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A PYGMY STEGODON FROM THE MIDDLE PLEISTOCENE OF EASTERN JAVA

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with pl. XIX

The material to be described below forms part of a collection of fossil vertebrates made by Dr. J. Cosijn North of Djetis and Perning in Eastern Java (Cosijn, 1931, 1932). The Cosijn collection has not yet been fully described, some preliminary identifications were made by the late Prof. Dr. J. H. F. Umbgrove (in Cosijn, 1931, pp. 118-119). The collection is preserved in the Geological Museum at Leiden; I have previously described the remains of rhinoceros (Hooijer, 1946, pp. 3, 55, 73, and 76) and those of hippopotamus (Hooijer, 1950, pp. 66, 69-72, and 87-108). It is a pleasure again to acknowledge my indebtedness to Prof. Dr. B. G. Escher and to Prof. Dr. I. M. van der Vlerk for permission to study this valuable material.

Umbgrove's first conclusion that the vertebrate fauna found by Cosijn is analogous to that of the Trinil bone beds is not shared by Von Koenigswald, who claims the mammalian fauna first discovered by Cosijn, the Djetis fauna, to be older than the Trinil fauna. The latter is Middle Pleistocene, and the Djetis fauna is placed in the Early Pleistocene (Von Koenigswald, 1935, p. 193).

I have presented arguments elsewhere (Hooijer, 1952) for regarding the Djetis fauna as similar in age to the Trinil fauna. Both are early post-Villafranchian faunas, and both are characterized by the presence of a series of forms (notably *Macaca, Hylobates, Pongo, Ursus, Crocuta,* and *Tapirus*) typifying the Southern Chinese *Stegodon-Ailuropoda* fauna (fully described in Colbert and Hooijer, 1953). The presence of these forms in the Javanese faunas shows that by the time of the formation of the Djetis and the Trinil beds these invading elements from the mainland of Asia had already reached Java (cf. Von Koenigswald, 1940, p. 72; 1950, p. 92). In our opinion the *Stegodon-Ailuropoda* fauna is Middle Pleistocene in age (Colbert and Hooijer, 1953, p. 20), an opinion also voiced by Von Koenigswald (1952, p. 306). How, then, could it be maintained that the Djetis fauna is older than the *Stegodon-Ailuropoda* fauna? The former fauna is of the same age as, or younger than, certainly not older than the latter.

Among the proboscidean material in the Cosijn collection I noticed a number of molar fragments of a very peculiar type of stegodont:

Stegodon hypsilophus nov. spec.

Diagnosis: A *Stegodon* of very small size; width of M3 64 mm. Ridges highly elevated; four-fifths to almost fully as high as wide. At least ten ridges in the upper last molar. Three to eight conelets on each ridge, ridges convex transversely at the apex. No trace of median cleft.

Holotype: A right and left M3 of the same individual described in the present paper (Geol. Mus. Leiden nos. 27837 and 27865).

Locality: North of Djetis and Perning, Eastern Java.

Age: Middle Pleistocene.

The material is as follows: Geol. Mus. Leiden no. 27837, anterior portion of M3 sin., and posterior portion of M3 dext.; Geol. Mus. Leiden no. 27865, anterior portion of M3 dext., and posterior portion of M3 sin. Each of these specimens was broken into several smaller fragments. They are so very similar in all respects that I have no doubt as to their belonging to one and the same individual; the right and the left molars are almost perfect mirror images of each other. The roots are broken off.

The serial position of these molars is clear from the shape of the posterior end, which is complete in one molar (the left) and shows four ridges and a talon gradually diminishing in width and height from front to back; such a tapering posterior end is found in the last molars only. That the molars belong to the upper jaw is evident from the divergence of the ridges from base to tip, as well as from the slight concavity toward the roots seen in the gingival borders of the crown. When viewed from the crown the molars appear to be slightly curved to the effect that one of the side surfaces is approximately straight, and the other slightly convex. The flattened surfaces are the internal or lingual surfaces.

In the following descriptions of the molars I shall proceed from the posterior end on forward, counting the ridges in Roman figures from back to front. Detailed measurements are contained in table 1. As the left molar is complete posteriorly I shall begin with the M^3 sin.

The posterior talon of the left M^3 (pl. XIX figs. 3, 9) bears three conelets of which the lingual is the highest and the buccal the lowest. The central conelet is the narrowest of the three, and is nearer to the buccal than to the lingual side. The grooves separating these conelets extend from the apex of the talon on the posterior surface rootward to just over one-half of its height. At the base of the talon the enamel is seen to bulge out, and this enamel swelling is well marked off from the talon by a horizontal groove. The gingival line of the enamel falls off rootward toward the lingual side. There is a tiny enamel point at the base of the talon buccally.

Ridge I from behind is larger, but of the same structure as the talon, having three conelets diminishing in height from lingual to buccal. The buccal conelet is relatively larger than that in the talon, however. At the base buccally there is a low enamel cone, while lingually the enamel presents several small basal excrescences. At the base this ridge is twice as wide as it is apically across the conelets. Of the converging lingual and buccal edges the former is more steep than the latter.

Ridge II from behind in the left M^3 has, again, only three conelets of which the central is the highest and placed somewhat nearer to the lingual than to the buccal side, due to a transverse enlargement of the buccal conelet. There is some damage to this ridge at the base buccally. This ridge is somewhat inclined forward at the apex.

In ridge II, as well as in ridges III and IV, we find the lingual edges to be more steep than the buccal; the conelets have a combined width one-half as great as the basal width. The ridges remain lower than wide, though not very markedly so, and, when seen in side view (pl. XIX fig. 4), appear to have a tendency to diverge crownward; the anterior ridges are more inclined forward than the posterior, which are the most erect.

In ridge III from behind the buccal conelet is subdivided into two small conelets, the outer of which has enamel points behind and buccally. The central conelet is now definitely to the lingual side of the median antero-posterior line of the crown.

Ridge IV, the foremost preserved ridge in this portion of M^3 sin., has four subequal conelets of which the original central conelet (second from the lingual side) is the highest. There is in addition a tiny fifth conelet, placed at the buccal end of the series and below the level of the others. Seen from in front (pl. XIX fig. 8) both the lingual and the buccal edges are slightly convex from above downward. The specimen is broken off just along the base of the transverse valley separating it from the (missing) ridge anterior to it; the base is not straight but forms an upward point in the middle and is curved upward at either end. The anterior surface of ridge IV thus exposed is convex from side to side, most markedly so in its basal part.

There is not very much cement on this posterior portion of the molar; the valleys between ridges I and II, II and III, and III and IV show in this order an increasing amount of cement which, however, still does not completely fill up the anterior valley; cement remains indicate that the cement extended to, but not upon, the lingual and buccal edges of the ridge, and left the conelets exposed.

The anterior portion of the same left M^3 unfortunately does not fit to the posterior portion. It consists of four ridges plus the anterior talon. The posterior surface of the hindmost preserved ridge shows the base of the valley along which it is broken off; the valley base is elevated in the middle and at both ends just as that in front of ridge IV, but the transverse concavity of this surface is less marked than the convexity of the anterior surface of ridge IV. The hindmost ridge on the anterior portion is only very slightly higher and wider than ridge IV, indicating that a few ridges are missing in between. As we shall see from the description of the M^3 dext. at least two ridges are missing. If we put x for the number of ridges missing between the posterior and the anterior portions, the hindmost ridge of the anterior portion might be indicated as ridge (x + V).

Ridge (x + V), then, possesses seven conelets, clearly derived from the five conelets seen in ridge IV by a subdivision of the original central conelet (second from the lingual side) into two, and the addition of a conelet at the lingual end of the series, which, in fact, is already faintly indicated in ridge IV. Of these seven conelets the second from the lingual side and the second from the buccal side are the largest. The three conelets in between form a transversely arched coronal edge (the middle conelet being the most prominent), and as the extreme lingual and buccal conelets are the least elevated the whole of the series of conelets forms a rather even curve from side to side. In ridge (x + V) as well as in ridge (x + VI) the lingual edge is steeper than the buccal, and the apical width taken over the two largest conelets is a little more than one-half the basal width. Cement remains on the posterior surface of ridge (x + V) show that the valley was completely filled.

Ridge (x + VI) is very similar to that behind it; the number of conelets is the same. The second conelet from the lingual side has somewhat diminished in size, becoming more equal to the others in size, while the second conelet from the buccal side has become more prominent, and so has the extreme buccal conelet. The valleys between the ridges in the anterior portion of the molar are filled up with cement; part of the cement is lost along the borders of the fragments into which this part of the molar was broken before I received it.

Ridge (x + VII), in contradistinction to the ridges behind it, is not higher but lower than the adjoining ridge behind, and the buccal edge is as steep as that on the lingual side. The conelets are eight in number, apparently due to twinning of the second conelet from the buccal side. The central triplets are relatively larger than those in ridge (x + VI), and consequently the conelet width is greater than that in any of the previously described ridges. This ridge is leaning forward more markedly than the others, a continuation of the tendency seen when passing along the molar from behind forward (pl. XIX fig. 2).

Ridge (x + VIII) is the anterior ridge of the molar. It is lower, and also narrower than the ridge behind it; the conelets are more crowded, too, and are six in number. The lingual edge is less steep than the buccal.

The anterior talon of M^3 sin. is very prominent buccally but is practically absent lingually. The main cone of the talon projects forward about as much as a true ridge and occupies the buccal third of the crown. Lingually there follow only two or three minor conelets, and the talon flattens out against the anterior full ridge in the lingual half (pl. XIX fig. 7).

The only signs of wear on this molar are on the anterior ridge (x + VIII) and on the anterior talon, but wear has been only slight; it has not yet exposed the dentine cores of the conelets. The anterior surface of the crown is oblique due to the asymmetrical development of the anterior talon, and is depressed in the middle as a result of pressure against the molar in front of it. The gingival border of the enamel is concave toward the root from side to side.

The thickness of the enamel is displayed only in the buccal base of plate II, and appears to be about 4 mm.

Ridges (x + V) to (x + VII) inclusive occupy an anteroposterior length of 49 mm, which gives a laminar frequency of 6. More behind the ridges become progressively narrower in anteroposterior direction so that ridges I to IV inclusive measure only 55 mm at the base anteroposteriorly, which gives a laminar frequency of $7\frac{1}{4}$.

Of the right M^3 in the Cosijn collection the posterior talon and ridge I are missing, while ridge II is only partially preserved; it is broken off transversely in the middle, showing the enamel in cross section as well as the depths of the clefts between the conelets. There are three conelets, as in the corresponding ridge of the left M^3, with the buccal conelet on a lower level than the others. The enamel has a thickness of 5 mm in cross section. The narrow clefts between the conelets are 12 mm deep, that is, over one-fourth of the height of the ridge. The enamel appears to consist of two layers which differ somewhat in structure.

TABLE 1

Measurements of left and right M^3 of *Stegodon hypsilophus* nov. spec.

No. of ridge from behind	(x + VIII)		(x + VII)		(x + VI)		(x + V)	
	l.	r.	l.	r.	l.	r.	l.	r.
Basal width	59	58	64	62	63	61	62	—
Apical width	32	31	38	38	33	35	33	—
Height	49	50	54	55	57	56	54	52
Height-width index	83	86	84	89	90	92	87	—

No. of ridge from behind	IV		III		II		I		posterior talon	
	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.
Basal width	59	54	53	51	45	44	41	—	32	—
Apical width	31	—	28	29	22	24	20	—	17	—
Height	52	51	49	48	44	43	39	—	34	—
Height-width index	88	94	92	94	98	98	95	—	106	—

Ridge III from behind is entire and, like ridge II, is very slightly smaller than the corresponding ridge in the left molar. As in that molar, there are four conelets, a result of twinning of the buccal conelet, and the second conelet from the lingual side is the highest. The lingual edge is steeper than that on the buccal side.

Of ridge IV only the posterior surface is preserved buccally. From this ridge on forward the right molar is broken along a vertical plane that passes through the middle of the plates. Of plates IV, V, and VI only the lingual halves are preserved in the collection, and the median longitudinal section has been polished in order to show the shape of the ridges and the valleys. Of these three ridges only the posterior is preserved in the left M^3; the right M^3 consequently has two ridges more than the left.

As seen in the section of ridges IV to VI (pl. XIX fig. 6) the ridges are rather uniformly high, and are leaning forward apically, mostly so the foremost ridge. The enamel shows two layers of which the inner (on the dentine core) is thinner and also darker in colour than the outer. It is also seen that the enamel coats of the opposed surfaces of neighbouring ridges meet for some distance above the base of the valley in the dentine. For approximately one-half of their height the valleys are reduced to mere lines between the ridges, and the valleys begin to open up and become filled with cement only in their coronal halves. The thickness of the enamel is about 5 mm, somewhat thinner toward the base, and thicker (up to 6 mm) at the posterior slopes of the ridges.

The number of conelets cannot be given for ridges IV to VI, but it can be seen that the extra lingual conelet, faintly shown in ridge IV of the right molar as well as in that of M^3 sin. is slightly stronger in ridges V and VI. The subdivision of the original central conelet (the second from the lingual side) has just taken place in ridge VI; in the left molar this subdivision of the central conelet must have occurred somewhere between ridge IV and ridge (x + V), as we have seen. The valleys of the right molar are completely filled with cement only from ridge IV on forward.

The posterior portion of M^3 dext. is broken off through the cement in front of the preserved lingual half of ridge VI. The anterior portion of the right molar consists of four ridges, and the talon, but the hindmost preserved ridge is not complete: only the anterior half of the lingual part is preserved. If the posterior half of this ridge had been present it might have fitted to the lingual half of ridge VI. As the fragments are, there is no point of contact, however. We can only conclude that the minimum number of missing ridges in the left M^3 is two, and we may designate the hindmost preserved ridge on the anterior portion of the right molar as ridge (x + V), in accordance with the system adopted for the left M^3.

Ridge (x + VI), fully preserved in the right molar, has seven conelets, as in the corresponding ridge in the left molar, and the largest conules are, again, the second from the lingual and the second from the buccal side. In ridge (x + VII) there are eight conelets, and the conelet width is greater than that in the ridge behind it. This penultimate ridge is distinctly curved forward at the apex. The anterior ridge (x + VIII) is incomplete at the base lingually and at the crown edge, along the median longitudinal fracture of the tooth, and has the conelets more crowded than the other ridges, from which it also differs in the lingual edge being less steep than the buccal. In all these points there is a very close resemblance between the right molar and the left already described before (pl. XIX figs. 1 and 5).

On the anterior ridge of the right molar and on its anterior talon wear is somewhat more advanced than on the left M^3, but dentine is nowhere exposed. The anterior talon, again, keeps well to the buccal side of the crown, forming a heavy cone at the antero-buccal angle. The conelets placed lingually of the main talon cone are slightly more developed than those in the left molar. The antero-lingual angle of the crown is damaged, exposing the dentine of ridge (x + VIII) and of the talon. The enamel coat is 4-5 mm thick, and shows the same two-layered structure as that on ridges IV to VI.

The plane of wear on the anterior end of the right M^3, as well as that on the left, is oblique: it falls off rootward toward the buccal side. This is the elephantine mode of wear. It is interesting to observe that the right molar is in a slightly more advanced stage of wear than the left, for this is what we usually find among the elephants (cf. Rühl, 1939, p. 64).

Table 1 shows that the measurements of the right M^3 agree well with those of the left M^3; the height-width indices of the right molar exceed those of the corresponding ridges in the left, indicating that the right molar is even more hypsodont than that of the left side.

Although the exact number of ridges of the M^3 of *Stegodon hypsilophus* nov. spec. cannot be determined, we have seen that it is at least ten, plus the talons, which at once excludes from comparison those species of *Stegodon* in which the number of ridges to M^3 is less than ten, such as *Stegodon bombifrons* (Falconer et Cautley), *Stegodon elephantoides* (Clift), *Stegodon licenti* Teilhard de Chardin et Trassaert, *Stegodon yüshensis* Young, and *Stegodon zdanskyi* Hopwood. Our *Stegodon hypsilophus* evidently belongs to the more progressive species of the genus, with *Stegodon aurorae* (Matsumoto), *Stegodon insignis* (Falconer et Cautley), *Stegodon orientalis* Owen, *Stegodon pinjorensis* Osborn, and *Stegodon trigonocephalus* Martin. The Javanese species, *Stegodon trigonocephalus* Martin (syn. *Stegodon airawana* Martin), is the most progressive species of its genus; in the elevation of its ridges it stands at the summit of the known Stegodontidae (Osborn, 1942, pp. 812, 855, 881 fig. 764 C). Even this species, however, is decidedly less progressive than the type of *Stegodon hypsilophus* nov. spec.

Table 2 gives the measurements of six specimens of M^3 of *Stegodon trigonocephalus* Martin, as follows: 1, Janensch, 1911, table 5, b; 2, Van der Maarel, 1932, table T, G; 3, Dubois collection no. 2490, ? Trinil; 4, Dubois collection no. 3408, Kebon Doeren; 5, Dubois collection no. 3412, Kedoeng Broeboes, and 6, Dubois collection no. 3474, ? Pati Ajam.

It is clear from the inspection of this table that the greatest width of M^3 of *Stegodon trigonocephalus* Martin is much greater relative to that of M^3 of *Stegodon hypsilophus* nov. spec. than is the height. The width of M^3 of *Stegodon trigonocephalus* Martin varies from 83 to 106 mm, while that of M^3 of *Stegodon hypsilophus* nov. spec. is only 64 mm (table 1). The molar ridges of the larger species decrease in relative height when passing along the molars from behind forward; the height-width index of the first ridge from behind in Janensch's specimen (89), and that of the posterior talon of Dubois collection no. 2490 (100) are not much less than the corresponding indices of the M^3 of *Stegodon hypsilophus* nov. spec. (95, and 106 respectively). From ridge 2 on forward, however, the ridges of

Stegodon hypsilophus nov. spec. are decidedly more hypsodont than those of the larger Javanese species; the indices vary in *Stegodon hypsilophus* nov. spec. from 83 to 98, against from 56 to 73 only in *Stegodon trigonocephalus* Martin.

TABLE 2

Measurements of M^3 of *Stegodon trigonocephalus* Martin

No. of ridge from behind	9	8	7	6	5	4	3	2	1	posterior talon
1. Basal width	86	86	85	85	83	77	69	60	44	32
Height	54	—	56	55	50	47	45	44	39	31
Height-width index	63	—	66	65	60	61	65	73	89	97
2. Basal width	—	86	85	83	77	71	68	63	55	—
Height	—	—	—	—	—	46	46	44	36	ca. 21
Height-width index	—	—	—	—	—	65	68	70	65	—
3. Basal width	—	—	97	95	94	90	84	78	67	43
Height	—	—	56	58	57	54	52	49	46	43
Height-width index	—	—	58	61	61	60	62	63	69	100
4. Basal width	—	—	—	—	—	86	76	69	60	50
Height	—	—	—	—	—	56	52	49	47	38
Height-width index	—	—	—	—	—	65	68	71	78	76
5. Basal width	—	—	—	—	—	83	78	72	65	47
Height	—	—	—	—	—	57	55	52	48	42
Height-width index	—	—	—	—	—	69	71	72	86	89
6. Basal width	—	—	—	—	106	98	85	78	56	39
Height	—	—	—	—	59	62	59	54	47	37
Height-width index	—	—	—	—	56	63	69	69	84	95

There appears to be no described species of *Stegodon* in which the molar ridges are as high relative to their basal width as in *Stegodon hypsilophus* nov. spec. As far as our present knowledge goes the molars of *Stegodon* show an elevation from brachyodont to subhypsodont, culminating in *Stegodon trigonocephalus* (Osborn, 1942, p. 853) with which species I have just compared *Stegodon hypsilophus* above.

Further, none of the known species of *Stegodon* are as small as that described in the present paper; as a matter of fact most of the progressive species in this genus are even larger than *Stegodon trigonocephalus*. An exception is *Stegodon aurorae* (Matsumoto), the type upper molar of which is only 75 mm wide. The height-width indices of the five unworn ridges, however, vary only from 50 (tenth ridge) to 70 (seventh ridge) (Matsumoto, 1918, p. 53). The median longitudinal section of the molar of *Stegodon aurorae* (Matsumoto, 1929, pl. VIII; see also Osborn, 1942, p. 893 fig. 781) shows that in this species, as in *Stegodon hypsilophus*, the enamel surfaces of the adjoining ridges remain in contact for some distance above the bottom of the valley, forming a Y in section, as they do in *Stegodon trigo-*

nocephalus too (Osborn, 1942, p. 881 fig. 764 C); this is a typical stegodontine character. Matsumoto even went so far as to create a new genus, *Parastegodon,* for the inclusion of his *Stegodon aurorae,* but this is not adopted by Osborn (1942, pp. 818 and 835), who writes that from a comparison with *Stegodon trigonocephalus* the species *aurorae* appears to belong in the true *Stegodon* group, an opinion with which I agree.

Molar crowns that are about as high as wide are found among primitive elephantines, *Archidiskodon planifrons* (Falconer et Cautley), that appear in Early Pleistocene deposits in Asia, Europe, and Africa beside the bunomastodontids from which they probably sprang (cf. Dietrich, 1951, p. 344). In these forms, however, the enamel layers of adjoining ridges part immediately at the bottom of the valley, the valley thus forming a V instead of a Y in section (Falconer and Cautley, 1845, pl. 2 figs. 5a, 5b; Matsumoto, 1918, p. 55 fig. 2; Osborn, 1934, p. 11; Hopwood, 1935a, p. 49) Moreover, these primitive archidiskodonts are characterized by the median expansions of the molar plates, sometimes even forming full enamel loops, evidently corresponding to the intermediate conules of the mastodonts, structures that we do not observe in progressive stegodonts such as that now under discussion. It has to be kept in mind, too, that the enamel of our new species consists of two layers that differ somewhat in structure; this is stegodontine (see Janensch, 1911, p. 162; Soergel, 1913, p. 6; Van der Maarel, 1932, p. 165, pl. XIII figs. 3-5).

It seems to me, from the fundamental resemblance of *Stegodon hypsilophus* to the stegodonts above discussed, especially *Stegodon trigonocephalus,* that my new species is referable to the same genus as that species.

Thus, *Stegodon hypsilophus* nov. spec. appears to be the most progressive species of its genus in the great relative height of the molar ridges. In this respect it represents the culmination of evolution in the stegodonts. The structure of the ridges, with two large conelets at either end and a number of smaller conelets in between that form a transversely convex edge, is essentially elephantine. Also noticeable is the total absence of a median cleft, a mastodontine feature that shows up in the anterior ridges of various species of *Stegodon.* The number of conelets on each ridge varies from three to eight; this character appears to be of little value systematically, although there is no doubt that the more primitive forms have fewer conelets than the more advanced (Hopwood, 1935b, p. 82).

Stegodon hypsilophus nov. spec. is also the smallest named species of its genus. The greatest width of its M^3 (64 mm) is less than that in any other species of *Stegodon.* I have recently described some fragmentary molars from the Pleistocene of Celebes that eventually might turn out to represent another pygmy species of *Stegodon* (Hooijer, 1953). Of this Celebes *Stegodon,* which remarkably enough is associated with a pygmy *Archidiskodon,* a 50 per cent scale reduction of *Archidiskodon planifrons* (Falconer et Cautley), an upper molar is only 63 mm wide. If this molar (Hooijer, 1953, pl. V fig. 5) is the last upper molar, which from the incomplete specimen it is impossible to make out, the Celebes form would be of the same size as *Stegodon hypsilophus* nov. spec. However, as the preserved lower molar in the Celebes collection shows, it would then be a "normal" pygmy *Stegodon,* for the height of an unworn ridge (40 mm) is decidedly less than the basal width (60 mm), giving a height-width index of 67, a normal figure for a *Stegodon.*

In conclusion, *Stegodon hypsilophus* nov. spec. demonstrates that in the progressive heightening of the molar ridges, an evolutionary change seen in all branches of the Proboscidea, the stegodonts have proceeded further than we knew. The superficial resemblance between the molar of *Stegodon hypsilophus* nov. spec. and one of a primitive elephantine, although the two differ in principle, is a remarkable case of parallel evolution.

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PLATE XIX

Stegodon hypsilophus nov. spec., North of Djetis and Perning, Eastern Java; figs. 1-2, anterior portion of M^3 sin.; fig. 1, crown view; fig. 2, lingual view; figs. 3-4, posterior portion of M^3 sin.; fig. 3, crown view; fig. 4, lingual view; fig. 5, anterior portion of M^3 dext., crown view; fig. 6, posterior portion of M^3 dext., buccal view, showing median sections of ridges IV to VI from behind; fig. 7, anterior portion of M^3 sin., anterior view; figs. 8-9, posterior portion of M^3 sin.; fig. 8, anterior view, showing ridge IV; fig. 9, posterior view.

All figures $^3/_4$ natural size.


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