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## PLEISTOCENE VERTEBRATES FROM CELEBES. VII. MILK MOLARS AND PREMOLARS OF ARCHIDISKODON CELEBENSIS HOOIJER

by

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Among the fossil proboscidean remains collected by Mr. H. R. van Heekeren in the T'jabengè area, Sopeng district, about 100 km Northeast of Macassar in Southwestern Celebes there are a number of very small teeth. They can be referred to the species of *Archidiskodon* of which I originally described two specimens of  $M^2$  or  $M^3$ , some molar fragments, the distal end of an ulna, and the proximal end of a tibia (Hooijer, 1949), to which could later be added a fine  $M_3$ , and an  $M_1$  or  $M_2$ , both completely preserved (Hooijer, 1953a).

*Archidiskodon celebensis* Hooijer is the smallest species of *Archidiskodon* known at present. Its molars are only one-half as large in linear dimensions as those of *Archidiskodon planifrons* (Falconer et Cautley), and they agree with the latter in their ridge-plate formula, configuration of the enamel figures of the worn plates, long roots, and degree of hypsodonty. As will be seen from what follows, the Celebes pygmy elephantine also agrees with *A. planifrons* in what is considered to be the most important distinguishing character of *A. planifrons*, viz., the presence of premolars.

Milk molars have been less intensively studied than molars; there are three of them, in *Archidiskodon* as well as in the recent species<sup>1)</sup>. Data on DM2-4 of *Archidiskodon planifrons* from the Upper Siwaliks of India, of *A. meridionalis* (Nesti) from the Villafranchian of Europe, and of *A. exoptatus* Dietrich from the Early Pleistocene of East Africa are given in Fal-

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1) A preantepenultimate milk molar (DM1) occasionally develops in the African elephant (Morrison-Scott, 1939).

coner and Cautley (1845-49), Falconer (1868), Adams (1877-81), Pohlig (1888-91), Weithofer (1890), Dietrich (1942), and Osborn (1942). These works have been drawn upon in the following study of the milk molars of *Archidiskodon celebensis*. All the specimens described below originate from Sompoh, near Tjabengè.

The anterior upper milk molar, DM<sup>2</sup>, is represented in Mr. Van Heeckeren's collection by a single specimen. It is of the right side, and complete except for the roots. The crown (pl. VII figs. 1 and 2) consists of three transverse ridges, and cingular elevations in front and behind, the talons. It is reniform in outline; the greatest anteroposterior diameter is just buccally of the median line of the crown. The buccal surface is slightly convex from before backward, while the lingual surface is depressed at the base of the second ridge. Only the anterior two ridges are worn, and the crown is distinctly higher on the buccal than on the lingual side. The anterior talon has a large buccal cusp, and two small points lingually; the anterior crown surface runs obliquely backward toward the lingual side, and passes into the lingual surface by an obtuse rounded angle.

Of the three transverse ridges present, the anterior is the widest, and irregular in shape; it has a buccal and a lingual portion separated by a median cleft. The lingual portion is placed forward relative to the buccal cone (which is pointed behind), and bears three conelets. The middle ridge is straight transversely and bears four conelets, equal in size. The posterior ridge is made up of three transversely placed conelets of which the central is the largest. The hind talon is formed only by two cingular points. There is hardly any crown cement except in the narrow valleys. Most of the roots is broken off, but from what is left it is evident that the specimen was two-rooted.

It will be noticed that the three ridges of this tiny tooth are built on three different basic plans: the first ridge is mastodontid (in the forward displacement of the lingual (pretrite) portion the ridge even reminds of the structure observed in bunomastodontids such as *Anancus*), the second ridge is stegodontid, and the third ridge, with its large central conelet, is elephantid in build.

The anterior upper milk molars of *A. planifrons*, *A. meridionalis*, and *A. exoptatus*, although varying in the number and development of the conelets to the ridges, are similar to the Sompoh DM<sup>2</sup> above described. From the measurements recorded in table 1 it can be seen that the DM<sup>2</sup> of *A. celebensis* is smaller than its homologue in any of these species, and also narrower relative to its length than the other specimens, except for one DM<sup>2</sup>

of *A. exoptatus* (recorded by Dietrich, 1942, p. 80, pl. V fig. 48) that measures 28 by 18 mm, and thereby has an index lower than that of the Sompoh tooth.

TABLE 1

Measurements of DM<sup>2</sup> of various *Archidiskodon* species

	<i>celebensis</i>	<i>planifrons</i>	<i>meridionalis</i>	<i>exoptatus</i>
Length	20	26	21-24.5	23-28
Width	14.5	21	17-20	18-23
Width-length index	73	81	78-87	64-100

Of the anterior lower milk molar, DM<sub>2</sub>, there is one specimen in the Celebes collection; it is of the left side (pl. VII figs. 3 and 4). The buccal surface is much higher than the lingual, and the crown bears, again, three transverse ridges of which the anterior two are worn. The crown is oblong, slightly constricted in the middle at the base, and is widest posteriorly. The anterior talonid forms one high pointed cusp with two points on its buccal slope. The anterior ridge is the narrowest of the three ridges and tapers markedly to its apex. There are three conelets, the central is pushed forward relative to the other two. The second ridge has four conelets and is inclined forward, especially so on the buccal side. The third ridge has two conelets only, of which the buccal is more forward than the lingual and much narrower at the base. The posterior talonid is merely a cingular triangular elevation, with a ridge running upward to the top of the lingual posterior conule, and a postero-external knob. Roots are not preserved, but the constricted pulp cavity shows that there was an anterior and a posterior root.

The DM<sub>2</sub> of *A. planifrons* (figured in Falconer and Cautley, 1846, pl. 14 figs. 10, 10a, as *E. hysudricus*, but see Falconer, 1868 I, p. 442; 1868 II, p. 92) is slightly larger than its homologue in *A. celebensis*, and so are most of the specimens of DM<sub>2</sub> of *A. meridionalis* (including some specimens examined by me in the Geological Institute at Florence, Italy, in September, 1953). The Sompoh DM<sub>2</sub> is narrower than any other DM<sub>2</sub> (table 2); there are, however, a few specimens which it exceeds in relative width.

TABLE 2

Measurements of DM<sub>2</sub> of various *Archidiskodon* species

	<i>celebensis</i>	<i>planifrons</i>	<i>meridionalis</i>	<i>exoptatus</i>
Length	19	20	18-24	20
Width	13	15	14.5-15.5	16
Width-length index	68	75	63-86	80

The second upper milk molar is not represented in the collection. Of the second lower milk molar there is a much worn down but complete specimen, a DM<sub>3</sub> dext. (pl. VII figs. 5 and 6). The crown is widest behind, and narrows gradually to the front. It carries six full ridges, all worn flat; no trace is left of the talonids which were apparently small, and the ridge-plate formula can be determined only by the incurvations of the enamel border of the crown lingually and buccally, the last remnants of the transverse valleys. As shown in buccal aspect (pl. VII fig. 6) there is an anterior and a posterior root. The latter is the larger, and most of it seems to have been resorbed, indicating that the tooth was about to be shed, or perhaps even was lost already, to be succeeded by a premolar (P<sub>3</sub>).

A DM<sub>3</sub> of *A. planifrons* (Falconer and Cautley, 1845, pl. 12 figs. 7 and 7a) has six ridge-plates and talonids and is almost twice as long and broad as the Sompoh DM<sub>3</sub> (table 3); in *A. meridionalis* there are either five or six plates to this tooth, and its variation ranges (ten specimens) include both *A. planifrons* and *A. exoptatus*. The laminar frequency (number of plates per 10 cm of anteroposterior length) is 20 in DM<sub>3</sub> of *A. celebensis* against 9-11.5, average 10.5, in *A. meridionalis*. Thus, the DM<sub>3</sub> of *A. celebensis* is one-half the size, and accordingly has twice as high a laminar frequency as its homologue in the large *Archidiskodon* species, and this is exactly the same ratio I found to exist between the molars of these species (Hooijer, 1949, pp. 221 and 223; 1953a, p. 315).

TABLE 3

Measurements of DM<sub>3</sub> of various *Archidiskodon* species

	<i>celebensis</i>	<i>planifrons</i>	<i>meridionalis</i>	<i>exoptatus</i>
Length	32	61	55-76	71
Width	20.5	36	31-43	36
Width-length index	64	59	44-64	51

Of the last milk molar, DM<sub>4</sub>, there is no complete specimen in the Sompoh collection. On pl. VII fig. 7 is represented the posterior part of a DM<sub>4</sub> dext. with three worn plates and a small talon. The enamel figures are entire, convex to the front and flattened behind. Cement fills the valleys and covers up most of the talon which bears five or six minute points. The penultimate plate figure has a median anterior loop of enamel. Slightly larger is the posterior portion of another DM<sub>4</sub> dext. (pl. VII fig. 11) which carries only two plates and a talon. The anterior preserved plate is worn into three enamel islets of which the central is the largest and the buccal the smallest. The wearing surface falls off toward the lingual side.

The last plate, just touched by wear, has six subequal conelets. The talon is embedded in cement.

In *A. planifrons* DM<sup>4</sup> has either six or seven plates, while in *A. meridionalis* there are seven or even eight plates in DM<sup>4</sup>. In addition, the crown height is less in *A. planifrons* than it is in *A. meridionalis*: Von Koenigswald (1951, p. 270) gives the height of the last plate of a DM<sup>4</sup> of *A. planifrons* figured by Falconer and Cautley (1845, pl. 6 figs. 4-5) as 35 mm, while in *A. meridionalis* DM<sup>4</sup> varies from 45 to 63 mm in height. The isolated DM<sup>4</sup> from Tjidjulung in Java, recorded by Von Koenigswald (l.c., p. 272) as *A. praeplanifrons*, resembles that of *A. planifrons* closely; its height is given as ca. 30 mm, and the crown is slightly longer and narrower than that of the Siwalik specimen. The measurements of the Javan specimen are included in table 4 under *A. planifrons*. It will be observed that *A. meridionalis* varies between wider limits.

TABLE 4

Measurements of DM<sup>4</sup> of various *Archidiskodon* species

	<i>celebensis</i>	<i>planifrons</i>	<i>meridionalis</i>	<i>exoptatus</i>
Length	—	102-112	100-116	—
Width	25 29.5	54-61	36-63	ca. 50-57
Width-length index	—	48-60	32-56	—
Height	ca. 23	ca. 30-35	45-63	—
Height-width index	ca. 78	ca. 56-57	73-117	—

The height of the last plate in the larger specimen of DM<sup>4</sup> of *A. celebensis* described above, a plate which has only just been touched by wear, is 22.5 mm; in the unworn state the height cannot have been more than 23 mm, which gives a height-width index of ca. 78. This is more than the same index in the two specimens of DM<sup>4</sup> of *A. planifrons* from the Siwaliks and Java which almost exactly agree in the value of this index, and falls within the variation limits of *A. meridionalis*. It would seem, therefore, that *A. celebensis* is more progressive than *A. planifrons* in the greater relative height of its DM<sup>4</sup>, and this can only be settled upon the study of more and better specimens which unfortunately are not available at present.

The laminar frequency of the two specimens of DM<sup>4</sup> of *A. celebensis* is 14 for both, that of *A. planifrons* is 6-7, and that of *A. meridionalis* is 7-8. Hence, the laminar frequency in *A. celebensis* is again twice as high as that in *A. planifrons* and *A. meridionalis*, which is what we found to be true for DM<sub>3</sub>, too.

The lower last milk molar, DM<sub>4</sub>, is preserved in the Celebes collection as

the middle portion of a left  $DM_4$  (pl. VII fig. 8). It shows three worn plates, while in front there is a small lingual portion of another plate, and part of the anterior root. The hindmost preserved plate has the enamel rings of the lateral conelets not yet coalesced with the central figure which shows an anterior median point. The middle plate has an anterior and a posterior enamel loop, and the anterior preserved plate, most worn down, shows a median expansion on the posterior surface only. The valleys between the plates are partially filled with cement. From the position of the anterior root it seems evident that the plates preserved are the third, fourth, and fifth from the front; in *A. planifrons*  $DM_4$  has seven plates, and in *A. meridionalis* there are seven or eight. Table 5 shows that the Sompoh specimen is

TABLE 5  
Measurements of  $DM_4$  of various *Archidiskodon* species

	<i>celebensis</i>	<i>planifrons</i>	<i>meridionalis</i>	<i>exoptatus</i>
Length	—	113-121	102-130	—
Width	22	61-63	43-71	52-58
Width-length index	—	52-54	34-58	—

rather narrow; it is half as wide as the smallest specimens of  $DM_4$  of *A. meridionalis* only. Nevertheless its laminar frequency points to a  $DM_4$ , as it is 13 against 6.5-7 in *A. planifrons*, and 6.5-8 in *A. meridionalis*. Thus it is intermediate between the  $DM_3$  recorded above and the  $M_1$  (or  $M_2$ ) recorded in my previous paper (Hooijer, 1953a) both in width ( $DM_3$ : 20.5 mm;  $M_1$ : 31 mm) and in laminar frequency ( $DM_3$ : 20;  $M_1$ : 11), being closer to the  $DM_3$  in width, and closer to  $M_1$  in laminar frequency.

Elephantine premolars are among the great paleontological rarities; they have been found to occur exclusively in the most primitive genus of Elephantinae, viz., *Archidiskodon*, and the specimens known thus far can be counted on the fingers of one hand. In the collection of *A. planifrons* from the Upper Siwaliks examined by Falconer there are three specimens proving that the penultimate and the last milk molars were vertically succeeded by premolars. The premolars in question are in situ in the jaws, with their milk predecessor or with the adjacent milk molar in place, and thus there is no doubt about their serial position. A  $P^3$  sin. was found in a palate with  $DM^4$  and  $M^1$  (Falconer and Cautley, 1845, pl. 6 figs. 4-6; Falconer, 1868 I, p. 427; 1868 II, p. 93/94); it has three ridges and talons, and is almost as wide as long. The crown is very slightly worn, and the ridges are not very distinctly shown. A  $P_3$  sin. in a left ramus of the mandible also containing  $DM_4$

(Falconer and Cautley, 1845, pl. 12 figs. 8-9; Falconer, 1868 I, p. 432/433; 1868 II, p. 93) does not show the ridges; it is decidedly smaller than the  $P_4$ , only part of which is preserved in another left ramus of the mandible with  $M_1$  (Falconer and Cautley, 1845, pl. 12 figs. 10-11; Falconer, 1868 I, p. 433; 1868 II, p. 93). The posterior portion of  $P_4$  preserved consists of the last ridge, with three conelets, and a small talonid. The measurements of these teeth will be given in table 6.

The next instance of premolars in an *Archidiskodon* to become known is that recorded by Pontier and Anthony (1933), who found a mandible of *A. imperator* (Leidy) from Chapala, Mexico, with a  $P_4$  below the much worn  $DM_4$ , the  $P_4$  consisting of two multimammillate ridges and talonids, and a bifurcated root. Finally, Von Koenigswald (1951) described and figured an isolated premolar from Tjidjulung (Java) as a  $P^3$  of a new species of *Archidiskodon*, *A. praeplanifrons* Von Koenigswald. There is no obvious reason for this serial determination but that the same locality provided a  $DM_4$  that Von Koenigswald takes to have belonged to the same individual as the premolar. As I have already shown above, the Javan  $DM_4$  is very close to that of *A. planifrons* in the relative height of the crown and can safely be referred to the same species. If the isolated premolar from Tjidjulung is taken as a  $P^4$  it would fit in nicely with the premolar dentition of *A. planifrons* as described by Falconer, being larger than the  $P^3$ , just as the  $P_4$  is larger than the  $P_3$ . If the Tjidjulung premolar is a  $P^4$  it cannot have belonged to the same individual as the  $DM_4$  from the same locality as the  $DM_4$  is not very much worn down and not yet in the shedding stage, while the premolar had already erupted as shown by its worn crown. With isolated finds like these, there is no proof for the assumption that the two teeth belong together. Consequently, there is room for a more conservative interpretation of the Tjidjulung premolar as a  $P^4$  of *A. planifrons*, and on the base of this material there is no need for the erection of a new species of *Archidiskodon* for the Tjidjulung fauna of Java.

There are three complete three-ridged teeth in the collection from Sompoh that I regard as premolars of *A. celebensis*. They can be interpreted as the penultimate and the last upper premolars, and the last lower premolar.

The largest specimen (pl. VII figs. 9 and 10) is probably a  $P^4$  dext. It is worn and shows the enamel figures of three cross ridges quite clearly. The crown is not much longer than wide, and is slightly higher buccally than lingually. The greatest width is in the posterior portion of the crown. The ridges are somewhat inclined forward, and are convex transversely to the front. The anterior talon is only a buccal column, with a small knob lingually, that rises from the base of the crown. The first ridge consists of two enamel

figures separated by a median cleft. The buccal figure is triangular with a posterior median point, and the lingual figure is an oblique oval placed more forward than the buccal figure; an enamel conelet at its lingual end would have become confluent with it upon further wear. The second ridge likewise exhibits a median cleft, but there is no dislocation of the enamel figures on either side. The buccal figure is single, and the lingual still shows two conelets. The third ridge has a central enamel figure instead of a cleft, flanked by two similar figures; the buccal of these has just coalesced with the central figure. The posterior talon consists of two centrally placed cones. There is cement between the ridges, but it does not encroach upon the buccal or lingual edges of the ridges or the talons. Although the specimen is broken off at the base of the crown, there seems to have been only a single root. There are no contact facets on the anterior or posterior surfaces of the crown. The measurements are given in table 6.

A smaller and more worn specimen (pl. VII figs. 14 and 15) I take to represent a  $P^3$  dext. There is an oblique contact facet posteriorly, and no trace of a posterior talon, unless the third ridge, which is narrower and apparently lower than the others, be taken as the talon in which case there are only two ridges. The anterior talon is a median cusp rising from the crown base. The first ridge is already worn into a single enamel figure; a constriction shows the position of the median cleft, and just buccally of this constriction there is a posterior enamel loop, the median posterior projection of the buccal enamel figure, very similar to that found in the first ridge of the  $P^4$  just described which is somewhat less worn. The second ridge presents two transverse ovals, one on either side of the median line, and the last ridge (or posterior talon) presents three conelets. The posterior contact facet has exposed the dentine core of his ridge, most markedly so on the lingual side. The valleys of the crown are filled with cement. Only the base of the root, which is single, is preserved.

Apart from their smaller size, the two upper premolars from Celebes just described resemble the Javan premolar described by Von Koenigswald (1951, figs. 2a, 2b) closely. The median cleft, essentially a mastodontid feature also shown in the first ridge of the  $DM^2$  figured in the present paper (pl. VII fig. 1), shows up in the Javan tooth, while it is also one-rooted. In the Siwalik  $P^3$  of *A. planifrons* (Falconer and Cautley, 1845, pl. 6 fig. 6) the ridges cannot well be distinguished.

There remains a complete three-ridged tooth that I consider to be a  $P_4$  sin. (pl. VII figs. 12 and 13). The crown is relatively longer than the upper P above described and presents an irregular oval: the buccal surface is less convex anteroposteriorly, and higher than the lingual, and the greatest



length is to the buccal side of the median axis of the crown. The anterior talonid consists of a median cusp, a buccal cusp slightly more forward than the latter, and two lingual points. The first ridge has three enamel figures, the central occupies one-half of the total width and the buccal and lingual figures are annular. In the second ridge the enamel figure is entire except for the lingual conelet that is still distinct. There is a posterior point buccally of the median line. The third ridge has two equally large enamel islets, the buccal with an anterior point and placed more forward than the lingual. The posterior talonid is low, buccally placed, and bathed in cement. The root is broken off, and appears to have been double. There are no contact facets on the anterior or posterior surfaces.

Such is the material that I regard as representing premolars of *A. celebensis*. In table 6 the dimensions of the Celebes premolars may be compared with those of their homologues in *A. planifrons*; under P<sup>4</sup> of this species are given the measurements of the supposed P<sup>3</sup> of *A. praeplanifrons* Von Koenigswald.

TABLE 6

Measurements of premolars of various *Archidiskodon* species

	<i>celebensis</i>	<i>planifrons</i>
P <sup>3</sup> , length	22	30.5
width	19	28
P <sup>4</sup> , length	28	37
width	24.5	35
P <sub>3</sub> , length	—	25.5
width	—	20.5
P <sub>4</sub> , length	28.5	—
width	20	ca. 30

If my interpretations are correct, the premolars of *A. celebensis* are about two-thirds as large in linear dimensions as their homologues in *A. planifrons*.

In my paper on the first found remains of *Archidiskodon celebensis* I pointed out that the Celebes pygmy elephantine represented an evolutionary stage corresponding to that of *A. planifrons* of the Lower Pleistocene of India (Hooijer, 1949, p. 223). Further confirmation of this view came from the study of the complete lower last molar several years later (Hooijer, 1953a). My theory that *A. celebensis* is a stranded descendant of *A. planifrons* that underwent a diminution in size, thereby preserving its archaic characters, receives additional support from the discovery of premolars, for these elements do occur in *A. planifrons* too, in contradistinction to the more progressive species *A. meridionalis*.

The evidence now available suggests further that in the general reduction in size, changes in relative size have also occurred. The anterior milk molars and the premolars of *A. celebensis* are larger relative to the penultimate and last milk molars and the molars than is the case in *A. planifrons*. Therefore, if we presume *A. celebensis* to have been derived from *A. planifrons*, the change apparently involved a less rapid reduction of DM<sub>2</sub> and P<sub>3-4</sub> than of DM<sub>3-4</sub> and M<sub>1-3</sub>. This points, at least, to correlated evolution of the upper and lower teeth. One of the specimens of DM<sup>4</sup> described above indicates that this tooth is more progressive than its homologue in *A. planifrons* in its greater relative crown height; this is an evolutionary trend not shown by the molars of *A. celebensis* which keep the low crown typical of *A. planifrons*.

The statements regarding the proportions throughout the dental series in *A. planifrons* and *A. celebensis* are, of course, subject to the reservations imposed by the scanty material. The two species agree in such a leading characteristic as the presence of functional premolars, but we do not know as yet to what extent these elements vary individually, which may be considerable. Only further collecting can lead to a better understanding of the affinities of these highly interesting primitive archidiskodonts.

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## EXPLANATION OF PLATE VII

*Archidiskodon celebensis* Hooijer, Sompoh, S.W. Celebes; figs. 1-2, DM<sup>2</sup> dext.; fig. 1, crown view; fig. 2, buccal view; figs. 3-4, DM<sub>2</sub> sin.; fig. 3, buccal view; fig. 4, crown view; figs. 5-6, DM<sub>3</sub> dext.; fig. 5, crown view; fig. 6, buccal view; fig. 7, DM<sup>4</sup> dext., crown view; fig. 8, DM<sub>4</sub> sin., crown view; figs. 9-10, P<sup>4</sup> dext.; fig. 9, buccal view; fig. 10, crown view; fig. 11, DM<sup>4</sup> dext., crown view; figs. 12-13, P<sub>4</sub> sin.; fig. 12, buccal view; fig. 13, crown view; figs. 14-15, P<sup>3</sup> dext.; fig. 14, crown view; fig. 15, buccal view.

All figures 1½ natural size.

