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PLEISTOCENE VERTEBRATES FROM CELEBES. XIV. ADDITIONS TO THE *ARCHIDISKODON-CELEBOCHOERUS* FAUNA

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With four plates

A joint Dutch-Indonesian expedition to Celebes in 1970 worked especially in the Beru area whence the first described Pleistocene Celebes vertebrate remains came. In the present contribution I shall describe the most important specimens that have been brought to light. My thanks are due to Mr. R. P. Soejono for permission to take certain specimens with me to the Netherlands for study and comparison. The expedition was financed by the Netherlands Foundation for the Advancement of Tropical Research (Wotro) at The Hague.

No further remains of Elasmobranchii (sharks and sting rays: Hooijer, 1954b) were found at Sompoh, so there are no additions on that score.

Of the giant land tortoise, originally described as *Testudo margae* Hooijer (1948), an abundance of material has been examined from Timor island (Hooijer, 1971). This has led to the conclusion that the fossil tortoise of Timor as well as that of Celebes are indistinguishable from *Geochelone atlas* (Falconer & Cautley) from the Early Pleistocene of the Siwaliks of India and of Java. The distribution of this species from the south-east Asiatic continent beyond Wallace's Line to Celebes and Timor is the result of overseas dispersal. In the 1970 collection from Celebes there are two first neurals from Sompoh, 15/7/1970, and Marale, 17/7/1970, respectively, the proximal end of a radius from Tjangkange, 1/8/1970, and shell fragments from Sompoh, Tjangkange, 31/7/1970, and Tjalio, south of the road, in orange sand.

The crocodile, which I described as *Crocodylus* spec. (Hooijer, 1954c), and which Dr. W. Hellmich of Munich (in litt.) believes may represent *Croco-*

dylus siamensis Schneider, still extant in the Malay Archipelago (Java and Borneo), is represented not only by tooth and bone fragments from Beru, 14/7/1970, and Tjangkange, 1/8/1970, but also by coprolites, up to 35 mm in diameters, from Sompoh and Tjalio, 3/7/1970, 50 m terrace south of the road, in orange sand.

It is among the proboscideans in particular that new data are to be recorded. Skull parts of *Archidiskodon celebensis* Hooijer (1949) with the last molars and the bases of the tusks and of the occiput are from Tjangkange. The stegodont molar fragments from Beru and Marale to be dealt with presently indicate, for the first time in Celebes, the presence of a form quite as large as *Stegodon trigonocephalus* Martin of Java. The pygmy stegodont of Celebes, *Stegodon sompoensis* Hooijer (1964), as a Tjalio M_3 shows, is rather hypsodont, in line with *Stegodon mindanensis* Naumann (1890) and *Stegodon timorensis* Sartono (1969).

Last, I report upon specimens of *Celebochoerus heekereni* Hooijer (1948) including skull parts of a male and of a female individual, and an upper molar of *Anoa depressicornis* (Smith), the extant pygmy buffalo of Celebes.

Archidiskodon celebensis Hooijer

The most complete specimen of *Archidiskodon celebensis* thus far recovered is a skull from Tjangkange, 27/7/1970, at an elevation of 80-85 m above sea level, the highest find of the 1970 expedition. The skull, which has remained at the office of the Lembaga Purbakala at Djakarta, is shown in ventral and left lateral view on pl. 1. Both of the last upper molars are in situ; the right M^3 is incomplete in front and behind, but the left M^3 is entire from end to end. Although the hinder end of the crown of M^3 sin. is covered by bone and matrix the basal outline of the back of the molar was exposed when I examined the skull; the skull was broken in various fragments when found. This made it possible to give the total length of M^3 as 160 mm, and the number of full plates, between the small end-plates or talons, as eleven. The M^3 sin. is shown separately on pl. 2 fig. 1. There can be no doubt that this molar belongs to *Archidiskodon celebensis*. It is only slightly damaged in front, and the anterior root is preserved. Behind the anterior talon there are five plates worn to the lozenge-shaped enamel figures, the 4th and 5th showing the median enamel loops that are so characteristic of *Archidiskodon celebensis*. The first few plates are 49-51 mm wide at base, and the greatest width, at plate 6 from the front, is 52 mm. Plate 6 is the hindmost worn plate, with four conelets the dentine cores of which are just touched by wear. From plate 7 on backward the width and full height of four

plates can be given (table 1). Beyond plate 9 the heights are not available for M^3 sin. as the last two plates and hind talon are enclosed in the jaw, but their bases were exposed. The M^3 dext., however, being broken off through the middle of plate 5 from the front, and behind plate 10, gives the height as well as the width of plate 10. The laminar frequency of the M^3 in the Tjangkange skull is 7.

TABLE 1

Measurements of M^3 of *Archidiskodon celebensis* (mm)

No. of plate	6	7	8	9	10	11	talon
Basal width	52	50	48	46	40	33	28
Total height	—	54	51	48	45	—	—
Height-width index	—	108	106	104	113	—	—

The present Tjangkange M^3 is the first complete last upper molar of its species to be placed on record. The number of plates, eleven, is the same as that in the entire lower last molar from Sompoh described before (Hooijer, 1953). The width-length index of M^3 is 33, or somewhat higher than that in the entire M_3 that is narrower and longer (length 164 mm, width 43 mm, width-length index 26). An upper molar is normally shorter and wider than a lower of the same serial position within the same species. Incomplete specimens of M^3 described in 1954 are 42-52 mm in width, with height-width indices of 106-116, and laminar frequencies of 6-7. The Tjangkange M^3, therefore, agree very well with M^3 of *A. celebensis* previously described. Now that we have the complete length of M^3 we find that it is a fifty per cent scale reduction of its homologue in *Archidiskodon planifrons* (Falconer & Cautley), but relatively longer and narrower, as was also the case with the Sompoh M_3. In *A. planifrons* M^3 the greatest width varies from 90 to 110 mm, and the greatest observed length is 292 mm (Maglio, 1970a: 21). The width-length index in *A. planifrons* M^3 varies from 34 to 47 (Hooijer, 1949: 219), and the number of plates, eleven, as well as the laminar frequency of 3 to 3½ (which would correspond to 6-7 in a molar half the length by the same plate formula) are quite characteristic of *A. planifrons* M^3.

Actually, *Archidiskodon planifrons* is a very variable species, but we lack stratigraphic control on the Upper Siwalik specimens recorded by Osborn (1942: 954-959). In a primitive *A. planifrons* from the Villafranchian of Bethlehem, which resembles the southern African *Archidiskodon subplanifrons* Osborn in the low crown height of its molars, the unworn plates of M^3 are less high than wide (height-width indices 82-87: Hooijer, 1958: 275). The height-width index is 110 in a full-sized plate of M^3 of *A. planifrons* from the Tatrot zone of the Upper Siwaliks, the earliest Siwalik specimen

known (Hooijer, 1956: 116). In the skull of *A. planifrons* in the British Museum (Natural History) the height-width index of M^3 is 115. Maglio (1970a: 21) gives the range of variation in height-width index of M^3 of *A. planifrons* as 84-109, the number of plates as 9-12, and the laminar frequencies as 2½ to 5½.

The molars of the Celebes pygmy elephantine agree with those of *A. planifrons* in the relatively thick and unfolded enamel, with median expansions or enamel loops to the enamel figures, and the wide, V-shaped valleys. Moreover, *A. celebensis* proved to have functional premolars, known among the early elephantines in *A. planifrons* exclusively (Hooijer, 1953). Finally, the occasional development of external tusks in the symphysis of the mandible (Hooijer, 1954d), not before recorded in any elephantine and considered a unique feature in *A. celebensis*, was reported by Maglio (1970a, b) in *Primelephas gomphotheroides* Maglio from the Late Pliocene of Lothagam, Kenya. Maglio placed *Primelephas gomphotheroides* in the Elephantidae, as a member of the basal group from which the later Elephantinae were derived.

In his recent papers, Maglio adopts three Pleistocene genera of Elephantinae, *Loxodonta, Mammuthus*, and *Elephas*, and the earliest representatives of these are rather alike in molar structure though very different in skull characters. The molars of *Loxodonta adaurora* Maglio, *Mammuthus africanavus* (Arambourg), and *Elephas planifrons* are very similar, and both in *Loxodonta adaurora* and *Elephas planifrons* vestigial incisive cavities were found in the mandible, although these apparently never developed into external tusks. These facts shed new light on the external tusks in the mandible of our Celebes elephantine; Maglio (1970a: 10) considers them to have reappeared possibly through paedomorphosis. For the sake of continuity I shall use *Archidiskodon* for *planifrons* and *celebensis*, as before.

The Tjangkange skull is incomplete; the side view (pl. 1 top fig.) shows the tusks were directed forward and downward, but we have nothing of the fronto-parietal surface, which is so flat in *A. planifrons* and convex in *Elephas* and *Loxodonta*, and the position of the orbit cannot be ascertained. The skull of *A. celebensis* appears to be quite narrow: the width of the palate between M^3 is 66 mm, and the width over the buccal surfaces of both M^3 170 mm. The premaxillaries are 195 mm wide, and the two tusks, which are 60 mm in diameters [1]), are only 60 mm apart. In the skull of *A. planifrons* in the Leiden Museum the palate is 6 cm wide only, and the width over the

1) A long portion of a tusk from Sompoh, weakly curved, is 70 mm in diameter at the proximal end, and 55 mm at the distal broken end. The pulp cavity, 35 mm in diameter at the proximal end, extends into the tusk for a length of about 30 cm. The total length of the tusk as preserved is 85 cm. The possibility that the tusk belongs to *Stegodon* cannot be ruled out.

buccal surfaces of M^3 is ca. 21 cm. The premaxillaries are 30 cm wide, and the two tusks, 6½ cm in diameters, are separated by an interval of 11½ cm. The close approximation of the upper tusks is a feature of *Stegodon* skulls: in skulls of *Stegodon trigonocephalus* Martin from Java they may be 65 mm in diameter and 50 mm apart, or 95 mm in diameter and 55 mm apart, and even in a very large skull with tusks 16 cm in diameters the interval is only 10 cm. However, the Tjangkange skull certainly does not belong to *Stegodon* as its molars show beyond any doubt. There is further the basal part of the occiput, but it does not fit on to the rest of the skull from Tjangkange. The condyles measure each 7 cm vertically and 4½ cm transversely, and the bicondylar width is 13 cm. In the skull of *A. planifrons* the condyle is 8 by 6½ cm, and the bicondylar width ca. 18 cm.

A portion of a right mandibular ramus with part of a molar originates from Sompoh, 23/6/1970. The ramus is rather damaged externally; the ventral border is preserved as well as the dorsal border buccally of the molar, but in between is a hollowed area in which part of the recurved main root is exposed (pl. 2 fig. 3). The height of the root is about 70 mm below the crown margin. The height of the ramus at the posterior end of the molar is 80 mm, and that at the broken anterior end 100 mm. The molar, which is presumably the last as there is no trace of a molar behind it, is broken off through the 5th plate from behind. Plates 4 through 1 from behind present imperfect lozenge-shaped enamel figures, with straight posterior borders but produced in the middle anteriorly (pl. 2 fig. 4). We find this wear pattern in many of the molars of *Archidiskodon celebensis*. The width decreases from the 4th to the first plate from behind as follows: 46, 42, 38, and 34 mm. The talonid is narrow and consists of two cones the outer of which is the larger and has an anterior point. Plates 4, 3, and 2 together occupy an anteroposterior length of 40 mm, giving 7½ for the laminar frequency. Last lower molars of *A. celebensis* previously described have a similar backward taper and a laminar frequency of 7½ to 8.

The stegodont material from Celebes available before the 1970 expedition had been described as *Stegodon* spec. (Hooijer, 1953), and later as *Stegodon sompoensis* Hooijer (1964). It has now become apparent that there are two species of *Stegodon* in Celebes: *Stegodon sompoensis*, a small species with high-crowned molars, very close to the Timor stegodont described in 1969 by Sartono, and a large form with relatively low-crowned molars, *Stegodon* cf. *trigonocephalus* Martin. The data on *Stegodon timorensis* Sartono (1969) used in this paper are derived from Hooijer (1969 and 1972), and those on *Stegodon trigonocephalus* from Hooijer (1955).

Until recently, I had regarded *Stegodon sompoensis* as a pygmy species with relatively low-crowned molars, as in *Stegodon trigonocephalus* from Java of which it is a fifty per cent scale reduction as far as the holotype is concerned. Further, I had no idea that another *Stegodon*, fully as large as *Stegodon trigonocephalus* from Java, would be present in Celebes along with the pygmy species. Evidence for the large *Stegodon* was found only during our 1970 Celebes expedition as well as better specimens of *Stegodon sompoensis* that showed this to be a high-crowned form. The type specimen of *Stegodon sompoensis* gives the actual size of the pygmy species, but not its molar crown height as it is worn. The crown height of *Stegodon sompoensis* was inferred from a referred specimen now removed from this species. The discussion will be given in the pages that follow.

Stegodon sompoensis Hooijer

The type specimen of the present species is a DM^4 or M^1 dext. from Sompoh, with either 6 or 7 ridges, ca. 50 mm long and 28 mm wide, and a laminar frequency of 14 (Hooijer, 1964). This specimen provided the first indubitable evidence for a true pygmy species of *Stegodon* in Celebes: length and width are just one-half those in DM^4 of *Stegodon trigonocephalus* (length 90-108 mm; width 48-57.5 mm), the laminar frequency of the Sompoh specimen (14) would correspond to 7 in a two times larger molar, which it is in DM^4 of *Stegodon trigonocephalus*, and the number of ridges is the same in both. The M^1 of *Stegodon trigonocephalus* is somewhat larger than the DM^4 so that as an M^1 the type specimen of *Stegodon sompoensis* would indicate a form less than one-half the size of *Stegodon trigonocephalus*, but I left this possibility open for the time being. We now know the M^1 in *Stegodon timorensis*, which is very close to *Stegodon sompoensis*, and with a width of 39 mm and a laminar frequency of 10 (Hooijer, 1972) it shows that the type specimen of *Stegodon sompoensis* is actually a DM^4. As the ridges of the DM^4 of *Stegodon sompoensis* are all worn height-width indices could not be given.

In 1953 I described as *Stegodon* spec. the anterior part of a left lower molar from Sompoh and the posterior part of a right upper molar from Tjeleko (Hooijer, 1953). They are 60-63 mm wide, with laminar frequencies of $6\text{-}6^2/_3$. The lower molar has ridges 60 mm wide by a height of 40 mm, giving a height-width index of 67, a normal index for *Stegodon trigonocephalus*. Not enough is preserved of these molars to determine their serial position: I stated that they would fit in as M_1 and M^1 of *Stegodon trigonocephalus*, but that it was also possible that they represented last molars. If

this were true, they would indicate a pygmy species as the M_3 and M^3 in *Stegodon trigonocephalus* are about one-half wider than the Celebes molars.

When, in 1964, I described the type specimen of *Stegodon sompoensis* I referred the Sompoh and Tjeleko molars of 1953 to this distinct pygmy species as M_3 and M^3. This was because I had no reason at the time to accept more than just one species of *Stegodon* in Celebes; there was no evidence in the Celebes collection of *Stegodon* molars larger than those described in 1953. I realized that even as last, and thereby largest, molars they were larger relative to their counterparts in *Stegodon trigonocephalus* than was the type of *Stegodon sompoensis*. I attributed this to individual variation, and in the diagnosis of *Stegodon sompoensis* I stated that the molars were from one-half to two-thirds as wide as their homologues in *Stegodon trigonocephalus* from Java. I added that the molar ridges were only two-thirds as high as wide, on the basis of the supposed M_3 from Sompoh that I had referred to *Stegodon sompoensis*.

The material collected at Beru, Marale and Tjalio during the 1970 expedition has proved me wrong in associating the Sompoh and Tjeleko molars of 1953 with *Stegodon sompoensis*. We have evidence now of fossil *Stegodon* molars in Celebes with laminar frequencies of 4-5, as large as the last molars in *Stegodon trigonocephalus* so that the 1953 molars are not the largest from Celebes any more. They will be referred to in this paper under the head *Stegodon* cf. *trigonocephalus* Martin. In the collections from Tjalio and Marale we have some molars (M_3, M_2, and M^2) that are just about fifty per cent scale reductions of their homologues in *Stegodon trigonocephalus*, just as is the DM^4 named *Stegodon sompoensis*. These molars are here referred to *Stegodon sompoensis*; the most important specimen is an entire M_3 sin. from Tjalio 25/7/1970, that is in part unworn and bears out all the distinctive characters of the Celebes pygmy form.

In the collection from Tjalio, 25/7/1970, there is an isolated left lower molar (pl. 3 fig. 1). It carries ten ridges and a sizable posterior talonid. The first four ridges are worn; the first ridge presents a hollow dentine area of which the enamel sides and the front, with the anterior talonid, are lost. However, the anterior root is preserved, showing that no ridges are lost in front. The total length is 135 mm, and from the posterior taper and curvature it is clear that this is a last lower molar, M_3 sin. The second ridge is worn to an entire enamel figure, with wrinkled enamel; the valley in front of it is very narrow, closed in at the base. The third ridge is worn, with a tripartite enamel figure, and the fourth ridge shows two large marginal conules, with four smaller conelets in between, just touched by wear. Neither this ridge nor any of the others, worn or unworn (with four or five conelets between

the large marginal ones), show the marked median expansions or the looped enamel folds characteristic of *Archidiskodon celebensis*; the enamel in the Tjalio molar is more wrinkled, too. Comparison with the splendid, eleven-ridged M_3 sin. of *A. celebensis* from Sompoh figured in 1953 (Hooijer, 1953) shows that the valleys in the Sompoh molar remain wider than those in the Tjalio molar although five plates of the Sompoh M_3 are worn. The last six ridges of the Tjalio M_3 are unworn, and their height can be taken as well as their basal width (table 2).

TABLE 2

Measurements of M_3 of *Stegodon sompoensis* (mm)

No. of ridge	1	2	3	4	5	
Basal width	—	41	43	44	45	
Total height	—	—	—	—	38	
Height-width index	—	—	—	—	84	
No. of ridge	6	7	8	9	10	talonid
Basal width	44	43	41	39	ca. 34	—
Total height	38	37	35	34	31	ca. 25
Height-width index	86	86	85	87	ca. 91	—

The unworn ridges are lower than wide, instead of the reverse as in *Archidiskodon* M_3; the height-width indices of the Tjalio molar ridges are 84-87, while in the M^3 of *A. celebensis* the height-width index is 107-115. The narrow valley bases and the absence of median expansions or enamel loops indicate that the Tjalio M_3 is a *Stegodon*, and a rather high-crowned *Stegodon* at that. The laminar frequency is 8 lingually and 9 labially, or 8½ on an average.

As an unquestionable M_3, the present Tjalio molar gives the actual size of its species, and it is a fifty per cent scale reduction of its homologue in *Stegodon trigonocephalus*. In this species M_3 is 240-304 mm long, 68-98 mm wide, with a laminar frequency of 4-6, which would correspond to 8-12 in a molar one-half the length by the same number of ridges. The Tjalio M_3 is in the same size class as the type of *Stegodon sompoensis*, but it gives further characters for the species: the Tjalio molar has only ten ridges, against 11-13 in the Java species, and it is higher-crowned than M_3 in *Stegodon trigonocephalus*, having a molar hight-width index of 84 against 56-66 in the Java species.

In every respect the Tjalio M_3 resembles the last lower molar in *Stegodon timorensis*, which has ten ridges in 118 to ca. 145 mm of length, greatest widths of 42-47 mm, laminar frequencies of 8-10, and height-width indices of 77-93. There is an astonishing resemblance between the Celebes and the Timor M_3, and if the Tjalio molar had come from Timor I would not have

hesitated to identify it as *Stegodon timorensis*. However, as we already have a type for the pygmy species from Celebes to which the Tjalio M_3 can be safely referred I prefer to use the name *Stegodon sompoensis* for the Celebes pygmy stegodont, and retain the name *Stegodon timorensis* for the Timor pygmy stegodont. If we would lump the two species, the name *sompoensis* would have to be used for both of the island forms as *sompoensis* has five years' priority over *timorensis*. It is, at any rate, highly probable that the Celebes pygmy stegodont and that of Timor evolved in geographic isolation and never formed one interbreeding population. The remarkable similarity in molar build may be attributed to parallel evolution.

An M_2 sin. from Marale, 31/7/1970, has seven worn ridges, but from what is preserved of the anterior root in the body of the mandible that holds it two ridges appear to be missing, making nine in all, in a length of ca. 115 mm. The ridges are all worn, and the posterior three show three to four conelets between the larger marginal ones, which are worn to entire enamel figures in ridges 3 to 6 from the front. The enamel figures are wrinkled with some expansion in the middle but nothing like that in an archidiskodont molar, and the valley is compressed at the base as seen in front of ridge 3 (pl. 3 fig. 2). Therefore, the Marale M_2 appears to represent *Stegodon* again. The width at base is 45 mm at ridge 4 from the front, 46 mm at ridges 5 to 7, inclusive, 45 mm again at ridge 8, and 38 in the last ridge, which is so little worn that its height can be given as 33 mm, giving a height-width index of 87, as in the penultimate ridge of the Tjalio M_3. The crown ends abruptly behind, with a very small talonid. The laminar frequency is 8.

The M_2 of the Java *Stegodon trigonocephalus* has either nine or ten ridges in a length of 185-213 mm, by greatest widths of 68-85 mm, and laminar frequencies of 3¾ to 6½. Of *Stegodon timorensis* we have three specimens of M_2 in situ, showing the number of ridges to be nine, in lengths of 114-116 mm. The greatest width varies from 40 to 43 mm, and the laminar frequency from 9 to 10. The height-width index of one specimen is 87. The Timor M_2 are rather narrower, with a higher laminar frequency than the Marale M_2, but the range of variation in the Timor M_3 given above indicate that the Marale M_2 could well be accommodated in the same species as the Timor M_2.

A number of skull parts were found at Tjalio I, 25/7/1970, including the palate with parts of M^2 in situ and M^3 in alveolo (pl. 3 fig. 3). All the ridges are worn; the left M^2 is broken off through the third ridge from behind, the right through the sixth. The width of the M^2 dext. is 48 mm at the fourth ridge from behind; those of the 3rd, 2nd and 1st ridges from behind are 47, 43, and 37 mm. The laminar frequency is between 7½ and 8. Of the M^3 only the apices of the front ridges are shown; this molar had not cut the

gums yet. From the wrinkled and slightly expanded enamel figures, which are quite close together in the front part of the M^2 dext., it is clear that this is *Stegodon sompoensis* again. In the M^2 of *Stegodon trigonocephalus* from Java the width runs from 76 to 94 mm, almost up to twice that in the Tjalio M^2, and the laminar frequency from 4 to 5. M^2 in *Stegodon timorensis* has a greatest width of 45-47 mm, and a laminar frequency of 8.

Stegodon cf. **trigonocephalus** Martin

Some remains of *Stegodon* found in Celebes during our 1970 expedition indicate molars of larger size than any so far found in that island.

The hinder end of an upper molar comprising two ridges, in a much rolled condition, was found in the second excavation at Marale, 20/7/1970, at a depth of 125-150 cm (pl. 3 figs. 4-5). The penultimate ridge is 20 mm thick anteroposteriorly, slightly concave to the front, bears seven conelets, slightly worn, and is 60 mm wide by a height of only 35 mm. The hindmost ridge, which may also be called talon, is lower still, 30 mm, by a basal width of 53 mm. The laminar frequency of the Marale specimen may be given as 5, which is less than that in the largest Celebes *Stegodon* molars known before $(6\text{-}6^2/_3)$.

Two ridge portions belong to stegodont molars with an even lower laminar frequency. One comes from north of the excavation at Beru I, 50 m terrace, 8/7/1970, and measures 25 mm anteroposteriorly at base, unworn height 40 mm, with one marginal and three central rather large conelets. It is 43 mm wide as preserved (pl. 4 figs. 2-3). The other is from Marale, 16/7/1970, likewise 25 mm anteroposteriorly and 40 mm high, with one large marginal and and six small central conelets, and is 35 mm wide as preserved (pl. 4 fig. 4). These ridge portions have a thickness that points to a laminar frequency of 4, far lower than that in the Sompoh and Tjeleko molars described in 1953 in which the ridges are only 15-17 mm thick anteroposteriorly. It is unfortunate that the full transverse width of the 1970 Beru I and Marale ridges is not known, but it is clear that they belong to larger, more posteriorly placed molars than the specimen described in 1953. A laminar frequency of 4 is found in second and third molars of *Stegodon trigonocephalus* from Java; even in *Stegodon trigonocephalus florensis* the laminar frequency of the last molars is already 4½ to 5.

The large Celebes stegodont of which we have evidence is quite as large as *Stegodon trigonocephalus*, and like it the Celebes form is not high-crowned: the height-width index of the full ridge of the specimen from the second excavation at Marale is only 58, within the limits of the Java M^3 (46-68) or M_3 (56-66). It is with these ridges that we should associate the 1953 Sompoh

and Tjeleko molars. The 1953 Sompoh lower molar is 60 mm wide and 40 mm high (index 67), and has a laminar frequency of 6. This is within the ranges of M_1 of *Stegodon trigonocephalus* (width 60-65 mm, height 38-46 mm, index 63-75, laminar frequency 6-7¼). The 1953 Tjeleko upper molar has a greatest width of 63 mm, and a laminar frequency of $6\,^2/_3$; the ranges of M1 in *Stegodon trigonocephalus* are 59-ca. 72 mm, and 6-6 $^1/_3$, respectively.

A half-ridge, unworn, 34 mm high and 19 mm thick anteroposteriorly at base, with one marginal and two central conelets, comes from Beru, 500 m east of km 168 in the field north of the road, 27/7/1970. The full width is unknown, but because of the laminar frequency, which is nearly 5, this specimen should be referred to as *Stegodon* cf. *trigonocephalus*.

Stegodon spec.

The remaining *Stegodon* finds belong to molars of small size, with high laminar frequencies, and could equally well be *Stegodon sompoensis* or *Stegodon* cf. *trigonocephalus*. A lateral ridge portion 13 mm thick at base and 34 mm high comes from Marale, 6/7/1970. It bears three conelets; the width is unknown. Two small, probably terminal ridges, only 12 mm thick anteroposteriorly, one 33 mm wide but worn, the other 32 mm high but of unknown width, are from Tjalio, obtained from the local people and hence of uncertain provenance. They belong to molars with a laminar frequency of about 8, which would fit either second or third molars of *Stegodon sompoensis* or last milk molars of *Stegodon* cf. *trigonocephalus*. A fragment of two adjoining ridge slopes and a cement-filled valley, closed in at the bottom, originates from Tjalio, 50 m terrace, south of the road, 5/7/1970. Finally, there is a small fragment of a stegodont molar obtained at Tjalio, 25/7/1970.

The small, hypsodont *Stegodon sompoensis* that we now have from Sompoh as well as from Tjalio and Marale is very close to *Stegodon timorensis*, but as said above I believe that these pygmy forms evolved independently on the two islands. *Stegodon timorensis* may be derived from *Stegodon trigonocephalus* of Java by a process of reduction in size and relative heightening of the molar crowns; we see the initial phase of this process in *Stegodon trigonocephalus florensis*, which averages slightly smaller and is more hypsodont than the Java species (Hooijer, 1957). The high-crowned pygmy stegodont of Celebes may be derived in a similar way from a species like *Stegodon trigonocephalus*, or the slightly larger *Stegodon insignis* (Falconer & Cautley) from India, or *Stegodon orientalis* Owen from China, which are close in ridge formula to the Java species, and have a laminar frequency of 4 or less in

their last molars. Since the entry of the stegodonts from the continent into Celebes was most probably by way of the Philippines it is of interest to look at the evidence for stegodonts in Mindanao and Luzon, scanty as it is.

Stegodon mindanensis Naumann (1890) is based on the posterior four ridges and talonid of a right lower molar. The specimen increases in width from 35 mm at the foremost preserved ridge to 37 mm at the last, is 33 mm high (height-width index 89), and has a laminar frequency of 10 (Naumann, 1887: 6; the figures are not quite natural size, as stated in the legend). This molar would fit in as an M_1 of *Stegodon timorensis*; we have the M^1 of this species, and it is at most 39 mm wide with height-width indices of 80-90 and a laminar frequency of 10. Naumann records a ridge of a *Stegodon* molar likewise from Mindanao that is 51 mm wide, 24 mm high (index 47), and 16 mm thick (laminar frequency 6). Such a ridge would fit in with *Stegodon trigonocephalus* as DM^4 (width 48-57½ mm, height 25-29 mm, index 46-58) although in the Java species the laminar frequency is somewhat higher (7-9).

Large molar portions from Luzon (one at least 70 mm wide figured by Beyer, 1949, pl. 1 fig. 1) have been recorded by Von Koenigswald (1956: 343) as *Stegodon* cf. *trigonocephalus*; a specimen 64 mm wide has a height of 46 mm, height-width index 72. A lower molar portion 5 cm wide, with at least six ridges but estimated to be 20 cm long (whereby it would be 10 per cent wider and 50 per cent longer than M_3 in *Stegodon sompoensis* or *Stegodon timorensis*) has been named *Stegodon luzonensis* Von Koenigswald (1956: 346). The crown height of the small Luzon molar is unknown.

The fossil *Stegodon* remains from Mindanao may be taken to represent a pygmy hypsodont, and a large, relatively low-crowned form, the same association that we have now found in Celebes. What the affinities of the Mindanao forms to those of Celebes are may perhaps become clear when we have much more material than is now available.

It is of interest to note that the very small stegodonts from Mindanao (*S. mindanensis*), from Celebes (*S. sompoensis*) as well as from Timor (*S. timorensis*) all have high-crowned molars, with height-width indices of about 80 or more. It would seem, therefore, a general rule that stegodonts diminishing in size develop higher molar crowns. All the pygmy forms may be derived from larger, low-crowned species, and remains of such forms have also been found in the same islands. The larger of the two forms on Timor already marks a step from *Stegodon trigonocephalus* in the direction of the pygmy species, but the larger of the two Celebes forms is fully as large as *Stegodon trigonocephalus*. More complete specimens may eventually show whether its affinities lie with this species or with any of the other large Pleistocene stegodonts of Asia.

Celebochoerus heekereni Hooijer

This is the most common element to the Pleistocene vertebrate fauna of Celebes, an endemic genus and species fully described in 1954 (Hooijer, 1954a). A skull portion from Tjalio I, 25/7/1970, is the most complete specimen so far found, showing the dorsal surface of the skull from above the front of the canine alveoli to above P^4 (pl. 2 fig. 2, pl. 4 fig. 7). Unfortunately, the specimen is rather damaged, crushed obliquely from behind and from the right side. The nasals are broken in small fragments and are depressed laterally on the right side; the right canine alveolus is placed a cm more forward than the left. The diameter of the canine alveoli, at least 35 mm, shows it to be a male individual (male canines average 34 by 30 mm in cross section). The canine alveolus curves outward at the level of P^3. There was no lateral angulation of the nasal region, so far as the state of preservation permits judgment. The broken crowns of P^4-M^2 are preserved; the palate is broken off behind M^2. The width of the palate between M^2 is 31 mm, and that over the outer borders of M^2 is 70 mm.

A palate from Marale, 19/7/1970, has P^{3-4} of the left side and M^{2-3} on both sides (pl. 4 fig. 1). The canine alveoli are not more than 25 mm in diameter, which shows this to be a female individual (female canines average 25 by 23 mm in cross section). The dimensions of the teeth (table 3) are on the small side. The palate between M^2 is 28 mm wide, and the width over the outer borders of M^2 is 58 mm.

A maxillary fragment with M^{2-3} sin. from Marale, 25/7/1970, has very large teeth, M^2 even exceeding the maximum size recorded in 1954 (table 3, last column).

TABLE 3

Measurements of teeth of *Celebochoerus heekereni* (mm)

		Marale ♀	Range (1954)	Marale ♂
P^4,	ant. post.	9.8	10.6-15.9	—
	transv.	11.5	11.4-15.9	—
M^2,	ant. post.	18.3	17.6-23.4	25.2
	transv.	15.8	15.2-18.7	19.2
M^3,	ant. post.	22.6	22.4-31.9	30.5
	transv.	16.1	15.0-21.5	19.8

The first lower molar was rather rare in the collection of *Celebochoerus* teeth; we now have an isolated M_1 dext. found at Tjalio, 15/7/1970, 50 m terrace south of the road, in orange sand. It is slightly worn, 18.1 mm long and 12.9 mm wide, within the limits of the six specimens available.

No elements of the milk dentition of *Celebochoerus* had so far been recovered. In the Marale collection, 16/7/1970, there is a DM_4 dext., un-

mistakable because of its being three-lobed, and decidedly narrower in front than behind. It measures 23.4 mm in length by a posterior width of 12.8 mm, and shows the simple potamochoeroid structure characteristic of *Celebochoerus* molars.

Much of the postcranial skeleton of *Celebochoerus* has already been recorded. Of the 1970 finds I mention the proximal part of a humerus dext. from Sompoh, lacking most of the lateral tuberosity. The greatest transverse diameter (over the head) is 77 mm. There are two distal portions of right radii, one from Tjalio, 26/7/1970, south of the road (with part of the ulna attached), and one from Tjalio II, 26/7/1970, which measure 27, and 32 mm anteroposteriorly at the distal articular surface; in a specimen recorded previously this is 29 mm. Further finds include the distal end of a radius from Tjalio, 29/7/1970, N.W. 50 m terrace, north of the road, measuring 33 mm transversely and 28 mm anteroposteriorly, and a first phalanx from Beru, 14/7/1970, 22 mm long, 19 mm wide proximally and 17 mm distally.

Anoa depressicornis (Smith)

Of the larger *Anoa* extant in Celebes, previously recorded fossil from Sompoh on the basis of a broken set of lower teeth (Hooijer, 1948), we now have an M^3 dext. found at Tjangkange, 1/8/1970. It is worn down to 13 mm from the crown base, and its metastyle is damaged (pl. 4 figs. 5-6). The antero-posterior diameter is 21 mm, the antero-transverse diameter 14.8 mm; it is indistinguishable from recent M^3 of *Anoa depressicornis* which vary up to 22.0 mm in length and 17.2 mm in greatest width. There is also an incomplete, rather small, calcaneum sin. from Tjalio 25/7/1970, that may belong here.

References

Beyer, O., 1949. Outline review of Philippine archaeology by islands and provinces. — Philippine Journ. Sci., 77: 205-374, 22 pls., 2 figs, 2 maps.

Hooijer, D. A., 1948. Pleistocene Vertebrates from Celebes. I. Celebochoerus heekereni nov. gen. nov. spec. II. Testudo margae nov. spec III. Anoa depressicornis (Smith) subsp., and Babyrousa babyrussa beruensis nov. subsp. — Proc. Kon. Ned. Akad. v. Wet. Amsterdam, 51: 1024-1032, 1 pl., 1 fig., 1169-1182, 1 pl., 1322-1330, 1 pl.

——, 1949. Pleistocene Vertebrates from Celebes. IV. Archidiskodon celebensis nov. spec. — Zool. Med., Leiden, 30: 205-226, pls. VIII-IX.

——, 1953. Pleistocene Vertebrates from Celebes. V. Lower molars of Archidiskodon celebensis Hooijer. VI. Stegodon spec. VII. Milk molars and premolars of Archidiskodon celebensis Hooijer. — Zool. Med., Leiden, 31: 311-318, pl. XIX, 32: 107-112, pl. V, 221-231, pl. VII.

——, 1954a. Pleistocene Vertebrates from Celebes. VIII. Dentition and skeleton of Celebochoerus heekereni Hooijer. — Zool. Verh., Leiden, 24: 1-46, 6 pls.

——, 1954b. Pleistocene vertebrates from Celebes. IX. Elasmobranchii. X. Testudinata. — Proc. Kon. Ned. Akad. v. Wet. Amsterdam, B 57: 475-485, 2 pls., 486-489, 1 pl.

HOOIJER, D. A., 1954c. Crocodilian remains from the Pleistocene of Celebes. — Copeia, 1954, 4: 263-266, 1 fig.
——, 1954d. Pleistocene Vertebrates from Celebes. XI. Molars and a tusked mandible of Archidiskodon celebensis Hooijer. — Zool. Med., Leiden, 33: 103-120, pls. XX-XXII.
——, 1955. Fossil Proboscidea from the Malay Archipelago and the Punjab. — Zool. Verh., Leiden, 28: 1-146, pls. I-XVII.
——, 1956. Archidiskodon planifrons (Falconer et Cautley) from the Tatrot zone of the Upper Siwaliks. — Leidse Geol. Med., 20: 110-119, 1 pl.
——, 1957. A Stegodon from Flores. — Treubia, 24: 119-129, pls. II-III.
——, 1958. An Early Pleistocene mammalian fauna from Bethlehem. — Bull. Brit. Mus. (Nat. Hist.), Geol., 3: 265-292, pls. 32-35.
——, 1964. Pleistocene Vertebrates from Celebes. XII. Notes on pygmy stegodonts. — Zool. Med., Leiden, 40: 37-44, 1 pl.
——, 1969. The Stegodon from Timor. — Proc. Kon. Ned. Akad. v. Wet. Amsterdam, B 72: 203-210, 3 pls.
——, 1970. Pleistocene South-east Asiatic pygmy stegodonts. — Nature, 225: 474-475, 3 figs.
——, 1971. A giant land tortoise, Geochelone atlas (Falconer & Cautley), from the Pleistocene of Timor. — Proc. Kon. Ned. Akad. v. Wet. Amsterdam, B. 74: 504-525, 2 pls.
——, 1972. Stegodon trigonocephalus florensis Hooijer and Stegodon timorensis Sartono from the Pleistocene of Flores and Timor. — Proc. Kon. Ned. Akad. v. Wet. Amsterdam, B. 75: 12-33, 3 pls.
KOENIGSWALD, G. H. R. VON, 1956. Fossil mammals from the Philippines. — Proc. Fourth Far-Eastern Prehistory Congress, Quezon City, 1: 339-362, 7 pls., 6 figs.
MAGLIO, V. J., 1970a. Four new species of Elephantidae from the Plio-Pleistocene of northwestern Kenya. — Breviora, Mus. Comp. Zool., 341: 1-43, 7 pls., 4 figs.
——, 1970b. Early Elephantidae of Africa and a Tentative Correlation of African Plio-Pleistocene deposits. — Nature, 225: 328-332, 2 figs.
NAUMANN, E., 1887. Fossile Elephantenreste von Mindanáo, Sumátra und Malakka. — Abh. Zool. Mus. Dresden, 1, 6: 1-11, 1 pl.
——, 1890. Stegodon mindanensis, eine neue Art von Uebergangs-Mastodonten. — Zeitschr. deut. geol. Ges., 42: 166-169.
OSBORN, H. F., 1942. Proboscidea. A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World. II. Stegodontoidea, Elephantoidea. New York, Amer. Mus. Press, 805-1675 + I-XXVII, pls. XIII-XXX, figs. 681-1225.
SARTONO, S., 1969. Stegodon timorensis: a pygmy species from Timor (Indonesia). — Proc. Kon. Ned. Akad. v. Wet. Amsterdam, B 72: 192-202, 1 pl., 6 figs.

EXPLANATION OF THE PLATES

Plate 1

Archidiskodon celebensis Hooijer, partial skull, Tjangkange, 27/7/1970; top figure, left lateral view; bottom figure, ventral view. Both figs. × 1/3. T. Asmar phot.

Plate 2

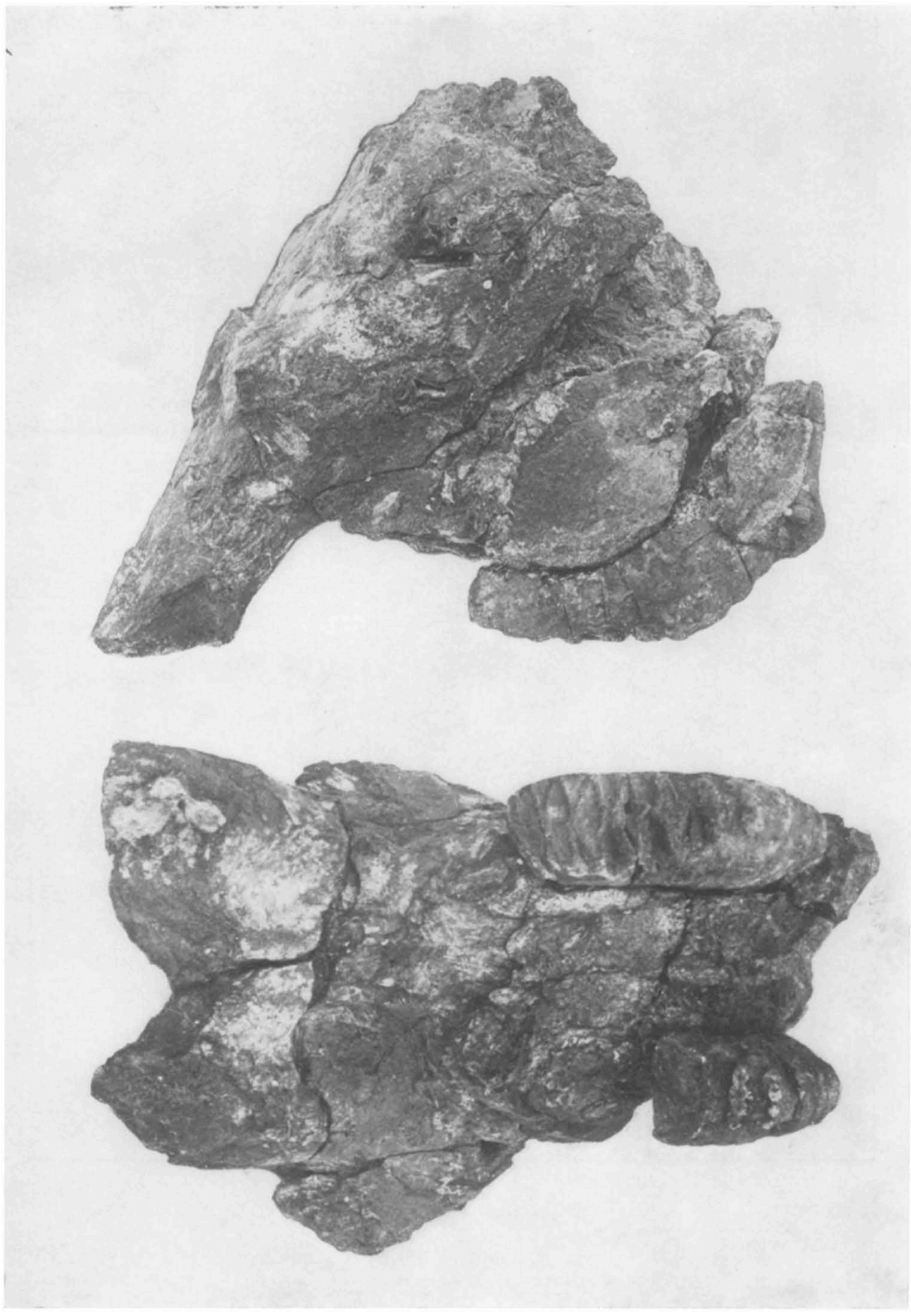
Figs. 1, 3 and 4, *Archidiskodon celebensis* Hooijer; fig. 1, M^3 sin. of skull from Tjangkange, 27/7/1970, crown view, × 2/5, T. Asmar phot.; figs. 3-4, right mandibular ramus with M_3, Sompoh, 23/6/1970; fig. 3, right lateral view, × 1/2; fig. 4, crown view, × 2/3; figs. 3-4 C. Hoorn phot. Fig. 2, *Celebochoerus heekereni* Hooijer, male skull, Tjalio I, 25/7/1970, dorsal view, × 1/2, C. Hoorn phot.

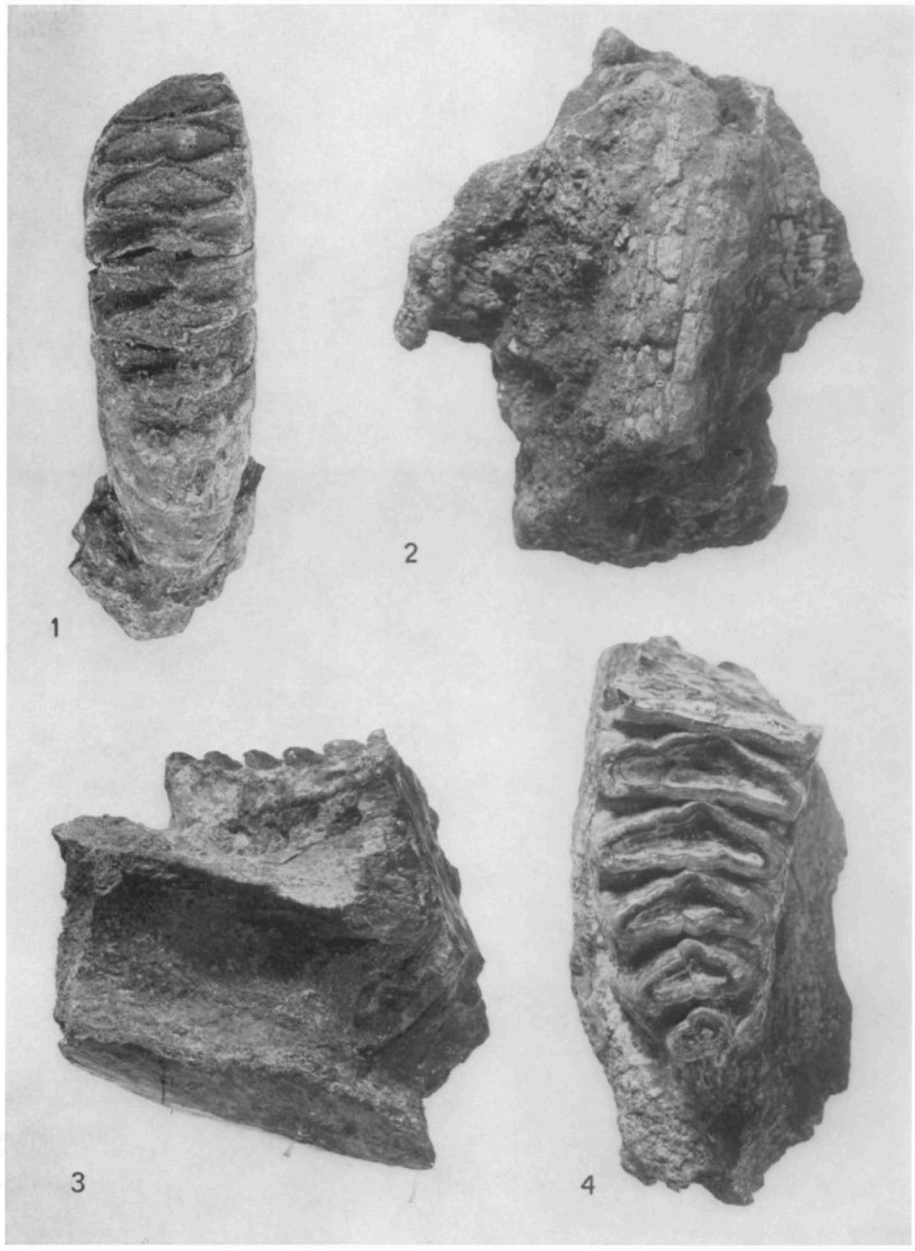
Plate 3

Figs. 1-3, *Stegodon sompoensis* Hooijer; fig. 1, M_3 sin., Tjalio, 25/7/1970, crown view, × 2/3; fig. 2, M_2 sin., Marale, 31/7/1970, crown view, × 3/4; fig. 3, palate with parts of M^{2-3}, Tjalio I, 25/7/1970, palatal view, × 1/3. Figs. 4-5, *Stegodon* cf. *trigonocephalus* Martin, posterior portion of upper molar, Marale, 20/7/1970; fig. 4, crown view, × 3/4; fig. 5, lateral view, × 5/6. All figs. C. Hoorn phot.

Plate 4

Figs. 1 and 7, *Celebochoerus heekereni* Hooijer; fig. 1, female palate, Marale, 19/7/1970, palatal view, × 4/5; fig. 7, male skull, Tjalio I, 25/7/1970, right lateral view, × 3/5. Figs. 2-4, *Stegodon* cf. *trigonocephalus* Martin; figs. 2-3, molar ridge portion, Beru I, 50 m terrace, 8/7/1970; fig. 2, anterior view, × 3/4; fig. 3, lateral view, × 4/5; fig. 4, molar ridge portion, Marale, 16/7/1970, anterior view, × 3/4. Figs. 5-6, *Anoa depressicornis* (Smith), M^3 dext., Tjangkange, 1/8/1970; fig. 5, external view; fig. 6, crown view. Both figs. × 4/5. All figs. C. Hoorn phot.

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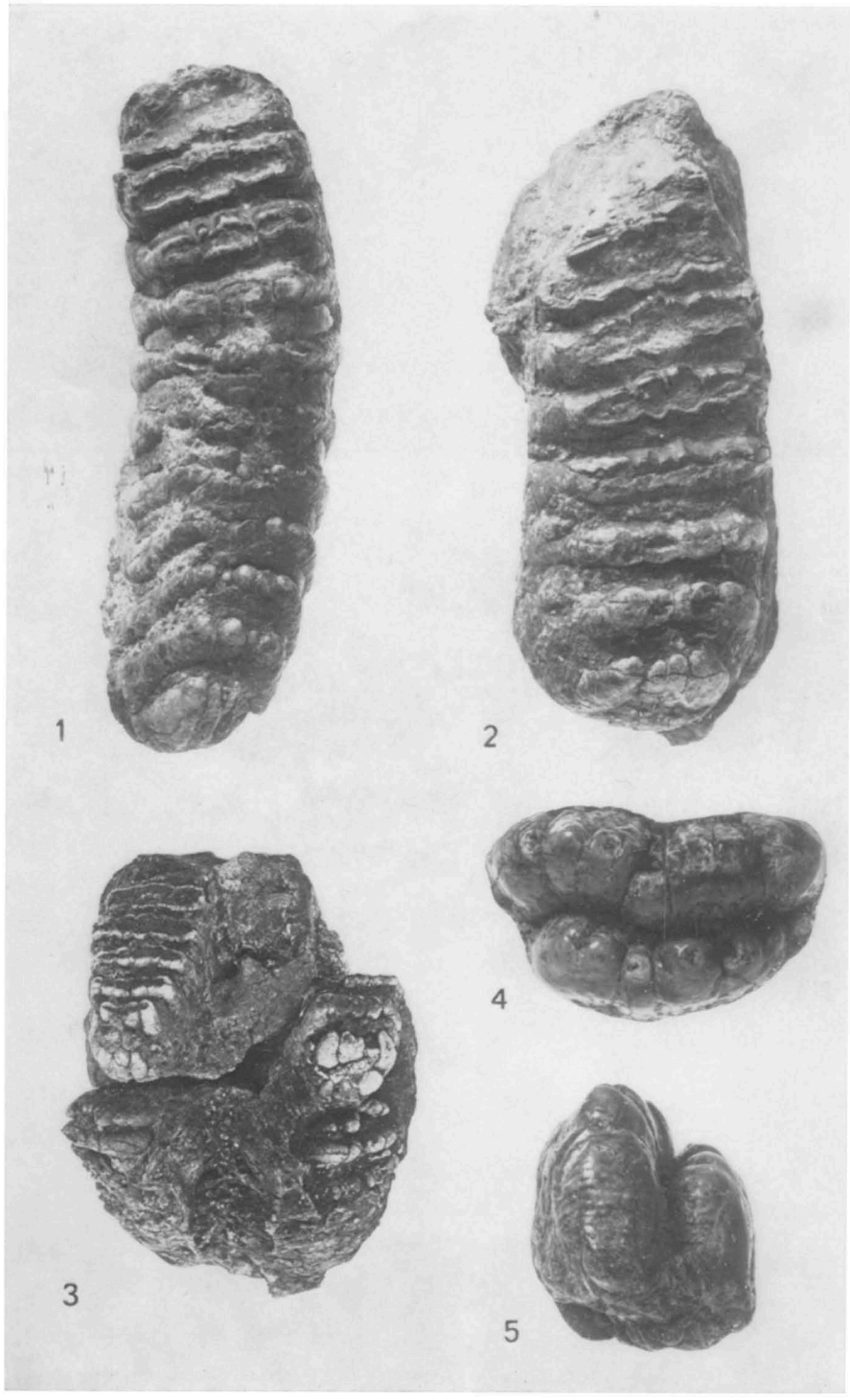
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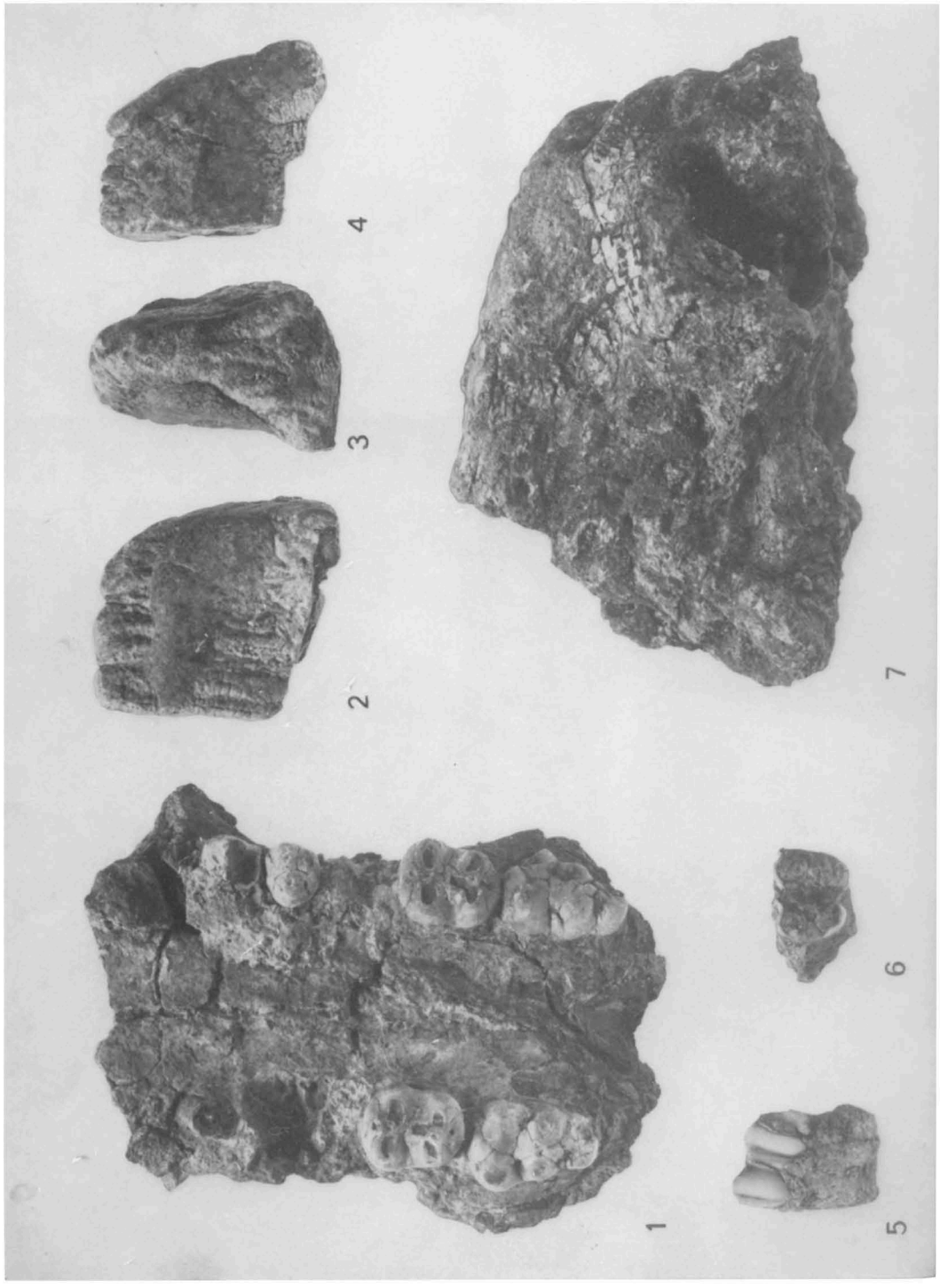
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