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PLEISTOCENE VERTEBRATES FROM CELEBES. XI. MOLARS AND A TUSKED MANDIBLE OF ARCHIDISKODON CELEBENSIS HOOIJER

by

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with pls. XX-XXII.

The species mentioned in the title of the present contribution was first described on the base of two incomplete upper molars, some fragments, and two portions of limb bones (Hooijer, 1949). The two and only complete molars were described later (Hooijer, 1953a). To this has been added the description of the milk dentition and of three premolars (Hooijer, 1953c). There are, however, important lacunae in our knowledge of the molar dentition to be filled. It remains as yet uncertain whether the type upper molar of 1949 represents M^2 or M^3, while the smaller of the complete lower molars of 1953 could be either M_1 or M_2. The prolonged study of the fragmentary molars in the Celebes collection has now made it possible to assemble the full set of upper and lower molars, and to determine the correct serial position of the previously described specimens. This study further showed the occasional presence of tusks in the mandible, the first time that incisive tusks have been found to occur in the lower jaw of an *Archidiskodon*. The problem of the descent of the archidiskodonts, and thereby of the elephantids in general, has to be reconsidered in the light of this unexpected discovery.

I wish, again, to express my feelings of gratitude toward Prof. Dr. A. J. Bernet Kempers, former Head of the Dinas Purbakala R.I. at Djakarta, Java, who entrusted the material to me for study, and to Mr. H. R. van Heekeren to whom we owe the discovery of the Pleistocene vertebrate fauna of Celebes.

Archidiskodon celebensis Hooijer

Archidiskodon celebensis Hooijer, Zool. Med. Museum Leiden, vol. 30, no. 14, 1949, p. 206, pls. VIII-IX; Chronica Naturae, vol. 105, 1949, p. 149; The Scientific Monthly, vol. 72, 1951, p. 5; Zool. Med. Museum Leiden, vol. 31, no. 28, 1953, p. 311, pl. XIX; Ibid., vol. 32, no. 20, 1953, p. 221, pl. VII.

Holotype: M^2 dext. described and figured in Hooijer (1949, pp. 206-209, pl. VIII figs. 1-2).

Locality: Sompoh, Beru, and Tjeleko, near Tjabengè (Sopeng district), about 100 km Northeast of Macassar, Southwestern Celebes.

Age: (?Early) Pleistocene.

Diagnosis: An *Archidiskodon* one-half as large in linear dimensions as *A. planifrons* (Falconer et Cautley); plate formula: M1 $\frac{}{8}$ M2 $\frac{}{9\text{-}10}$ M3 $\frac{}{11}$; molar plates low as in *A. planifrons*, with thick enamel, expanded in the median line, forming an imperfect loxodont sinus when worn, separated by V-shaped valleys; plentiful cement also on outer sides of plates. Molar crowns relatively narrower than the average in *A. planifrons*, roots long. Functional premolars both in upper jaw ($P^{3\text{-}4}$) and in mandible (P_4), about two-thirds as large as their homologues in *A. planifrons*. The mandible is downturned anteriorly, symphysis tuskless (?female) or provided with vertically compressed and grooved incisors (?male).

M^3 (pl. XX figs. 1, 7)

The posterior portion of an M^3 sin. from Sompoh (pl. XX fig. 1) is the first unequivocal sample of the last upper molar of *A. celebensis* to be put on record. It holds four plates, and a small terminal plate at the back; only the foremost preserved plate is worn. The crown is covered with cement all over except at the conelets and at the buccal and lingual bases of the plates where the enamel is exposed. Very little of the root is preserved.

This is the last molar because it tapers markedly posteriorly: from front to back the plates diminish regularly both in width and in height. Each of the plates also tapers toward its summit, whereby the buccal edges are slightly convex from above downward, and the lingual edges almost straight. The lingual bases of the plates are placed on a straight anteroposterior line, while the buccal surface of the crown is convex anteroposteriorly at the base. The plates diverge somewhat from base to top, and each of them carries four conelets except, perhaps, the last (which takes the place of the hind talon) in which there may be three conelets only. As is evident from the inspection of table 1, the unworn plates are higher than wide, though not

TABLE I

Measurements of M^3 sin. of *Archidiskodon celebensis*

No. of plate from behind	5	4	3	2	1
Basal width	42	42	39	34	23
Unworn height	—	49	47	42	30
Apical width	—	22	21	18	15

very markedly so, and the width over the conelets (the apical width) is slightly over one-half the basal width.

The occlusal surface of plate 5 from behind falls off rootward toward the lingual side; this is the mode of wear typical of mastodonts (Dietrich, 1951, p. 360 fig. 13).

In all its characters the present specimen is a typical *Archidiskodon celebensis* molar, i.e., a fifty per cent scale reduction of *A. planifrons*. The height-width index (plate 4) is 116; that of the M^3 in the skull of *A. planifrons* figured by Falconer and Cautley (1845, pls. 9-10) is 115 (cf. Falconer, 1868I, p. 430). The laminar frequency of the M^3 of *A. celebensis* is 6, which corresponds to 3 in molars that are two times larger. Actually, a laminar frequency of 3-4 is considered typical of the last molars of *A. planifrons* (Hooijer, 1953d, p. 197). The base of the front plate of the present fragment is expanded in the middle; this would lead to a lozenge-shaped enamel figure upon wear, which is as characteristic of *A. planifrons* as it is of *A. celebensis*.

The laminar frequency of the M^3 is lower, and the height-width index is higher than that of the upper molars described in my first paper on *A. celebensis* (Hooijer, 1949). This indicates that the 1949 molars are more advanced in position, and represent M^2 rather than M^3, although the width of one of them exceeds that of the M^3.

Next comes the anterior portion of an M^3 sin. from Sompoh (pl. XX fig. 7). The state of preservation is not as good as that of the posterior portion just described; there are various cracks and the fragments are somewhat displaced along these fractures, notably in the anterior part of the molar. It is, however, well worth recording as it clearly shows various primitive archidiskodontine features.

The specimen comprises four plates and an anterior half-plate. The full-sized plates are all worn and show expansions in the middle of their enamel figures. In their slightly advanced stage of wear the plates still show a median anteroposterior cleft, on either side of which the enamel figures expand in fore and aft direction. In plate 2 from the front there is even a slight tendency toward dislocation of the two plate halves, the lingual enamel figure projecting forward, the buccal backward toward the median line.

This is a structure reminding us of the molars of bunomastodontids, the ridges of which have pretrite (lingual in upper molars) and posttrite (buccal) cones separated by a median cleft, and which are further complicated by the development of various intermediate conules such as the anterior pretrite central conule and the posterior posttrite buttress. We find this mastodontoid structure displayed in the slightly worn molar plates of primitive archidiskodonts (Falconer and Cautley, 1845, pl. 11 figs. 1, 5, 7; 1846, pl. 18A figs. 1-2; Dietrich, 1942, pl. VII fig. 64; Arambourg, 1952, p. 409 fig. 2). Upon further wear of a plate the median cleft disappears but the median expansion of the enamel figure remains. Either the enamel figure assumes an imperfect lozenge-shape, such as that seen in the worn paratype upper molar of *A. celebensis* (Hooijer, 1949, pl. VIII fig. 3), or there remain only central enamel projections, occasionally even full enamel loops, as seen in the lower molars of *A. celebensis* already described (Hooijer, 1953a, p. 313, pl. XIX). These structures, which can be traced back to the intermediate conules of the mastodont molar, are characteristic of primitive archidiskodonts; further examples will be give in the sequel.

In the anterior full plate of the M^3 sin. of pl. XX fig. 7 the enamel figure is continuous from side to side, although the mastodontoid cleft still forms an enamel inflection between the posterior central lobes of the pretrite and posttrite halves. This plate is split transversely, and at the buccal edge there is a 3-4 mm wide fissure filled with matrix. The anterior half-plate is placed buccally and exhibits three conelets; in front of it rises another enamel cone that marks the antero-buccal edge of the crown. There is an extensive contact facet anteriorly. The anterior surface of the crown slopes backward from buccal to lingual, and in its centre is a vertical fissure, 2-3 mm wide, again filled with matrix. Nothing of the roots is preserved.

The occlusal surface, weakly convex anteroposteriorly, falls off rootward toward the lingual side, in the mastodont manner. In width the present fragment exceeds that first described: the basal width of plate 4 from the front is 50 mm, that of plate 3 is 51 mm, and that of plate 2, 52 mm. The laminar frequency of the present fragment is 6 at the occlusal surface, but is rather higher (7) at the base as the plates converge rootward. The least worn plate, plate 4, is 53 mm high, and the height-width index consequently is at least 106. Thus, like the first described M^3 fragment, the present specimen differs from the upper molars described in 1949 in their greater height-width index and lower laminar frequency. This specimen is the widest molar of *A. celebensis* that has come to my notice.

M^2 (pl. XX figs. 2, 3, 6, 8)

A much worn right upper molar (pl. XX figs. 6, 8) closely resembles the paratype upper molar of *A. celebensis* (Hooijer, 1949, pp. 209-212, pl. VIII fig. 3) in showing the imperfect loxodont sinus of the plates, occasioned by the median expansion of the anterior borders of the plates. The posterior borders are straight except for a slight enamel projection just buccally of the median longitudinal axis of the crown, visible in plates 2 and 3 from behind. The molar is broken off in front of plate 5 from behind, and the buccal edges of this plate and that of plate 4 are damaged. The occlusal surface is slightly convex from before backward, and falls off toward the lingual side.

This is not the last upper molar since there is a posterior contact facet. The hind talon is a relatively small affair that consists of two enamel cusps only. The hindmost plate is worn into a tripartite figure, the central part is the largest. In the wide V-shaped valley in front of it cement is developed buccally only. The other valleys likewise have hardly any cement in the lingual halves, which is what I observed in the paratype molar too (Hooijer, 1949, p. 210). As in that specimen, cement does extend upon the inner and outer sides of the plates, which agree in their imperfect lozenge-shaped figures and relatively thick enamel (up to 3½ mm). The complete figures of plates 2 and 3 from behind correspond in stage of wear to the anterior two plates of the paratype molar. Plate 4 from behind in the present specimen is confluent in the median line with plate 5, indicating that the valley is deeper on the sides than in the middle.

A large portion of the root is still attached to the crown (pl. XX, fig. 8); it is 70 mm long, and its posterior surface is concave vertically to accommodate the molar behind it. As seen in side view the posterior plate is strongly inclined backward, while the other plates are more erect; the laminar frequency on the occlusal surface is 7½, the same figure I found for the paratype upper molar.

The present specimen is interesting for its long root, a characteristic of primitive archidiskodonts (Hooijer, 1953a, p. 313), and, of course, for the imperfect loxodont sinus of the worn plates. The hindmost plate in this specimen (as well as that in the paratype molar) is elephantine in build (lat. an. med. lam.) but the mode of wear is mastodont-like, as is often the case in primitive archidiskodonts (Dietrich, 1942, p. 85; 1951, p. 359). The basal width both of plate 2 and of plate 3 from behind is only 42 mm; this molar represents the penultimate molar, M^2.

Of the same serial position is the anterior portion of a left upper molar (pl. XX figs. 2-3) with five plates and an anterior talon, very similar to the holotype upper molar of *A. celebensis* (Hooijer, 1949, pp. 206-209, pl. VIII figs. 1-2) and likewise originating from Sompoh. Only the anterior two plates are touched by wear. Cement is abundant, exposing only the bases and the conelets of the plates. The lingual edges of the plates are more steep than the buccal, and the plates are slightly higher than wide, rounded transversely above, and each carrying four or five conelets. Passing forward along the crown we notice that the plates become increasingly inclined forward; added to that the base of the crown is concave rootward antero-posteriorly, indicating that the molar is of the upper jaw.

The hindmost plate lacks the lingual posterior part, which allows of the enamel to be seen in cross section. The enamel is 3 mm thick basally and even 3½ mm apically. Of the five conelets the second from the buccal side is the highest, and the depth of the cleft separating the two low cusps at the lingual end of the series is 10 mm. This plate is expanded at the base anteriorly; its height is 45 mm, the basal width 42 mm, just as are those in the largest plate of the holotype specimen. Plate 4 from the front resembles the last closely, being only slightly less high (43 mm) and wide (41 mm). In plate 3 from the front the second and third conelets from the lingual side are the largest and stand well above the other conelets; the height of this plate is 44 mm, and its basal width is only 40 mm. Plate 2 from the front has the conelets slightly worn; this plate is 39 mm wide basally. The anterior plate is again narrower at the base (38 mm), and has only four conelets which are worn down to enamel rings except the extreme lingual. The occlusal surface of this specimen falls off rootward in the elephantine manner, toward the buccal side. The anterior talon forms two high cusps, one in front of the buccal conelet, and the other in front of the third conelet from the buccal side in plate 1, and has further three smaller enamel cusps; the talon is not developed at the lingual edge of the crown. There is an anterior contact facet.

The distance from the middle of plate 5 to the middle of plate 1 from the front is 57 mm at the apex but is not more than 43 mm at the base (roots are broken off). Thus, as a result of the convergence of the plates toward the root the laminar frequency would increase from 7 to over 9 as the occlusal surface approaches the base of the crown with the increasing amount of wear.

The four incomplete molars thus far described are the largest specimens of upper molars in the Sompoh collection. It is clear now that the two upper molars of 1949, then described as either M^2 or M^3 are both M^2s. The exact plate formula of these molars cannot be given; in *A. planifrons* M^2 has 8-9 plates, and M^3 10-11 plates, plus the talons (Hooijer, 1949, p. 218).

M^1 (pl. XX figs. 4-5)

There remains one incomplete upper molar that for its size and other characters cannot be but an M^1. It is of the left side (pl. XX figs. 4-5) and consists of six plates and the anterior talon. The first three plates are worn; they are more inclined forward than the posterior plates. All the preserved plates are complete, and those unworn are definitely higher than wide, their height-width index even exceeding that of the M^3 sin. There are four conelets per plate except in plate 4 from the front in which there are five. The second conelet from the lingual side in plate 2 has an anterior point. The foremost plate is interesting as it has a structure strongly reminiscent of the bunomastodonts (pl. XX fig. 4); there are two transversely elongated enamel figures separated by a median cleft, and both in front and behind this median cleft there is a small enamel figure in the valley, the central intermediate conules as in a bunomastodontid. The anterior talon is enclosed in cement, as are all the plates, and shows one worn point lingually and a smaller point buccally only.

Plates 1 to 6 inclusive are contained in 55 mm, which gives a laminar frequency of 11, intermediate between that of the M^2s mentioned above and that of the DM^4s described at an earlier occasion (Hooijer, 1953c, p. 225).

Table 2 contains all the essential data of the upper milk molars and molars of *A. celebensis* thus far described.

TABLE 2

Upper milk molars and molars of *Archidiskodon celebensis*

	length	width	width-length index	height	height-width index	plate formula	laminar frequency
DM^2	20	14.5	73	—	—	x3x	
DM^4	—	25	—	—	—	-3x	14
DM^4	—	29.5	—	ca. 23	ca. 78	-2x	14
M^1 sin.	—	33	—	39	118	x6-	11
M^2 (type)	?120	42	?35	45	107	-7x	8
M^2 (B)	?145	47	?32	—	—	-7x	7½
M^2 dext.	—	42	—	—	—	-5x	7½
M^2 sin.	—	42	—	45	110	x5-	7-9
M^3 sin.	—	42	—	49	116	-4x	6
M^3 sin.	—	52	—	—	106+	½4-	6-7

M_3 (pl. XXI figs. 2-3)

In the mandible the number of plates to the molars is occasionally greater than that in the upper jaw (up to 11 in M_2, and up to 13 in M_3 of *A.*

planifrons; Hooijer, 1949, p. 218). The very best specimen of lower molar of *A. celebensis* is the M_3 sin. in situ in a ramus fragment (Hooijer, 1953a, pp. 312-315, pl. XIX, upper left and lower right), with 11 plates, a greatest width of 43 mm, and a laminar frequency of 7½, higher than that of the M^3s described above.

There are several specimens of lower molars in the Celebes collection, none of which is complete, however. Three doubtlessly represent the hinder ends of M^3s, and two of these even form a pair. They carry six plates, steadily increasing in height and width from back to front, and parts of a seventh plate, along which they are broken off anteriorly. Cement is abundant all over the crown; roots are not preserved. Wear has proceeded to the fifth plate from behind, and in both M_3s the occlusal surface falls off toward the buccal side, as in mastodonts.

As can be seen in table 3, in which the measurements of the fragmentary M_3s are compared with those of the complete M_3 sin. described in 1953, the differences are so slight as to be accounted for by individual variation. In the posterior portion of a left M_3 last recorded in this table, with five

TABLE 3

Measurements of M_3 of *Archidiskodon celebensis*

No. of plate from behind	6	5	4	3	2	1
M_3 sin. (Hooijer, 1953a)						
Basal width	—	—	—	—	—	—
Unworn height	47	45	41	37	33	28
M_3 sin. (pl. XXI fig. 3)						
Basal width	44	42	39	34	28	ca. 16
Unworn height	47	44	41	39	35	27
M_3 dext.						
Basal width	42	40	37	31	25	ca. 14
Unworn height	46	44	42	41	36	30
M_3 sin. (pl. XXI fig. 2)						
Basal width	—	41	39	35	30	ca. 18
Unworn height	—	47	43	39	37	32

plates preserved only, the common base of dentine extends behind the last plate as a shelving notch (pl. XXI fig. 2). In all of these specimens the plates remain higher than wide, but, when passing backward along the plates of the crowns the widths decrease more rapidly than do the heights, so that the small posterior plates have the greatest relative heights. The laminar frequency of all these incomplete specimens is 8, slightly greater than that of the 1953 M_3 (7½).

M_2 (pl. XXI figs. 1, 4, pl. XXII figs. 1-2)

An incomplete molar in a large portion of a left mandibular ramus from

Sompoh (pl. XXI fig. 1) is of value as its full length can be measured in the ramus. It is further instructive as it shows the plates in all stages of wear, from hardly worn behind to worn down to the base of the valley in front. There are eight plates, and a small talonid preserved on the occlusal surface; the anterior portion of the crown is broken off. The anterior root of the molar is, however, preserved in the ramus, which makes it clear that two plates are lost; the plate formula, therefore, must have been x10x. It is not the last molar as the crown terminates rather abruptly behind. Cement is developed on the inner and outer sides of the plates, and envelops the talonid of which a central enamel point only is seen.

The hindmost plate has formed three enamel rings on the worn surface. In the second plate from behind these conelets are already worn out. The enamel figure of this plate as well as those of the two plates following it in front show a median expansion caused by enamel loops both in the anterior and in the posterior border of the plate; the former are larger than the latter. These enamel projections make a contact across the valleys between the plates; on either side the valleys are wide open. With advancing wear, as seen in plate 5 from behind, the median enamel loops flatten out; the enamel figures become broader anteroposteriorly at either end and expand more gradually anteriorly toward the median line. In the valley between plates 7 and 8 from behind the occlusal surface has reached the middle of the bottom; these plates would have formed a continuous dentine surface with the anterior two plates that are lost.

The anterior root, preserved in the ramus of the mandible, would have supported the anterior two plates only; the junction between this root and the main root supporting the remainder of the crown is just below the third plate from the front, as is also the case in the earlier described lower molars of *A. celebensis* (Hooijer, 1953a, pp. 313 and 316).

In size as well as in plate formula and in laminar frequency the present molar is intermediate between the complete M_3, which measures 164 by 43 mm and has 11 plates, and the smaller complete lower molar described earlier as either M_1 or M_2, which measures 85 by 31 mm and has 8 plates (Hooijer, 1953a). The total length of the present molar, from the front of the anterior root to the back of the talonid, is 120 mm; its greatest width, 37 mm, which gives a width-length index of 31. Height measurements cannot be given as all the plates are worn. Plates 3 to 7 inclusive occupy an anteroposterior length of 55 mm, which gives a laminar frequency of 9. The present specimen is so perfectly intermediate between the two complete molars described in 1953 that there can be no doubt that it represents M_2; the smaller of the 1953 molars must be M_1.

The ramus of the mandible which holds this M_2 is broken off behind the molar, and does not present any unusual features. The height below M_2 is 78 mm. It is much expanded laterally beside the hinder part of M_2 at the origin of the coronoid process. On the inner surface the mylohyoid groove is weakly indicated. What little is preserved of the symphysial region shows that the lower border of the ramus is slightly downwardly curved. The symphysis is edentulous.

In this connexion another left ramus of the mandible, originating from Tjeleko, is very remarkable indeed; it is presented on pl. XX fig. 9, pl. XXI fig. 4, and pl. XXII fig. 2 of the present paper. It holds part of a worn molar which will be described first.

The molar in the Tjeleko ramus is worn to the last plate, and has a posterior contact facet. The height of the posterior root, exposed in the broken surface of the ramus, is about 70 mm. Altogether four plates and the lingual half of a fifth plate are preserved on the occlusal surface, which is concave anteroposteriorly and falls off toward the buccal side. The front part of the crown is broken off. However, the anterior root of the tooth is preserved in the ramus, which enables us to determine the total length at the base of the crown, which is 133 mm, much shorter than the M_3 in the ramus described in 1953 although somewhat longer than the M_2 recorded above.

The preserved plates show all stages of wear, and are embedded in cement also on the sides of the crown. The posterior talonid is a small affair, and only one point of it can be seen above the cement coating. The posterior plate is worn into two enamel figures, of which the buccal has an anterior point. The plates following in front have single enamel figures, expanded in the middle, and mostly so in front, with their hinder borders almost straight. The resemblance of their patterns to those in the M_2 just described is striking (cf. pl. XXI fig. 1).

Since the total length of the crown is known, it is possible to determine the number of plates that the molar possessed when entire, which is nine. This is one plate less than that in the M_2 above described, but a number that corresponds well and only with that of the M_2 in *A. planifrons* (Hooijer, 1949, p. 218). The greatest width of the present molar (at plate 4 from behind) is 48 mm, greater than that of the M_3s thus far described (41-44 mm). The resulting width-length index is 36, a figure also found for the small M_1 of 1953. Plates 2 to 5 inclusive measure 57 mm anteroposteriorly at the worn surface; the laminar frequency consequently is 7, a figure even lower than that of the M_3s (7½-8).

The present molar, as shown by the presence of a posterior contact facet, is not an M_3; it is a penultimate molar (M_2) remarkable for its great width, relatively as well as absolutely, and low laminar frequency.

Incidentally, the width-length index of the large M_2 from Tjeleko is just within the range of that index in the M_2 of *A. planifrons*. It is typical of the molars of *A. celebensis* to be narrower-crowned than the average of those of *A. planifrons* (table 4, partly after Hooijer, 1953a, p. 314).

TABLE 4

Width-length indices of lower molars of *Archidiskodon*

	A. celebensis	*A. planifrons*	*A. meridionalis*
M1	36	39-67	35-48
M2	31-36	35-53	31-47
M3	26	26-49	27-43

The difference in size between the M_2 of the Sompoh ramus above described and that in the Tjeleko ramus may be connected with a difference in sex of their owners, the Sompoh ramus belonging to a female, and the Tjeleko ramus to a male.

It is now possible to present the plate formula of the lower molar series of *A. celebensis* as follows:

$$M_1,\ 8;\ M_2,\ 9\text{-}10;\ M_3,\ 11,$$

a formula that corresponds with those both of *A. planifrons* and of *A. meridionalis,* although it is to the lower side of the range of variation observed in the latter species (Hooijer, 1949, p. 218; 1953a, p. 316). *A. celebensis* represents the same evolutionary stage as *A. planifrons,* equal to that of the most primitive specimens of *A. meridionalis.* Indeed, as far as the molars are concerned, there is such a gradual transition between *A. planifrons* and *A. meridionalis* that there is no definite break in the series at which the boundary line between the two species can conveniently be placed (for a discussion of this, see Hooijer, 1953d, pp. 195-198).

Table 5 contains the essential data of the lower dentition (milk molars

TABLE 5

Lower milk molars and molars of *Archidiskodon celebensis*

	length	width	width-length index	height	height-width index	plate formula	laminar frequency
DM2	19	13	68	—	—	x3x	
DM3	32	20.5	64	—	—	x6x	20
DM4	—	22	—	—	—	-3-	13
M1 dext.	85	31	36	29	94	½8x	11
M2 sin.	120	37	31	—	—	x10x	9
M2 sin.	133	48	36	—	—	x9x	7
M3 dext.	164	43	26	47	109	½11x	7½
M3 sin.	—	44	—	47	107	-7	8
M3 dext.	—	42	—	46	110	-7	8
M3 sin.	—	41	—	47	115	-5	8

and molars) of *A. celebensis* described in the present and earlier papers of this series.

EVIDENCE OF INCISIVE TUSKS IN THE MANDIBLE

While the ramus of the mandible from Sompoh (with the small M_2) only shows a slight downward curve anteriorly, that from Tjeleko shows this feature much more clearly (pl. XXII fig. 2). Actually, the downward prolongation of the symphysial region into a sort of beak is observed in *A. planifrons* (Falconer, 1868I, p. 429), and has also been demonstrated in European mandibles referred to that species (Osborn, 1942, p. 962 fig. 849, and p. 1024 fig. 914).

There is much damage to the anterior part of the mandible from Tjeleko: the descending alveolar border in front of the molar is partially lost, and what is preserved of the symphysis has a shape totally different from what would be seen in a normal, tuskless, elephantine mandible.

To begin with, the Tjeleko ramus is much higher and more massive than that from Sompoh, and increases more markedly in height to the front below the M_2, the height of the ramus below the posterior part of M_2 is about 100 mm, that below the anterior part of the molar at least 120 mm. The origin of the coronoid process is much more strongly marked in the Tjeleko ramus than in that from Sompoh too. Unfortunately both rami are broken off just behind the molars that they contain. The mylohyoid sulcus forms a much more distinctly depressed area on the inner surface of the ramus in the Tjeleko than in the Sompoh specimen.

In the Tjeleko ramus, the lower border is gently curved downward anterior to the level of the anterior root of the molar, forming a very open angle (about 155°) with the straight lower border of the ramus below the molar. In one of the *A. planifrons* mandibles (Osborn, l.c., lower fig.) the downward curve of the "beak" is even stronger. The lateral surface of the ramus, however, does not diminish as rapidly in height to the front as does that of the *A. planifrons* mandibles; the descent of the alveolar edge in front of the molar is not as steep, it is hardly steeper than that of the lower border of the ramus in its anterior part. Thus, the ramus remains of about the same height in front of the molar as far as preserved.

On the outer surface we observe two mental foramina, one rather large, 21 mm in diameter, and situated below the anterior root of the M_2, and another, 12 mm in diameter, placed 22 mm in front of the large foramen and on the same level. In normal archidiskodont mandibles these foramina are much smaller. The larger foramina seem to indicate the need of a greater nutritive supply toward the end of the mandible.

On the lingual surface of the ramus one would expect to find remains of the body of a symphysis, which presents more or less an oval when cut in the median line. Its upper border forms the symphysial channel, a gutter between the descending alveolar ridges, and hence is concave transversely. The body of a symphysis slopes away in front to the chin projection, and behind to the posterior end of the symphysis, at the point of divergence between the rami. The upper surface of a symphysis, therefore, is convex anteroposteriorly.

Instead, the lingual surface of the Tjeleko ramus curves inward anteriorly only to form an oblique projection that is much depressed from above downward. Its lower surface is convex anteroposteriorly and concave transversely, and clearly represents the lower surface of the body of the symphysis, curving upward behind. The upper surface of the projection is regularly concave from side to side but perfectly straight anteroposteriorly except in its proximal part where it is slightly curved upward. It forms part of an almost cylindrical hollow, ca. 50 mm in diameter proximally and ca. 45 mm in diameter distally; it is 95 mm long as far as preserved. The axis of this hollow slopes downward in front at an angle of 130° with the lower border of the ramus below the molar, more steeply so than does the anterior part of the lower border of the ramus, to the effect that the bone becomes very thin vertically at the anterior end of the mandible. The subcylindrical hollow terminates abruptly behind, being marked off from the upturned posterior surface of the symphysis by a sharp edge. The axis of the cylinder would form a tangent of the linguai surface of the ramus if prolonged backward.

At the distal end of the subcylindrical hollow the bone is very thin, and broken off. Laterally the boundary of the hollow is not preserved either because the descending alveolar edge of the ramus is damaged. The median boundary of the hollow is broken too (pl. XX fig. 9). Does this surface represent the upper surface of the symphysis? If so, it would indeed be concave from side to side, but it would be convex anteroposteriorly and not straight and even concave behind. It would pass into the posterior surface of the symphysis by a gently curved surface and not by a sharp edge. The axis of the symphysial gutter would not form a tangent to the lingual surface of the ramus but would pass medially of that surface; it would mark the median line of the mandible, passing midway between the rami on either side. Moreover, if the hollowed surface would be the upper surface of the symphysis the body of the symphysis would be very thin and weak, only some 25 mm thick, which is impossible mechanically.

The conclusion is inevitable that the subcylindrical hollow lingually of the descending alveolar border of the ramus is not the upper surface of the symphysis. The only possible interpretation is that it formed part of the alveolus of a large tusk, the left lower incisor. Its perfect straightness and its proximity to the ramus exclude any other interpretation. The alveolus evidently lodged a tusk that was not yet fully grown as the horizontal diameter increases from ca. 45 mm at the alveolar edge to ca. 50 mm at the bottom of the alveolus. This is in accord with the stage of growth of the mandible; its owner was not yet fully adult, having M_2 in use.

We are forced to accept that the individual to which the Tjeleko mandible belonged carried real tusks in the lower jaw in the mastodont fashion. And even relatively large tusks at that, the proximal horizontal diameter being about 50 mm. As only the lower part of the alveolus is preserved it is not possible to determine whether the incisor was round or compressed in cross section. However, if we insert a cylinder in the alveolus its proximal upper end would project above the level of the descending alveolar edge of the ramus, which seems to indicate that the tusk was vertically compressed in cross section, at least at its proximal end. What the form and the length of these tusks were, beyond the alveolus, we can only surmise.

As far as our present knowledge of fossil proboscideans goes, mandibular tusks occur only in the moeritheres, deinotheres, and mastodonts. The stegodonts and elephants are characterized by the very early complete loss of the lower incisor teeth, one prime distinction in these superfamilies (Osborn, 1936, p. 25; 1942, p. 1550). As in our collection from Celebes we have evidence only of stegodonts (*Stegodon* spec.: Hooijer, 1953b) and archidiskodonts, the present find is remarkable, to say the least.

There is another puzzling specimen in the Celebes collection that in the present state of our knowledge does not fit in either with stegodonts or with elephants. This is a portion of a tusk that is much compressed in cross section, with a shallow median groove on one of the broad surfaces, and regularly convex on the opposite surface. The fragment originates from Sompoh (pl. XXII figs. 3-4) and is 8 cm long, perfectly straight. The diameters diminish along its length; at the broad end the greater diameter is 56 mm, the smaller diameter 39 mm. At this end is seen the apex of the pulp cavity, a small pointed hole only a few mm deep. Evidently this section was just about at the distal end of the pulp cavity. At the opposite end the diameters are 51 by 36 mm. The longitudinal groove on one of the broad surfaces is shallow, 20 mm wide and 3 mm deep in its middle part. There is no trace of an enamel band along any part of the surface. The broken ends show in places the system of decussating curved lines by which the ivory of the elephant's tusk is characterized.

There can be no doubt that this is a proboscidean tusk, but it is equally certain that such compressed and even grooved tusks have never been observed either in stegodonts or in elephants, which have the tusks round in cross section.

Flattened incisors such as the one just described do occur in the mandible of various longirostrine bunomastodontids known as "prod-tuskers", "oblique-tuskers", or "shovel-tuskers". In a number of genera such as *Trilophodon, Amebelodon,* and *Tetralophodon,* the incisors, if any, in the decurved mandibles are vertically compressed, and often have a depression or groove along their upper surface. Our Celebes specimen closely resembles the lower tusks of, e.g., the "shovel-tusker" *Amebelodon sinclairi* (Osborn, 1936, p. 337), as well as those of some "sub-shovel-tuskers" (Osborn, l.c., pp. 442, 446), which possess the same compressed cross section and the shallow longitudinal groove along their upper surface. Although these inferior tusks evidently were used for feeding purposes, they are not invariably present: the mandible is tuskless in *Trilophodon lulli* (Osborn, l.c., p. 294/295), *Tr. phippsi* (l.c., p. 315), *Tr. cruziensis* (l.c., p. 323), and in *Tr. joraki* (l.c., p. 326). It is considered probable that the absence of lower tusks is a female character, a view supported by the minimum dimensions both of the jaw and of the molars of some tuskless types (Osborn, l.c., p. 326). In *Tetralophodon* the lower incisors are retrogressive; it seems likely that only the males were provided with them (Osborn, l.c., pp. 344, 354, 362, and 369).

After this excursion among the bunomastodonts, let us return to the Celebes material. As said above, the Celebes collection contains only two types of proboscideans, *Stegodon* and *Archidiskodon.* The peculiar isolated tusk from Sompoh reminds us of the lower incisive tusks in certain bunomastodontids. The Tjeleko mandible resembles these mastodonts in the presence of lower incisors. Both the compressed incisor and the tusked mandible are beyond anything which experience thus far has led us to believe to exist in archidiskodonts.

Although the association cannot at present be proved to be correct, it seems preferable to assume that a tusk like that described above occupied the alveolus partially preserved in the Tjeleko mandible.

We have next to consider whether a mandible with a pair of compressed and grooved incisors may still be considered to belong to the genus *Archidiskodon.* The molar in the Tjeleko ramus is a typical *Archidiskodon celebensis* M_2, remarkable only for its great size; it is not any more mastodontoid than the M_2 in the Sompoh ramus which has a tuskless symphysis. The presence of mandibular incisive tusks in *Archidiskodon celebensis* may be regarded as a sexual character, the Tjeleko ramus with tusks being male, the Sompoh ramus without, female. The difference in size between the M_2s of the two rami dealt with above is also suggestive of a difference in sex between the individuals to which these mandibles belonged (above, p. 113).

In this connexion it is interesting to recall (above, p. 114) that the few lower jaws of *A. planifrons* in which the symphysis is preserved are characterized by a peculiar downturned anterior symphysial projection, a character that reminds us of the prolonged deflected rostrum of the longirostrine bunomastodontids referred to above, although the symphysis in *Archidiskodon planifrons* thus far has been found tuskless (cf. Osborn, 1942, p. 962 fig. 849, and p. 1024 fig. 914). This is only one among various mastodontoid features by which a primitive *Archidiskodon* is characterized. The most important character of *Archidiskodon planifrons* as well as of *A. celebensis* is the presence of premolars, waning inheritances from the past, essentially mastodontoid in structure (see Hooijer, 1953c, pl. VII figs. 9-10, 12-15). The median expansions of the plates of these early archidiskodonts can be traced back to the intermediate conules of the bunomastodontids, and even in the mode of wear, with the occlusal surface falling off rootward toward the lingual side in the upper molars, and toward the buccal side in the lower, the molars of archidiskodonts often remind us of the mastodonts.

On the base of all these observations Dietrich (1951, pp. 344, 372) suggests the derivation of the archidiskodonts from bunomastodontid ancestors, a change that involves mainly a heightening of the molar ridges. This is in opposition to the usual view, viz., that the archidiskodonts arose from primitive stegodonts. However, in the most primitive member of the Stegodontidae, *Stegolophodon,* the valleys of the molars are closed at the bottom (in contradistinction to *Archidiskodon*), and the mastodontoid intermediate conules have already merged with the ridge-plates, while in *Archidiskodon* these structures are still discernible (Dietrich, l.c., p. 344/345).

The new facts that have emerged from the present study of the Celebes archidiskodont are well in harmony with the theoretical views expressed by Dietrich quoted above. It is, after all, not too startling to discover that compressed lower tusks occasionally develop in a very primitive species of the genus *Archidiskodon* such as *A. celebensis.* These lower incisors belong in the same category as the premolars (neither of these are known in *Stegolophodon*) as characters inherited from the bunomastodontids from which *Archidiskodon* has most probably sprung. In *A. celebensis* the lower tusks are apparently confined to the male sex, as they were in certain bunomastodontids too.

Of *Archidiskodon planifrons* two mandibles with complete tuskless symphyses are figured by Falconer and Cautley (1845, pl. 8 fig. 2, and pl. 11 fig. 2). The M_3s in these two jaws differ very markedly, that in the first being very short (224 mm) but rather wide (97 mm), that in the other being very long (300 mm) but extremely narrow (77 mm). The contrast between these two molars is so wide (they represent almost the extremes of variation observed in this molar, see Hooijer, 1953a, p. 314, table 1) as to make it seem very improbable that there is any positive correlation between molar size and the presence or absence of lower incisive tusks in *A. planifrons* such as that found in *A. celebensis*. In other words, it is unlikely that *Archidiskodon planifrons* will ever be found to possess tusks in the mandible. In this respect *A. planifrons* seems to have evolved further from its mastodont ancestors than has *A. celebensis*.

On the whole, *Archidiskodon celebensis* represents the same evolutionary stage as *A. planifrons* which is twice as large in linear dimensions, as shown by its plate formula, long roots, enamel configuration, and degree of hypsodonty of the molars (Hooijer, 1949, 1953a). The two species further agree in the presence of premolars (Hooijer, 1953c). I have regarded *A. celebensis* as a dwarfed descendant of *A. planifrons*, retaining the archaic characters of the latter species.

The occasional retention of mastodontoid lower tusks in *A. celebensis* stamps this species as more primitive than *A. planifrons* (or any other named form of *Archidiskodon*, for that matter), and leads us to assume an independent origin of *A. celebensis*, independent from the species of *Archidiskodon* already known, that is.

It seems, therefore, likely that the most primitive elephantines, the archidiskodonts, arose polyphyletically from longirostrine bunomastodontids.

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EXPLANATION OF THE PLATES

PLATE XX

Archidiskodon celebensis Hooijer, S.W. Celebes; fig. 1, posterior portion of M^3 sin., Sompoh, buccal view; figs. 2-3, anterior portion of M^2 sin., Sompoh; fig. 2, crown view; fig. 3, buccal view; figs. 4-5, anterior portion of M^1 sin., Sompoh; fig. 4, crown view; fig. 5, buccal view; figs. 6 and 8, M^2 dext., Sompoh; fig. 6; crown view; fig. 8, lingual view, showing the long root; fig. 7, anterior portion of M^3 sin., Sompoh, crown view; fig. 9, left ramus of the mandible with M_2 and alveolus for incisive tusk, Tjeleko, upper anterior view.

Figs. 1-8, ¾ natural size; fig. 9, ½ natural size.

PLATE XXI

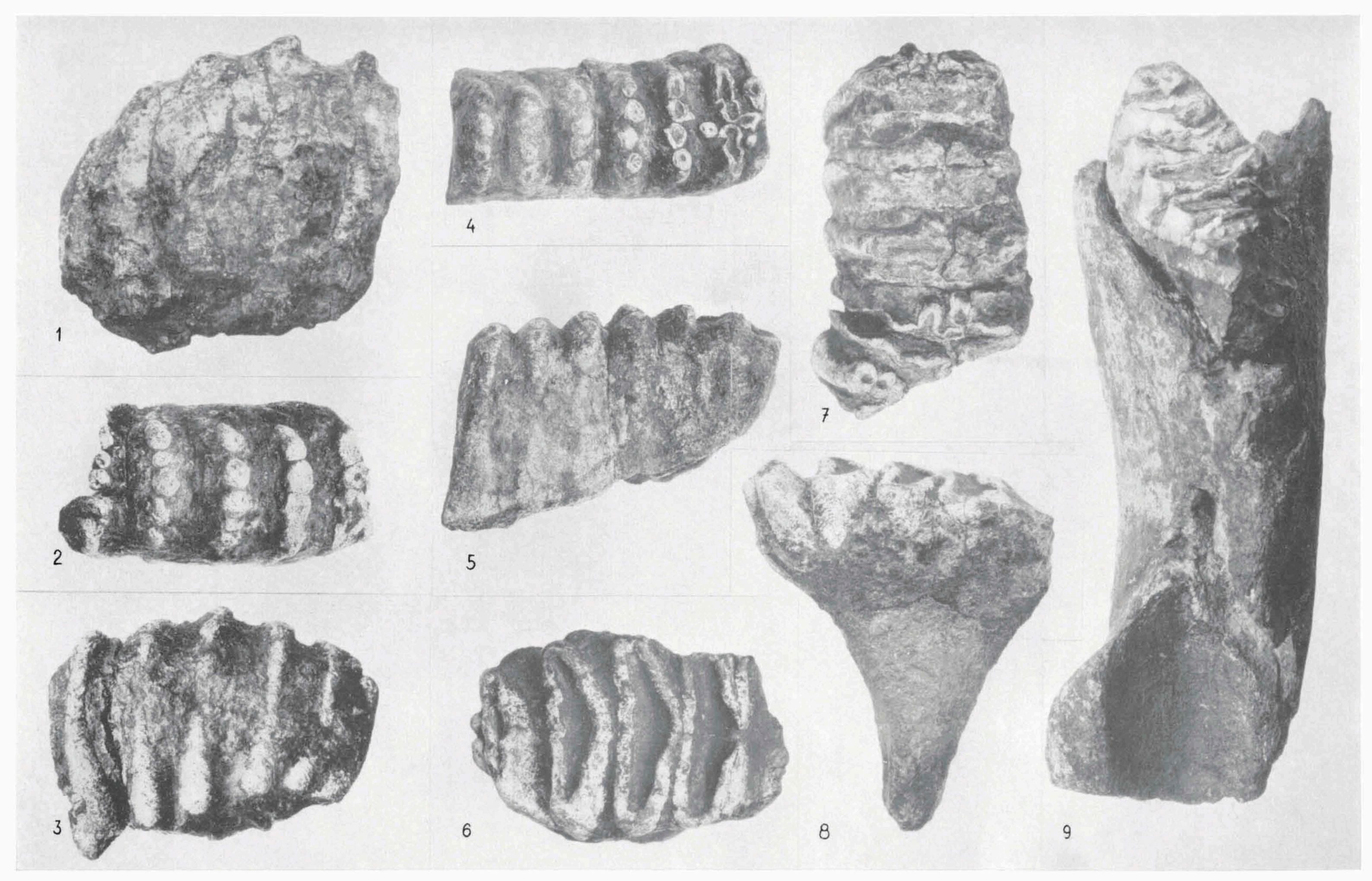
Archidiskodon celebensis Hooijer, S.W. Celebes; fig. 1, left ramus of the mandible with M_2, Sompoh, upper view; fig. 2, posterior portion of M_3 sin., Sompoh, lingual view; fig. 3, posterior portion of M_3 sin., Sompoh, buccal view; fig. 4, left ramus of the mandible with M_2 and alveolus for incisor, Tjeleko, upper view.

Fig. 1, 2/3 natural size; figs. 2-4, ¾ natural size.

PLATE XXII

Archidiskodon celebensis Hooijer, S.W. Celebes; fig. 1, left ramus of the mandible with M_2, Sompoh, inner view; fig. 2, left ramus of the mandible with M_2 and alveolus for incisor, Tjeleko, inner view; figs. 3-4, lower incisive tusk, Sompoh; fig. 3, proximal view; fig. 4, upper view, showing longitudinal groove.

Figs. 1-2, ½ natural size; figs. 3-4, ¾ natural size.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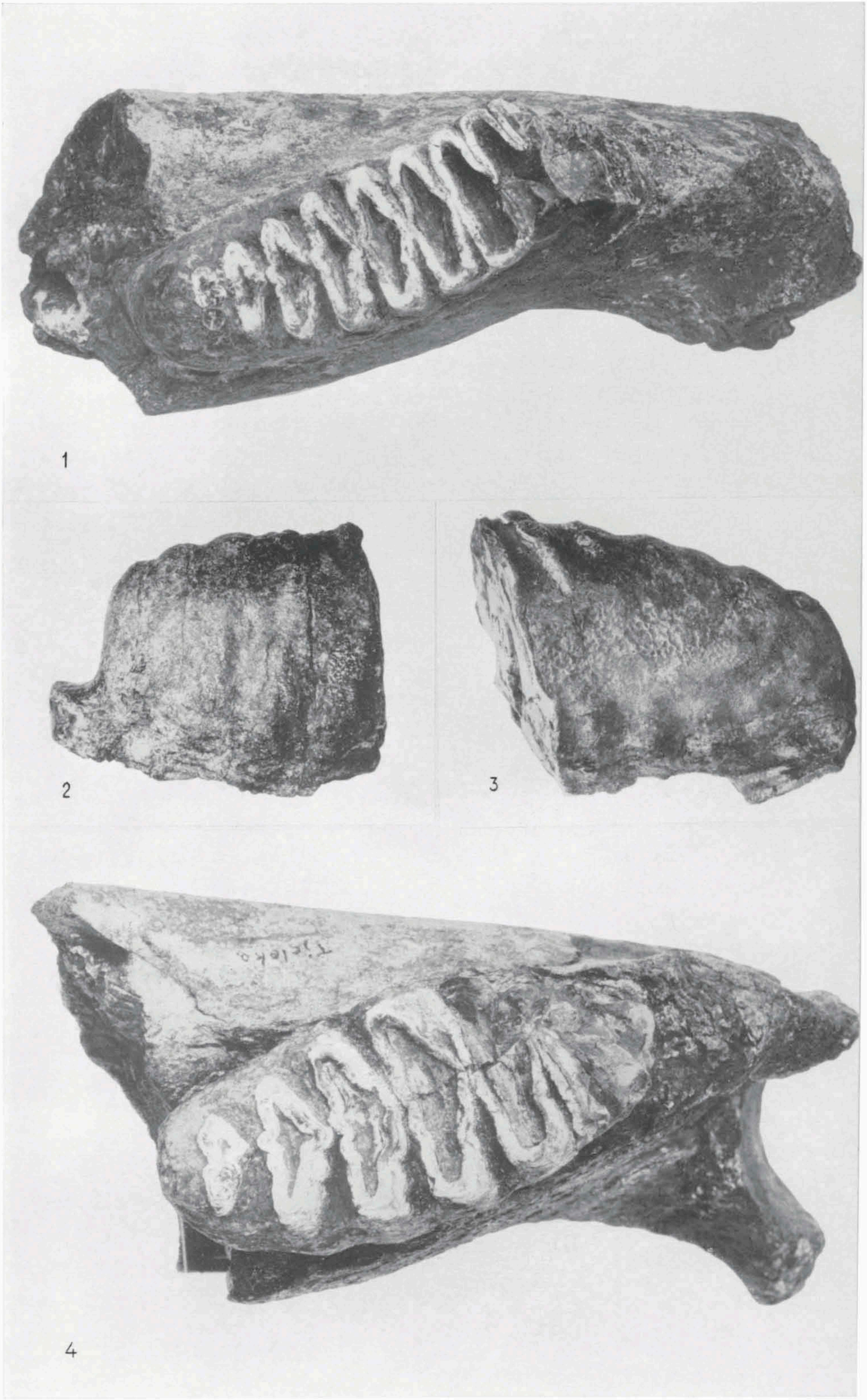
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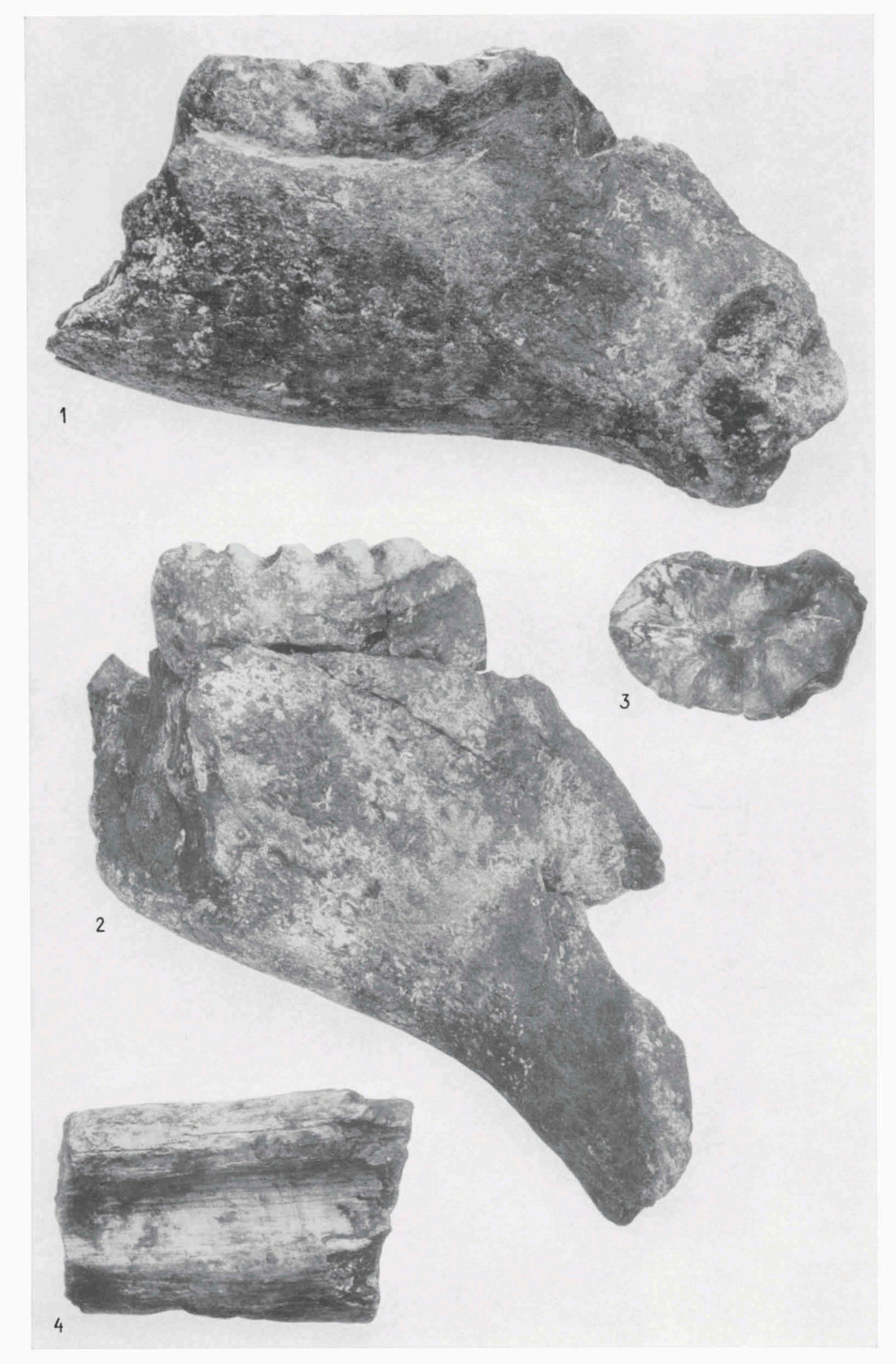
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