of Val d'Arno, also Brit. Mus. M12641, M12642.	Crowns relatively narrow, 86–94 mm. Enamel thick. Transverse crests 6–8. Cement areas narrower, not enveloping crown. Valleys U-shaped (*M. griqua*). Post-sinus fold very prominent. Total enamel length unknown. The mass of cement exceeds the mass of dentine. Cf. *A. planifrons rumanus* Stefanescu.	Crowns of M^3 relatively narrow, 70 mm. (*P. wilmani*) to 110 mm. (*P. transvaalensis*). Indices = 41 to 51. Enamel relatively thin; conelets finely crimped, i.e. numerous. Cement areas progressively narrower than dentinal areas. Cemented valleys greatly reduced. Ridge plates narrow and increasingly lofty, 128 mm. (*P. wilmani*), 259 mm. (*P. hanekomi*). Ridge plates per 100 mm. 4–6. Sinus foldings extremely reduced or progressively wanting. Valleys V-shaped (*P. andrewsi*).	Crowns relatively narrow, 74 mm. (*L. prima*) to 92 mm. (*L. subantiqua*). Enamel relatively thin, coarsely crimped; conelets numerous. Cement thin in middle, thick at edge. Ridge plates per 100 mm. = 4 (*L. africana obliqua*) to 5½ (*L. subantiqua*). Broad typical loxodont sinus expansion, double sinus foldings in contact. Total ridge plates 9 (*L. prima*) to 12–13 (*L. zulu*).

Table II—*Continued*

In this group are the following species: *A. proplanifrons, A. subplanifrons, A. milletti, A. yorki, A. vanalpheni, A. broomi.* The ridge plate height increases from 55 in *A. proplanifrons* to 62 e. in *A. subplanifrons*, to 118 in *A. milletti*, to 129 in *A. vanalpheni* and 110+ in *A. broomi.* Meanwhile the number of ridge plates in 100 mm. remains constant, namely, 3 in *A. proplanifrons*, 4½ in *A. planifrons* of India and 3 in *A. broomi.*	In this group may be the following species: *M. griqua, P. andrewsi, A. loxodontoides.* The generic relationships of this group are doubtful; the narrow crowns separate the types of *M. griqua* and of *P. andrewsi* from the broad crowns of the typical *Archidiskodon.* The U-shaped valley of *M. griqua* of Fig. 3 is quite distinct from the V-shaped valley of *P. andrewsi;* similar teeth have been discovered in Europe. It is probable that these teeth represent a genus distinct either from *Archidiskodon* or *Palaeoloxodon*, namely *Metarchidiskodon.*	In this group are the following: *P.* [= *Pilg.*] *kuhni, P.* [= *Pilg.*] *yorki, P.* [= *Pilg.*] *wilmani, P. archidiskodontoides, P. sheppardi, P. transvaalensis* and *P. hanekomi.* Also possibly *?P. andrewsi.* These seven or eight types are much more uniform in character than members of the *M. griqua* group, *P. sheppardi* and *P. transvaalensis* formerly being referred by Dart to *Archidiskodon. P. kuhni, P. yorki* and *P. wilmani* were referred by Dart to *Pilgrimia;* the prevailing characters relate them more closely to *Palaeoloxodon.*	In this group are the following: *L. zulu, L.* [= *Pilg.*] *subantiqua, L. africana obliqua, L. prima.* These occur only on the more recent levels and are clearly related to the existing African elephant, distinguished by the above characters.

The above phylogenetic arrangement is provisional. Only by the longitudinal sectioning method of Falconer is it possible to ascertain the true structural relationships of these Proboscidean molars. This is illustrated in the wide difference between sections of *M. griqua* (Fig. 3)

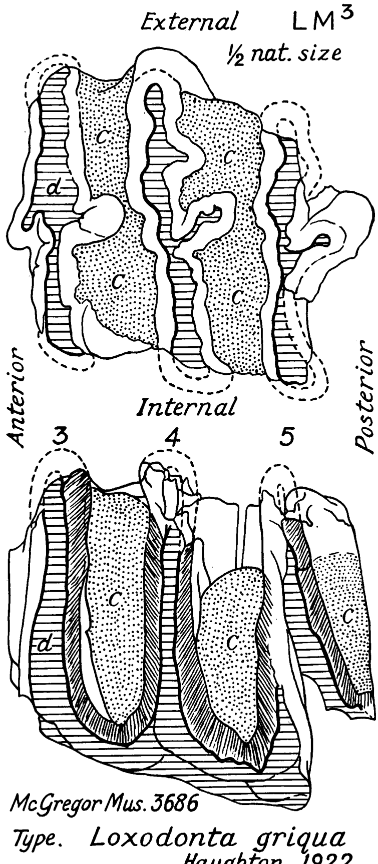

Fig. 3. Type of "*Loxodonta*" *griqua* Haughton, 1922. McGregor Museum 3686, Kimberley, South Africa. Supposed third, fourth and fifth ridge plates of an LM^3. Observe very deep U-shaped valleys, thick simply folded enamel with very prominent looped post-sinus folds. Type figure of *Metarchidiskodon*, new genus. One-half natural size.

and *P. andrewsi* (Fig. 5), also in the wide difference between the sections of *A. subplanifrons* (Fig. 1) and *A. proplanifrons* (Fig. 2). A very interesting comparison is that of the *planifrons* series of Africa and the Siwaliks of India analysed as follows (Table III):

TABLE III.—COMPARATIVE MEASUREMENTS OF THE PRIMITIVE SPECIES OF *Archidiskodon* FROM THE TRANSVAAL AND FROM THE UPPER SIWALIKS OF INDIA

	Tooth	Ridge plate height	Number of ridge plates	Ridge plates per 100 mm.	Enamel thickness	Loxodont sinus and folds	Conelets and crimping	Length	Breadth	Index	Enamel length
A. proplanifrons	RM^3	55	5½–6	3	5	Pre- and post sinus folds	Conelets = 4–6. Foldings	179	104	58	690
A. subplanifrons	RM_3	62e.	6	4	4	Pre- and post sinus folds.	Conelets = 6–8.	153	101	66	650
*A. planifrons**	RM_3	55	8e.	4½	3½	Pre- and post sinus folds, greatly reduced.	Conelets = 16 e. in ridge plate 4.	179	86	48	810e.

*This is No. 19965, American Museum Brown Collection (Fig. 4) from near Siswan, India. This is the most primitive stage found in the large series of the *Archidiskodon planifrons* molars collected by Barnum Brown in the Upper Pliocene Pinjor horizon of the Siwaliks, India.

A. proplanifrons proves to be by far the most primitive elephantoid thus far discovered; the types of *A. subplanifrons* and of *A. proplanifrons*, although recorded from the middle terrace, were probably washed from older Pliocene deposits into the Pleistocene terrace gravels. Both types are much more primitive than the most primitive molars thus far discovered by Falconer and Barnum Brown in the Upper Pliocene Siwaliks of India.

Archidiskodon subplanifrons group

The author owes the present rare opportunity to revise his own previous opinions and those of Haughton and Dart to the courtesy and confidence of Curator Wilman of the McGregor Museum in Kimberley, South Africa, who forwarded the original fossil types of *A. subplanifrons* (Fig. 1) and *P. andrewsi* (Fig. 5), enabling us to distinguish ancestral *Palaeoloxodon* from ancestral *Archidiskodon*. First, let us briefly review and expand the characters of the first-mentioned species:

Archidiskodon subplanifrons Osborn, 1928

Type: Right third inferior molar, five ridge plates exposed, sixth buried in cement, ridge plate 1 imperfect. McGregor Museum 3920, cast Amer. Mus. 21924.

Length of type molar = 153 mm., breadth = 101 mm., index = 66.

Enamel length, restored = 650 mm., enamel area = 2600 sq. mm.

Average enamel thickness = 4 mm.

Ridge plates, number = 6, postconvex, preconcave, 5–6 suboval to round conelets with double central folds in the ridge plate.

Ridge plates per 100 mm. = 4.

Erroneously referred by Haughton (1932, page 2) to *Archidiskodon subplanifrons* is the much more primitive specimen (McGregor Museum 4334), herewith made the type of *Archidiskodon proplanifrons*.

Archidiskodon proplanifrons, new species

Type: Third superior molar of the right side with six complete ridge plates. McGregor Museum 4334, cast Amer. Mus. 26969.

Recorded from Gong-Gong "at a depth of 56 feet in the 'Middle Terrace,' under a boulder, at a distance of 450 yards from the Vaal River, thus occurring at a depth of from 10–15 feet below the level of the present river bed."[1]

Length = 179 mm., breadth = 104 mm., index = 58.

Height of 5th ridge plate = 55 mm.

Enamel length, restored = 690 mm.

Average enamel thickness = 5 mm.

Ridge plate, number = 5½–6. Postconcave, preconvex, with 4–5 rounded conelets in the posterior plates and 6–6+ conelets in the anterior plates, slight median foldings in each transverse plate.

[1]Haughton, 1932, page 2.

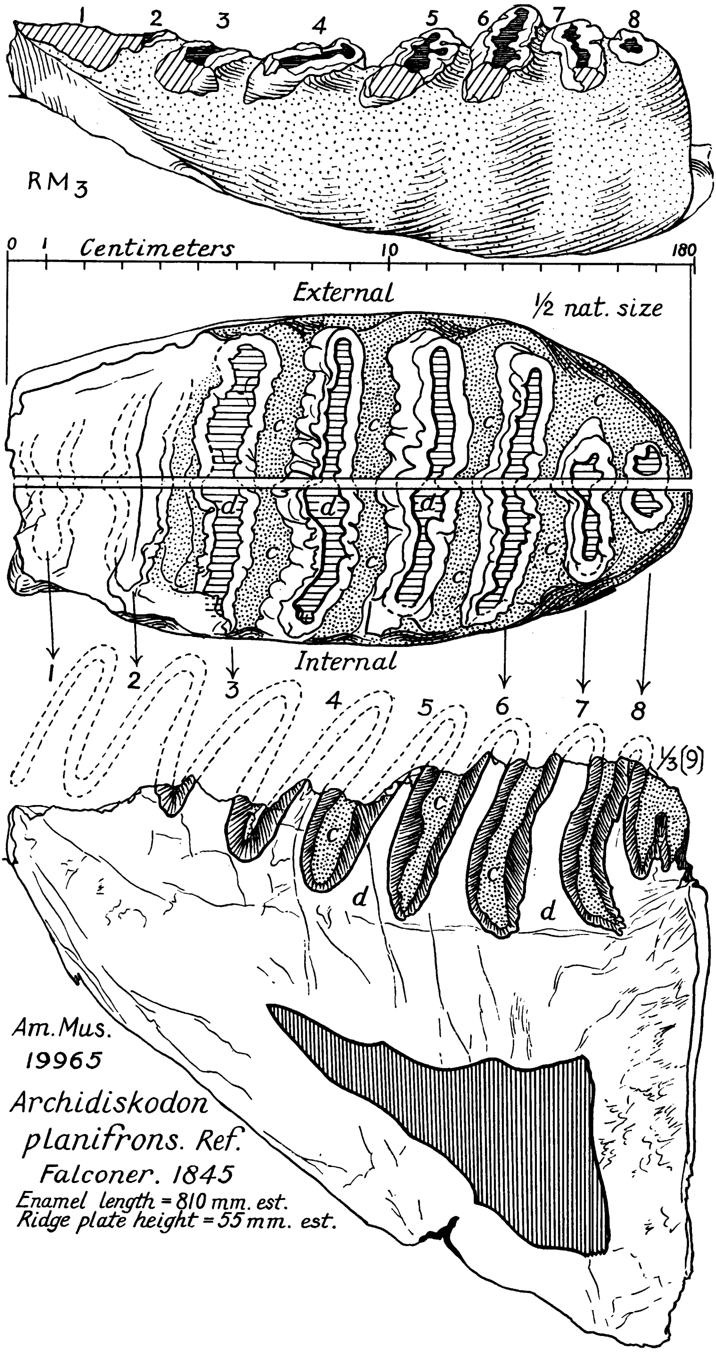

Fig. 4. Referred third right inferior molar, RM_3, of *Archidiskodon planifrons* Falconer, 1845, from three miles north of Siswan, India. 8⅓ [9] ridge plates. Internal aspect exhibiting the gently folded section of the entire molar with relatively low enamel ridge plates and estimated total enamel length of 810 mm. One-half natural size.

According to these measurements by Osborn, 1934, and those of Haughton, 1932, this type third right superior molar is the most primitive elephant tooth thus far discovered, even more primitive than *Archidiskodon subplanifrons*; it is indubitably an ancestral *Archidiskodon* with widely open valleys, summits of ridge plates much more widely separate than in *A. subplanifrons*, cement bathing the entire surface of the crown, median pair of conelets entirely distinct and undivided, total number of conelets estimated in the crown 26, as compared with total estimated number 34 in *A. subplanifrons.*

The above species, *Archidiskodon subplanifrons* Osborn, 1928, and the new species *Archidiskodon proplanifrons*, as tested by these thickly enameled, deeply cemented, low and spreading ridge plated, relatively broadened, third superior and inferior grinding teeth, are totally distinct from certain of the relatively thin enameled, high ridge plated, less deeply cemented, relatively narrow molar types which have been erroneously referred by Haughton, Dart and Osborn to *Archidiskodon*, but more properly belong to *Palaeoloxodon* including its synonym *Pilgrimia.*

Metarchidiskodon griqua group

Metarchidiskodon, new genus

This group includes the fragmentary type (Fig. 3) of "*Loxodonta*" *griqua* Haughton, 1922, in which we observe the following distinctive characters: (1) Cement areas equal or exceed dentine areas; (2) presinus folds absent or inconspicuous; very prominent post-sinus folds; (3) very deep U-shaped valleys extending to the bottom of the crown; this is a very important point. (4) These valleys are filled to the summit with cement. (5) Enamel ridge plates very deep, extending to the bottom of the crown, closely compressed with very narrow dentinal areas between.

This specimen appears to belong to a distinct form of grinding tooth to which the new generic name *Metarchidiskodon* may be applied, and distinguished from *Archidiskodon* as follows: (1) M3 with a relatively long narrow crown; index cannot be estimated at present. (2) Deep U-shaped valleys filled with cement. (3) Enamel ridge plates extending to the bottom of the crown. (4) Very prominent post-sinus folds instead of median sinus expansion of the typical *Archidiskodon* (Figs. 1, 2, and 4). Type species: *Loxodonta griqua* Haughton, 1932. Type figure 3, to be compared with the relatively narrow grinding teeth of similar molars observed in the Val d'Arno specimens and in British Museum M12641, M12642.

Palaeoloxodon transvaalensis group

The sectioned fragments of the type LM_3 (McGregor Museum 435) named *Archidiskodon andrewsi* by Dart in 1929, differ very widely both from the sectioned grinders of "*Loxodonta*" *griqua* just described in the relatively shallow enamel folds which are V-shaped and penetrate to only half the depth of the grinder as a whole.

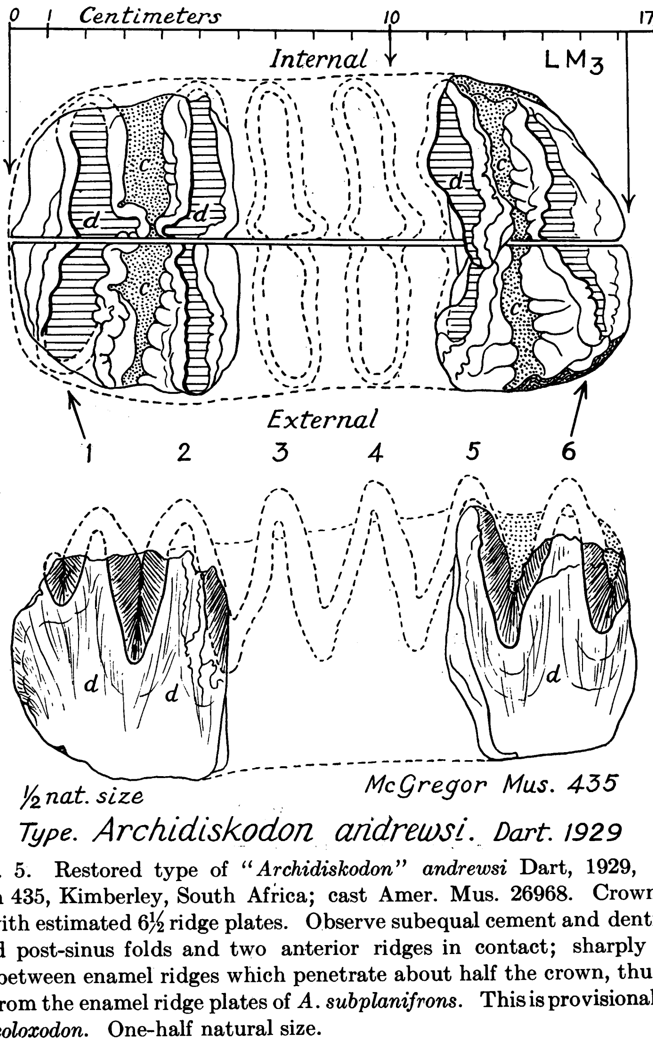

Fig. 5. Restored type of "*Archidiskodon*" *andrewsi* Dart, 1929, McGregor Museum 435, Kimberley, South Africa; cast Amer. Mus. 26968. Crown view restored with estimated 6½ ridge plates. Observe subequal cement and dentinal areas; pre- and post-sinus folds and two anterior ridges in contact; sharply V-shaped valleys between enamel ridges which penetrate about half the crown, thus differing widely from the enamel ridge plates of *A. subplanifrons*. This is provisionally referred to *Palaeoloxodon*. One-half natural size.

?PRIMITIVE *Palaeoloxodon.*—A primitive or ancestral member of the *Palaeoloxodon* group may be this problematic *A. andrewsi* Dart (Fig. 5), a type which on sectioning and very careful reëxamination by the present author, proves to be distinct both from *A. planifrons* (Fig. 4) and *A. subplanifrons* (Fig. 1). The fragmentary type, f.LM_3, displays the following characters: Ridge plate height =48 mm. est., estimated number of ridge plates =6. Feeble pre-sinus fold; very prominent post-sinus fold. Valleys V-shaped. Estimated length =164 mm. Estimated breadth =83 mm., estimated index =50. Enamel thick, crimped. It has been extremely difficult to restore this terribly shattered type specimen and deduce its outstanding characters as listed above, from the enamel folds which certainly belong at the front and back of the third inferior grinding tooth.

TYPICAL *Palaeoloxodon.*—The type molars of the eight species referred to *Palaeoloxodon* above are readily distinguished from *Archidiskodon* by the following five characters: (1) Dentine areas equal or exceed cement areas by relatively close compression of the ridge plates. (2) Absence of pre- and post-sinus central foldings, faint median expansion of the loxodont sinus. (3) Enamel relatively thin and more or less strongly and finely crimped. (4) Height of ridge plates increasing: *P. kuhni* =100 mm., *P. wilmani* =128 mm., *P. archidiskodontoides* =145 mm., *P. sheppardi* =188 mm., *P. transvaalensis* =231 mm., *P. hanekomi* =259 mm. (5) Number of ridge plates. It seems probable that Dart's type of *A. sheppardi*, displaying 1–13 ridge plates, is an LM^2, in which case *A. sheppardi* becomes a synonym of *A. transvaalensis* Dart with 1–14 ridge plates.

CONCLUSION

The present author trusts that this statement of his own errors in treating members of this group together with the introduction of the section method of Falconer may facilitate the reëxamination and fresh interpretation of the generic and phylogenetic relations of these very important Transvaal types.

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