MINISTERIE VAN ONDERWIJS, KUNSTEN EN WETENSCHAPPEN

ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN

Vol. 40 no. 7 8 juli 1964

PLEISTOCENE VERTEBRATES FROM CELEBES. XII. NOTES ON PYGMY STEGODONTS

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There is a reason for adding to the series "Pleistocene vertebrates from Celebes", which was brought to a conclusion just a decade ago, and which has since been summarized, with bibliographic references, e.g., in Van Heekeren (1957) and Hooijer (1959, 1960). The discovery of a pygmy stegodont in the island of Flores, Lesser Sunda Islands (Hooijer, 1964) brought me to a reconsideration of the evidence for a pygmy *Stegodon* in Celebes, which was considered inconclusive at the time, and restudy of all the fragmentary specimens in the Celebes collection not included in the published reports. As a result, all doubt concerning its status is removed; the Celebes *Stegodon* is decidedly smaller than *Stegodon trigonocephalus* Martin from Java. The evidence will be presented in the pages that follow; it rounds off the account of the Pleistocene Celebes vertebrates.

The pygmy elephantine *Archidiskodon celebensis* Hooijer (1949), nearly all the dental elements of which (including premolars and the lower tusk) are now known, is not the only proboscidean in the Pleistocene fauna of Celebes. In 1953 descriptions and figures were given of two unmistakable *Stegodon* molars (Hooijer, 1953), a left lower and a right upper, with basal widths of 60-63 mm, wider than the last molars of *Archidiskodon celebensis* (42-52 mm in M^3, 41-44 mm in M_3: Hooijer, 1954: 109 and 113). I could not, then, make up my mind as to whether these did represent the last molars, and left them as *Stegodon* spec.

The stegodont molars differ from those of the pygmy archidiskodont in various characters, as follows:

1. The ridges are only two-thirds as high as wide in the unworn state, whereas in *Archidiskodon celebensis* the plates in M^3 and M_3 are higher than wide.

2. The valleys between the ridges are closed in at the bottom, and thus the enamel walls form a Y in longitudinal section, whereas in *Archidiskodon* the valleys are open down to the bottom, and are V-shaped in section. As a result of this, the worn enamel figures in a *Stegodon* molar approach each other more closely across the valleys in advanced wear than they do in an *Archidiskodon.*

3. The enamel figures of worn *Stegodon* ridges do not show the marked median expansions, less even median enamel loops occurring in an archidiskodont (these loops or expansions in an archidiskodont may block the valley in the middle, and a section through the valley at that point shows the stegodont Y instead of the archidiskodont V; this point has to be carefully checked).

4. The molar crowns terminate abruptly, and do not taper off as in an archidiskodont.

5. The enamel in a *Stegodon* molar is rather grooved, and produces more finely wrinkled figures in the worn state than it does in *Archidiskodon.*

The first-mentioned character loses its significance only in the most progressive stegodont known, viz., *Stegodon hypsilophus* Hooijer (1954a) from Java. In this species the molar ridges are from four-fifths to almost fully as high as wide, and therein resemble those of an archidiskodont. However, the Y-shaped valleys and the absence of median expansions to the ridges prove it to be a stegodont.

In *Stegodon* molars the crown edge of the ridges bears a number of conelets, which are usually very nearly equal in size and separated by shallow grooves that are soon worn off. The resulting enamel figure is much wrinkled, and may be expanded in the middle. Some interesting variations from this pattern may be observed, e.g., in the Java *Stegodon trigonocephalus* of which abundant material is available. In the anterior ridges of the molars there may be a median cleft, rather deep, apparently an ancestral character reminiscent of the mastodont cleft that separates the pretrite and posttrite ridge portions. On the other hand, especially in the posterior ridges, we may see a tripartite division of the crown edge, with the median portion either smaller or larger than those flanking it. This is the characteristic of the plate crown edge in elephantines; the median portion then is the highest. The clefts between these portions are very deep, and the structure remains visible until the plates are well worn down. The most primitive elephantines, the archidiskodonts, have a median portion of their molar plates composed

of two conules, whereas the lateral portions are made up each of one large conule (*Archidiskodon africanavus* Arambourg, 1952: 409, fig. 3; *Archidiskodon planifrons* (Falconer & Cautley) from the Tatrot: Hooijer, 1956, pl. 1, and from Bethlehem: Hooijer, 1958, pl. 35 fig. 1). In more advanced elephantines such as *Elephas trogontherii* Pohlig the median cleft does not show up, except occasionally, and the plates are divided into a broad lamellar median portion and two narrower but still transversely oval lateral portions. In *Elephas antiquus* Falconer the lateral portions of the plate figures become annular (this species, moreover, characteristically preserved the median expansions or "loxodont figures" of the plates that we find in primitive archidiskodonts and in the modern African elephant).

A specimen hitherto left undescribed and originating from Sompoh represents a right stegodont DM^4 or M^1 (pl. 1 fig. 1-2). It is incomplete in front and carries five ridges (the last may be called talon), 28 mm wide. They are much more worn down on the convex buccal side than on the lingual. The occlusal surface is convex from before backward, and convexo-concave from buccal to lingual. The enamel figures approach each other very closely except lingually. On the buccal side the bottom has been reached, and the figures have coalesced. On the lingual side the valleys are still wide open and cement-filled apically, but they are closed in at the basal portion. These are stegodont features. There is a large posterior root, supporting four ridges, and a smaller anterior root of which only the portion supporting the fifth ridge from behind (the foremost preserved ridge) remains. Since in stegodont molars the anterior root supports two, or three ridges at most, the full number of ridges of the specimen was either six or seven.

This number of ridges suggests DM^3, DM^4, or M^1. Determination of the present tooth as DM^3 is out of the question, for a DM^3 narrows distinctly from back to front over three ridges, whereas in the Sompoh molar these ridges are of uniform width. Hence, the Sompoh molar is a DM^4 or an M^1. In *Stegodon trigonocephalus* DM^4 has seven ridges, M^1 has either seven or eight, plus the talons (Hooijer, 1955: 28, 30). In *Stegodon orientalis* Owen from China DM^4 has six or seven ridges, and one worn M^1 has only six (Colbert & Hooijer, 1953: 73). Good series of the milk molars from Java and China, and of the first molars from Java, are available (table 1). The length of the Sompoh specimen may be given as ca. 50 mm if it had seven ridges. The width can be taken exactly, as well as the laminar frequency, and these show the tooth to be a fifty per cent scale reduction of DM^4 in both the Java and the China species. *Stegodon insignis* (Falconer & Cautley) from the Siwaliks is rather larger than the Java form, as the single specimen found in situ (Sahni & Khan, 1961) suggests.

TABLE I

Measurements of DM^4 and M^1 in *Stegodon* (mm)

	Sompoh	*S. trigonocephalus*		*S. orientalis*	*S. insignis*
		DM^4	M^1	DM^4	DM^4
Length	ca. 50	90-108	118-157	97-125	112
Width	28	48-57.5	59-ca. 72	53-66	66
Height	—	25-29	36-39	26-35	—
Height-width index	—	46-58	55-59	47-58	—
Laminar frequency	14	7-9	6-6 1/3	—	7
Ridge formula	(2-3)4x	x7x	x7x-x8x	x6x-x7	7 1/2

The height of the Sompoh DM^4 (or M^1) cannot be given, but the *Stegodon* molars of which the height can be taken show that the Celebes stegodont is just about as hypsodont as is the Java *Stegodon trigonocephalus*; an unworn ridge is two-thirds as high as wide (Hooijer, 1953: 108). This excludes at once the possibility of the Celebes pygmy stegodont and the Java pygmy stegodont *Stegodon hypsilophus* being identical; in the latter species, moreover, DM_4 is 39 mm wide, and DM^4 therefore a few mm wider still.

The Celebes *Stegodon* DM^4 (or M^1) is equal in size to DM^4 in *Archidiskodon celebensis* two incomplete specimens of which have been described (Hooijer, 1953a: 224-225, pl. VII fig. 7 and 11). The width is 25 mm in one, and 29.5 mm in the other, and the height-width index is ca. 78, higher even than that in DM^4 of *Archidiskodon planifrons*. The laminar frequency (14) is the same as that in the *Stegodon* DM^4 (or M^1). The *Archidiskodon* DM^4 differ from the *Stegodon* molar in the greater width of the valleys, and the presence of median expansions and even an enamel loop to the figures; in *Stegodon* the enamel is more wrinkled, especially in the least worn lingual portion of the crown.

The crown of the *Stegodon* DM^4 (or M^1) was evidently lower than that of the *Archidiskodon* DM^4; the height at the lingual end of the last ridge, which is only slightly worn, may not have been more than 16 or 17 mm in the former as opposed to 23 mm in the latter. Compared with the M^1 in *Archidiskodon celebensis* the Sompoh molar is smaller: the M^1 is 33 m wide, with a height-width index of 118 and a laminar frequency of 11 (Hooijer, 1954: 109). It differs from the stegodont tooth in the same points as does DM^4, and beautifully shows the bunomastodontid build in its anterior plate, complete with median cleft and a detached cylinder, the intermediate pillar, behind it (l.c., pl. XX fig. 4).

As related in full before (Hooijer, 1954) the archidiskodonts most likely sprang from brevirostrine bunomastodontids, and not from stegodonts as

was the consensus of opinion until recently. The characters of the Celebes pygmy archidiskodont, notably the (occasional) retention of mandibular tusks, are strongly in favour of this view first advanced by Dietrich (1951).

There are more *Stegodon* specimens in the Celebes collection that have not been described before, but these unfortunately add little or nothing to our knowledge. There is a molar fragment comprising the lingual or buccal half of one ridge and a half (pl. 1 fig. 5-6) that shows substantial tubercles at the entrances to the valleys, and the stegodont Y in section at the middle. The serial position of the specimen cannot be determined; its full width was probably about 50 mm. A smaller fragment (pl. 1 fig. 3-4) shows a row of three tubercles blocking the valley entrance; the height of the valley above the enamel base is not less than 14 mm.

Now that the Celebes stegodont has been proven to be a pygmy, we may once more consider the two molars described in 1953. The last molars in the Java *Stegodon trigonocephalus* are rather variable in size, as seen by the widths in table 2. The Celebes molars, the largest of their kind in the collection of that island, are at least ten per cent narrower than the smallest Java specimens and at least forty per cent less wide than the largest Java specimens.

TABLE 2

Greatest width of last molars of *Stegodon* (mm)

	Celebes	Java
M^3	63	76-113
M_3	60	68-98

The high variability in third molar size in the Java stegodont has not remained unnoticed, and the smallest specimens, viz., those with widths of less than 76 mm (M_3) have at times been regarded as evidence for a dwarfed form. The long series of lower last molars in the Dubois collection, however, shows that the very large specimens (width over 90 mm) are almost as rare as the small ones, suggesting unimodal distribution. The M_3 of *Stegodon trigonocephalus* averages 86 mm in greatest width, that is, one-half wider than that of the Celebes *Stegodon*. The sample available may well be biased in favour of the large specimens, and moreover it should be kept in mind that the species ranges from Early to Late Pleistocene, during which period dwarfism may have occurred; this is most likely toward the end of its existence in Java.

As I wrote in 1953, it seemed most probable that the Celebes *Stegodon* would be a pygmy species just as *Archidiskodon celebensis,* and among

the postcranial proboscidean material there was no evidence of any large forms either. The serial position of the two incomplete molars being uncertain, however, I refrained from naming them. The DM^4 (or M^1) above described is even smaller relative to its homologue in *Stegodon trigonocephalus* than are the 1953 molars when compared with the last molars in the Java species. Therefore, it is quite certain that the 1953 molars do represent the last molars; they could not very well be M2 or M1. The slightly worn lower molar (Hooijer, 1953, pl. 5 fig. 1-4) has the elephantine tripartite ridge structure all over, and thereby represents an advanced type although its height-width index is only 67. In the holotype upper molar of *Archidiskodon celebensis* the plates vary in height-width index from 87 in plate I to over 110 in plate V. The archidiskodont has the same crown edge build as has the Celebes stegodont, which of course makes the identification of isolated, worn, and incomplete ridges a very difficult matter. The height-width index is the only feature we can rely on.

Von Koenigswald (1956: 354) stated that the isolated plate D of the first described specimens of *Archidiskodon celebensis* (see Hooijer, 1949, pl. 9 fig. 5) is a *Stegodon,* but this does not seem to be correct at all. Its height-width index is 89, too high for the Celebes stegodont but within the range for this index in *Archidiskodon celebensis* (see above). There is (although this is denied by Von Koenigswald) a tripartite division, the marginal conules being separated from the five in the centre by clefts that are deeper than the others. This, as we have seen, is the structure of both the *Stegodon* and the *Archidiskodon* from Celebes; the number of conelets between the two marginal ones varies from two to five.

The similarity in ridge-plate edge structure between the stegodont and the archidiskodont from Celebes, two forms that have become populations of pygmies, is another example of parallel evolutionary development of which the proboscideans provide so many striking cases.

Certain fossils found in two Philippine Islands, Mindanao and Luzon, have been described and named as pygmy stegodonts also. *Stegodon mindanensis* Naumann (see Hooijer, 1949: 222) is based on a right lower molar fragment, 37 mm wide and with a height-width index of 88 (Naumann, 1887: 6, pl. 1 fig. 1-2). This suggests either a progressive stegodont or an archidiskodont, a point to be decided upon examination of the actual specimen. A ridge also from Mindanao is 51 mm wide (Naumann, 1887: 8, pl. 1 fig. 3-4), and has a height-width index of only 47, which is stegodontine. The two specimens are from different sites, and may represent different genera. *Stegodon luzonensis* Von Koenigswald (1956: 346, pl. 3-4) is based on photographs and sketches of an incomplete molar in the right half of

a mandible. The molar is stated to be only 5 cm wide, and it has at least six ridges. The height of the ridges cannot be determined, but other molar fragments found in Luzon and referred to as *Stegodon* cf. *trigonocephalus* are from 61 to 64 mm wide, with an index of 72 (Von Koenigswald, 1956: 343). The serial position of these is, however, uncertain.

In conclusion, then, the pygmy *Stegodon* may be named and diagnosed as follows:

Stegodon sompoensis nov. spec.

Diagnosis. — Size small; molars from one-half to two-thirds as large in linear dimensions as their homologues in *Stegodon trigonocephalus* Martin from Java. Ridges two-thirds as high as wide, with tripartite edge structure.

Holotype. — The DM^4 or M^1 dext. described and figured in the present paper.

Paratypes. — An M_3 and an M^3 described and figured in Hooijer (1953).

Locality. — Sompoh, near Tjabengè, Sopeng district, about 100 km N.E. of Macassar, southern Celebes.

Age. — Pleistocene.

The pygmy stegodont from Flores, known thus far only from two milk molars, appears to be similar in size to that of Celebes. It seems rather unlikely that they would belong to the same species, but we have as yet no means of differentiating between the two. Both were probably derived from large-sized continental stegodonts, and underwent evolutionary change to the pygmy condition on each island independently. The same may apply to the Mindanao and the Luzon forms, although the evidence for these is not conclusive. Insular dwarfism of proboscideans is known from the Mediterranean as well as from Santa Rosa off the California coast. It has now been shown to be rather widespread in the eastern Malay Archipelago also.

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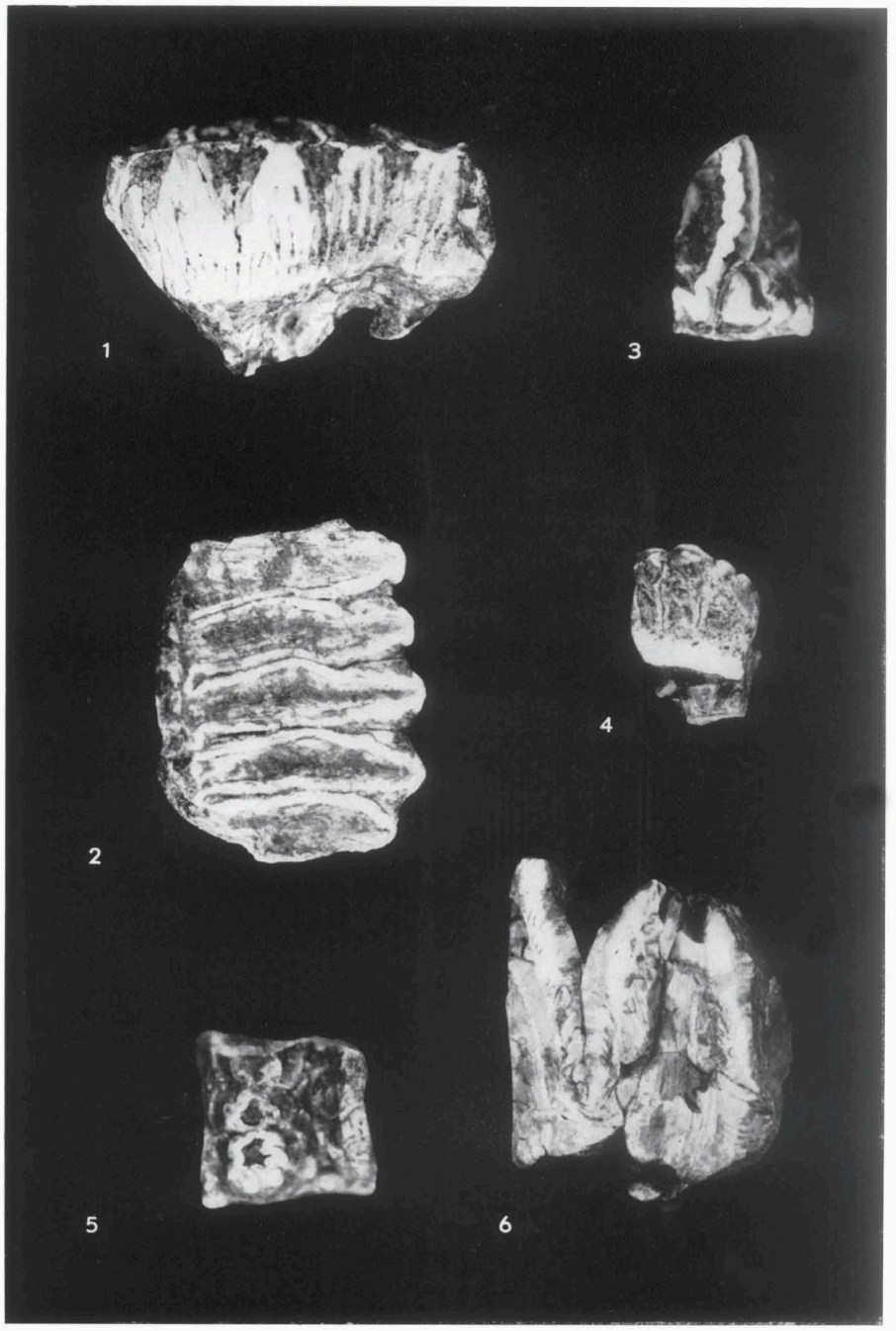

Stegodon sompoensis nov.spec., Sompoh near Tjabengè, Sopeng district, southern Celebes. Fig. 1-2, DM^4 dext. (holotype); fig. 1, lingual view, × 1.4; fig. 2, crown view, × 1.4. Fig. 3-4, molar fragment; fig. 3, crown view, × 1.4; fig. 4, lateral view, × 1.3. Fig. 5-6, molar fragment; fig. 5, crown view, × 1; fig. 6, median section, × 1.5.