

1957 Simpson, George Gaylord.....
Dupl. The Mastodonts
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H. R. ANTHONY

THE MASTODONTS OF BRAZIL

GEORGE GAYLORD SIMPSON AND
CARLOS DE PAULA COUTO

BULLETIN
OF THE
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Corrections for

THE MASTODONTS OF BRAZIL

George Gaylord Simpson and
Carlos de Paula Couto

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Page 141, column 2, text, line 4 from bottom: For table
8, read table 6.

Page 150, column 1, line 19 from bottom, should read: mm.,
or over 2 per cent, longer than any in

Page 153, column 2, line 26 from bottom: For fine,
read five.

Page 166, column 1, line 20 from top, should read: stick
to it, even if it is ~~arbitrary~~ arbitrary.

Page 167, column 2, line 22 from bottom, should read:
three axes

Page 167, column 2, line 16 from bottom, should read:
atlases has the foramina and that his axes

Plate 6, figure 1, line 2 of legend: delete ?M₂₋₃ or
M₃ alone?

Plate 16, add to legend: 6. Haplomastodon waringi (Holland),
A.M.N.H. No. 45875, from Ceará, right M₃, crown view.
Approximately x 1/2.

Morris J. Skinner

THE MASTODONTS OF BRAZIL

THE MASTODONTS OF BRAZIL

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INTRODUCTION

THE OCCURRENCE OF MASTODONTS in Brazil has been a matter of scientific record since at least 1838. Since then many publications have mentioned or summarily described Brazilian mastodonts, but aside from the simple fact that there are indeed fossils of mastodonts in Brazil the total scientific contribution of those publications has been slight. That is true to such an extent that probably not even one of the hundreds of specimens reported has been correctly identified up to now.¹ Now at last it is possible to make a good start, at least, in that direction. The possibility arises mainly from the discovery and preservation of a large number of mastodonts at Águas do Araxá, herein described. With this basis for comparison, numerous other finds can be placed with some probability. This occasion is taken to summarize also other Brazilian finds reported in the literature or known to us by the specimens. The Brazilian mastodonts, and especially the Araxá collection, also contribute to a general understanding of the systematics of South American mastodonts, and that subject is reviewed.

This joint study was made possible by the visit of the senior author to Brazil from October, 1954, to January, 1955, under the auspices of the Conselho Nacional de Pesquisas. We are deeply indebted to the Conselho and its officers not only for this opportunity as a whole but also for support of special phases of the present work. Generous aid was also given by numerous other institutions and persons. First of all we are indebted to the Departamento Nacional de Produção Mineral, its Director, Dr. Alberto Ribeiro Lamego, and Dr. Llewellyn Ivor Price of the Divisão de Geologia e Mineralogia. Most of the preliminary work and collecting of the mastodonts of Águas do Araxá were done by Dr. Price, most of the specimens are in the

Divisão, and much of this study was done there. Dr. Price most generously made all specimens, data, and facilities available to us and aided in innumerable ways.

At the Termas de Águas do Araxá the management made available all the specimens *in situ* and gave us other assistance. In Belo Horizonte Mr. Harold V. Walter gave full access to his private collection, and the Director and professors of the Faculdade de Filosofia da Universidade de Minas Geraes did the same for the university's collection. In São Paulo Dr. Victor Leinz authorized study of specimens in the Departamento de Geologia e Paleontologia da Faculdade de Filosofia, and Dr. Josué Camargo Mendes aided us and provided photographs of specimens. In Pôrto Alegre Dr. Dante de Laytano similarly gave access to specimens in the Museu Julió de Castilhos, and Dr. Irajá Pinto (of the Instituto de Historia Natural da Universidade de Rio Grande do Sul) aided us and obtained photographs.

Broader review of the South American mastodonts was greatly aided during a later visit to Argentina by the senior author, to whom Drs. Noemí Cattoi (Museo Argentino de Ciencias Naturales, Buenos Aires), Rosendo Pascual (Museo de La Plata), and Galileo J. Scaglia and Jorge Lucas Kraglievich (then of the Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata) were especially helpful in this connection.

Some of the statistics were calculated by Dr. Anne Roe and others by Mrs. Mary Patsuris, who also assisted in numerous other ways in final preparation of the manuscript. Mrs. Rachel H. Nichols helped with the bibliography. Figures 1-3 and 6-8 were drawn by Ulisses Bastos Freitas, figure 6 after an original by Dr. L. I. Price and the others from the specimens. Figures 10 and 11 were drawn by Chester Tarka. With regard to the plates, it has not been practicable to bring the photographic figures to a uniform scale or to a particular enlargement. Whenever possible, the scale of each separate figure has been indicated by a measurement given in the legend.

The following abbreviations are used:

¹ A partial exception is the type of "*Mastodon waringi*" Holland, 1920, by virtue of the almost accidental fact that the specific name is valid, but the original publication elucidated neither the true characteristics nor the affinities of the species, and even the name has been completely overlooked in subsequent studies prior to the present one (except of course in the previously published abstract of this monograph).

A.A., Águas do Araxá

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MEASUREMENTS AND STATISTICS

L, maximum length

W, width (taken as further specified in the text)

N, number of specimens

OR, observed range

\bar{x} , mean

s, standard deviation

V, Pearson's coefficient of variation

(The sign \pm precedes standard errors of sample statistics.)

Measurements are in millimeters unless otherwise specified.

SUMMARY CLASSIFICATION OF SOUTH AMERICAN MASTODONTS

SUGGESTED CHANGES IN CLASSIFICATION and nomenclature and a discussion of general affinities of the South American mastodonts are presented after the detailed review of Brazilian specimens and occurrences. The latter provide our point of departure and much of the evidence for our more general conclusions and therefore are best presented first. It is, however, necessary to use a modi-

fied nomenclature in referring to the Brazilian specimens. In order that this nomenclature may be understood from the outset, an outline classification is presented here and defended later. The synonymy is not complete but includes names now most current in the literature. Genera and species are South American only, not all those referred to the family or subfamily.

Family Gomphotheriidae¹ Cabrera, 1929, p. 74

= Mastodontidae Girard, 1852, *pars*, p. 328

= Trilophodontidae Simpson, 1931, p. 281

Includes:

Palaeomastodontidae Andrews, 1906, p. 130

Bunomastodontidae Osborn, 1921a, p. 2

Humboldtidae Osborn, 1936, pp. 575, 687, 722

Serridentidae Osborn, 1936, pp. 30, 287, 381

Subfamily Anancinae Hay, 1922, p. 101

Includes:

Brevirostrinae Osborn, 1918, p. 136

Rhynchorostrinae Osborn, 1918, p. 136 (= Rhynchotheriinae Hay, 1922, p. 101)

Notorostrinae Osborn, 1921b, p. 330 (= Cuvieroniinae Cabrera, 1929, p. 76)

Humboldtinae Osborn, 1934, p. 180; 1936, p. 575

Cuvieroniinae Cabrera, 1929, p. 76

Stegomastodon Pohlig, 1912, p. 193

Stegomastodon platensis (Ameghino, 1888, p. 7)

(Numerous synonyms; see Cabrera, 1929, pp. 97, 98)

Stegomastodon superbus (Ameghino, 1888, p. 7)

(Numerous synonyms; see Cabrera, 1929, p. 120)

Notiomastodon Cabrera, 1929, p. 90

Notiomastodon ornatus Cabrera, 1929, p. 91

Haplomastodon Hoffstetter, 1950, p. 24

Haplomastodon waringi (Holland, 1920, p. 229)

= *Masthodon chimborazi* Proano, 1922, on an unnumbered page slipped into article

= *Bunolophodon Ayora* Spillmann, 1928, on an unnumbered page preceding p. 70

= *Bunolophodon postremus* Spillmann, 1931, p. 73

= *Haplomastodon guayasensis* Hoffstetter, 1952, p. 208

= *Stegomastodon brasiliensis* Hoffstetter, 1952, p. 222

Cuvieronius Osborn, 1923, p. 1

= *Cordillerion* Osborn, 1926, p. 15

Cuvieronius hyodon (Fischer, 1814, p. 341)

= *Mastodon andium* Cuvier, 1824, p. 527

(Many other synonyms; see Hoffstetter, 1952, p. 186)

¹ Under the tentative and not yet legal "Copenhagen decisions" (see Hemming, 1953), the prior name Palaeomastodontidae would apply to this family, unless (as is quite possible) there is some still older, obscure "family group" name available. We have no sympathy for the general principle of strict priority and equivalence for "family group" names, which would cause great confusion in the nomenclature of mammalian families, at least. In any event, it may fairly be claimed that retention of the names Gomphotheriidae here "would lead to greater stability and universality of nomenclature

than would strict application of priority," and we therefore invoke the procedure for retention of customary names also envisioned in the recommendations of the Copenhagen Colloquium. The family now generally called Gomphotheriidae is not at all the group intended to be included in Palaeomastodontidae by Andrews or now understood when the latter name is used. "Bunomastodontidae" is invalid because not based on a generic name, and the other available family names are antedated.

HAPLOMASTODON WARINGI FROM ÁGUAS DO ARAXÁ

THE COLLECTION OF remains from about 30 to 40 individuals of *Haplomastodon waringi* in a single deposit at the Águas do Araxá, in Minas Geraes, provides a basis of comparison for other, more isolated specimens of that species. It also provides a unique opportunity to study variation in what is inferred to be a single population of mastodonts. Elsewhere in South America only the Valley of Tarija, Bolivia, may have yielded more individuals of a single species, in that case *Cuvieronius hyodon*. Those remains were, however, scattered over a large area and through a great thickness of strata. They cannot be assigned to a single population. Moreover, although several excellent studies have been based on collections from Tarija, no adequate study of their variation is available. Indeed there seems to be no fully adequate study of such variation in any species of proboscideans, in spite of the enormous literature on that subject.¹

The Araxá material is fragmentary. It includes no skulls and relatively few complete bones from any part of the skeleton. It does, however, include a large number of complete teeth, and for them, at least, it is possible to make a first step towards a population study rather than the classical but biologically inadequate typological studies of the past.

Part of the Araxá collection was left *in situ* at the Águas do Araxá and part is preserved in the Divisão de Geologia y Mineralogia of the Departamento Nacional de Produção Mineral in Rio de Janeiro. Detailed study in the present paper is based principally on the latter material. The material remaining at Águas do Araxá has, however, also been seen, and notes on it are included. Also studied are one specimen from Araxá in the Faculdade de Filosofia of the Universidade de Minas Geraes and two in the private collection of H. V. Walter, both in Belo Horizonte.

¹ Some large collections have been described, but generally without adequate population data or concepts. An outstanding recent example is the excellent body of information and figures on large numbers of isolated teeth of Portuguese mastodonts by Bergounioux, Zbyszewski, and Crouzel (1953). Yet they did not have large samples of fully unified origin, and some of their criteria and methods for taxonomy and interpretation are purely intuitive or otherwise inadequate.

OCCURRENCE

The Araxá mastodonts were discovered in 1944 in the course of development of the mineral springs at Águas do Araxá, a few kilometers from the town of Araxá in the State of Minas Geraes. The find was brought to the attention of the Divisão de Geologia y Mineralogia by Dr. José Ferreira de Andrade Junior, then Engenheiro Chefe das Obras do Balneário do Araxá. The deposit was examined and collections made by Llewellyn Ivor Price, of the Divisão de Geologia y Mineralogia, and Rubens da Silva Santos. Price (1944) has described the occurrence, and the following briefer account is mostly based on his.

The fossils were found in a pothole, *caldeirão*, in the bed of an old, evidently Pleistocene stream. The pothole is 6 meters long, 4 meters wide, and 1.2 meters deep. It is irregular, consisting of a confluent series of cavities rounded and polished by stream abrasion. After its original formation, the pothole was filled with sediments and fossils. The deepest material was poorly sorted and included rounded boulders up to 30 cm. in diameter. Most of the bones, frequently broken but with little stream wear, were in this poorly sorted part. Towards the top, sorting became greater and the sediments finer. The bones in this upper part of the deposit were more fragmentary and water-worn. The uppermost sand, with well-rounded pebbles and a few small, much worn bone fragments, was later cemented by iron oxide, forming a hard covering of *canga* which sealed and preserved the deposit. We were informed in Belo Horizonte and at the Águas do Araxá that a few specimens were also found around but not in the pothole, and it is possible that a considerable deposit of unexcavated bones still exists in the valley gravels around this site.

The coarse lower part of the pothole filling, containing the well-preserved bones and teeth, was deposited by fast-flowing water. The filling was also rapid. It is the most probable assumption that the bones washed into the pothole by freshets all represented animals that were contemporaneous or nearly so.

There was no association of bones of one individual with the sole exception of a radius and an ulna. In no case was the whole or any considerable part of a single individual buried in the pothole. The flesh of the animals must have decayed and the bones must already have been separated and scattered before rapid stream action washed some of them into this catchment basin. The bones in the deposit were about 98 per cent mastodonts. Rarer remains reveal the presence of *Eremotherium*, *Equus*, and *Macrauchenia*, all Pleistocene in aspect. (The identification of *Equus* is by Price and was based on material not seen by us.) Price suggests that the concentration of animals in this valley may have been due to the mineral springs, which have a salty taste. In recent times they have attracted cattle from long distances around. Price naturally assumed that the animals dying here were senile or sick, or defenseless juveniles. Our subsequent study reveals the unexpected and unexplained fact that in reality most of the animals preserved in this deposit died in the most vigorous stages of early to middle adulthood, very young animals being absent and very old ones comparatively few.

DENTITION

UPPER TUSKS

The Divisão de Geologia y Mineralogia collection contains one nearly complete young tusk, one complete old adult tusk, and fragments of six others of varying ages. The youngest fragment (162M), considerably water-worn and incomplete proximally, has a maximum diameter of 29 mm. In the region of its maximum diameter there is preserved part of an enamel band about 18 mm. in width. The enamel has spalled off distally. No other tusks show enamel, but most of them have spalled or exfoliated over much of the surface, and it is possible that an enamel band has been lost. The oldest tusk in the Divisão de Geologia y Mineralogia, apparently associated with a palate and lower jaw in which only worn M_3^s are retained (81M), has the surface well preserved, and there is no trace of enamel. That tusk has a strong, simple curve. It measures about 98 cm. from alveolus to tip along the curve and about 16 cm. in maximum diameter near the

alveolus. (It is not certain that insertion in the restored alveolus is exactly at the point where it was in the living animal, but the reconstruction is probably approximately correct.)

A nearly complete female or young, but not strictly juvenile, tusk (62M) measures about 51.5 cm. from the worn tip to the end of the hollow intra-alveolar portion. Near the middle it is 65 mm. in greatest, and 51 mm. in least, diameter, and with a somewhat flattened oval cross section. It has a very slight curve, including a trace of torsion suggestive of *Cuvieronius* but less definite than in that genus. Older tusks developed a more pronounced simple curve and became more nearly circular in section. A fragment (included under the collective or lot No. 60M), for instance, has maximum and minimum diameters 79 and 67 mm., respectively, with a ratio of 1.18, to be compared with 1.27 in the younger tusk previously mentioned.

Three relatively old tusks, partially restored and fixed in place so that both diameters cannot be measured, are preserved at Águas do Araxá. All have a moderate, simple (non-spiral) curve. The largest is 128 cm. long on the outer curve as preserved and presumably was larger in life. Its maximum diameter near the proximal end is 16.4 cm. Corresponding measurements of a second specimen, also broken at the proximal end, are 119 and 15.5 cm. The third specimen has a similar curve but is broken and restored at both ends and gives no additional useful information.

In summary, these animals had comparatively straight, compressed oval tusks when young, with an enamel band sometimes, at least, in the most juvenile stages, and in the adults the tusks tended to become more curved and less compressed and no longer had enamel. The observations are in agreement with those on *Haplomastodon* from Ecuador (Hoffstetter, 1952).

GENERAL REMARKS ON MOLARS

Cheek teeth anterior to dm_4^4 are represented only by two specimens so deeply worn and so uncertain as to homologies as not to warrant description. $Dm_4^4-M_3^s$ are represented by good series. $Dm_4^4-M_2^s$ are all clearly trilophodont, with variable anterior and posterior cingula

and cuspsules but no tendency to form a true fourth loph. M_3^3 always have four complete lophs. A fifth loph may be well developed, especially on M_3 , or may, especially on M_3^3 , be represented only by cones not forming a really distinct loph. Additional conules usually, but not always, occur posterior to the fifth loph. Some account of these variations is given below.

Each loph of dm_4^4 - M_3^3 is formed by two main cusps, the pretrite (external on the lower and internal on the upper molars) and the posttrite cones. Variable intermediate conules occur between them in the loph. Accessory buttresses or conules form strong trefoils on the pretrites, from near their apex so that the trefoil pattern appears on the grinding surface in early stages of wear. The posttrites may be almost completely simple but usually have small basal buttresses which form, with the main cone, poorly or occasionally even well-developed trefoils in the latest stages of wear. In short, these are bunolophodont molars with (on the whole) single trefoils, as in *Cuvieronius* among other South American mastodonts and as in *Gomphotherium* and its allies in North America and the Old World. The molar pattern tends to be distinctly different from

variable. The conelets that form (with the pretrite cones) the trefoils are somewhat, at least, on the pretrite side of the midline, but this is generally true to about the same extent in the Gomphotheriinae (essentially Osborn's "Bunomastodontidae"). Indeed we see no reason to doubt that the pretrite trefoils are homologous in *Gomphotherium*, *Serridentinus*, and all the South American mastodonts and that all of these could be and probably were derived from forms with molars essentially as in *Gomphotherium*, if not from that genus itself. (*Serridentinus* of Osborn's phylum A, which includes the genotype, seems even to intergrade with *Gomphotherium*, "*Trilophodon*" of Osborn, but his phylum B is more distinctive.) Posttrite trefoils may have originated independently in some of the various lines that have them, but they are incipient, at least, in all South American mastodonts, including *Cuvieronius* and *Haplomastodon*, and may well have been so in the common ancestry of these genera, and of *Notiomastodon* and *Stegomastodon*.

Corresponding upper and lower molars are nearly mirror images of each other and may be difficult to distinguish. They can, however, almost always be identified by the following characters:

DM_4^4 - M_3^3

Average absolutely shorter, but with overlap of range

Relatively wider; often absolutely wider but with overlap

Three roots; anterior root relatively small and buccal; third root anterolingual

Pretrite (trefoil) cones of middle and posterior lophs tending to be somewhat anterior to posttrites

and simpler than that of *Stegomastodon* or *Notiomastodon*.

Osborn (especially 1936) made a decisive difference between trefoils formed by "ectoconelets" (in the lower teeth) or "entoconelets" (in the upper teeth) and those formed by "mesoconelets." The former condition was considered diagnostic of the "Serridentidae" as opposed to the "Bunomastodontidae" and the "Humboldtidae." In the Araxá specimens the conelet position is

DM_4 - M_3

Average absolutely longer, with overlap

Relatively narrower; often absolutely narrower but with overlap

Two roots, anterior and posterior; posterior root large and complex, with some tendency to division, especially on M_3

Pretrites of middle and posterior lophids tending to be somewhat posterior to posttrites

The last character, also noted by Hoffstetter (1952) for Ecuadorian *Haplomastodon*, makes the posterior lophs (including lophids) somewhat oblique. The obliquity is not evident on the first loph of dm_4^4 - M_3^3 or on the first two lophs of M_3^3 . It is variable on the middle and posterior lophs and is rarely strongly pronounced, but is usually perceptible on the most posterior complete loph, at least. When strongly developed this is a distinction from the otherwise extremely

similar molars of *Cuvieronius hyodon*. *Cuvieronius* does, nevertheless, have a slight tendency to have lophs oblique in the same way (visible, for example, in Boule and Thévenin, 1920, pl. 4, figs. 8, 14), and the distinction is neither invariable nor sharply diagnostic. In *Notiomastodon* and *Stegomastodon* the obliquity is usually definitely present and stronger than is usual in *Haplomastodon*, but even in *Stegomastodon* the pretrites and posttrites may be nearly opposite (for example, the M^3 of *S. platensis* figured by Cabrera, 1929, fig. 15). The obliquity is incipient in *Gomphotherium*, in which it is often developed to about the same degree as in *Haplomastodon*. This character is thus

TABLE 1
LOWER TOOTH REPLACEMENT IN THE
ARAXÁ MASTODONTS

Specimen	dm_3	dm_4	M_1	M_2	M_3
D.G.M. I	3	?	?	?	?
D.G.M. No. 141M	—	A	2	0	?
D.G.M. No. 72M	—	—	3	0+	0
D.G.M. No. 139M	—	—	3	1	0
A.A.	?	?	3	1	0
D.G.M. No. 113M	?	?	A	2	?
A.A.	—	—	A	2	0
D.G.M. D	—	—	3	2	0
D.G.M. No. 132M	?	?	4	3	?
D.G.M. No. 138M	?	?	?	3	1
D.G.M. No. 137M	—	—	—	A	1
D.G.M. No. 70M	—	—	—	4	3
D.G.M. No. 131M	—	—	—	—	3
D.G.M. No. 134M	—	—	—	—	3
D.G.M. C	—	—	—	—	3
D.G.M. No. 133M	—	—	—	—	3
A.A.	—	—	—	—	3
A.A.	—	—	—	—	4
Walter collection	—	—	—	—	4

Symbols:

- , Tooth known to have been shed
- ?, Absence or presence unknown
- A, Alveoli; tooth present but amount of wear unknown
- 0, Tooth formed but not erupted
- 0+, Erupted but unworn
- 1, Wear on anterior lophids only
- 2, Light wear on all lophids
- 3, Extensive wear but pattern still clear
- 4, Severe wear, pattern partly or wholly obliterated

suggestive, but it is not so clearly diagnostic as Hoffstetter (1952) implies.

On the other hand, in some of the Old World Anancinae, notably *Anancus* itself, the obliquity of pretrites and posttrites is so strong that one can hardly speak of distinct lophs, and the effect is of alternating buccal and labial cones. That condition is diagnostic and clearly indicates that some, at least, of the Old World Anancinae followed a line of specialization distinct from that of any of the American mastodonts.

TOOTH REPLACEMENT AND AGE GROUPS

As in all proboscideans (and otherwise only in some sirenians), replacement of cheek teeth is by postero-anterior movement, worn anterior teeth being shed and their alveoli obliterated as replacing teeth erupt from behind. As in other short-jawed proboscideans, usually only two and at most three molars (including deciduous molars) are in use at any one time, and the process continues until late adult and old individuals have only M^3 retained in the jaws.

There are 14 partial lower jaws in the Divisão de Geologia y Mineralogia, four at Águas do Araxá, and one in the Walter collection in which the simultaneous presence or absence of two or more molars in the same individual can be determined. The data are given in table 1, which also indicates the state of wear of each tooth present. The scale used for wear is approximate and involves subjective decision in many instances, but it gives at least a rough idea of relative wear. A possibly more objective alternative, measurement of crown height at a given point, was

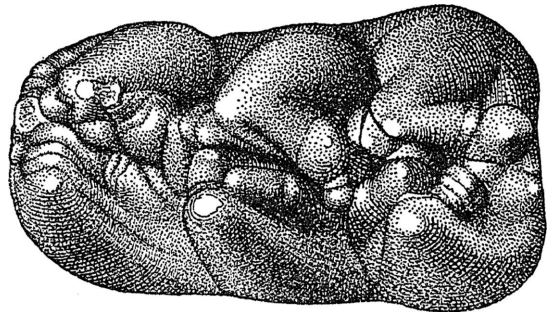


FIG. 1. *Haplomastodon waringi* (Holland). D.G.M. No. 75M, right M_2 , from Águas do Araxá, crown view, in stage 0 of wear. $\times \frac{1}{2}$.

TABLE 2
UPPER TOOTH REPLACEMENT IN THE
ARAXÁ MASTODONTS

Specimen	dm ³	dm ⁴	M ¹	M ²	M ³
D.G.M. No. 73M	—	2	1	—	—
D.G.M. No. 136M	—	—	3	2	—
D.G.M. No. 127M	—	—	—	—	3
D.G.M. No. 81M	—	—	—	—	3

Symbols:

- 1, Wear on anterior lophids only
- 2, Light wear on all lophids
- 3, Extensive wear but pattern still clear

considered but seemed to give no better results, the original (unworn) crown height being highly variable and not necessarily closely correlated with total size of the tooth.

The specimens do not definitely show more than two teeth in use at any one time, but

they do not exclude the possibility that M_{1-3} may briefly all be in use in animals of about the age of D.G.M. No. 132M. For a very brief period M_1 may function alone (72M, 139M), but that does not appear to be true of M_2 . M_2 is retained until M_3 is in early stage 3 of our scale. In later stage 3 and in stage 4 M_3 functions alone.

Table 2 gives similar data for upper jaws, but they do not add significantly to the information on replacement.

In individuals with two (or more) molars in place, an anterior molar is of course more worn than the one (or ones) posterior to it in the same jaw. Thus an M_2 , for example, in wear stage 3 is younger than an M_3 in stage 3, not of the same age. The data of table 1, incomplete as they are, make it possible to designate very approximate corresponding ages for different molars. Thus M_1 in wear stage 4 belonged to an animal of roughly the

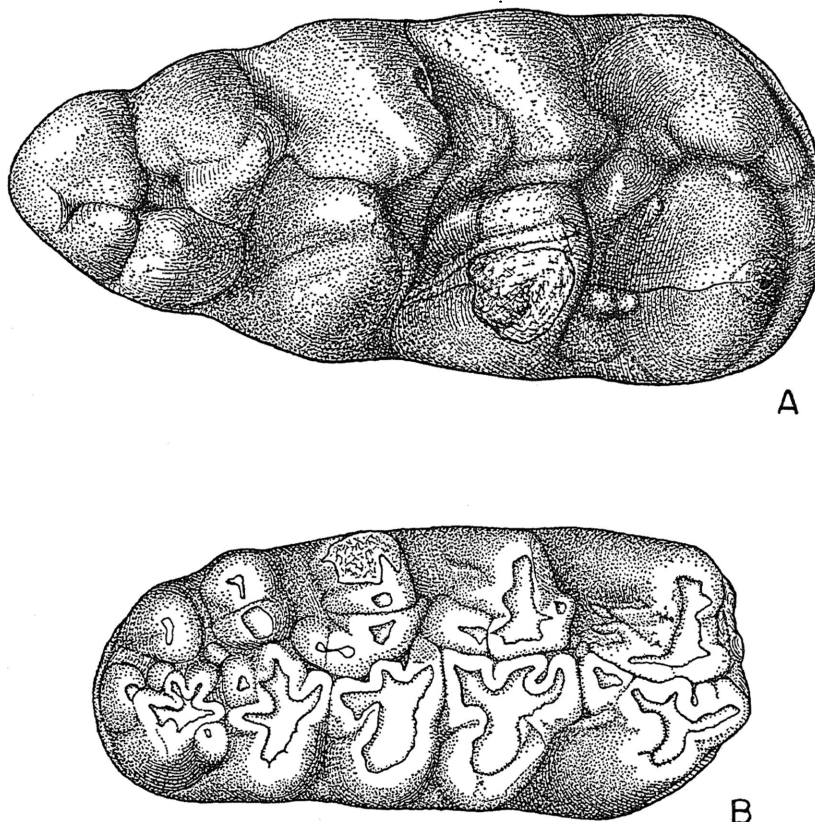


FIG. 2. *Haplomastodon waringi* (Holland). Crown view of M^3 's from Águas do Araxá showing different stages in wear. A. D.G.M. No. 116M, left M^3 in stage 0 of wear. B. D.G.M. No. 126M, right M^3 in stage 3 of wear. Both figures $\times \frac{1}{2}$.

same age as an animal with M_2 in wear stage 3 (see specimen 132M in table 1). In this way M_{1-3} can be very roughly assigned to six age groups, as shown in table 3. Table 4 (A) shows the stage of wear of available M_{1-3} in the whole sample, and table 4 (B) shows their assignment to age groups in accordance with the scheme of table 3.

There is some duplication of individuals in table 4 (B), and there are other imperfections in the data. Nevertheless, these data do give

TABLE 3
APPROXIMATE GROUPING BY AGE AND WEAR^a
OF M_{1-3} IN ARAXÁ MASTODONTS

Age Group	M_1	Stages of Wear M_2	M_3
A	0-1	Forming	Not formed
B	2	0	Forming
C	3	0+-2	0
D	4	3	1
E	—	4	2-3
F	—	—	4

Symbols:

- 0, Tooth formed but not erupted
- 0+, Erupted but unworn
- 1, Wear on anterior lophids only
- 2, Light wear on all lophids
- 3, Extensive wear but pattern still clear
- 4, Severe wear, pattern partly or wholly obliterated

^a The equivalence in age of molars in different stages of wear is based mainly on the data in table 1. Information is incomplete, so that this grouping is correspondingly uncertain.

some idea of distribution of age at death in this accumulation of mastodont remains. The great majority of individuals was obviously adult at the time of death but not, as a rule, senile. Heavy mortality occurred before M_2 was lost, and the peak of mortality probably occurred at about the time when that tooth was shed. Few animals had lived until M_3 were in latest wear stages. Only four M_3 's and four M_3 's are in wear stage 4. These inferences do not take account of the deciduous molars, but those are comparatively few in the collections, as shown in table 5. That fact tends to confirm the inference that most of the animals buried in the Araxá deposit were adults. There is a contrast with the

TABLE 4
DISTRIBUTION BY STAGES OF WEAR AND BY
APPROXIMATE AGE GROUPS OF
ARAXÁ LOWER MOLARS

(Figures in the body of the table are observed frequencies.)

	M_1	M_2	M_3	Totals
(A) Stages of wear				
0 ^a	0	2	6	
1	3	6	7	
2	0	4	6	
3	5	3	8	
4	3	3	4	
(B) Approximate age groups				
A ^b	3	—	—	3
B	0	3	—	3
C	5	10	6	21
D	3	3	7	13
E	—	3	14	17
F	—	—	4	4

^a For wear stages, see table 1.

^b For age groups, see table 3.

collections from the caves, *lapas*, of the Lagoa Santa region, where juvenile animals are comparatively common.

SIZE AND METRICAL VARIATION

Table 6 gives essential data on the dimensions of $dm_4^1-M_3^3$ in the combined collections from Araxá. Uncertain measurements have been omitted. Some teeth in wear stage 4 are

TABLE 5
NUMBERS OF TEETH^a IN THE ARAXÁ COLLECTIONS

Tooth	Frequency in Collection
dm_{2-3}^{2-3}	3
dm_4^1	3
M_1	11
M_2	18
M_3	32
dm_4^1	6
M^1	10
M^2	11
M^3	20

^a Homologous teeth of right and left jaws of the same individual are counted as only one, but non-homologous teeth possibly or surely of a single individual are counted separately.

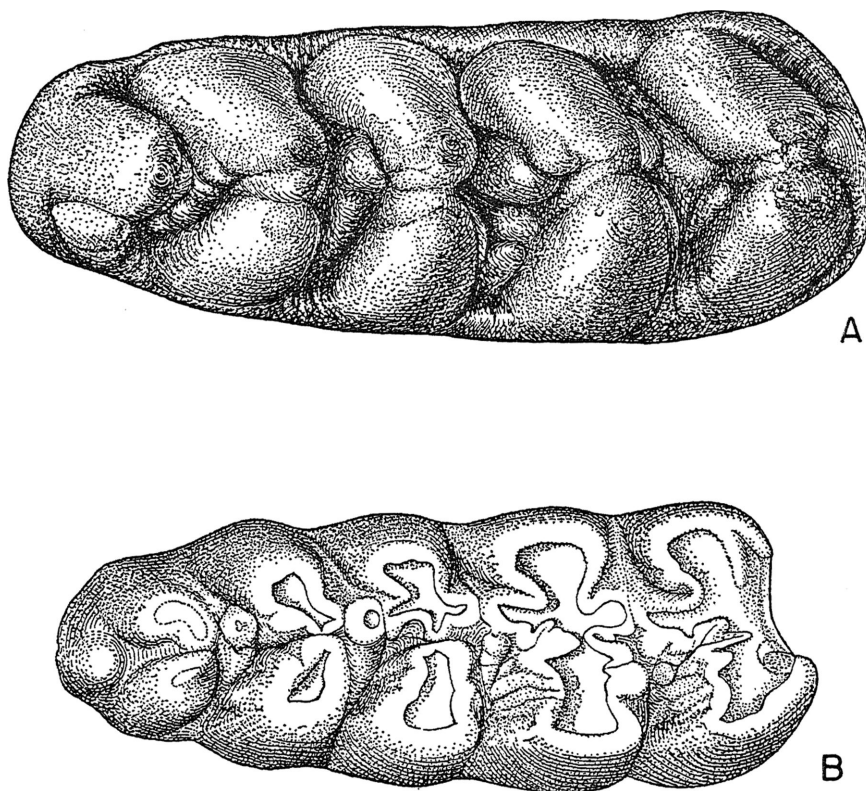


FIG. 3. *Haplomastodon waringi* (Holland). Crown view of left M_3 's from Águas do Araxá showing different stages in wear. A. D.G.M. No. 72M, in stage 0 of wear. B. D.G.M. No. 133M, in stage 3 of wear. Both figures $\times \frac{1}{2}$.

TABLE 6

METRICAL DATA^a ON TEETH OF *Haplomastodon waringi* FROM ARAXÁ

Variate	N	OR	\bar{x}	s	V
L dm_4	3	85-86	85.3	—	—
W dm_4	3	45-60	54.3	—	—
L M_1	10	99-111	105.0	—	—
W M_1	9	55-68	60.9	—	—
L M_2	18	107-149	131.7 ± 2.6	11.2 ± 1.9	8.5 ± 1.4
W M_2	18	65-90	74.2 ± 1.4	6.2 ± 1.0	8.3 ± 1.4
L M_3	22	180-239	208.1 ± 3.0	13.8 ± 2.1	6.7 ± 1.0
W M_3	24	69-90	80.8 ± 1.0	4.8 ± 0.7	5.9 ± 0.8
L dm^4	6	74-80	77.7	—	—
W dm^4	6	52-55	53.2	—	—
L M^1	9	86-101	96.0	—	—
W M^1	8	63-71	67.0	—	—
L M^2	11	115-132	125.0 ± 1.8	6.0 ± 1.3	4.8 ± 1.0
W M^2	11	69-89	76.7 ± 2.0	6.5 ± 1.4	8.5 ± 1.8
L M^3	17	165-216	188.2 ± 2.8	11.5 ± 2.0	6.1 ± 1.0
W M^3	19	75-110	86.4 ± 1.8	7.7 ± 1.2	8.9 ± 1.4

^a For abbreviations, see p. 132.

evidently shorter than they had been when unworn, but the effect seems to have been slight, and measurements of those teeth are included in the tables. Wear has little or no effect on width. "Length" is maximum length near the base of the tooth and along its long anteroposterior axis. For dm_1-M_2 and dm_4-M^3 "width" is maximum width near the base transversely across the second loph. This generally is the greatest width for the tooth as a whole, although the third loph of $dm_4-M_2^3$ may be widest. On M^3 the first and second

curves, but it is evident that the samples could be drawn from approximately normal or slightly platykurtic and skewed distributions. There is no suggestion of bimodality. That fact supports the conclusion that only one species is present, and it also suggests that there is no great difference, at least, between males and females in the grinding teeth. There may, of course, be a slight average difference between the sexes, and that may contribute to the flatness of some of the distributions.¹

TABLE 7
COMPARISON OF SOME BIOMETRICAL DATA^a ON YOUNGER AND OLDER
INDIVIDUALS OF *Haplomastodon waringi* FROM ARAXÁ

Variate	Age Group ^b	N	OR	\bar{x}	s	V
L M_2	0-2	13	124-149	134.4±2.1	7.5±1.5	5.6±1.1
	3-4	6	107-148	124.3±6.2	15.2±4.4	12.2±3.5
W M_2	0-2	13	67-102	76.2±3.0	10.6±2.1	13.9±2.7
	3-4	6	65- 80	73.5±2.1	5.0±1.5	6.9±2.0
L M_3	0-1	10	187-239	212.3±5.2	16.5±3.7	7.8±1.7
	2-4	18	189-220	202.9±2.8	11.9±2.0	5.9±0.98
W M_3	0-1	10	69- 90	81.6±1.9	6.1±1.4	7.5±1.7
	2-4	18	71- 90	80.4±1.1	4.9±0.8	6.1±1.0

^a For abbreviations, see p. 132.

^b Defined by stage of wear.

lophs usually have nearly the same width, with the second a little wider. It is, however, also common for the first loph to be slightly wider; that is true of eight out of 19 M^3 's in the sample. The maximum excess of width of the first loph over the second is only 4 mm., or about 4 per cent.

"Width" on M_3 is the maximum width near the base on the third, not the second, lophid. That is usually the widest point on the whole tooth, but the first three lophids usually are of nearly the same width. In five specimens out of 25 the second lophid is wider than the third, and in one of these (included in the lot D.G.M. No. 60M) the excess is considerable, 7 mm., or over 8.5 per cent.

Table 8 gives grouped frequency distributions for the most abundant teeth, M_2^{2-3} . The samples are too small to give good frequency

The normal curve statistics given for the variates of highest sample frequencies in table 8 show that M_2^{2-3} are highly variable in size, but no more so than might occur in a variable single species. Correlation between length and width is low, as is evident in

¹ Bergounioux, Zbyszewski, and Crouzel (1953) have designated nearly all the mastodont teeth studied by them as either "forme mâle" or "forme femelle." They remark that, "En réalité cette distinction ne nous paraît pas fort objective, faute de critères suffisants. Toutefois dans une même catégorie de dents, on observe facilement deux types, le premier que l'on pourrait appeler massif, que nous avons affecté au sexe mâle, et le deuxième qui est plus gracile dont nous avons fait le sexe femelle. Nous n'avons pu concrétiser autrement les différences observées sur les diverses pièces." After study of their measurements and figures, we remain somewhat skeptical of their interpretation. In any case, we see no way to sex our Brazilian specimens.

figures 4 and 5. There is correspondingly great variation in the proportions of the teeth. The slope of the regressions for M_3^3 is <1 , so that longer teeth (especially for M_3) tend to be relatively narrower. In figure 5 are entered two pairs of measurements of M_3 , each pair representing right and left teeth of a single individual. The radical differences between the two sides of one animal, both in size and in proportions, dramatically illustrate the variability present in this population. In at least one of these instances the two teeth of a single individual, if they had been found isolated, would unhesitatingly have been referred to different species by standards frequently used.

COMPARISON OF YOUNGER AND OLDER INDIVIDUALS

We have made a brief comparative study of some biometrical characteristics of younger and older individuals in the fauna. The results are all inconclusive, but they may suggest possibilities for future work and are therefore published in summary form in table 7. The age groups, defined by wear stages, are of course different for M_2 and M_3 , and for reasons previously given would be different even if the same wear stages were covered in the two.

In all four dimensions the older animals have smaller means than the younger, but none of the differences are statistically sig-

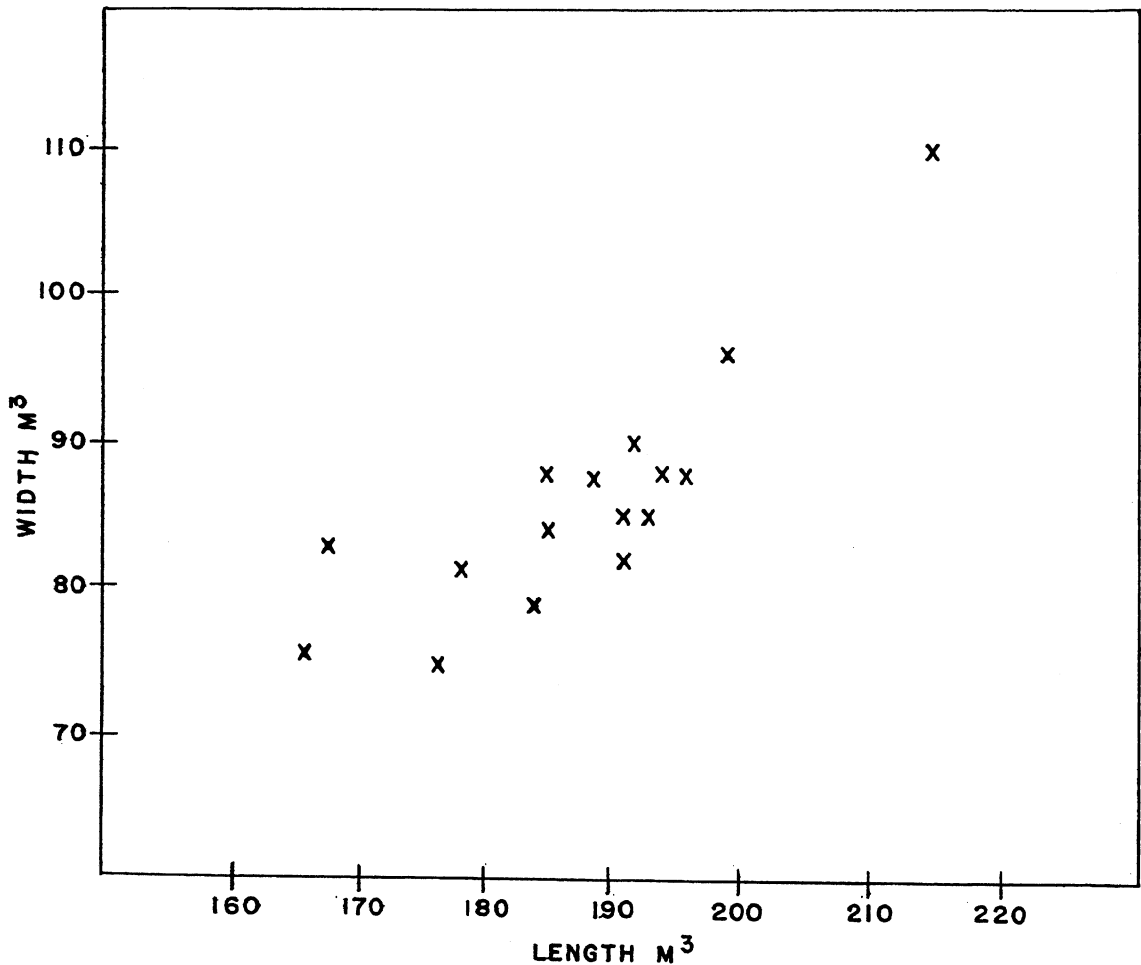


FIG. 4. Scatter diagram of length and width of M_3 of *Haplomastodon waringi* from Águas do Araxá.

nificant. For length measurements the teeth do actually become shorter with age because of interstitial wear, but even at its maximum this factor could hardly account for a decrease of 10 mm., which occurs between the means for these samples of both LM_2 and LM_3 . There can be no appreciable aging factor in width measurements for individuals. It is possible, but is not established, that in this population there was some selective mortality against the larger individuals, or that selec-

and other studies cited by them) that mortality in various animals often tends to reduce variance with increasing age—in other words, that centripetal or stabilizing selection by mortality is acting within the population. If it could be established by larger or more decisive samples, the combination of shift in the mean and reduction of variance by differential mortality would be unusual and of great theoretical interest for its bearing on natural selection.

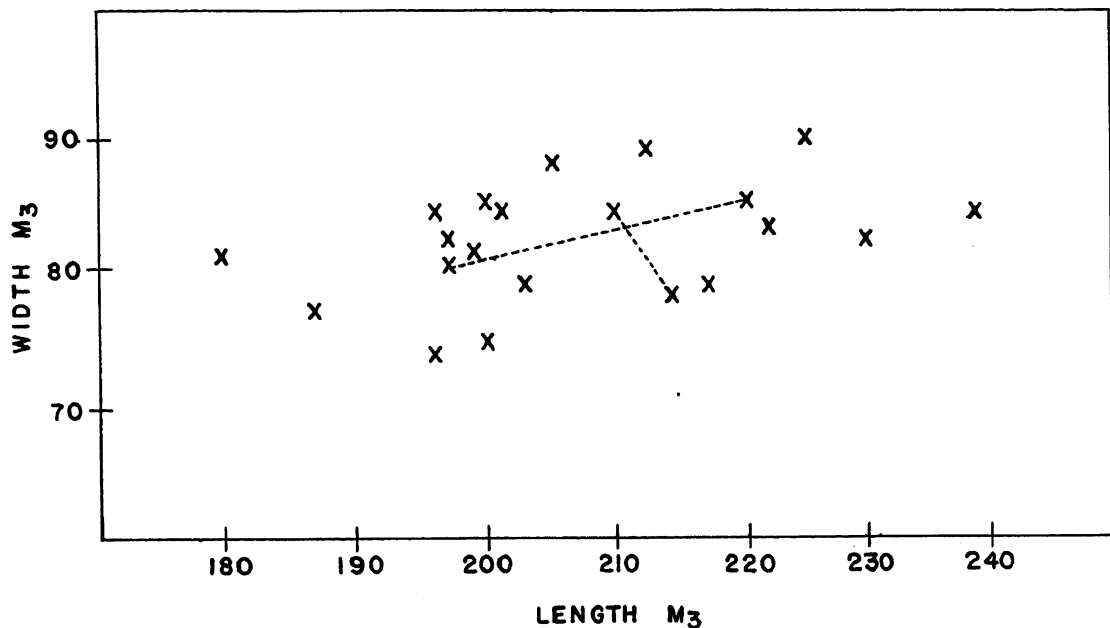


FIG. 5. Scatter diagram of length and width of M_3 of *Haplomastodon waringi* from Águas do Araxá. The points connected by dotted lines represent right M_3 and left M_3 of single individuals.

tion by youthful mortality was favoring a decrease in size—an unexpected but by no means impossible result. The animals are probably from the late Pleistocene, and there is some evidence elsewhere (e.g., Hooijer, 1949) of evolutionary trends for decrease in size from late Pleistocene to Recent.

In three of the four dimensions there is a decrease in variance, both absolute and relative, from younger to older sample moieties. Again, the observed change is not statistically significant, and it is further made questionable by the decided increase in variance of one dimension, LM_2 . It is, nevertheless, in the expected direction. It has repeatedly been found (e.g., Haldane, 1954; Kurtén, 1953;

These particular samples, or indeed mastodons in general, are not very favorable materials for such a study. Because of the mode of tooth replacement, age groups for homologous variates can generally be established only tooth by tooth and not for the dentition as a whole. Thus the younger and older animals here compared intergrade in age, and their combined age span covers only a fraction of the life of the animal. Comparison of truly juvenile and truly aged animals is impossible, because they do not have homologous teeth formed and in place. Nevertheless these results suggest that significant results might appear with larger samples and especially if, say, stage 0 and stage 4, without

TABLE 8
GROUPED FREQUENCY DISTRIBUTIONS FOR
DIMENSIONS OF M_2^3 IN *Haplo-*
mastodon waringi FROM ARAXÁ

Length	f ^a	Width	f ^a
M₂			
105-112	2	65-68	2
113-120	1	69-72	7
121-128	2	73-76	4
129-136	7	77-80	3
137-144	3	81-84	1
145-152	3	85-88	0
		89-92	1
M₃			
180-189	2	66-69	1
190-199	4	70-73	1
200-209	6	74-77	3
210-219	5	78-81	8
220-229	2	82-85	8
230-239	2	86-89	2
		90-93	1
M₃			
160-168	2	75- 80	3
169-176	0	81- 86	7
177-185	5	87- 92	7
186-194	6	93- 98	1
195-203	3	99-104	0
204-212	0	105-110	1
213-221	1		

^a Frequency in combined collections.

intervening stages, were sufficiently well represented for statistical comparison.

MORPHOLOGICAL VARIATION

Pretrite and posttrite cones are present in all complete lophs (and lophids), and the pretrites always have accessory conules (or conelets, the distinction is not clear) which form trefoils with the pretrite cones. Conules entering into the trefoil and on the posterior slope of the pretrite cone are generally better developed than those on the anterior slope and often tend to be double. An additional conelet may be present between the conules of successive trefoils. From one to four conelets, early obliterated by wear, may also be present on the lophs between the main cones. The posttrites usually have basal buttresses, at least, and often conelets which develop trefoils on this side also, when the tooth is

deeply worn. Additional conelets may also appear between lophs and at anterior and posterior ends of the tooth.

With all these accessory elements, *Haplo-**mastodon* molars, although simpler than those of some other late mastodonts, may really be very complicated in detail, and they are extremely variable in the presence and positions of conules and conelets. A count of Osborn's "conical elements" or "aristogenes" has a large subjective element, because it is difficult to decide when a tendency towards twinning of a cusp or when a small convexity is to be called a separate "element." (We cannot make our counts on Osborn's specimens agree exactly with his.) Nevertheless such counts do give some idea of the proliferation of cusps and of variation in that characteristic. On four unworn M_3 's our counts of "conical elements" are 28, 31, 34, and 38, and on three unworn M_2 's they are 29, 32, and 36. Incidentally, the criteria used by Osborn would have assigned variants within this single population not only to different species but also to different geological epochs. In a broader way, however, a range of complexity is established.

The development of the fifth loph (and lophid) and of conules posterior to it is one of the most conspicuously variable characters of M_3 . Data for M_3 are given in table 9. The total number of conical elements posterior to the fourth lophid and its trefoil conule varies from two (cones of fifth lophid, none posterior to it) to eight (four in fifth lophid, four posterior to it). A single individual (in the Águas do Araxá collection) has two (in fifth lophid) plus one (posterior to it), or three on

TABLE 9
POSTERIOR CONICAL ELEMENTS ON M_3 OF
*Haplo-**mastodon waringi* FROM ARAXÁ

	No.	Frequency
(A) Elements in fifth lophid	2	9
	3	7
	4	4
	5	5
	0	5
(B) Elements posterior to fifth lophid	1	9
	2	7
	3	3
	4	1

the left M_3 , and five plus two, or seven on the right M_3 . Again, these parts of one individual would have been placed in different species by standards usual in the older taxonomy of mastodonts.

When the fifth lophid has three to five conical elements, it tends to be convex anteriorly, and in about one-fifth of the specimens it is strongly arched, practically semi-circular.

The fifth loph is less developed on M^3 than on M_3 , although it is always represented by at least two cones. It consists of only two cones (one sometimes vaguely bifid) in nine out of 14 specimens. One has a fairly definite loph with three conical elements. Four have four conical elements arranged in a somewhat irregular cluster, the pattern different in each case. Posterior to the fifth loph, four specimens have no conical elements, three have a vague or tiny single element, and six have one distinct conule. None has more than one conule in this position.

Variation in the obliquity of the lophs or in the alternation of pretrite and posttrite cusps has already been mentioned. It reaches an extreme in an M_3 in lot 60M. The first two pretrites of this M_3 are nearly opposite the posttrites, but the third is decidedly posterior to the corresponding posttrite. The fourth pretrite lies between the fourth and fifth posttrites. The fifth posttrite (which has a bifid apex) is anterior to, but nearly lined up with, a row of three conules on the posttrite side. Posterior to these elements is a row of three lower conules across the tooth, giving the effect of a sixth loph. This is perhaps the most aberrant tooth in the collection and, if found isolated, might well have been placed in a new species or even genus. Yet it represents only an extreme of a tendency shown to varying degree in the whole collection, and we believe that it must be considered as a variant member of the same population as all the other Araxá specimens.

If we are right in assigning all the Araxá specimens to one species and if their extent of variation in size and morphology is at all typical of mastodonts, it is necessary to become more skeptical about the taxonomy of these animals. On this basis it would appear that very few indeed of the numerous species currently assigned to single genera are valid or, at least, have been correctly defined.

It would further appear possible that some genera, perhaps of a split classification such as that of Osborn, may have been based on merely individual variations.

MANDIBLE

The Divisão de Geologia e Mineralogia collection includes four nearly complete and several partial mandibular rami, and there are four partial jaws at Águas do Araxá. These represent a short-jawed form, with very short, somewhat down-turned symphysis and a short, narrow, lingual gutter. Aside from those general characteristics, as in Ecuadorian *Haplomastodon* and essentially as in *Stegomastodon*, the mandible does not seem to have any special or diagnostic characteristics.

VERTEBRAE

The combined Araxá collections include parts of six atlases and six axes. Their importance is great, because it was on the presence or absence of transverse foramina in these bones that Hoffstetter (1952) based generic separation of *Haplomastodon* and *Stegomastodon* and a proposed subgeneric division of both those genera.

D.G.M. No. 144M is a nearly complete atlas that closely resembles one from Ecuador figured as *H. chimborazi* by Hoffstetter (1952, fig. 48A) except that it has large, symmetrical, transverse foramina. An also nearly complete atlas in the Águas do Araxá collection has no trace of a transverse foramen on the left side, but has two complete and separate foramina and canals on the right side, the upper foramen being the larger. A somewhat less well-preserved Águas do Araxá specimen has a large transverse foramen on the left side and a distinctly smaller one on the right side. Above this foramen on the right is a large pit on the distal face, not piercing the bone and not communicating with the transverse canal. In the collection in the Divisão de Geologia e Mineralogia there are also three incomplete half-atlases. One has and the other two do not have a transverse foramen.

Measurements in millimeters of the Águas do Araxá specimens are as follows:

Maximum height	203	224
Maximum width	290	—
Height of neural canal	80	104
Width of neural canal	70	90

The most completely preserved axis resembles one referred by Hoffstetter (1952, fig. 48D) to *Hapломastodon guayasensis* in its broad, massive neural spine and large, wide neural canal, rounded above. The centrum, however, is somewhat broader, more as in a specimen referred by Hoffstetter (*ibid.*, fig. 48C) to *H. chimborazi*. The other, less well-preserved specimens seem to vary between

slender bridge of bone when the vertebrae were complete and that it represents, in fact, a transverse foramen. A somewhat similar notch was probably present on one side of a fourth, badly damaged specimen, the other side of which is too imperfect for the presence or absence of the notch to be determined.

A fifth, relatively well-preserved specimen has a similar notch, which was probably a

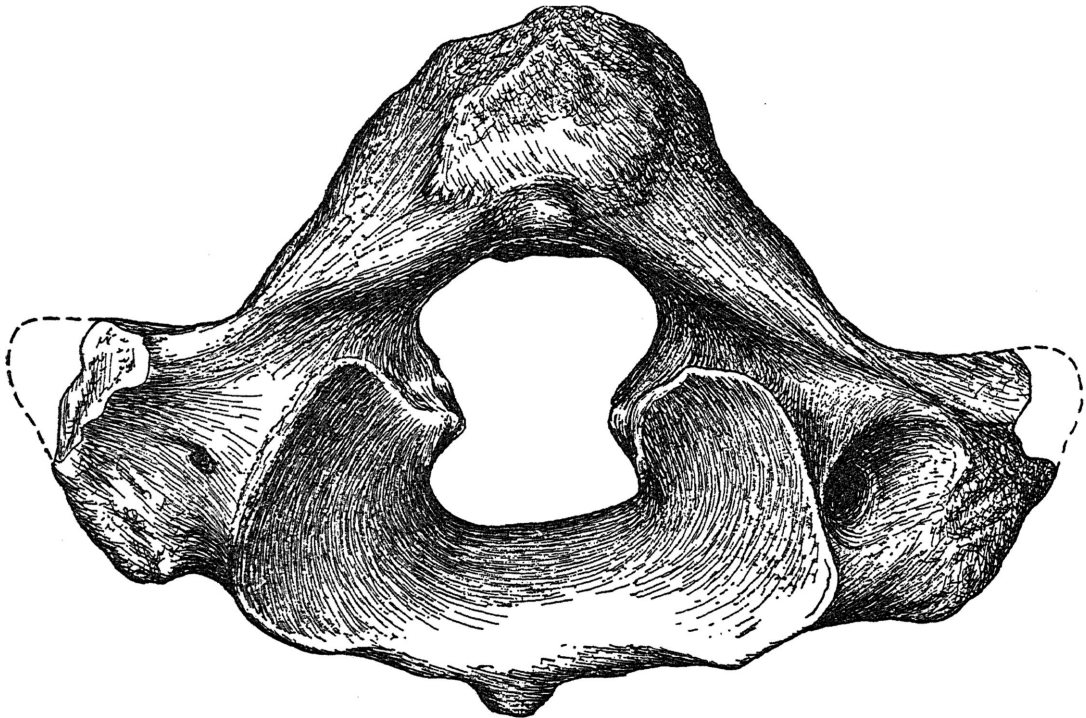


FIG. 6. *Hapломastodon waringi* (Holland). Nearly complete atlas at Águas do Araxá, posterior view, showing asymmetrical development of transverse foramina. $\times 0.45$.

those two Ecuadorian specimens, which we believe to be conspecific.

Because the transverse processes are worn and broken in all six specimens, it is unfortunately impossible to be absolutely certain about the transverse foramina. In three specimens there is on each side, on the posterior face of the transverse process and lateral to the articular surface for the third cervical, a broad notch or groove which communicates anterodorsally with a nearly vertical groove running towards the lateroventral part of the anterior face of the base of the neural arch. It is probable that the notch was closed by a

transverse foramen, on the right side. On the left side there is merely a shallow depression in the same position, with a smaller notch above it. This specimen probably had a transverse foramen on one side only. In any case, the structure of the two lateral processes was certainly not symmetrical. Finally, the sixth axis known to us from Araxá has no sign of notch or foramen on either side, and the possibility of the presence of a foramen is almost excluded. The ridge that, on specimens with notch or foramen, runs ventrally from the neural arch to a point above the notch and that bridged the foramen (if the notch

was closed and was a foramen) here runs down to and beyond the position of the notch without being interrupted or pierced.

Among these six axes, we judge that four probably had two transverse foramina, one probably had a foramen on one side and not on the other, and one probably had no transverse foramina. Although these observations are admittedly not quite certain, it is certain that the specimens differ considerably in the structure of the lateral processes and the region where the transverse foramen occurs if present. It is further certain that one specimen was markedly different in this region on the two sides.

It is clear that the transverse foramina of both axis and atlas are highly variable in this sample. As elsewhere emphasized, there is every reason to think that the sample rep-

resents a single species and even, in a fairly restricted sense, a single deme. It follows that no taxonomic value can at present be assigned to the individual presence or absence of transverse foramina in this group of mastodonts.

The collection includes a few partial vertebrae posterior to the axis, but they do not seem to be distinctive or of any particular interest.

LIMB BONES

HUMERUS

There is one essentially complete humerus in the Divisão de Geologia e Mineralogia collection from Araxá. It is adult, with the epiphyses fully fused, but measures only about 68.5 cm. in total length as opposed to 79 cm. for a specimen referred by Hoffstetter

TABLE 10
COMPARISON OF SOME LIMB BONES OF *Haplomastodon* FROM BRAZIL AND ECUADOR

	Length	Width of Distal Articulation	Antero- posterior Depth, Distal Articulation	Proximal Width	Proximal Depth	Ratio
Humerus						
<i>H. waringi</i> , D.G.M. Araxá	68.5	20.5	—	—	—	—
<i>H. waringi</i> , M.N. No. 553-V	—	23	—	—	—	—
<i>H. waringi</i> , M.N. No. 554-V	74	23	—	—	—	—
<i>H. "chimborazi"</i> , after Hoffstetter	79	21	—	—	—	—
<i>H. "guayasensis"</i> , after Hoffstetter	78	21.5	—	—	—	—
<i>H. "guayasensis"</i> , after Hoffstetter	—	21	—	—	—	—
<i>H. "guayasensis"</i> , after Hoffstetter	—	21.5	—	—	—	—
<i>H. "guayasensis"</i> , after Hoffstetter	84.5	21.5	—	—	—	—
Femur						
<i>H. waringi</i> , D.G.M. Araxá	—	18.3	20.1	—	—	1.10
<i>H. waringi</i> , M.N. No. 550-V	—	20.2	21.4	—	—	1.06
<i>H. "guayasensis"</i> , after Hoffstetter	99.0	21.0	21.2	—	—	1.01
<i>H. "guayasensis"</i> , after Hoffstetter	99.5	22.3	23.2	—	—	1.04
Tibia						
<i>H. waringi</i> , M.N. No. 79-V	53.8	—	—	21.7	15.2	0.70
<i>H. "guayasensis"</i> , after Hoffstetter	60.6	—	—	24.6	17.6	0.72
<i>H. "guayasensis"</i> , after Hoffstetter	61.3	—	—	24.7	16.5	0.68
<i>H. "guayasensis"</i> , after Hoffstetter	63.8	—	—	25.2	19.3	0.77
<i>H. "guayasensis"</i> , after Hoffstetter	64.9	—	—	24.6	18.1	0.74
<i>H. "guayasensis"</i> , after Hoffstetter	68.1	—	—	27.2	21.6	0.79
<i>H. "guayasensis"</i> , after Hoffstetter	69.5	—	—	26.9	20.6	0.77

(1952, fig. 49) to *H. chimborazi* and (in round numbers) 78 and 84.5 cm. for specimens referred by him to *H. guayasensis*. Morphologically, our specimen is very similar to Hoffstetter's *H. "chimborazi"* (*loc. cit.*) and almost equally similar to specimens referred to *Stegomastodon platensis* (Cabrera, 1929, fig. 20) and to *Cuvieronius hyodon* (Boule and Thévenin, 1920, pl. 8, figs. 2-3). It differs slightly from Hoffstetter's *H. "guayasensis"* (*ibid.*, fig. 57A), but the difference seems to us well within the probable range of individual variation. In short, it appears that the South American mastodonts, at least, show no specific or, indeed, generic differences in this bone, unless such differences appear in the mean dimensions and proportions of larger samples than have yet been available for comparison. A second humerus, at Águas do Araxá, was larger and probably in the size range of the Ecuadorian specimens. It has, however, been extensively restored and gives no other useful information.

RADIUS AND ULNA

The Araxá collection in the Divisão de Geologia e Mineralogia includes nearly complete, adult, associated radius and ulna, two nearly complete adult dissociated ulnae, and another dissociated ulna lacking the olecranon. The maximum length of the most complete ulna is 57.5 cm. The two dissociated ulnae, each of which may have lost some bone distally, are 57.5 and 51 cm. in length as preserved. An ulna referred to *H. "guayasensis"* by Hoffstetter (*ibid.*, fig. 57B) is 81 cm. in total length. Our specimens otherwise seem to present no important differences from Hoffstetter's, although the olecranon may tend to be a little more extended proximally.

FEMUR

The Divisão de Geologia e Mineralogia collection includes one femur, lacking the distal end, and the distal half of another. One nearly complete femur and another extensively restored are preserved *in situ* at Águas do Araxá. The successive studies of Boule and Thévenin, Cabrera, and Hoffstetter have established a fairly probable distinction between the femora of *Cuvieronius*, on one hand, and those of *Stegomastodon*

and *Haplomastodon*, on the other. In *Cuvieronius* the head of the femur is set at a stronger angle to the shaft, extending proximomedially and rising little above the greater trochanter. In *Stegomastodon* and *Haplomastodon* the head projects more proximally and rises markedly above the greater trochanter. The Araxá specimens are of the *Stegomastodon-Haplomastodon* type. The head projects even farther proximally than in the specimen referred by Hoffstetter (1952, fig. 58A) to *H. "guayasensis,"* and the greater trochanter is somewhat less massive. In these respects the Araxá specimens resemble those referred by Cabrera (1929, figs. 33-34) to *Stegomastodon superbus*. The possible taxonomic distinctions within the *Stegomastodon-Haplomastodon* type of femur suggested by Cabrera and by Hoffstetter are, however, based on so few specimens that their taxonomic validity cannot be accepted as established. We also question whether the general similarity of *Stegomastodon* and *Haplomastodon* femora indicates special relationship of the genera.

The distal view of the Divisão de Geologia e Mineralogia specimen closely resembles that of *Stegomastodon* (their "*Mastodon Humboldtii*") given by Boule and Thévenin (1920, fig. 23). The transverse width across the articulation is 183 mm., and the antero-posterior depth is 201 mm., ratio 1.10. These figures for the better Águas do Araxá specimen are 213 and 245 mm., ratio 1.15. Corresponding measurements of two specimens referred to *H. "guayasensis"* by Hoffstetter (1952, p. 216) are 209.5 by 212 mm. and 223 by 232 mm., ratios 1.01 and 1.04. In this respect, too, the Araxá form is like some specimens referred to *Stegomastodon*, but again the taxonomic significance is uncertain.

CONSPECIFICITY OF THE ÁGUAS DO ARAXÁ SAMPLE

The mastodonts of Araxá must be referred to a single species. It is probable, moreover, that they represent a single deme or "Mendelian population." As regards the deeper part of the deposit at least, which contained all the well-preserved bones and teeth, the filling of the pothole was evidently rapid. The animals represented here must be considered contemporaneous for taxonomic purposes.

Their remains could not have been carried far, and all these animals must have died within a small area. None of the distributions of variates is demonstrably, or even suggestively, bimodal or polymodal, even to the extent of reflecting possible sexual dimorphism. With all their variation, these mastodons are obviously all closely related. All these circumstances make it biologically incredible that more than one species is present, and so closely associated a sample from a single species is practically certain to have come from one deme.

The Araxá teeth differ among themselves as much as do those of many proposed species and even some proposed genera of mastodons. In our opinion this does not invalidate the reference of the Araxá specimens to a single species. On the contrary, it strongly suggests that species and genera founded on differences comparable to those within the Araxá sample are invalid or at least have not been adequately distinguished or defined.

For reasons fully given on later pages, the Águas do Araxá mastodons are referred to *Haplomastodon waringi*.

OTHER OCCURRENCES OF MASTODONTS IN BRAZIL

THE FOLLOWING LIST, by territories and states in sequence roughly from north to south, includes all finds of mastodonts in Brazil known to us from specimens or publications. Many discoveries recorded in the literature are now completely indeterminable taxonomically. Even specimens in hand, or well figured, are commonly not determinable with complete assurance. The only adequate sample of unified origin is that from Águas do Araxá. Identifications of single teeth do not carry conviction, and generally one wants at least an association of cheek teeth and tusks, represented by few finds in Brazil. In general, however, we feel that well-preserved teeth known at first hand may be referred with sufficient probability to *Haplomastodon waringi* if their characters are definitely within the range of the Águas do Araxá sample. As will be seen, that is true of most of the adequately known finds in Brazil. A few exceptions do occur and are individually discussed.

TERRITORY OF AMAPÁ

A well-preserved crown of M^2 (D.G.M. No. 423M) in early wear stage 3 was found in a *garimpo de ouro* in the Rio Araguari in 1940. This is a large tooth (L 135 by W 88 mm.), 3 mm., or over 2 per cent, larger than any in the Águas do Araxá collection and within, but near, the upper limit in width for that collection. It is morphologically similar to the Araxá teeth and may belong to the same species.

STATE OF AMAZONAS

A good right M_3 from the region of the upper Juruá River is in the Departamento de Geologia e Paleontologia of the Faculdade de Filosofia Ciências e Letras, Universidade de São Paulo (No. 2538, former Paixão collection No. 2738). The tooth is the fully simple *Haplomastodon* type. The measurements are: L 182 by W 79 (W on second lophid, 81). The fifth lophid has three nearly fused conules and no definite conule posteriorly. The tooth is within the range of the Águas do Araxá sample.

TERRITORY OF ACRE

Mastodont remains are reported as having been found at several localities in the territory, in white and red argillaceous beds in the cut banks of the rivers Juruá, Jaminaua, Jordão, and others (Moraes Rêgo, 1930, p. 10).

A fragment of the posterior part of the crown of a mastodont molar was collected by Epaminondas Jácome, in 1926, at the mouth of the Chandless River, tributary of the upper Purus River, and sent to the Museu Nacional (No. 310-V). The fragment is insufficient for exact identification, but it is probably from *Haplomastodon*.

From the region of the upper Juruá River came a fragment of right mandible with roots of M_{1-2} and part of a left lower jaw with dm_4 , broken and in late wear stage 4, and roots of M_1 . Both fragments are in the Museu Nacional (Nos. 309-V and 311-V.) Both of them demonstrate the presence of a short-jawed mastodont in that region but are otherwise unidentifiable. The dm_4 of M.N. No. 311-V measures approximately 85 by 45 mm. (at the lower limits of OR in the Águas do Araxá sample). The coronal pattern is completely obliterated by wear. There is no evident difference from the Araxá sample, but the specimen is not positively identifiable.

In 1949, the Museu Nacional received from Luis Antonio M. Pedreira a fragment of right lower jaw with the M_3 preserved (M.N. No. 2.122-V), two fragments of pelvis (M.N. Nos. 2.123-V and 2.124-V), a fragment of scapula (M.N. No. 2.125-V), a centrum of a vertebra (M.N. No. 2.126-V), and the capitulum of a femur (M.N. No. 2.127-V) from a mastodont, which were collected, together with megathere remains, in the "Cachoeira do Museu," Juruá River, in the *município*¹ of Cruzeiro do Sul. The mandible is of the brevirostrine type, and the M_3 is essentially tetralophodont, with a small fifth lophid which bears four small cusps in line, its measurements

¹ In Brazil a *município* is an administrative unit within a territory or state, corresponding more nearly to a county than to a municipality.

being 200 by 90 mm. The molar is well within the range of the Araxá sample, and is structurally indistinguishable from the specimens of the Araxá collections. It is in stage 3 of wear. Single trefoils are well developed on the pretrites, and three small cusps are present behind the fifth lophid.

The Museu Paraense Emílio Goeldi, in Belém do Pará, has some isolated fragments of lower jaws and several lower molars of mastodonts from Acre Territory. All the lower molars have single trefoils as in *Cuvieronius* and *Haplomastodon*. A fragment of a right lower jaw has M_{1-2} preserved. Both molars are trilophodont, with two small posterior cusps, both lateral to the main axis of the tooth. The M_1 is in stage 2 of wear, and the M_2 is not completely erupted and is in 0 degree of wear. The anterior accessory cuspule of the pretrites is higher than the posterior one. Wear begins on the pretrite and on this cuspule. The posterior accessory cuspule begins to wear only when the anterior cuspule and the main pretrite cusp are in an advanced stage of wear. The posttrites are simple and essentially without accessory cusps. Rudimentary accessory cusps are sometimes present, especially in the two anterior posttrites, but they are insignificant in size. The posttrites are formed of two coalesced, transversely placed cusps of the same height. Wear on the posttrite begins on the two cusps at the same time, so that two islands of dentine are first formed by wear on the posttrite. With further wear these coalesce. The measurements (in millimeters) of the two molars are: M_1 , L 111.5 by W 73; M_2 , L 133 by W 80. This specimen was collected by Teixeira da Costa in 1903 in a spot called "Cachoeira," on the upper Juruá River.

A fragment of a left lower jaw from a completely adult individual bears the last molar (M_3). The molar is essentially tetralophodont, with a fifth small lophid with three transverse cusps, and with one posterior cuspule immediately behind the more external of those three. The molar is in stage 4 of wear and was collected in the region of the upper Juruá River or in the region of the upper Purus River, its exact locality being uncertain. The measurements of the M_3 are L 215 by W 90 mm.

The other fragmentary specimens in the

same collection were collected in the region of the upper Juruá River. An anterior fragment of a right M_3 is from Iracema, Juruá River, where it was collected by Brito in 1904.

All the specimens from Acre preserved in Belém agree in size and morphology with the Araxá sample. They are almost certainly from *Haplomastodon waringi*.

A fragment of right mandible with M_2 in late stage 4 of wear was collected in the region of the upper Juruá River and given to the Museu Nacional (No. 311-V) by Rego Barros in 1915. The M_2 measures L 210 by W 87 mm. The posterior lophids are distinctly oblique, and the fifth lophid is well developed. The specimen is well within the range of the Águas do Araxá sample.

STATE OF PARÁ

An anterior fragment of a right M_3 with the two first lophids preserved comes from a steep bank of an *igarapé*, near the small town of Chaves, in the county of the same name, on the island of Marajó. It is simple, with few conelets and single trefoils. The wear is incipient. No standard measurement is possible, but the fragment is like the simpler Araxá variants on parts present. The specimen was collected by Orlando Luciano Martins de Moraes Rêgo in 1952 and is in the collection of the Museu Nacional (M.N. No. 2098-V).

A posterior fragment of a right (?) lower molar, perhaps M_1 , in stage 4 of wear, was collected in one of the islands of the Amazonas delta (Marajó, Condeixa, or Pacoval) and given to the same museum (M.N. No. 284-V) in 1941 by Rubens Ayres do Nascimento. It resembles M.N. No. 2098-V and may be tentatively referred to the same species, probably *Haplomastodon waringi*.

The presence of these fragmentary molars on islands of the Amazonas delta is probably due to transportation from farther up the river, along with the enormous amounts of sediments constantly being deposited on the delta.

STATE OF MARANHÃO

Fossil remains of "*Mastodon*" are reported as having been collected in a sandstone deposit near Turiassú, in the northern part of the state (Gomes, 1934, p. 64).

STATE OF CEARÁ

Large fragments of bones of a mastodont were discovered in the *município* of Baturité (Burlamaqui, 1855, p. 5), and in Lagoa de São Pedro, Maria Pereira (Moraes, 1924, p. 53). Additional mastodont remains (mandible and tibia) were discovered in Jaguaribe-Mirim (Moraes, 1924, p. 52).

"Bones of huge Mammals, Mastodons and Megatheria, are abundant in various parts of the province, and perfect skeletons have been found. Some of the localities are the following: Santa Catharina (lagoa), Sítio Cronzó, at the foot of the Serra Ybiapaba at Inhamuns; between Cratheús and Quixeramobim; Timbauba; in the place called Sucatinga a skeleton was found in an excavation, and part was sent to Rio; at Sta. Cruz, in a lagoa, another skeleton was found" (Hartt, 1870, p. 471).

A right lower jaw, with M_2 preserved, found in the *município* of Quixadá, and now in the collection of the Museu Rocha in Fortaleza, was referred by Paula Couto (1955, pp. 209-210), with doubt, to *Notiomastodon*. We can say now that it is almost certainly from *Haplomastodon waringi*. M_2 is in stage 3 of wear, and its measurements are L 220 by W 82. The fifth lophid bears three nearly fused conules and a short talonid. The mandible is morphologically similar to those from Pernambuco and Araxá. It has single trefoils and is of the simple *Haplomastodon* type.

A right M_3 , probably of the same species, from the Pleistocene of Ceará is in the collection of the American Museum of Natural History (No. 45875). It is in stage 2 of wear, and its measurements are L 245 by W 89.

Some mastodont bones in the Museu Nacional (Nos. 554-V and 561-V) were collected in the southern part of the state in 1919. The humerus (No. 554-V), with the supinator crests broken, is more robust than a humerus from Araxá in the collection of the Divisão de Geologia e Mineralogia and nearly as long as Ecuadorian specimens referred by Hoffstetter to *H. chimborazi*, but wider distally.

The palatal part of a young skull, with left M^2 , roots of left dm^4 and M^1 , roots of right dm^4 , and partial alveoli of M^{1-2} , from Lagoa São Pedro, Maria Pereira *município*, is in the Divisão de Geologia e Mineralogia (No. 26M). The left M^2 is in stage 0 of wear,

and its measurements are L 146 by W ca. 85 mm. It resembles *Haplomastodon* but is relatively complex, with fairly well-developed posttrite trefoils. The alveoli for the tusks are already large, the diameter in the socket being about 75 mm.

STATE OF RIO GRANDE DO NORTE

During the dredging of the port of Natal, in the locality of Baixinha, at the entrance of the port, parts of a skeleton and two tusks of a mastodont were discovered. The fossils were buried in the calcareous sandstone of the reefs. The localization of the bones in that spot was probably due to transportation by running water (Moraes, 1924, p. 52).

A tusk from the same locality was given to the Museu Nacional (No. 548-V) by Artur Neiva in 1924. The tusk is gently curved upward, with no band of enamel and no torsion, as in *Stegomastodon* and *Haplomastodon*. The species is possibly *Haplomastodon waringi*.

A rolled fragment of the posterior end of a left M_3 , collected by Dioclesio Duarte in the *município* of Parelhas is in the Divisão de Geologia e Mineralogia (No. 21M). The third and fourth lophid are distinctly oblique. The fifth lophid is represented by two large cones, and they are followed by a single conule. No standard measurements are possible. The tooth, as far as preserved, can be almost exactly matched in the Araxá collection, but that does not amount to a positive identification.

STATE OF PIAUÍ

A small fragment of a right lower jaw, with M_2 almost complete (the anterior end of the first lophid is lacking), was collected in a small lake on the farm of São Vitor, *município* of São Raimundo Nonato. The molar is tetralophodont, with a fifth small lophid composed of three conules, the middle one very small. The tooth is in degree 3 of wear, and its measurements are L 210 by W 70. This fragment was presented by Antonio Coelho and P. do Aragão in 1933 to the Museu Nacional (No. 400-V). The species is almost certainly *Haplomastodon waringi*.

STATE OF PERNAMBUCO

Branner (1902, p. 134; 1906, p. 284) mentions the occurrence of fossil bones of mas-

todonts and other animals in a locality known as Lagoa de Lagea, 8 leagues east of Águas Belas. The bones were discovered in 1873 during the excavation of an artificial reservoir for water. Many fragments of bones of mastodonts and of other mammals, some of enormous size, were obtained from a similar excavation made in Lageiro, about 3 leagues from Lagoa de Lagea on the road leading to Pedra Pintada.

At Cabôclo, a small town in the western part of the state, near the border of the State of Piauí, Moraes Rêgo (19—), cited by Moraes (1928, p. 11), discovered several fossil bones of mastodonts in siliceous argillaceous beds.

Fossil remains of Pleistocene mammals, including mastodonts, were found in alluvial deposits filling natural pools at several localities, such as Serra Verde, Riacho da Onça, Sítio Chata, in Santa Terêsa, Alagoinhas, and Rio Branco. The mastodonts were classified as *Mastodon humboldti* Cuvier (Moraes, 1928, pp. 77–78). They have not been available for restudy, but were probably *Haplomastodon*.

Paula Couto (1944, pp. 201–202) referred to *Mastodon humboldti*, with doubt, a fragment of a left lower jaw with a molar (M_3) preserved, collected in Sítio Laje Grande, *município* of Pesqueira, by Gerson de Faria Alvim (Alvim, 1939, p. 9). The specimen is in the collection of the Divisão de Geologia e Mineralogia (No. 28M). The M_3 is broken anteriorly. Its fifth lophid has two small conelets followed by two large ones, each pair on each side of the longitudinal axis of the tooth. The molar is in degree 1 of wear and measures L 205 (ca.) by W 87. The species may now be reidentified as probably *H. waringi*.

Liais (1872, p. 415) mentioned a molar tooth of a mastodont from the Pleistocene of Pernambuco with two opposite trefoils, and classified it with doubt as *Mastodon humboldtii* (sic). If Liais' observation of double trefoils is correct, the tooth may have belonged to *Stegomastodon* or *Notiomastodon*, but it could be from *Haplomastodon waringi*, which frequently has apparent double trefoils in an advanced stage of wear.

Halfeld (in Burlamaqui, 1855, p. 5) mentions fossil bones, like those of mastodonts, found in the locality of Cabôclo, *município* of Boa Vista.

A tusk of a mastodont was found in Rio

Branco, together with several other fossil remains. From Cabôclo and Jatobá come some remains of mastodonts which are in the collections of the Divisão de Geologia e Mineralogia (Moraes, 1924, pp. 52–53).

Fossil bones of mastodonts are reported as having been discovered in 1954 in the "Fazenda Pau Ferro," district of Águas Belas, *município* de Águas Belas. To judge by previous discoveries, it is possible that the remains are from *Haplomastodon waringi*.

The collections of the Divisão de Geologia e Mineralogia and the Museu Nacional include several specimens of mastodonts from Sítio Laje Grande, *município* of Pesqueira. D.G.M. No. 28M is a fragment of right mandible, with slightly broken M_3 in late stage 3. M_3 measures L 215 by W 74 mm., and has single trefoils. Its fifth lophid is well developed, and the third and fourth lophids are slightly oblique. The tooth is well within the range of the Araxá sample in all respects.

Another fragment of right mandible with the same number (No. 28M) in the Divisão de Geologia e Mineralogia collection, collected in that same spot, has dm_4 shed, M_1 in place but in stage 4 and badly broken, M_2 complete, in stage 1. This is one of a lot of fine specimens accessioned with the same data as the preceding specimen of this list. It is obviously a different individual from the preceding. M_2 measures L 164 by W 81 mm. It is distinctly wider on the third lophid (91 mm). The pretrite is distinctly posterior to the posttrite on the first lophid, slightly posterior on the second lophid, and nearly opposite on the third lophid. There are strong pretrite but not posttrite trefoils. Each lophid has two conules between the main cones. Those characters can be closely matched in the Araxá sample and in (other) *Haplomastodon*. This tooth is, however, unique in having a strong fourth lophid, narrower than the third but otherwise nearly as well developed, with two main lateral cones and two intermediate conules, here arching somewhat anterior to the main cones. The fourth lophid is followed by two tiny median conelets. The fourth lophid of this M_2 is more fully developed than in any other South American specimens known to us. It is decidedly larger and more truly loph-like than the M_2 of *Curieronius hyodon* selected by Boule and Thévenin (1920, pl. 5, fig. 2) as an extreme variant

and considered tetralophodont. In *Haplomastodon* and, as far as we know, the other South American genera, the third lophid of M_2 is normally followed by a single median cone. Variable additional conules and conelets commonly occur, but not quite to the extent of forming a true lophid as in the present specimen. Even here, however, the fourth lophid is somewhat less developed than is usual in the genus *Tetralophodon* and its established close allies or probable synonyms.

In correlation with the development of a fourth lophid, this tooth is much longer than any in the Araxá collection. The critical ratio $(x-\bar{x})/s$ in comparison with that of the Águas do Araxá sample is 2.8, corresponding

tooth is wider, but not precisely measured on the third lophid). There is considerable complexity of conelets, but the trefoils are essentially single. There is a short symphysis and no trace of a lower tusk even at this early stage, the youngest of any specimens examined by us. No difference from the Araxá population is demonstrated. In the same collection is a young upper tusk (No. 56-V) most surely of the same individual as 55-V. As preserved, with the distal end of the tusk and the thin edge of the proximal, intra-alveolar end somewhat broken, this tusk is about 36.5 cm. in length. Near the middle of the preserved part it is 41 mm. in maximum, and 36 mm. in minimum, diameter, ratio 1.28.

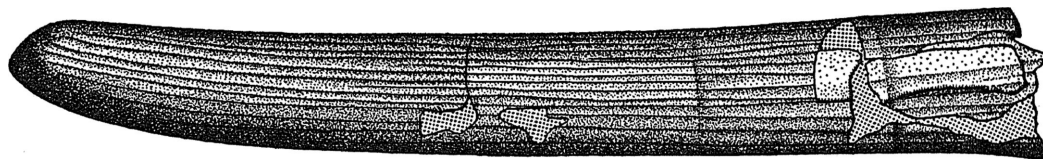


FIG. 7. *Haplomastodon waringi* (Holland). M.N. No. 56-V, tip of upper tusk of young individual. From Sítio Laje Grande, Pernambuco. $\times 0.40$.

with a random sampling probability around 0.005, a highly significant lack of agreement with the hypothesis that the specimen is from a species or population with LM_2 distributed as in the Araxá sample. The tooth might represent a genus otherwise unknown in South America, but it seems more likely that it is an aberrant (mutant?) *Haplomastodon*.

Vidal (1946, pp. 9-10, pls. 15-18) referred to *Cuvieronius humboldtii* (sic) a collection of mastodont remains made by himself in Sítio Laje Grande, Pesqueira, in 1939, together with fossil bones and teeth of crocodiles, *Macrauchenia*, *Toxodon platensis*, *Equus*, deer (*Hippocamelus sulcatus*?), megatheres, and mylodonts (*Mylodon*?). The collection is in the Museu Nacional.

Castellanos (1948) proposed a new specific name, *Notiomastodon vidali*, for two of those specimens (M.N. Nos. 55-V and 56-V). One of these specimens is part of a right mandible (No. 55-V) with dm_2 shed, posterior half of dm_3 in stage 3 of wear, and dm_4 in early stage 1. Dm_3 is 55 mm. in width, and the measurements of dm_4 are L 87 by W 50, W having been measured on the middle lophid (the

proximal end an enamel band 16 mm width is preserved. The band probably extended originally to the distal tip but spalled off except for 72 mm. of its length near the proximal end, in a position it was probably still all intra-alveolar in. The tusk has a slight longitudinal curvature and still slighter, barely noticeable, spiral sion. Both M.N. No. 55-V and M.N. No. 56-V were included by Castellanos (op. cit.) in the type of his species *Notiomastodon vidali*. They are not distinguishable from Araxá specimens and probably belong to *H. waringi* with which *N. vidali* must be considered synonymous.

One mandible from this locality, with both sides preserved, has M_{2-3} preserved, M_1 having been shed. M_2 is in late stage 3, and M_3 in early stage 1, of wear. M_2 is broken and stored in both sides, but it originally measured very approximately L 140 by W 85 mm. M_3 is not fully erupted and cannot be precisely measured, but the approximate measurements are L 225 by W 100 mm. The molars have single trefoils, and the pretrites and posttrites are nearly opposite. In length M_{2-3} are within the range of those of Araxá.

but near the upper limit. The width of M_2 is about 5 mm., or 6 per cent, and the width of M_3 is about 10 mm., or 11 per cent, above the limit for the Araxá collections. The critical ratio $(x - \bar{x})/s$ for the length of M_3 compared with the Águas do Araxá mean is about +1.9. The unworn cones of M_3 are high, compared to those of the Araxá sample, and they are

M.N. No. 88-V is a fragment of left mandible with scant remains of badly broken M_3 . The specimen is a mastodont but is otherwise unidentifiable.

M.N. No. 83-V is a fragment of right lower jaw with M_1 , broken and worn, and anterior root of M_2 . M_1 measures roughly L 115 by W 70 mm. The third lophid has double tre-

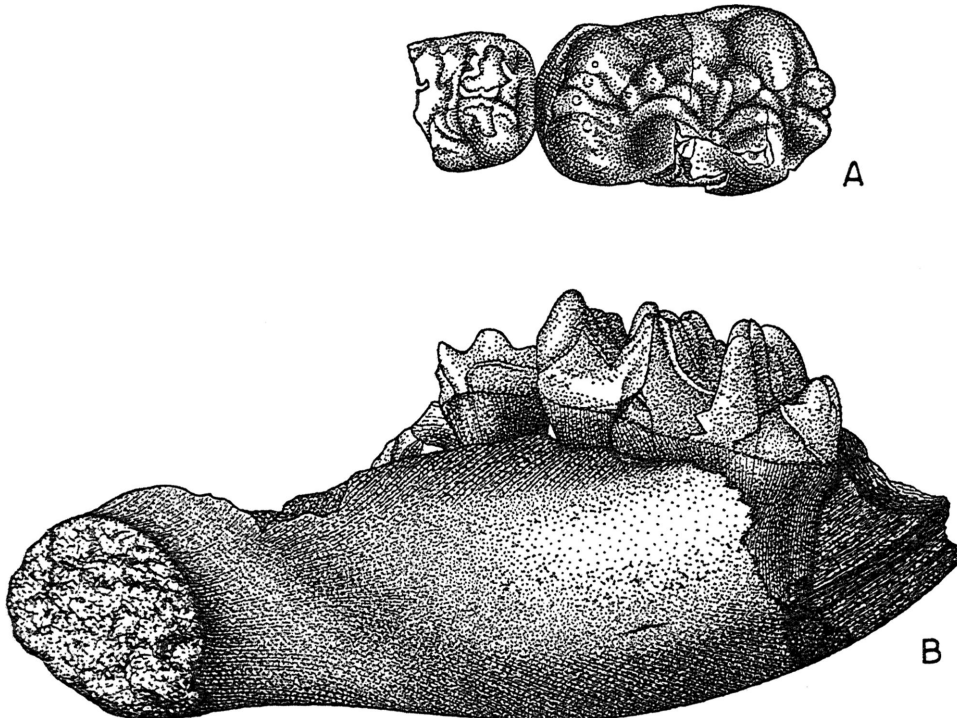


FIG. 8. *Haplomastodon waringi* (Holland). M.N. No. 55-V, part of right mandible, from Sítio Laje Grande, Pernambuco. A. Crown view showing posterior half of dm_3 in stage 3 of wear and dm_4 in early stage 1. B. Lateral view with dm_3 shed, half of dm_3 , and dm_4 . $\times \frac{1}{2}$.

more nearly vertical, less procumbent, than is usual in that sample. The differences from the Araxá sample are similar to the differences of Hoffstetter's (1952) Ecuadorian *Haplomastodon guayasensis* from *H. chimborazi*, two names which we believe to be synonymous with *H. waringi*. As in the case of the Ecuadorian specimens referred by Hoffstetter to *H. guayasensis*, the present jaw may represent merely a robust individual variant or a slightly different population or subspecies of *H. waringi*. The specimen is indistinguishable from *H. "guayasensis"* on any grounds, but reference to that probably invalid taxon, even as a subspecies, would be unjustified.

foils, but the posttrite trefoil is poorly developed, no more distinct than in equally worn specimens from Araxá. M_1 is somewhat more robust than in the latter. The specimen is not identifiable as to species, but shows no clear distinction from the Araxá sample.

M.N. No. 59-V is a right M^3 in stage 1 of wear. It measures L 182 by W 79 mm. Its enamel is unusually rugose. Many cusplets are present (six poorly separated cusplets on the crest between the main cones of the second loph). Keels are seen on the anterior and posterior sides of the posttrite cones. A fairly good fifth lophid, with four united conules, is present and followed by one vague talon

conule. The tooth is not quite like any Araxá specimen, but could well be a variant of the same species.

M.N. No. 78-V is a fragment of right M^3 bearing the lophs 3 to 5, in stage 0 or stage 1 of wear. Its width is 81 mm. The pattern is simple, with single trefoils and few cusplets. The fifth lophid has two large cones. This fragment is closely similar to Araxá specimens.

M.N. No. 74-V is a rolled and broken posterior end of right M_2 . Its fifth lophid is represented by a single large, median cone, nearly circular in section. It is probably less developed than in any Araxá specimen, but the difference is slight.

M.N. Nos. 60-V, 61-V, and 75-V are also fragments of molars probably referable to *Haplomastodon*.

M.N. No. 57-V is a left M_2 , broken antero-obliquely, in stage 1 of wear. Its measurements are L roughly 220–225 by W 82 mm. It is closely similar to Araxá specimens.

M.N. No. 79-V and 80-V are a tibia and restored fibula. They are somewhat smaller than Hoffstetter's "*guayasensis*" series. The size of the proximal end is in the range for "*guayasensis*," but the relative depth is well below the average for that series.

The whole collection from Sítio Laje Grande demonstrates with exceptional clarity that the common form, at least, at that locality is a *Haplomastodon*. Association of the single-trefoiled molars with an only faintly spiral juvenile tusk bearing an enamel band is conclusive as to the genus. Except for the tetralophodont M_2 (included under D.G.M. No. 28M), all the specimens are within the probable population range indicated by the Araxá sample and can be referred to *H. waringi* with some confidence. The significance of the aberrant M_2 is not clear.

STATE OF PARAIBA

There are fragments of bones of mastodonts from Paraíba in the Museu Nacional (Paula Couto, 1944, p. 202). They are from the *município* of Caiçara and were given to the museum (M.N. No. 278-V) by Antonio Novarro da Costa in 1931. They are not more precisely identifiable.

According to Burlamaqui (1855, pp. 9–10), the French naturalist Brunet made a good

collection of mastodont remains in the interior of the state.

A posterior end of left M_2 from Fonte do Brejo das Freiras, Rio de Peixe basin, Antenor Navarro, was sent to the Divisão de Geologia e Mineralogia (no number) by David Felinto Cavalcanti. The fourth lophid is oblique and has a semicircle of four poorly distinguished cones, and it is followed by two strong conules of different heights. No standard measurements are possible, but the fragment suggests a tooth similar to teeth from Araxá but unusually robust.

Remains of a mastodont were found in Fazenda Damião, *município* de Cuité, and sent to the Museu Nacional by Valdir de Andrade Vaz in January, 1955.

STATE OF ALAGOAS

According to Branner (1902), large fossil bones were reported to have been found at Meirús, a small town 3 leagues northeast of Pão de Açúcar. Branner did not see either the excavation (a watering pond for cattle) or the fossils, but he learned that some of the bones were many times as large as those of an ox. It is possible that those bones were from mastodonts.

Mastodont remains have also been found in "Lagoa dos Elefantes" (Branner, 1906). A tusk from the "Lagoa dos Elefantes" is in the Museu Nacional (No. 545-V). It is restored in part and is morphologically similar to tusks of *Stegomastodon* and *Haplomastodon*. It is gently curved upward, with no band of enamel and no torsion.

Halfeld (*in* Burlamaqui, 1855, p. 5) said that large bones like those of mastodonts were collected near the Pão de Açúcar, on the left bank of the São Francisco River. The same Halfeld also referred to fossil bones of a mastodont found by himself at the mouth of the Riacho da Vaca, in Lagoa da Pedra (Hartt, 1870, p. 418).¹

From the vicinity of Lagoa da Pedra an

¹ Halfeld (*loc. cit.*) gives the position of the mouth of the Riacho da Vaca as being "on the south side of the river [São Francisco]." According to the millionth map of Hispanic America of the American Geographical Society, Lagoa da Pedra is therefore in Bahia and not in Alagoas. It should be noted, however, that Lagoa da Pedra is situated quite close to the meeting point of the present boundaries of Alagoas, Bahia, and Sergipe.

immense collection of bones and teeth of mastodonts was sent to Rio de Janeiro (Hartt, 1870, p. 419), but the present location of those fossils is unknown.

Rodrigues Carvalho (*in* Burlamaqui, 1855, p. 18) made a good collection of fossil remains of several genera of mammals, including glyptodonts (plates of carapace) and mastodonts (tusks and bones), during the excavation of a *cacimba*¹ in the small town of Aldêa, or Poço Grande *município* of São Luiz de Quitunde. Mastodont remains were also found in Poço, *município* of Penedo, together with fossil remains of another mammal (Burlamaqui, 1855, p. 18).

Oliveira (1920, p. 38) refers to fossil remains of mastodonts found in the *município* of Anadia in the vicinity of the São Francisco River.

A fragment of left M³ with the first three lophs was found in Villa de Caçambinha, *município* of Palmeiras dos Índios, and given to the Divisão de Geologia e Mineralogia (No. 415-M) by Flavio da Rocha. The width across the second loph is 95 and across the first loph 98 mm. In size and morphology the specimen agrees well with some from Araxá.

STATE OF SERGIPE

Mastodont bones were reported from Sítios Novos, 5 leagues northeast of Propriá (Burlamaqui, 1855, p. 5).

STATE OF BAHIA

Ayres de Casal (1817, pp. 77-78) mentioned a skeleton of an animal similar to an elephant found in a water hole near the small town of Rio das Contas, saying that one molar, lacking the fangs, weighed 4 *libras*. The animal was doubtless a mastodont.

Holland (1920, pp. 224-232) refers to mastodont remains collected by Waring in Pedra Vermelha, and "uncovered by some workmen, who were engaged in enlarging and cleaning out a 'water hole.'" Among the fossils were fragments of mastodont molars and a right lower jaw, with three teeth preserved, the middle one greatly fractured. These specimens are the types of "*Mastodon*"

waringi Holland, and they are discussed on a later page. The mastodont remains were found together with remains of *Smilodon neogaeus* Lund (?), *Toxodon burmeisteri* Giebel, horses, *Megatherium*(?), and glyptodonts.

Moraes Rêgo (19—), cited by Moraes (1928, p. 11), mentions fossil bones of several Pleistocene mammals, among them mastodonts, found in clay beds of his "Formação das Vasantes," in the state of Bahia.

Branner (1906) refers to mastodont remains found in Santa Luzia and Monte Alto.

According to Burlamaqui (1855, p. 4) part of a skeleton of a mastodont was discovered by Fernando Halfeld in the year 1853, during the excavation of a *cacimba* (water hole) on the right bank of the São Francisco River, immediately below the Paulo Afonso fall, 1 league from the Sal River or from "Pedra do Navio." The bones had been deposited in a concavity in granite, filled with sandstone and humus.

Similar remains were found in Caldeirões, near the locality of Jeremoabo (Halfeld, *in* Burlamaqui, 1855, p. 5).

Two incomplete mandibles of mastodonts, with the teeth broken away, are reported by Moraes (1924, p. 54) as having been found in Santa Luzia.

According to Moraes Rêgo (1926, p. 36) fossil bones of mastodonts and megatheres were found near Pilão Arcado, Chique Chique, and in the "Serra do Assuruá."

Hartt (1870, p. 298) refers to bones and teeth of mastodonts found in the vicinity of the Rio de Santo Antônio, near Villa do Rio das Contas, and near the old "fazenda de Bom Jesus de Meira," 8 leagues from the Villa, buried in the soil.

Spix and Martius (1828) discussed remains of mastodonts and other extinct animals from the shallow hollows excavated by the *sertanejos* in the hills of the west side of the base of the "Serra de Tiuba"² in order to make tanks for holding rain water (Hartt, 1870, p. 325). The same authors (1828, pp. 747-748) refer to fossil bones of mastodonts discovered in Caldeirões, between "Serra de Tiuba" and Monte Santo. In addition, they

¹ A natural excavation on the surface of crystalline rocks, filled with alluvial material.

² Hartt (1870, p. 324) incorrectly refers to this mountain as the "Serra de Itauba."

refer to finds made at the Fazenda das Almas¹ and in caves at Morro de Chapeo, near the source of the Rio de Salitre. The remains were referred by them, with doubt, to *Mastodon giganteus* Cuvier, *M. humboldtii* Cuvier, or to an unknown species. The suggested identifications cannot now be taken seriously.

A posterior part of a right M_3 from Monte Alto is in the Departamento de Geologia e Paleontologia, Faculdade de Filosofia, University of São Paulo (No. 3-1201, former Paixão collection No. 2076). It has single trefoils as in *Haplomastodon*. Its fifth lophid has three well-defined cones, followed by a talonid with one cone and two vague conelets on the sides. The molar is said to be from Monte Alto, Bahia. It is 142 mm. long.

The distal end of a humerus of a mastodont was found in Jacobina (M.N. No. 554-M).

STATE OF MINAS GERAES

Mastodont remains are particularly abundant in this state, and they were among the first fossils reported from Brazil. Spix and Martius (1828, pp. 747-748) said that mastodonts had been found in Vila do Fanado, Itacambira, Formiga, and Brejo das Almas as well as in caves and deposits of marl in Santo Antônio do Curvello² and Tamanduá. Saint Hilaire (1830, pp. 314-315) also mentioned Vila do Fanado³ as the locality of a mastodont tooth. The remarkable collections of Lund (1893a, 1893b, 1846) included mastodonts from the caves (*lapas*) of the Lagoa Santa region in the Rio das Velhas Valley. He did not describe or name the specimens, but included "*Mastodon* sp." in faunal lists and figured a juvenile skull. Winge (1906) later described Lund's specimens and identified them as "*Mastodon andium* Cuvier," which in modern terminology is *Cuvieronius hyodon*. The molars are, indeed, difficult or perhaps sometimes impossible to distinguish from those of that species, but there is little doubt that all these specimens, as do most, at least, of the others from the Minas Geraes

lapas (see below), belong to *Haplomastodon waringi*. Recent collections from the caves are mostly those of H. V. Walter, some of whose specimens are described below. He (Walter, 1949, pp. 102-104) has mentioned but not described or figured several of his mastodont discoveries near Lagoa Santa and Pedro Leopoldo.

In addition to those localities, the remarkable Águas do Araxá collection, described in this monograph and first recorded by Price (1944), is from the State of Minas Geraes. A small collection of Pleistocene mammals from Frutal, made by Juvenal Queiros and Antonio Barboza, included fragments of mastodonts. The specimens eventually were taken to the Escola de Minas of Ouro Preto, where Gomes (1934) classified them as *Mastodon* (*Dibyledon* [sic!]) *humboldtii*. The specimens, a very incomplete molar (probably left M^2) and the anterior part of a left lower jaw with a very broken M_2 , are too fragmentary to be classified. Paula Couto (1953, p. 362) reported an isolated mastodont molar from near Governador Valadares in the Rio Doce Valley. The specimen is probably *Haplomastodon waringi*.

Besides two specimens from Águas do Araxá, included in our description of that series, the Walter private collection includes a juvenile skull from the Lapa do Caetano da Cerca Grande and an isolated left M^3 from the Lapa do Borges.

The juvenile skull from Lapa do Caetano lacks the occipital region, and some matrix is present on the left side. The left orbit is more or less clean. Little or no crushing was noted. The dm^{2-3} were in use, the degrees of wear being 2 and 1, respectively. The next tooth is visible on the right side, where the bone is broken. It is formed but not erupted. Dm^2 is oval in outline and has two crests and a cingulum or small talon. Dm^3 has three complete crests, with anterior and posterior cingula. The posttrite trefoils are feeble and of *Haplomastodon* type. The measurements are as follows: left dm^2 , L 33 by W 31; right dm^2 , L 32 by W 31; left dm^3 , L 55 by W ca. 38; right dm^3 , L ca. 56 by W ca. 38. The left tusk is unerupted, its tip being in the alveolus. It is completely covered with dark, shiny, rugose material, probably enamel. The skull is distinctly low and is flattened above and behind the orbits. Certainly it did not rise to

¹ This was a farm visited by Spix and Martius. It has not been possible to locate it on any map.

² Now known simply as Curvello.

³ Now known as Minas Novas. The tooth of which St. Hilaire speaks was given to him at Vila do Fanado but was found in the "*Sertão*," or bush, presumably in the same vicinity.

the pulp cavity and retaining the worn tip. The most important feature of this fragmentary tusk, which apparently belonged to an adult but not aged individual, is the presence of a strong band of enamel on one side, thus distinguishing it sharply from all other tusks of comparable individual age from Brazil examined by us, including several other tusks from the same spot. The tusk and its enamel band have a slight spiral torsion. It is gently concave antero-posteriorly on its upper face, and the dentine is well polished. Its diameters at the broken proximal end are 68 by 53 mm. The length of the enamel band from the tip to the broken proximal end is 240 mm., the width at the proximal end being 55 mm. The tusk is oval in cross section.

U.M.G. No. LB-2 is the tip of a broken tusk with enamel. It is not symmetrical with U.M.G. No. LB-1, but probably comes from the same individual. The length of the preserved part is 51 mm.

U.M.G. No. LB-3 is a broken large tusk with a worn and rounded tip. No trace of enamel is present, but a very slight torsion is noted on the longitudinal grooves of the dentine. The longitudinal curvature is almost nil. The length of the broken tusk is 382 mm. Its diameters about one-third of the distance from the proximal end (where it is worn to a slight polish, giving way to grooving) are 83 by 72 mm.

U.M.G. No. LB-4 is a fragment of tusk, broken at both ends. It possibly represents mainly the intra-alveolar part of the tusk. The distal part tapers abruptly and is worn (probably) or spalled. No enamel band is present. No evidence of longitudinal curvature or spiral torsion is seen. The total length as preserved is 317 mm., the length of the tapered part, as preserved, being *ca.* 10.5 cm. The cross section was originally oval. The diameters of the intra-alveolar part are 88 by 80 mm.

U.M.G. No. LB-5 is a fragment of large spalled tusk. It was nearly straight, but presents no other reliable information.

U.M.G. No. LB-6 is an M_2 , much worn (early stage 4). The third lophid bears a double trefoil, but this is no more complex than in some variants of *Haplomastodon*. The measurements are: *L ca.* 128 (slightly rounded by wear) by *W* 78 (second lophid) and 85 mm. (third lophid).

U.M.G. No. LB-7 is a broken dm_4 (or possibly M_1) in early stage 3 of wear. Posttrite trefoils are present, but poorly developed. Measurements: *L* not measurable; *W* (on second lophid) 57 mm.

U.M.G. No. LB-9 is a deeply worn and broken M_3 , not useful.

U.M.G. No. LB-10 is a partial left M_3 , with the first two lophids preserved. Its wear is in advanced stage 1. The third lophid was the widest. Posttrite trefoils are poorly developed, within the Araxá range. On the second lophid the posttrite is slightly anterior to the pretrite.

U.M.G. No. LB-11 is a fragment of the symphyseal region of a lower jaw. It is short, with a slight spout. No teeth are preserved.

U.M.G. No. LB-12 is a right mandible, with the posterior end of M_2 , very worn (advanced stage 4), and *situs* of M_3 and part of ascending ramus present. Although M_2 was still present in final wear stages (only a posterior rim of external enamel, no crown pattern), M_3 had been shed during life, its alveoli having been almost filled with secondary bone, by reossification, which was certainly owing to a pathological condition (probably dental infection). The posterior end of M_2 (U.M.G. No. LB-13) was found separately, but it is probably from this individual, as it fits perfectly into the remaining alveoli in the mandible.

Two other mastodont specimens, both unidentified, are represented in the Walter collection of the University of Minas Geraes: one wrist bone (U.M.G. No. LB-8) and a fragment of upper jaw, with roots of molars and no crown present.

Except for the tusks, all the material from the Lapa do Borges is consistent with reference to *Haplomastodon waringi*. The molars are well within the range of the Águas do Araxá series. The tusks, however, are unlike the few available from that locality, or, indeed, any other tusks known to us from Brazil. All the fragments are nearly straight, whereas tusks of comparable size known to belong to *Haplomastodon* are generally (always?) distinctly curved. Two of the tusks (U.M.G. Nos. LB-1 and LB-3) have a slight spiral torsion, also usually or always absent in comparably large tusks known certainly to be of *Haplomastodon*, but another Lapa do Borges tusk of comparable size (U.M.G. No.

LB-4) lacks the torsion. One individual (Nos. LB-1 and LB-2, probably of the same individual) has an enamel band, but this is absent in the other tusks which seem to be of comparable individual age. The torsion and adult enamel suggest *Cuvieronius*, to which the molars could also conceivably belong, but the torsion is decidedly less than in any positively identified *Cuvieronius*, and it also occurs here in a tusk without enamel. On the other hand, the peculiar characters of various of these tusks (low degree of curvature, vague torsion, and enamel band) are all known to occur in younger, juvenile tusks positively identifiable as *Haplomastodon*. We may, then, have in the Lapa do Borges a population of *Haplomastodon waringi* with a tendency to retain juvenile characters into (early?) adult life. Indeed, because few tusks of *Haplomastodon* are known, these characters may normally have been variable in young adults of that genus. If so, the really positive identification of South American mastodonts, already so difficult, would be further complicated. Only larger collections can eventually answer these questions.

Unworn or little-worn molars of *Haplomastodon* and South American *Stegomastodon* are usually readily distinguished, but some variant specimens may nearly if not entirely intergrade morphologically. As has been noted, *Haplomastodon* does commonly have feeble posttrite trefoils, and in deeply worn teeth these may appear about as in *Stegomastodon*. The possibility cannot be excluded that some of the occurrences listed on previous pages may represent *Stegomastodon*, but this seems unlikely for most if not all of them. The probability may be greater for some of the following specimens.

In the Departamento de Geologia e Paleontologia of the University of São Paulo there is a water-worn left M³ (U.S.P. No. 3-1238, Paixão collection No. 2553), with apparently well-developed double trefoils. The specimen is labeled as from Araxá and is within the Araxá size range (L 175 by W 80), but is peculiar not only in having unusually strong posttrite trefoils but also in having an extremely small fifth loph, probably only a single cone. The specimen could represent *Stegomastodon*, but the identification is uncertain. There is also possible question as to the locality data.

One other Minas Geraes mastodont locality can be added from specimens seen by us. José Froes Filho of Belo Horizonte has a mastodont M₂ from Patos de Minas. The tooth, in wear stage 4, is trilophodont, with single trefoils and opposite pretrites and posttrites, as in *Haplomastodon*.

STATE OF ESPÍRITO SANTO

Fragments of molars from Cachoeiro de Itapemirim were given to the Museu Nacional, Rio de Janeiro (No. 283-V), by José Guilherme de Azevedo. The molars are of the single trefoil type and are very likely from *Haplomastodon waringi*.

STATE OF SÃO PAULO

An incomplete molar of a mastodont was discovered in a *cacimba* in the locality of Águas da Prata, by R. W. Tibiriçá, and classified by Moraes Rêgo (1933) as *Mastodon* sp. It is a broken right M₂, apparently from *Haplomastodon*, and is in the collection of the Departamento de Geologia e Paleontologia of the Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Its measurements are L 130 by W 76 mm.

Haplomastodon remains were collected in Minas das Furnas, *município* of Apiaí, in 1940, by Thomaz Skulski, and sent to the Instituto Geográfico e Geológico, São Paulo. The fossils are very fragmentary and include a right M₂ (L ca. 120 by W ca. 70), poorly preserved (No. 64-V), fragments of an M₃, in stage 0-1 of wear (No. 63-V), and small fragments of another molar (Nos. 65-V to 67-V).

STATE OF RIO GRANDE DO SUL

The posterior end of a left M₃ was collected by José Protasio Pereira da Costa in Irai and is in the Divisão de Geologia e Mineralogia collection (No. 46M). The fourth lophid has a single trefoil and is moderately oblique. The fifth lophid is well developed and is followed by a comparatively large talonid without a strongly distinct apex. As far as it goes, the specimen seems to be within the range of the Araxá sample. It is probably *Haplomastodon waringi*.

In the Museu Júlio de Castilhos in Pôrto Alegre there is a right lower jaw with two incomplete alveoli and the posterior root of a molar, along with a separate fragment of a

right lower molar, found at Irai by José Protasio Pereira da Costa in 1936. The specimen was made the type of a supposedly new species, *Bunomastodon iraiensis* Tupi Caldas, 1938, but the name is a *nomen nudum*, as it was not accompanied by a diagnosis or description and the illustrations given are not recognizable as to genus or species. Paula Couto (1940, pp. 146–147; 1944, p. 202) referred the same material doubtfully to *Mastodon* or *Stegomastodon humboldti*. Elsewhere (Paula Couto, 1943, p. 43) he applied the name *Cuvieronius humboldti*. The same identification was then given for other specimens in the same museum: an incomplete mandible of an old individual with left M_3 , a fragment of a tusk, parts of two molars, and other fragments from the *município* of Uruguaiana; and an incomplete left lower molar from the region of Barra do Ouro, Maquiné Valley, *município* of Osório. These specimens, although poorly preserved, seem to have stronger posttrite trefoils than are usual in *Haplomastodon*, and Paula Couto (1953) recently referred the Osório molar to *Stegomastodon*.

The Irai specimen is really entirely unidentifiable, and it is noteworthy that a *Haplomastodon*-like molar is known from the same locality, as previously noted. The Uruguaiana and Osório specimens may be *Stegomastodon*, but that is quite dubious.

SUMMARY

With few exceptions, all the specimens listed above are comparable with the Águas

do Araxá *Haplomastodon waringi* as far as they preserve diagnostic characters. The molars have single trefoils, or as nearly so as in Águas do Araxá variants, the adult tusks are simply curved and without enamel, and the juvenile tusks are straight and have enamel. In size (table 11) the observed ranges are rather large in comparison with the range of the Águas do Araxá specimens and in view of the smaller number of specimens. That, however, would be expected in a heterogeneous lot of materials from so large an area (measurable M_3 from five states or territories, Acre to Pernambuco) while the Águas do Araxá sample is probably from a single deme. A few measurements are above the observed range of the Araxá sample, but still could be in the range of the corresponding population. The means for the widely scattered specimens are also slightly above Araxá means. Those facts suggest, but do not prove, that the Araxá sample may represent a local population somewhat small (in individual size) for the species. The available data are consistent with the hypothesis that throughout the great area covered by these scattered finds the common mastodonts, at least, belonged to a single species and that the species was *H. waringi*.

The most exceptional specimens are the tetralophodont M_2 from Sítio Laje Grande, Pernambuco, and the relatively straight adult tusk with enamel from the Lapa do Borges, Minas Geraes. They are decidedly outside the observed Araxá ranges, but their characters do not agree with those of any other known

TABLE 11
COMPARISON OF DIMENSIONS OF M_3 FROM ÁGUAS DO ARAXÁ AND FROM
OTHER LOCALITIES IN BRAZIL

	N	OR	\bar{x}
Length of M_3			
A.A.	22	180–239	208.1 ± 3.0
All other measurable specimens	9	182–245	211.3
Width of M_3			
A.A.	24	69– 90	80.8 ± 1.0
All other measurable specimens	9 ^a	70– 90	83.1

^a An additional specimen not exactly measurable, from Laje Grande, Pernambuco, is unusually wide, perhaps as much as 100 mm.

species either, and they may, after all, prove to be aberrant *H. waringi*.

As noted above, a specimen in São Paulo labeled (perhaps incorrectly) as from Araxá and a few specimens from Rio Grande do Sul may belong to *Stegomastodon*. Those identifications are far from positive, but it would not be surprising if *Stegomastodon*, so widespread on the pampas along the Rio de la Plata, did turn up in extreme southern Brazil.

AGES: In no case is it possible to be more definite about age than to say that all these finds in Brazil are Pleistocene or possibly in a few cases early Recent. Most of the scattered finds have no stratigraphic data. Even the carefully excavated and recorded Águas do Araxá find cannot at present be referred to any limited part of the Pleistocene. No reliable guide fossils or faunal sequences have yet been firmly established within the Brazilian Pleistocene. It is questionable, depending on

decision as to the Pliocene-Pleistocene boundary, whether the mastodonts had yet reached South America in the earliest Pleistocene. From what little is known of their scanty stratigraphy and associations, an impression is given that many or most of the Brazilian finds are from rather late in the Pleistocene. There is some hint that the latest of them may have been early Recent. Association with man in the *lapas* has been claimed but not clearly established. There is no evidence for evolutionary advance among the Brazilian mastodonts. Indeed such evidence would be difficult or even impossible to obtain, in view of the wide variation at Águas do Araxá where by usual criteria very primitive and very advanced forms occur in one population. We suspect that mastodonts may not have inhabited Brazil long enough for speciation to occur.

REVIEW OF SOUTH AMERICAN MASTODONTS

THE SOUTH AMERICAN MASTODONTS are abundant, widespread, and varied. All are Pleistocene (perhaps into earliest Recent) in age. There is some possibility of succession in species or lesser taxa, but in no case has such succession been clearly established. It is highly probable that all the genera at least, and little less probable that all the valid species, were contemporaneous through much of their age spans. Large collections are at hand, and they have been studied by, among others, the most eminent vertebrate paleontologists for well over a century and a half. Under these circumstances of occurrence and of research, it would be reasonable to expect that the taxa would be fairly clear cut and that their classification and nomenclature would now be beyond serious confusion or dispute. That expectation is still very far from being fulfilled. The extraordinarily large literature is also extraordinarily confusing. Even in comparatively recent publications, hardly any two authors recognize the same taxa, and if quite exceptionally they do agree as to the taxa, they are likely to use different names.

The nearest approach to clarification has come from the work of Cabrera (1929) on Argentine and of Hoffstetter (1952) on Ecuadorian mastodons. The intervening work of Osborn (1936) is incomparable as a continent-wide compilation of data and citations, but is less clear in classification and is eccentric in nomenclature. Those three authors have reviewed much of the tangled history of the subject, and we need not go into historical questions here except as they affect the status of certain particular taxa and names considered in the following pages. Our suggestion of a modified taxonomy and nomenclature owes much to the work of Cabrera, Osborn, and Hoffstetter, plus our present study of Brazilian mastodons and less intensive review of materials in Argentine museums (Buenos Aires, La Plata, and Mar del Plata) and in the American Museum of Natural History. In general we endorse, but

can now add somewhat to, the excellent work of Hoffstetter. This is particularly true of the most essential point: there are three (and only three) clear-cut and well-defined major taxa (well ranked as genera) among South American mastodons (*Cuvieronius*, *Stegomastodon*, *Haplomastodon*), plus at least one more of dubious status (*Notiomastodon*). The principal emendations of Hoffstetter's arrangement now to be suggested are as follows:

1. Known South American specimens of *Haplomastodon* do not clearly indicate the presence of more than one species, the prior name of which is *H. waringi*. *Haplomastodon chimborazi*, *H. guayasensis*, and "*Stegomastodon*" *brasiliensis*, recognized as distinct species by Hoffstetter, are here all considered synonyms of *H. waringi*.

2. We thus agree with Hoffstetter's earlier opinion (1950) that the common mastodons of Brazil, and notably those from Águas do Araxá, belong to *Haplomastodon*, and disagree with his later view (1952) that they represent an unnamed subgenus of *Stegomastodon*.

3. It further follows from the suggested specific synonymy that Hoffstetter's subgenera *H.* (*Haplomastodon*) and *H.* (*Aleamastodon*) are considered to be synonyms.

4. *Haplomastodon* does not seem to us to be more nearly related to *Stegomastodon* than to *Cuvieronius*.

5. That and other considerations cast serious doubt on the validity or usefulness of the placing of the South American mastodons in two subfamilies, Anancinae and Cuvieroninae, by Cabrera, accepted and accentuated by Hoffstetter. (*A fortiori* we reject Osborn's placing of these forms in several different families and subfamilies.) For the present, at least, we think that all South American genera, as well as some in North America and the Old World, may best be placed in one subfamily, the Anancinae.

The reasons for these proposals are given in sufficient detail in what follows.

CLASSIFICATION AND MUTUAL AFFINITIES OF SOUTH AMERICAN FORMS

CUVIERONIUS OSBORN, 1923

Mastodon (part) AUCT., nec Cuvier, 1817, p. 233.

Cuvieronius OSBORN, 1923, p. 1.¹

Cordillerion OSBORN, 1926, p. 15.

Teleobunomastodon REVILLIOD, 1931, p. 21.

TYPE: *Cuvieronius hyodon* (Fischer, 1814, p. 341).

INCLUDED SPECIES: *Cuvieronius hyodon* only, in South America. One or more species (needing revision) in North America.

KNOWN DISTRIBUTION: Pleistocene, perhaps especially or wholly early Pleistocene, in the Andine region and adjacent lower regions to the south (northern Chile). Probably latest Pliocene and Pleistocene in southwestern United States and perhaps Mexico.

DIAGNOSIS: Brevirostrine, bunolophodont, trilophodont mastodonts with single trefoils or with posttrite trefoils poorly developed. Pretrite and posttrite cusps opposite or slightly alternating on posterior lophs of M₃. Tusks twisted in a long, open spiral and with a spiral band of enamel persisting in the adults. Skull comparatively low and elongate.

DISCUSSION: This is the best-known and most clearly defined of the South American genera. It has, however, been involved in an unusual nomenclatural confusion.

The problem stems from Cuvier, who in 1806 described a "*mastodonte des cordillères*," based on an isolated M² from near the volcano of Imbabura in the then Kingdom of Quito, and a "*mastodonte humboldien*," based on an isolated dm⁴ from "La Conception du Chili." Later Cuvier and others applied the Linnaean names "*Mastodon andium*" (with numerous variants) and "*Mastodon humboldti*" (also with variants), respectively, to the two supposed species. It was soon found that there are, indeed, at least two quite distinct mastodonts in South America, one most common in the Andine region, especially Bolivia, and one in the lowlands, especially

the Argentine pampas. It was natural to assume that the former (our *Cuvieronius*) was Cuvier's "*Mastodon andium*" and the latter (our *Stegomastodon*) his "*Mastodon humboldti*." (For fuller accounts of the earlier history, see Osborn, 1936, and Hoffstetter, 1952.)

In 1923 Osborn decided that the two groups here in question are distinct genera and for one of them he proposed the name *Cuvieronius* with the designated type "*Mastodon humboldti*." His brief but at the time adequate definition clearly and correctly (Cabrera, 1929, to the contrary notwithstanding) applied to the Pampean mastodonts and also correctly and explicitly excluded the Andine form.² In 1926 Osborn proposed that the quite different Andine genus, also clearly and correctly defined, be called *Cordillerion*, type "*Mastodon andium*."

In 1929 Cabrera concluded that both of Cuvier's original specimens, types of the subsequent names³ *Mastodon humboldti* and *Mastodon andium*, came from Andine, not Pampean, mastodonts. After examination of the originals in Paris, Hoffstetter agreed. From study of good casts, we also agree that neither one is likely to be a Pampean mastodont, although we are skeptical as to whether they are otherwise precisely identifiable. (They could, indeed, be *Haplomastodon*.) Cabrera therefore transferred the name *Cuvieronius* to the Andine mastodonts or Osborn's *Cordillerion*. Logically and scientifically it is surely absurd that a name be transferred from the genus obviously intended by its author to a genus explicitly excluded by that author. Nevertheless the legalistic nomenclatural argument is clear and apparently conclusive under the rules: the type of *Cuvieronius* is "*Mastodon humboldti*," and

¹ Designation of *Cuvieronius* in this sense as of "Osborn, 1923, nec 1926" (e.g., in Hoffstetter, 1952) is incorrect. Osborn used the name in exactly the same way in 1926 as in 1923. Neither in 1923 nor at any later date did he ever really apply it to the genus now known by that name.

² Osborn (1923) then referred the Andine mastodonts to *Dibelodon* Cope, which has a North American type. As everyone, including Osborn in all later publications, has subsequently agreed that that generic reference is incorrect, we need not devote further space to this additional complication.

³ This wording is deliberate. Despite the wording of the rules, nomenclatural "types" are actually used as types of names, not of species. Indeed Cabrera's argument requires that usage.

the type specimen of that specific name is probably an Andine mastodont (or at any rate probably does not belong to the genus actually defined by Osborn).

Osborn, who refused to follow the International Rules just because of such absurdities, rejected Cabrera's usage and continued to call the Pampean genus *Cuvieronius* and the Andine genus *Cordillerion*. Other students (e.g., Simpson, 1945; Hoffstetter, 1952) have more commonly followed Cabrera and applied *Cuvieronius* to the Andine genus, with *Cordillerion* as a synonym. The case does not seem to us nearly so clear-cut as Cabrera indicated, especially because we still have misgivings as to the exact identification of Cuvier's highly inadequate types. Nevertheless the only possible way to stabilize the nomenclature is to pick one solution and stick to it, even if it is arbitrary. We therefore follow Cabrera, because that has been done by Hoffstetter and other recent authorities and because this usage may be less likely to be upset again by some other arbitrary application or interpretation of the Rules.

Cuvieronius hyodon (Fischer), 1814

Mastotherium hyodon FISCHER, 1814, p. 341.

Mastotherium Humboldtii FISCHER, 1814, p. 341 (specific name ascribed to Cuvier).¹

Mastodon rhomboides RAFINESQUE, 1814, p. 182.

Mastodon cordillerarum DESMAREST, 1818, p. 446 (specific name ascribed to Cuvier).¹

Mastodon Andium CUVIER, 1824, p. 527.

Mastodon argentinus AMEGHINO, 1888, p. 7.

Mastodon chilensis PHILIPPI, 1893, p. 88.

Mastodon bolivianus PHILIPPI, 1893, p. 89.

Mastodon tarijensis AMEGHINO, 1902, p. 2.

(For numerous variants of these specific names and other combinations with generic names, see Hoffstetter, 1952.)

TYPE: Isolated M² in the Muséum d'Histoire Naturelle, Paris; original of figure 1 on plate 50 of Cuvier (1806).

KNOWN DISTRIBUTION: As for the genus in South America. Occurrence of the species in North America not established but possible.

DIAGNOSIS: Only surely valid species of the genus. Conclusively differential diagnoses of

the several supposed Mexican and United States species (all with names of later dates) have not yet been made.

DISCUSSION: Cabrera (1929) and Hoffstetter (1952) both concluded that all the specific names referable to South American members of this genus are synonymous. We have not revised all the pertinent materials, but study of a number of them and review of the literature strongly suggest to us, also, that only one species is known from South America. The genus unquestionably occurs in North America, but the situation there is quite confused as regards species and is mostly outside our present scope, although it is mentioned again below in this monograph.

Within South America, *Cuvieronius hyodon* is decisively distinct from any or all species referred to *Siegomastodon* and *Notiomastodon*. Although all are within the scope of the broad subfamily Anancinae (as here redefined), *C. hyodon* can have no further and particularly close relationship to members of the latter two genera. On that basis, placing the species in a separate genus is clearly justified. The distinction from *Haplomastodon waringi* is also clear at the specific level, but we believe the species (hence also the genera) to be more closely related than hitherto noted, as discussed under *Haplomastodon*.

HAPLOMASTODON HOFFSTETTER, 1950

Haplomastodon HOFFSTETTER, 1950, p. 22.

Haplomastodon (Aleamastodon) HOFFSTETTER, 1952, p. 208.

(No other full generic name has been based on specimens surely referable to this genus, but many specimens and species now referred to this genus have been referred to numerous other genera; for a partial list, see Hoffstetter, 1952.)

TYPE: *Haplomastodon waringi* (Holland, 1920, p. 229).

KNOWN DISTRIBUTION: Pleistocene, especially but probably not exclusively late Pleistocene (and perhaps earliest Recent), throughout most of tropical South America except, as far as surely known, the Andine region south of Ecuador; also into temperate southwestern Brazil. Occurrence in Mexico, the United States, or both is possible on the basis of recorded finds, but the generic identification there is not now positive.

¹ These specific names were in fact intended as Latin translations of Cuvier's earlier purely vernacular names.

DIAGNOSIS: Brevirostrine, bunolophodont, trilophodont mastodonts with single trefoils or with posttrite trefoils poorly developed (about as in *Cuvieronius*). Pretrite and posttrite cusps of posterior lophs of M_3^1 generally oblique, with stronger mean tendency towards alternation than in *Cuvieronius*. Juvenile tusks usually straight or very slightly spiral, with enamel band; adult tusks usually simply upcurved and without enamel. Skull probably less elephantoid than in *Stegomastodon* but probably somewhat less depressed and elongate than in *Cuvieronius*.

DISCUSSION: *Haplomastodon* now seems to be the most abundant and widespread of South American mastodonts, and it is easily distinguished from all others if both molars and tusks are available. It is, however, part of the peculiarly complex and confused history of the study of South American mastodonts that until 1950 specimens of this group were invariably confused with and assigned to one or the other of the really quite distinct groups now designated as *Cuvieronius* and *Stegomastodon*. In the literature up to 1950 it is usually impossible to tell which of the three genera is really involved without a new study of the actual specimens.

In 1950 Hoffstetter pointed out that some of the specimens previously referred to *Cuvieronius* (as "*Mastodon andium*" or under various other names) have adult tusks much as in *Stegomastodon* and quite different from those diagnostic of *Cuvieronius*. He also noted that many specimens earlier referred to *Stegomastodon* (as "*Mastodon humboldti*" and numerous other names) have molars as in *Cuvieronius* and definitely not as in *Stegomastodon*. Hoffstetter referred all those specimens to *Stegomastodon*, but in a then new subgenus, *Stegomastodon* (*Haplomastodon*), characterized by the presence of single, not [fully] double, trefoils. As Hoffstetter noted, *Haplomastodon* does frequently have poorly developed posttrite trefoils, and worn teeth can be confused with those of *Stegomastodon*, *sensu stricto*. The distinction is usually clear, however, and there can be no doubt that *Haplomastodon* is a valid taxon at some level in the hierarchy. Its separation from *Cuvieronius* and *Stegomastodon*, *sensu stricto*, greatly clarified an extremely confused taxonomic situation and was a stroke of genius for which

all students of the subject must be grateful to Hoffstetter.

In 1952 Hoffstetter raised *Haplomastodon* to full generic rank on the basis that it lacks transverse foramina in the atlas. He also split his Ecuadorian specimens into two subgenera, *H.* (*Haplomastodon*) and *H.* (*Aleamastodon*), in the belief that the former lacked and the latter had transverse foramina in the axis. At that time he also stated that a third subgenus, unnamed and left in *Stegomastodon*, *sensu lato*, occurs in Brazil, notably at Araxá. That supposed subgenus was characterized as having teeth like those of *Haplomastodon* but an axis with transverse foramina as in *Stegomastodon*.

Surprising as this result may seem, the Araxá material described above in this monograph demonstrates beyond possible doubt that the presence or absence of transverse foramina in both atlas and axis of *Haplomastodon* is an individual variation. Within the Araxá sample, which seems surely to represent a single population, there are both axes and atlases with and without transverse foramina. Moreover, in both axis and atlas the foramen may occur on one side and not on the other; the character varies even within single individuals. Hoffstetter's treatment of the Ecuadorian specimens was based on four atlases, all lacking transverse foramina, and three atlases, one without and two with transverse foramina. It could well happen, purely by chance, that these specimens were derived from a single species in which the foramina are variable on both bones. We believe that it is merely a coincidence that none of his atlases has the foramina and that his atlases with and without the foramina are from different regions in Ecuador. The frequency of occurrence or absence of the foramina might, of course, differ in different populations, and it might then be a taxonomic character, although hardly one of generic rank. However, neither the Ecuadorian nor the Brazilian samples are adequate for one to estimate the frequency in the corresponding populations, or to demonstrate any differences among those populations.

We conclude, therefore, that the subgenus *H.* (*Aleamastodon*), based only on the presence of the foramina in the axis, is invalid. Although the generic rank of *Haplomastodon*

was also based by Hoffstetter on what now appear to be invalid grounds, it does not follow that that genus is invalid. The original definition of *Haplomastodon* as a subgenus remains valid, and we believe that there are grounds other than those given by Hoffstetter for raising that subgenus to the generic level.

When Spillmann (1931) first recognized the taxon now called *Haplomastodon* (his "*Bunolophodon Ayora*" and "*Bunolophodon postremus*"), he suggested its direct derivation from the taxon we call *Cuvieronius* and, somewhat more obscurely, implied that it is less nearly related to the taxon we call *Stegomastodon*. Osborn (1936), on the other hand, believed that Spillmann's Ecuadorian mastodons had no special relationship to the genus we call *Cuvieronius* and placed the two groups in different families. He put Spillmann's species in the same genus as *platensis* and *superbus*, which in our terms (Osborn's concept but not his nomenclature) amounted to referring them to *Stegomastodon*. The arrangement was confusing because he defined the genus (his but not our "*Cuvieronius*") as typically having double trefoils and yet noted that the Ecuadorian forms have single trefoils.

Hoffstetter more nearly agreed with Osborn than with Spillmann. Even after he removed *Haplomastodon* from *Stegomastodon* he still considered them closely allied¹ and distinguished both sharply from *Cuvieronius*, placed in a different subfamily. The evidence stated (Hoffstetter, 1952) was that *Haplomastodon* has (adult) tusks simply curved and without enamel and has an elephantoid skull, both as in *Stegomastodon* and not as in *Cuvieronius*. We believe that one of those points is, at best, inconclusive and that the other may be at least partially erroneous. The evidence of the molars must also be considered, and it opposes Osborn's and Hoffstetter's views. The question requires reconsideration on the three essential points of molar, tusk, and skull characters.

1. MOLAR STRUCTURE: This is virtually identical in *Haplomastodon* and *Cuvieronius*, to such an extent that isolated teeth may be

difficult, perhaps in some cases impossible, to distinguish. The structure is distinctly different from the more complex teeth of *Stegomastodon*.² Only in the last wear stages or in extreme variants is there any likelihood of mistaking one for the other. It is true that this resemblance between *Haplomastodon* and *Cuvieronius* is mainly in primitive characters, their molars being more *Gomphotherium*-like than those of *Stegomastodon*, but at least it indicates that *Haplomastodon* and *Cuvieronius* have both been separate from *Stegomastodon* for a long time and does suggest a common ancestry at a pre-*Stegomastodon* stage. The alternation of pretrite and posttrite cones, cited by Hoffstetter as a resemblance between *Haplomastodon* and *Stegomastodon* and a difference from *Cuvieronius*, does also occur in *Cuvieronius* although, to be sure, less frequently and usually less markedly. It is rarely strong in *Haplomastodon*, generally less than in *Stegomastodon*. It seems to have been a very early tendency (already present by middle Miocene) in all the forms here placed in the Anancinae, although arrested or perhaps even reversed in *Cuvieronius*. It has progressed less far in *Haplomastodon* than in most anancines.

2. TUSKS: The adult tusks of *Cuvieronius*, spiral with enamel band, and of *Haplomastodon*, usually (at least) simply upcurved without enamel, are markedly different, and this is doubtless the principal reason why closer relationship between the genera has not previously occurred to most students. The juvenile tusks of *Haplomastodon* are, however, more like those of *Cuvieronius* than like those of *Stegomastodon*. They are nearly straight, with slight torsion, and with an enamel band. The tusks from Lapa do Borges, probably although not surely of *Haplomastodon*, suggest that an enamel band, slight torsion, or both were sometimes retained beyond strictly juvenile stages. There is thus, even in the tusks, some reason to suspect special relationship of *Haplomastodon* to *Cuvieronius*. There are several possible evolutionary interpretations. The two genera may have developed from forms with adult tusks more or less as in

¹ Indeed, as will be noted under the species, he continued to refer Brazilian specimens of *Haplomastodon* to *Stegomastodon*.

² A few North American specimens referred to *Stegomastodon* are not so distinct from *Haplomastodon*, but they are also not so characteristic of *Stegomastodon* and, indeed, may not really belong to that genus.

juvenile *Hapломastodon*, from which *Hapломastodon* itself evolved by "adult variation" or "reduction" in the sense of de Beer (1951), with the adult stage convergently resembling *Stegomastodon*, while in *Cuvieronius* the enamel was retained and the spiral intensified by progressive evolution. Or (in our opinion less likely) the band and incipient spiraling may have been caenogenetic in the ancestry, retained as such in *Hapломastodon* but projected into the adult stage paedogenetically in *Cuvieronius*, probably again with intensification of the spiraling. In any event, there seems to be no evidence that anything like the juvenile *Hapломastodon* tusks occurs in *Stegomastodon*, and this speaks against a close relationship of the two.

3. SKULL: Boule and Thévenin (1920)

stated that the skull of *Cuvieronius hyodon* (their "*Mastodon andium*") is much lower and less elephant-like than the skull of South American *Stegomastodon* (their *Mastodon humboldti*). Hoffstetter placed *Hapломastodon* among the more elephant-like forms in this respect. The evidence is, however, equivocal, and there are some data suggesting that *Hapломastodon* may have had a somewhat more, although not precisely, *Cuvieronius*-like skull.

The elephant-like skull used by Boule and Thévenin to represent *Stegomastodon* ("*M. humboldti*") is not from Argentina but from Colombia. That is far outside the really positively established range of *Stegomastodon* in South America and in a region where *Hapломastodon* would seem, *a priori*, somewhat more likely to occur. Boule and Thévenin

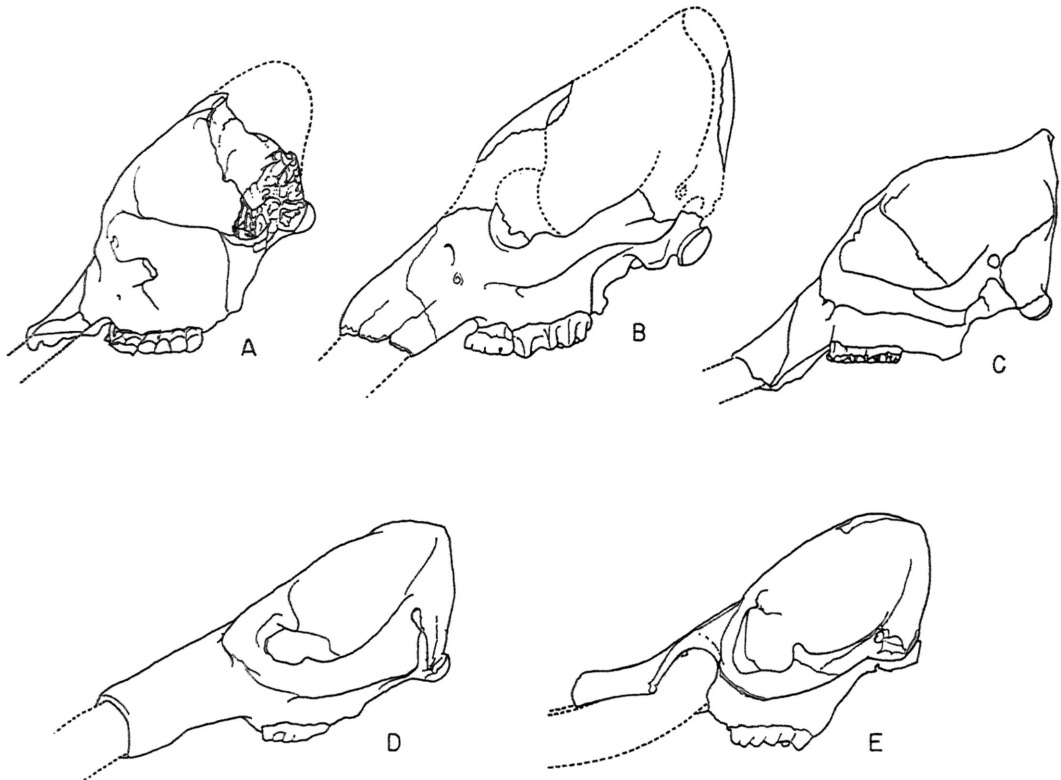


FIG. 10. Comparative left lateral views of skulls of fully adult mastodonts. A. *Stegomastodon?* sp., from Colombia, redrawn after Boule and Thévenin (1920, fig. 32). B. *Stegomastodon platensis*, from Argentina, redrawn after Cabrera (1929, fig. 6). C. *Stegomastodon texanus*, from Texas, redrawn after Osborn (1936, fig. 642B). D. *Cuvieronius hyodon*, from Bolivia, drawn from a photograph in Boule and Thévenin (1920, pl. 1, fig. 1). E. *Hapломastodon waringi*, from Ecuador, drawn from Spillmann's photograph reproduced by Osborn (1936, fig. 548). All $\times \frac{1}{10}$.

said that the teeth have double trefoils, but the teeth are deeply worn, and such worn teeth of *Hapломastodon* do sometimes seem to have strong double trefoils. Hoffstetter (1950) questioned the identification. Known adult skulls of Argentine *Stegomastodon* (see Cabrera, 1929) are heavily restored, and the skull proportions are not really certain, but the parts preserved do suggest that the elephant-like fore-and-aft compression and the great elevation of the occiput were much as in Boule and Thévenin's specimen and also North American *Stegomastodon*.

The only undoubted adult skulls of *Hapломastodon* found to date were the Ecuadorian specimens called "*Bunolophodon ayorae*" and "*Bunolophodon postremus*" by Spillmann (1931 and earlier). Both specimens were destroyed by fire, but they had previously been photographed for Spillmann. The photographs are most widely available in Osborn (1936, especially fig. 548). They show skulls that are distinctly lower, less elephantine, and more *Cuvieronius*-like, than any skulls attributed to *Stegomastodon*. They are not exactly as in *Cuvieronius*; after all, the genera

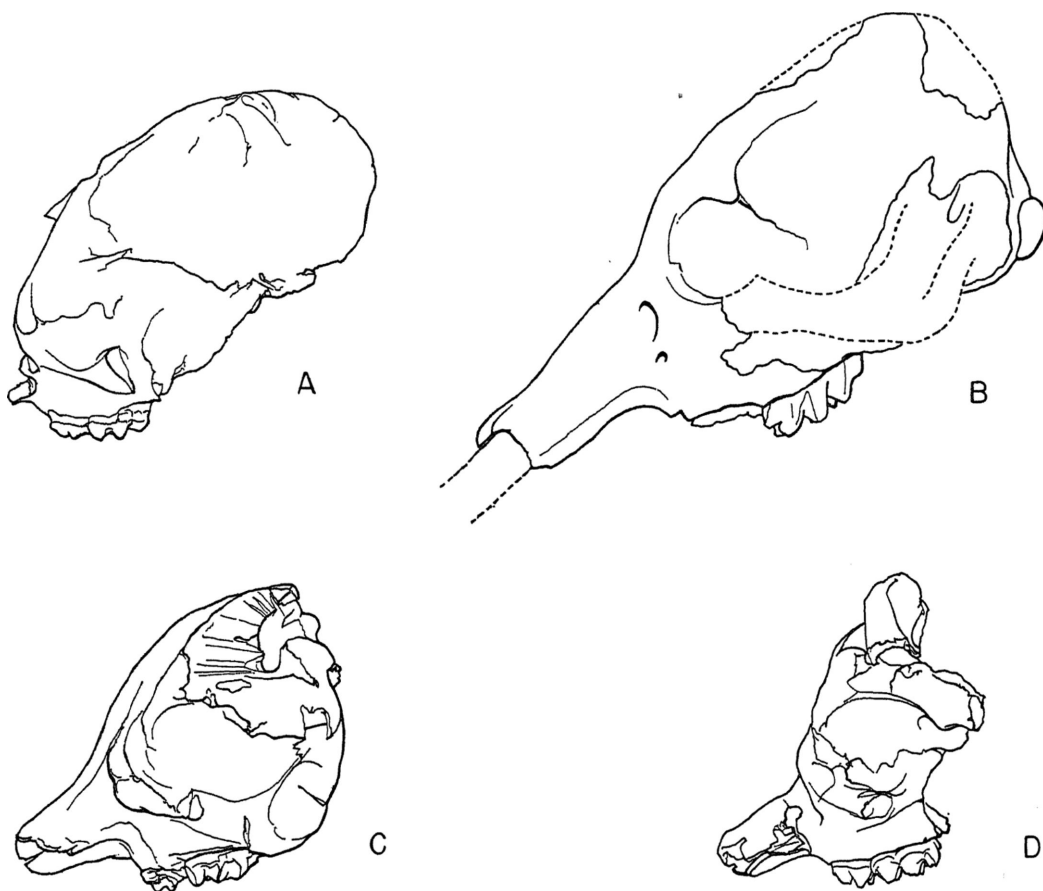


FIG. 11. Comparative left lateral views of skulls of juvenile and young adult mastodonts. A. *Stegomastodon platensis*, from Argentina, drawn from a photograph of M.A.C.N. No. 12046. B. *Stegomastodon platensis*, from Argentina, redrawn after Cabrera (1929, fig. 8). C. *Hapломastodon waringi*, from Minas Geraes, drawn from a photograph of the specimen in the Walter collection, Belo Horizonte. D. *Hapломastodon waringi*, from Minas Geraes, drawn from a photograph of Lund's specimen in Copenhagen. A, C, and D are of almost exactly the same age, juveniles with dm^2 in place and dm^3 erupting. B is a young adult with M^1 in place and M^2 erupting. A, C, and D are $\times \frac{1}{2}$; B is $\times \frac{1}{4}$.

are distinct, and we know that the adults had quite different tusks to which the skull shape must be mechanically adapted. Nevertheless, these data, such as they are, suggest that the probable skull proportions make relationship of *Haplomastodon* to *Cuvieronius* at least as likely as affinities with *Stegomastodon*.¹

Winge (1906, pl. 9) figured a juvenile skull from Lagoa Santa which is probably referable to *Haplomastodon*. His specimen has been studied and photographed (the present paper, pl. 17) by one of us (Paula Couto). The skull seems to be short, with a high occiput, but it is obviously crushed and its high appearance is due largely if not entirely to a large postero-superior fragment that has clearly been misplaced and does not naturally continue the true, lower skull profile. In the H. V. Walter collection at Belo Horizonte there is a skull of almost exactly the same age and almost uncrushed, although incomplete posteriorly. This skull is also probably referable to *Haplomastodon*, and it is from Lapa do Caetano in Minas Geraes, the same general region as Winge's specimen collected by Lund.

Fortunately there is available for comparison an Argentine skull of *Stegomastodon* also of about the same age as the two skulls of *Haplomastodon* from Brazil: M.A.C.N. No. 12046. The skull is more globose and less elevated posteriorly than in adult *Stegomastodon*, as would be expected of a juvenile. Nevertheless even at this early age it seems evident² that the frontal region is more rounded and rises to a higher level posteriorly than in the juvenile *Haplomastodon*, which has the frontal region distinctly flattened. That is

¹ In these comparisons it should be noted that the elongation and dorsoventral compression of the *Cuvieronius* skull vary greatly in different specimens, as is evident in the figures assembled by Osborn (1936) from various sources, in the other publications on the genus, and in the scattered specimens, among which we have examined about six skulls. Note also that the sectioned specimen figured by Boule and Thévenin (1920, fig. 4) and often used as a basis for comparison is one of the most dorsoventrally compressed of those known. It is, indeed, quite different in proportions from other specimens in the collection they studied (e.g., fig. 5; pl. 1, fig. 1).

² From direct comparisons of photographs only. Both the Walter and the Argentine juvenile skulls have been studied at first hand by us, but it was not practicable to bring them together for direct comparison.

also true of another, older but still young *Stegomastodon* skull figured by Cabrera (1929, fig. 8). This evidence, too, is not all that could be desired, but it also suggests that the skull proportions in *Haplomastodon* were different from those of *Stegomastodon* and probably more as in *Cuvieronius*.

On the evidence available, it seems to us probable that *Haplomastodon* and *Cuvieronius* were at least as nearly related to each other as either was to *Stegomastodon*. On this basis, if a distinction between Anancinae and Cuvieroninae were retained, we would favor the tentative transfer of *Haplomastodon* to the Cuvieroninae. We are, however, now inclined not to make that subfamily distinction, for reasons more fully considered below in this study.

POSSIBLE OCCURRENCE OF *Haplomastodon* OR *Cuvieronius* IN ARGENTINA

With a single exception, all the mastodont molars from Argentina known to us from the literature or at first hand have strong post-trite trefoils and are almost certainly referable to *Stegomastodon* or *Notiomastodon*. The exception is M.A.C.N. No. 13009, a fragment of left lower jaw with M_2 nearly complete, from "five leagues" (about 25 kilometers) north of La Banda in Santiago del Estero. This is a comparatively simple tooth, with weaker trefoils than in positively identified *Stegomastodon* and probably within the morphological range of *Haplomastodon* or of *Cuvieronius*. The tooth is also somewhat smaller than in positively identified *Stegomastodon platensis* or *superbus*, and it is within the size range of *Haplomastodon waringi* from Araxá and probably within that of *Cuvieronius hyodon* from Tarija. It seems likely that the tooth belongs to one of those two species. The locality is closer to the known range of *C. hyodon* in Bolivia,³ but extension of the range of *Haplomastodon* would hardly be less probable.

Haplomastodon waringi (Holland), 1920

Mastodon brasiliensis LUND, 1842, in Lesson, p. 157, *nomen nudum*.

³ Several students have, indeed, reported *C. hyodon* (seldom by that name) in northwestern Argentina, but Cabrera (1929) has shown that the reports are all dubious either as to locality or as to identification.

Mastodon andium WINGE, 1906, p. 48, *nec* Cuvier, 1806, p. 413.

Mastodon waringi HOLLAND, 1920, p. 229.

Masthodon chimborazi PROAÑO, 1922, on an unnumbered page slipped into the article.

Bunolophodon Ayora SPILLMANN, 1928, on an unnumbered page preceding p. 70.

Bunolophodon postremus SPILLMANN, 1931, p. 73.

Notiomastodon vidali CASTELLANOS, 1948, p. 139.

Haplomastodon chimborazi (Proaño, 1922), HOFFSTETTER, 1952, p. 192.

Haplomastodon guayasensis HOFFSTETTER, 1952, p. 208.

Stegomastodon brasiliensis HOFFSTETTER, 1952, p. 222.

TYPE: C.M. No. 11033, originally described (Holland, 1920) as including a partial lower jaw and other fragments, collected by Gerald Waring at Pedra Vermelha, Bahia, Brazil. A search in the Carnegie Museum collections by J. Le Roy Kay in 1954 turned up only the following, all under the type number 11033: three molar fragments, the largest with most of the (probably) posttrite part of a loph or lophid; the tip of a tusk; a fragment of tusk dentine; and part of the distal end of a tibia.

KNOWN DISTRIBUTION: As for the genus in South America.

DIAGNOSIS: The only currently defined species now recognized in the genus.

DISCUSSION: The synonymy given above lists, as far as we know, all the original binomials with types now believed to belong to this species. Specimens now placed in the species have of course also been referred in error to several other species. (The type of "*Masthodon chimborazi*" was, indeed, first referred to *Elephas primigenius* by Proaño!) Other combinations of generic and specific names have also been used.

Mastodonts from Lagoa Santa, Minas Geraes, Brazil, now known to belong to this species, were first mentioned by Lund (1839a), but he gave no description or illustration then or later. Lesson (1842) listed "*Mastodon brasiliensis* Lund," but only the bare name, an unquestionable *nomen nudum*. Winge (1906, pl. 9) figured one of Lund's specimens and described others, but he referred them to "*Mastodon andium*" (i.e., to *Cuvieronius hyodon* of present nomenclature) and did not mention, hence of course did not

define or validate, the name *Mastodon brasiliensis*. Hoffstetter (1952) gave what amounts to a legal, even though tentative, definition of "*Stegomastodon brasiliensis*." He credited the specific name to Lund, but under the Rules the name is available only as of Hoffstetter, 1952, and is thus antedated by at least six other names for the same species.

The name *Mastodon waringi* Holland, 1920, has apparently been overlooked by all other students of the group, but it was defined within the words of the Rules and is clearly available in nomenclature. It is the oldest available binomial known to us for this species and must therefore be accepted as the valid name.¹

Holland's definition of "*Mastodon*" *warangi*, although sufficient to make the name available under the Rules, does not in fact distinguish the species clearly from others now recognized. His principal specimen has been lost, and what remains of his type lot is fragmentary in the extreme. Nevertheless we believe that the species can be recognized with sufficient probability and that the name can therefore now be fixed without ambiguity. Fortunately two of the fragments do demonstrate requisite diagnostic characters. The tusk tip preserved is simply curved and has no enamel, which excludes *Cuvieronius hyodon* and *Notiomastodon ornatus*. One of the molar fragments is a large posttrite cone and adjacent conule, with evidence that the trefoil was feeble. The specimen can be exactly matched in the Araxá collections. Reference to *Stegomastodon* is extremely improbable, and only *Haplomastodon* remains among known possibilities in South America. It is shown in detail above in our listing of Brazilian mastodonts that all the well-definable specimens of mastodonts from anywhere within many hun-

¹ The collected volume in which the name appeared is dated 1922, and this might raise the question of priority as against *Masthodon chimborazi* Proaño, 1922, but that volume was issued in parts. There is conclusive evidence in the original publication that the part including definition of *Mastodon waringi* was published in October, 1920. It is thus unnecessary here to discuss whether Proaño's name was really published by him in a requisite technical sense: it appeared in an unpaired leaflet inserted in a religious tract! The question would, nevertheless, arise again if, contrary to our opinion, the Ecuadorian specimens were believed to be specifically distinct from the Brazilian forms.

dreds of kilometers of the type locality of *waringi* apparently represent a single species of *Haplomastodon*, a species which is unusually well definable on the basis of the Araxá population. The surviving type fragments of *waringi* are all within the known range of that species. The probability that Holland's specimen belonged to the same species as our Araxá series is thus adequately high if not, indeed, conclusive.

The type of *vidali* is also within the demonstrated range of the common Brazilian species, and the name must be considered synonymous with *waringi*. "*Stegomastodon*" *brasiliensis* refers to Lund's specimens from Lagoa Santa but has no technically designated type. Winge's descriptions of Lund's specimens and our own study of other Lagoa Santa specimens, although somewhat equivocal, do not demonstrate that those specimens are surely separable from the species of Araxá, also in Minas Geraes. Thus *brasiliensis* is also now to be considered a synonym of *waringi*. (In other terms, this was, indeed, the opinion of Hoffstetter when he almost inadvertently made the name *brasiliensis* available in nomenclature, for he applied it to the Araxá specimens and implied that it included the whole series of Brazilian finds; he was not aware that the name *waringi* had been given to a member of that group.) All names hitherto based on Brazilian types may thus now be considered synonymous.

The other names listed in synonymy above have Ecuadorian types. "*Bunolophodon Ayora*" (emended to *Ayorae* or *ayorae* in all publications after the first) is an objective junior synonym of "*Masthodon chimborazi*," having the same specimen as type. "*Bunolophodon postremus*" has a different type, but Hoffstetter (1952) has convincingly shown that it is inseparable from *chimborazi* (the name accepted by Hoffstetter) or *ayorae*.

Hoffstetter based *guayasensis* on the supposedly subgeneric distinction of the atlas and axis. As already mentioned, we now know that the stated character is individually variable and that Hoffstetter's diagnosis does not distinguish the subgenus and species. Hoffstetter also mentioned the following differences between *H. guayasensis* and *H. chimborazi*:

1. Teeth of *guayasensis* average a little

larger. But there is much variation and overlap, and the samples are small. Hoffstetter did not consider this in itself an established difference between the species, and we agree.

2. Molars of *guayasensis* have the main cones higher and more vertical, the talon less developed, and less distinct conelets in the valleys. The differences, also based on small samples, seem to be less than occur within our Araxá sample.

3. The supinator crest of the humerus is less expanded in *guayasensis*. The difference is slight, and the extent of variation of the crest in these or other mastodonts is virtually unknown.¹

We do not consider these differences sufficient basis for separation of the supposed species. It is possible, or indeed even probable, that there were differences of subspecific or lesser value between the coastal and Andine populations, but even that is not established by the actual specimens. In this conclusion, we are merely confirming the original opinion of Hoffstetter himself (1950). It was only after he had separated the supposed species on the now untenable basis of the transverse foramina that he suggested that other small differences might be specific. He considered them individual variations in his earlier study, and we agree. Thus all the described Ecuadorian specimens of *Haplomastodon* seem to belong to one species.

It thus remains to compare the Ecuadorian forms, conspecific among themselves, with the Brazilian *H. waringi*, and especially with the Araxá sample which is essentially our hypodigm for that species. We have not seen the surviving Ecuadorian materials at first hand, but rely on Hoffstetter's excellent data.

Morphologically the Araxá teeth embrace the whole range of variation of the Ecuadorian specimens and provide no possible diagnostic separation. Table 12 compares available measurements of molars, and some comparable measurements of limb bones are given in table 10 above.

Hoffstetter (1952), from whom all the

¹ It is possible that Hoffstetter's artist may unconsciously have exaggerated this difference in the schematic comparative figure (Hoffstetter, 1952, fig. 50). The less schematic separate figures (*ibid.*, figs. 49 and 57A) of the same bones resemble each other more closely.

TABLE 12
MEASUREMENTS (IN MILLIMETERS) OF MOLARS OF *Haplomastodon* FROM
ARAXÁ, BRAZIL, AND ECUADOR

	<i>H. "chimborazi,"</i> from Hoffstetter	<i>H. "guayasensis,"</i> from Hoffstetter	Hoffstetter's Combined Data		<i>H. waringi</i> from Araxá	
			Range	Midpoint	Range	Mean
dm ⁴						
L	100	—	100	100	74–80	78
W	68	—	68	68	52–55	53
M ¹						
L	115	—	115	115	86–101	96
W	76	—	76	76	63–71	67
M ²						
L	133	141	133–141	137	115–132	125
W	97	101	97–101	99	69–89	77
M ³						
L	170–194	173–207	170–207	188.5	165–216	188
W	87–103	91–110	87–110	98.5	75–110	86
dm ₄						
L	—	88	88	88	85–86	85
W	—	50	50	50	45–60	54
M ₁						
L	—	100–107	100–107	103.5	99–111	105
W	—	65–70	65–70	66.5	55–68	61
M ₂						
L	121–138	135	121–138	129.5	107–149	132
W	80–84	83	80–84	82	65–90	74
M ₃						
L	190–245	199–245	190–245	217.5	180–239	208
W	80–100	83–102	80–102	91	69–90	81

Ecuadorian data are derived,¹ gives either a single measurement or a range and does not give the numbers of specimens involved. In all cases the numbers were evidently small, apparently one to five or six. It is evident, with due allowance for the small samples, that in almost all cases the size ranges for Ecuadorian and Araxá populations overlapped widely. The only serious question might arise as regards dm⁴–M¹, but these are particularly small samples and even here overlap in the populations is not excluded. Note, too, that

¹ Other published measurements from Ecuador are few and are evidently unreliable.

the ranges for the corresponding lower teeth clearly overlapped.

On the available data, these molar dimensions seem to have ranged and averaged somewhat smaller for the Araxá than for the Ecuadorian specimens. This is true for 11 of the 16 dimensions compared, and the differences are slight in the other five. A proper statistical estimate of probabilities cannot be made with the available data, and it seems possible that the apparent difference could be due to sampling error. It is, however, at least possible that the Araxá population averaged a little smaller than populations in Ecuador. Among

the few comparable skeletal elements there is also a tendency for the Araxá specimens to be a little smaller. It has also been noted previously that there are minor differences of form and proportions in Araxá and Ecuadorian limb bones, compared individually, but the range of variation in those characters cannot be even roughly estimated.

There is some suggestion that the Araxá animals may average somewhat smaller than other Brazilian *H. waringi* (see table 11). This tends further to decrease the possible difference between Brazilian specimens in general and those from Ecuador.

Populations in localities as distant as Ecuador and southeastern Brazil would certainly be different demes and would quite possibly belong to different subspecies. It would be far more likely than not that there would be differences in the means of their characters. The available data do not, however, suggest that they belong to different species and provide no sound basis on which even possible subspecific distinction could be defined. The conclusion is somewhat negative: specific or subspecific distinction is not demonstrated. Specific identity is, however, positively probable in our opinion. There is nothing in the distance itself or in the different geographic surroundings to make specific distinction probable. Many single species of medium-sized to large animals, including some mastodonts (certainly *Mammuth americanum*), have ranged over equally large and varied areas.

Larger samples from Ecuador might warrant some small taxonomic distinction, but we conclude that at present the described Ecuadorian specimens of *Haplomastodon* should all be referred to *H. waringi*.

STEGOMASTODON POHLIG, 1912

Stegomastodon POHLIG, 1912, p. 193.

Rhabdobunus HAY, 1914, p. 373.

(Species now placed in this genus have also been referred to *Mastodon*, *Gomphotherium*, *Anancus*, *Cuvieronius* and probably other genera; see Cabrera, 1929; Osborn, 1936.)

TYPE: *Stegomastodon mirificus* (Leidy, 1858, p. 10).

KNOWN DISTRIBUTION: In South America, Pleistocene of the Pampean region of Argen-

tina and adjacent Paraguay, Uruguay, and perhaps Brazil. Probably also in northern South America (Colombia?, Venezuela?). Widespread in late Pliocene and early Pleistocene of central and western United States.

DIAGNOSIS: Brevirostrine, bunolophodont, trilophodont mastodonts. Less bunodont or choerodont than any but the most primitive Old World anancines but more so than *Haplomastodon* or *Cuvieronius*. Alternation or obliquity of main cones present, moderate. Tusks simply curved to nearly straight, without enamel. Skull short and high, elephantoid.

DISCUSSION: As noted above, Osborn meant his name *Cuvieronius* to apply to the South American species now referred to this genus, but by a peculiar working of the rules of nomenclature and a somewhat arbitrary identification of types the name has been transferred to Osborn's *Cordillerion*. Osborn noted the close relationship of these South American forms to the North American *Stegomastodon*. In fact neither his original (1923) nor final (1936) diagnosis really cites any difference between his "*Cuvieronius*" and *Stegomastodon* apart from slight formal differences in wording only.¹ He placed both in the same subfamily ("Humboldtinae," an invalid name under the Rules), and Osborn's subfamilies are often approximately equivalent to the genera of more conservative classifications.

When Cabrera (1929) rejected the name *Cuvieronius* for the South American species included under that generic name by Osborn, he did not propose a substitute but simply referred those species to *Stegomastodon*. In this he has been followed by later authors except Osborn, and indeed the published work (even that of Osborn) does not indicate any objective generic distinction between the pertinent South American and North American species.

Adequate specimens of this genus are

¹ In 1936 Osborn gave among the characters of "*Cuvieronius*," "Single trefoils and down-turned tusks in primitive species (*Cuvieronius ayora*, *C. postremus*)," which is not true of *Stegomastodon*. But as a matter of fact it is also untrue of the South American species actually referable to this group. The two species cited belong to the (later recognized) quite distinct genus *Haplomastodon*, and incidentally it is not correct that they have down-turned tusks.

readily recognizable among South American mastodonts. The adult tusks, the double trefoils, and the elephantoid skull are quite unlike *Cuvieronius*. The double trefoils, at least, and probably also the juvenile tusks and the more elevated cranium are also unlike *Haplo-mastodon*. Although, as previously discussed, *Haplo-mastodon* is in some respects intermediate between *Cuvieronius* and *Stegomastodon*, the three genera all seem sufficiently clear-cut. The distinction between *Stegomastodon* and *Notiomastodon* is more debatable, as is noted under the latter genus.

***Stegomastodon platensis* (Ameghino), 1888**

Elephas Humboldtii BLAINVILLE, 1845, p. 249, nec Cuvier, 1824, p. 527.

Mastodon platensis AMEGHINO, 1888, p. 7.

Mastodon bonaerensis MORENO, 1888, pp. 17, 18, *nomen nudum*.

Mastodon rectus AMEGHINO, 1889, p. 643.

Mastodon maderianus AMEGHINO, 1891, p. 243.

(See Cabrera, 1929; other combinations of these names have been used, specimens of this species have been erroneously reported under other names, and still other names with types as yet not adequately restudied will doubtless eventually fall into this synonymy.)

TYPE: M.L.P. No. 8-63, an isolated tusk.

KNOWN DISTRIBUTION: Typically Pampean, Pleistocene, and perhaps mainly early Pampean in the Argentine provinces of Buenos Aires, Santa Fé, and Entre Rios. More widespread finds in South America have not been positively distinguished from this species, the distribution of which may coincide with that of the genus in South America.

DIAGNOSIS: Tusks long, comparatively slender, nearly straight to gently curved. Lophs on M_3^s $4\frac{1}{2}$ – $5\frac{1}{2}$. Double trefoils (as for all species of the genus), but pattern relatively simple, with few secondary conules or conelets. Somewhat less robust than typical *S. superbus*.

DISCUSSION: See the next species.

***Stegomastodon superbus* (Ameghino), 1888**

Mastodon superbus AMEGHINO, 1888, p. 7.

Mastodon pirayuiensis GEZ, 1915, p. 35.

(The remarks on the synonymy of *S. platensis* are also applicable to this species.)

TYPE: M.L.P. No. 8-8, a pair of tusks and a senile mandible.

KNOWN DISTRIBUTION: Typically Pampean, Pleistocene, and perhaps mainly late Pampean, in the Argentine provinces of Buenos Aires and Córdoba. If the species is valid (see discussion below) some extra-Argentine finds may also belong to it.

DIAGNOSIS: Generally very similar to *S. platensis* but comprising somewhat more robust individuals generally, at least, with heavier, more curved tusks and with somewhat more complex grinding teeth.

DISCUSSION: Ameghino named four species of Argentine mastodonts. Cabrera (1929) convincingly argued that three of these are synonymous, the prior name being *platensis*. Cabrera retained *superbus* as a separate species, in which he also placed various specimens previously customarily classified as *Mastodon humboldti*. The two supposed species are essentially sympatric. Cabrera pointed out (in other words) that it is extremely unlikely that two such closely similar groups, if they are taxonomically distinct and not variants in one population, should be both sympatric and synchronous. He concluded that they are probably not synchronous, and believed *platensis* to be earlier than *superbus*. However, as he recognized, the available stratigraphic evidence is exiguous and does not objectively establish that succession.

A summary review of the fine series of specimens in the Museo Argentino de Ciencias Naturales in Buenos Aires was made by Simpson early in 1955 in connection with the present monograph, although this review does not permit a further revision of Cabrera's excellent work. There is certainly a wide difference between smaller, straighter tusks and larger, more curved tusks. Molars (associated with tusks in only a few instances) also have a wide range from smaller and usually simpler to larger and usually more complex. Nevertheless the two groups do intergrade, and data available do not show that the distribution is definitely bimodal. There is wide overlap or intergradation, both in size and structure, and reference to one supposed species or the other is frequently arbitrary. The range in size and structure for all specimens of *Stegomastodon* in the Museo Argentino de Ciencias Naturales is not greater than demonstrably occurs in Brazilian *H. waringi*.

Decision as to the validity and significance

of *S. platensis* and *superbus* must await discovery of adequate samples of known relative dates. If *platensis* and *superbus* were successive, they probably represent a single lineage that was acquiring more complex molars and more curved tusks along a chronocline. Whether they should or could then be distinguished as chronological species or as lesser categories would be largely arbitrary. If it should turn out that the two morphological groups are synchronous, we would consider the two supposed taxa identical.

NOTIOMASTODON CABRERA, 1929

Notiomastodon CABRERA, 1929, p. 90.

TYPE: *Notiomastodon ornatus* Cabrera (1929, p. 91).

KNOWN DISTRIBUTION: Positively identified only from the Pleistocene at Playa del Barco, Monte Hermoso, Province of Buenos Aires, Argentina.

DIAGNOSIS: Cheek teeth and jaws, as far as known, essentially as in *Stegomastodon platensis* (and *superbus*), but tusks with a strong band of enamel.

DISCUSSION: Mastodont remains from Playa del Barco were mentioned by Ameghino as early as 1908, but until 1929 they were referred to "*Mastodon humboldti*," equivalent in modern terms to assigning them to *Stegomastodon platensis* or *superbus*. The few described teeth do seem indeed to be indistinguishable from those of *Stegomastodon*. Cabrera (1929) says that this is the smallest South American mastodont, but his type or syntype M_{1-2} are larger than any he referred to *S. platensis* or *superbus* and his two referred M_3 's are not enough smaller to be placed, on account of size, in a different species. However, three partial tusks from the same locality all have enamel bands,¹ which are absent on several known tusks, probably of equally young individuals, of *S. platensis* and *superbus*. On this basis Cabrera placed them in a separate genus. He distinguished the genus sharply from *Stegomastodon* and considered it more closely related to *Cuvieronius* and a member of the Cuvieroninae, as distinct from the Anancinae, to which *Stegomastodon* was referred. The only apparent

grounds for this allocation were the presence of an enamel band on the tusks of both *Notiomastodon* and *Cuvieronius*.

Osborn (1936) separated *Notiomastodon* still more widely from *Stegomastodon* and equally from *Cuvieronius* (of Cabrera's and our, not Osborn's, nomenclature). He erected for it a monotypic subfamily, *Notiomastodontinae*, of the "Serridentidae," a family based on the genus *Serridentinus*. He believed that the accessory ridges or trefoils are not homologous in *Serridentinus* and *Stegomastodon* and that those of *Notiomastodon* are homologous with the former and not with the latter. We cannot wholly follow Osborn on either of those points. Whatever the more exact homologies of the structures may be, Osborn's *Serridentinus* of group "(B) Sharp ridge-crests" does indeed seem to have developed distinctive molars, which are, however, quite unlike those of *Notiomastodon*. The molars of group "(A) Blunt ridge-crests," which includes the type of *Serridentinus*, seem to us comparatively little modified from the more primitive gomphothere pattern and through that ancestry to have, aside from variable details, trefoils homologous with those of *Stegomastodon*. The *Notiomastodon* molars are virtually identical in pattern with those of *Stegomastodon*, and closer relationship with the longirostrine *Serridentinus* seems extremely unlikely.

Hoffstetter (1950, 1952) has noted the near identity of *Notiomastodon* and *Stegomastodon* in every known respect except the enamel band and has argued that the mere presence (or persistence?) of that band is insufficient basis for subfamily or perhaps even for generic separation. Indeed, except for that one feature, even the tusks of *Notiomastodon* are like those of *Stegomastodon* and quite different from those of *Cuvieronius*. Hoffstetter tentatively reduced *Notiomastodon* to subgeneric status in *Stegomastodon*.

We agree that *Notiomastodon* is almost certainly a close relative of *Stegomastodon* and that its generic status is uncertain. It is known only from a few inadequate specimens from a single locality. Even the association of *Stegomastodon*-like jaws and teeth with enameled tusks, although probable, is not certain. Cabrera assumed that his type mandibular ramus and (upper) tusk are of one individual, but even if they were found together

¹ There is, nevertheless, a tusk in Buenos Aires, M.A.C.N. No. 5451, which is from Playa del Barco and has no enamel. It is, however, somewhat spalled and could have lost an enamel band.

(which does not seem to be a matter of record) the individual association is questionable. There is also the possibility that the Playa del Barco specimens represent a local population of *Stegomastodon*, or even of *S. platensis* or *superbus*, some members of which retained or acquired enamel bands as a developmental anomaly or mutation. Only further and better material can settle these doubts. Our summary investigation in Argentina, including a brief visit to Monte Hermoso, did not yield clues to any specimens other than the few known to Cabrera.

***Notiomastodon ornatus* Cabrera, 1929**

Notiomastodon ornatus CABRERA, 1929, p. 91.

TYPE: M.A.C.N. No. 2157, a young right mandibular ramus with M_1 and M_2 (unerupted) and an isolated (upper) tusk. It is not established that these belong to the same individual. The tusk is more distinctive, and we therefore now designate it as lectotype.

KNOWN DISTRIBUTION: As for the genus.

DIAGNOSIS: Sole species referred to the genus.

WIDER AFFINITIES AND ORIGINS OF THE SOUTH AMERICAN GENERA

COMMUNITY OF ORIGIN

With the possible exception of *Notiomastodon*, distinctions among the South American genera here recognized have been shown to be fairly clear-cut. Nevertheless they do all share numerous characters and in comparison with the mastodonts as a whole they are a rather uniform assemblage. All are:

Fully brevirostrine, with sharply downturned symphyseal spouts and without even vestiges of lower tusks in known specimens (although such may occasionally have occurred in these species).

Trilophodont. (The term refers, of course, to the usual condition of M_3^2 , which do occasionally, in *Haplomastodon* and *Cuvieronius* at least, have variants with some tendency towards tetralophodonty.)

With ridge formulas of M_3^2 $4\frac{1}{2}$ – $5\frac{1}{2}$ (usually somewhat smaller on M^2 than on M_3).

Bunolophodont, with bunodont pretrite trefoils and usually some tendency towards posttrite trefoils, least in *Haplomastodon* and *Cuvieronius* and most in *Notiomastodon* and *Stegomastodon*. The latter do become somewhat complex, with more conules but not truly choerodont or ptychodont.

Brachyodont. Crown height varies considerably, but not beyond a range that may still be considered brachyodont.

With some tendency towards alternation of opposite molar cones or obliquity of lophs on posterior parts of M_3^2 , weakest in *Cuvieronius* and strongest in *Stegomastodon* (and *Notiomastodon*).

These characters are, to be sure, mainly rather primitive as Pleistocene mastodonts

go, except for the brevirostry. We were at first inclined to agree with the implications or statements of Cabrera, Osborn, Hoffstetter, and others that they do not indicate any special unity of origin for the South American mastodonts as a group. Their retention of the primitive characters could date back to a quite remote common ancestry, in an early gomphothere stage, and their brevirostry could have arisen independently two or more times. (It probably did arise independently in the Mammutidae [Mastodontidae, *sensu stricto*, *auctorum*] and the Elephantidae.) On further consideration, however, it seems to us more likely that the known South American forms (along with some from North America and perhaps also some from the Old World) represent the radiation of a distinct systematic group of common origin at no very remote time, perhaps as late as middle Pliocene.

NORTH AMERICAN ALLIES

Much, if not all, of the generic radiation evidently occurred before the mastodonts spread to South America. *Stegomastodon* and probably *Cuvieronius* have been identified in North America at dates almost certainly earlier than their appearance in South America. Although *Haplomastodon* has not yet been certainly identified outside South America, there are North American specimens that may well prove to belong to that genus.

North American specimens of *Stegomasto-*

don are so closely similar to the South American specimens that their common origin at a time not earlier than Blancan (of the North American provincial age sequence) seems virtually certain. The genus was clearly already differentiated before it spread from North to South America. That could even be true of the species, for the necessary intercontinental comparisons have not yet been carried out in sufficient detail and the specific identifications or definitions of North American forms also seem to require further inquiry.

Although Osborn (1936) agreed that North and South American forms here united in *Stegomastodon* were closely related, he nevertheless suggested that the South American group was derived from *Morrillia*. *Morrillia* is a fairly typical longirostrine gomphothere except that it had lost the lower tusks and had molars slightly more complex than is usual in *Gomphotherium* itself. We see no reason to infer any special relationship to any of the forms of *Stegomastodon*.

The situation as regards *Cuvieronius* and *Haplomastodon* is complicated by the fact, previously emphasized, that their molar structure is almost the same and probably not generically identifiable, in itself, in some variants. It seems at present necessary to have tusks of *Cuvieronius* to be certain of distinguishing it from *Haplomastodon* and to have both tusks and molars of *Haplomastodon* to be certain of distinguishing it from, respectively, *Cuvieronius* on one hand and *Stegomastodon* on the other.

At least two North American finds of *Cuvieronius*-like tusks are known. In the Eden formation (late Pliocene) of California, tusks with a spiral enamel band were found in apparent association with rhynchothere-like molars and jaws (Frick, 1921). Frick accepted the association and named the whole complex *Trilophodon shepardi edensis*. Osborn (reviewed in 1936 with citations to earlier comments) rejected the association, placed the molars and jaws in *Rhynchotherium* but referred the tusks to the genus we call *Cuvieronius* (his *Cordillerion*).¹ We thus have here

either a rhynchothere with spiral tusks, a *cuvieronine* with rhynchothere-like jaws and molars, or a remarkably fortuitous occurrence of *Rhynchotherium* and *Cuvieronius* in immediate association with no duplication of parts.

In the Benson fauna (early Pleistocene) of Arizona Gidley (1926) found a partial skull without tusks which he named *Anancus*² *bensonensis*. Near by but not individually associated was a *Cuvieronius*-like tusk, which Gidley referred to the same species. Osborn (1936) accepted the association and referred the species to the genus we call *Cuvieronius*. M^{2-3} are, indeed, similar to those of *Cuvieronius hyodon*, but they are even closer to those of *Haplomastodon waringi* and hardly if at all separable morphologically from some specimens of that species. Moreover, Gidley also found in the same deposit, but did not collect, another tusk that was "of the short, thick, much curved, and rapidly tapering variety; also there was no evidence of an enamel band." The description, such as it is, could apply to an adult tusk of *Haplomastodon*. The Benson occurrence thus includes a skull that could be either *Haplomastodon* or *Cuvieronius*, with slightly greater resemblance to the former, a tusk that is with considerable probability *Cuvieronius*, and a tusk that could be either *Haplomastodon* or some other genus but not *Cuvieronius*.

Other occurrences so far reported in the literature are even more equivocal. Many brevirostrines with (essentially) single trefoils have been reported from Mexico and several from Texas. Osborn (1936), reviewing the earlier literature, listed and accepted two species, one of them with five subspecies, from Mexico and three species from Texas. (More than one species may be represented, but that is not established, and the whole morphological range is no greater than can occur in a single species.) He referred them all to "*Cordillerion*," our *Cuvieronius*, but no *Cuvieronius*-like tusks have been reported from those regions, still less in association with these teeth and jaws. Some if not all of the teeth are at least as suggestive of *Haplomastodon* as of *Cuvieronius*. Cope (1884) and Villada (1903) did mention the presence of enamel on the upper tusks of some of the

¹ In so doing, Osborn created an unusual nomenclatural problem that we do not intend to try to solve here. He placed the former subspecific and then specific syntypes in two different genera but retained the original specific name, *edensis* or *edense*, for both.

² The generic reference, certainly incorrect, stems from an earlier error by Hay.

Mexican forms, but they did not say that it was spiral and did not give any data that would distinguish these tusks from those of *Rhynchotherium*, which occurs in the same general regions. Freudentberg (1922), in direct contradiction, said that all the Quaternary Mexican mastodonts lack enamel on the upper tusks, but again the association is uncertain.

Most recently, Savage (1955) has pointed out that certain specimens previously described from Kansas by Hibbard and Riggs (1949) and others as yet undescribed from Mexico (now in the California Institute of Technology) have cheek teeth similar to those of *Cuvieronius* and *Haplomastodon*.¹ He refers the Kansas specimens to *Stegomastodon* but as representing "a population very close to the origination [of *Stegomastodon*] from *Haplomastodon*-like forms and close to the rhynchotheres and cuvieronines." Actual reference to *Haplomastodon* is apparently not excluded for some or even for all of these specimens.

The data are certainly not satisfactory at present, but they suggest that both *Cuvieronius* and *Haplomastodon* may well occur in North America, along with true *Stegomastodon*. Still less certainly, they suggest that *Cuvieronius*, *Haplomastodon*, and *Stegomastodon* were of common origin and were not yet so clearly distinct in the late Pliocene as they became in the Pleistocene.

There is further a hint that the rhynchotheres may also belong in this same complex, from which, in that event, they would have split off at a somewhat earlier date. If the Eden specimens do belong together and represent a rhynchothere-like cuvieroniine or a *Cuvieronius*-like rhynchothere, they would constitute important evidence for this view. Without special discussion, Savage (1955, fig. 8) shows them as annectant between *Rhynchotherium* and a *Cuvieronius*-*Haplomastodon*-*Stegomastodon* complex. In molars and upper tusks the rhynchotheres are, on the whole, more primitive than the other genera named. The down-turned symphysis and small lower tusks could also be primitive, for this could have been a stage in the evolution of fully brevirostrine types with down-

turned symphyseal spouts (so called descriptively, not functionally).

POSSIBLE OLD WORLD ALLIES

The ultimate source of this whole complex must be sought in the Old World, and a relationship between the classical brevirostrines of the Old World (*Anancus*) and the New (*Stegomastodon*) has long been claimed. Cabrera (1929) explicitly referred the South American stegomastodonts to the Anancinae and so, until his final work, did Osborn in substance but with his different, idiosyncratic nomenclature. In his latest work, however, Osborn (1936 and early mention there cited) first put the South American stegomastodonts in a separate subfamily, then family, with a definition that distinguishes them from the most specialized but not from the more primitive Anancinae (his "Brevirostrinae," an invalid name). Then, finally (in the last proof stages of his 1936 memoir), Osborn also removed North American *Stegomastodon* from the Anancinae because of their resemblance to the (in our opinion congeneric) South American stegomastodonts. The sequence is odd: it might seem more logical to refer the South American forms to the Anancinae (or to leave them there) because of their resemblance to the *Anancus*-like North American stegomastodonts.²

Hoffstetter (1952) rejected Osborn's arrangement and referred both *Stegomastodon* (following Cabrera and others) and *Haplomastodon* to the Anancinae, but (also following Cabrera and essentially Osborn except in nomenclature) kept *Cuvieronius* in a subfamily of its own.

The better-known among the Old World Anancinae are too specialized to have given rise to *Stegomastodon*, or *a fortiori* to *Haplomastodon* or *Cuvieronius*. The genera *Anancus*, *Pentalophodon*, and *Synconolophus* (so similar and closely related that all their species could well be referred to the single genus *Anancus*) rapidly developed extreme alternation of

¹ We are indebted to Dr. D. E. Savage and also to Dr. C. W. Hibbard and to Mr. W. Otto for further data on these specimens.

² Osborn did leave the anancines and stegomastodonts in adjacent phylogenetic positions, even though he finally referred them to different families. His graphic phylogeny of 1934 (republished in Osborn, 1936) indeed shows a common ancestry, but in the Cretaceous! His final chart of 1935 (published posthumously in Osborn, 1936) does not definitely show a common ancestry but suggests that one may have occurred in the Oligocene.

posterior cusps of M_3^s and became choerodont-ptychodont to higher degree than any New World mastodonts. They also developed a higher number of ridge crests and tetralophodont to pentalophodont M_2^s . There are, however, a few known teeth from Africa (Arambourg, 1945, reidentifying specimens referred to other groups by MacInnes, 1942) and from Portugal (Bergounioux, Zbyszewski, and Crouzel, 1953) that seem to be those of anancines and to be sufficiently primitive to indicate a possible ancestry for the American brevirostrine bunolophodonts. This group, *Protanancus* Piveteau, if the various isolated specimens are correctly referred, was trilophodont, with only four and one-half crests on M^3 , with single trefoils, and with the alternation of pretrites and posttrites comparatively slight, hardly more than in some specimens of *Cuvieronius*, which on an average has the least alternation of any of the New World forms in question here. Neither upper tusks nor lower symphysis is known. To be noted also is the tantalizing fragment from Moghara, Egypt, called *Mastodon spenceri* by Fourtau (1918), a trilophodont with a long but sharply down-turned symphysis suggestive of *Rhynchotherium*, to which Osborn (1936) tentatively referred it. Its only cheek tooth is a worn M_2 , not very characteristic but not clearly distinct from M_2 referred to *Protanancus*. It is also pertinent that some of the later Old World anancines have moderately elongated and down-turned symphyses, rather like those of the rhynchotheres except that the lower tusks had then been lost in the adults at least.

There is thus a hint, no more, that there may possibly have existed in the middle to late Miocene of the Old World a stock from which there could have evolved in the Old World *Anancus* (with *Pentalophodon* and *Synconolophus*) and in the New World *Rhynchotherium* (with several subgenera or synonyms), *Stegomastodon*, *Haplomastodon*, and *Cuvieronius*.

SUBFAMILY POSITION

In view of the many uncertainties and of the trend of such evidence as is at hand, past and current supergeneric classifications of the South American forms are decidedly unsatisfactory. If *Stegomastodon* really arose from and is referable to the Anancinae, then it is likely or, at best, is not excluded that the other South American genera arose from the same source and at no earlier date. If *Rhynchotherium*, *Stegomastodon*, and *Cuvieronius* are referred to different subfamilies, this is merely giving subfamily rank to each of several divergent but probably related genera. *Haplomastodon* could also be given its own subfamily, or could be referred to the Cuvieroniinae rather than the Anancinae. In fact it tends to unite the supposed subfamilies if the latter is represented by *Stegomastodon*. *Haplomastodon* is even less like the most typical Anancinae, true advanced *Anancus*, than is *Stegomastodon*.

The previously proposed subfamily allocations simply do not correspond with the balance of acceptable evidence now at hand. As of now, it seems to us that the alternatives lie between assigning each of the genera *Anancus*, *Rhynchotherium*, *Stegomastodon*, *Haplomastodon*, and *Cuvieronius* to its own separate subfamily, a cumbersome arrangement with one genus per subfamily, or putting them all together tentatively as a rhynchorostrine-brevirostrine group of possible common origin from, ultimately, longirostrine gomphotheres. For the present we tentatively favor the latter arrangement. Or, of course, one could simply abandon subfamilies within the Gomphotheriidae.

As far as we know, the earliest name formed according to the Rules and available for a subfamily uniting these genera is Anancinae Hay, 1922. Tentatively and pending further clarification, especially regarding the North American and Old World forms, we refer all the South American mastodonts to that subfamily.

PROGRESSIVE SPECIALIZATION IN SOME ANANCINAE

An interesting method of scoring over-all evolutionary advance has been developed especially by Olson (1944), Westoll (1949), and Schaeffer (1952). It is enlightening as to

advance along parallel lines (Olson) or as averages in long temporal sequences (Westoll, Schaeffer). Neither pattern occurs precisely among the mastodonts here under discussion,

but the method is applicable to them with certain reservations. A known or postulated ancestral form is selected and its characters are (in one form of the method, see Simpson, 1953) assigned zero score. Progressive changes in specified features are assigned increasingly higher integral scores. Combined scores for particular species or genera or for the whole group at a particular time can then be totaled or expressed as a percentage of the highest possible score.

Protanancus might be the appropriate scoring base for this group, but its characters are

vance that as a very tentative postulate. We also postulate that spiral and upcurved tusks are equally specialized but in different directions and that the same is true of a short, high, "elephantoid" skull (typical *Stegomastodon*) as against one that is especially long and low (*Cuvieronius hyodon*). There is comparatively little doubt about the sequentially specialized nature of loss of enamel on the tusks and development of trefoils and additional lophs on the molars. A scale worked out on these frankly hypothetical considerations is as follows:

A. Shape of upper tusks	0, moderately down-curved 1, straight to upcurved; spiral
B. Enamel on upper tusks	0, present 1, present in juveniles, absent or variable in adults 2, absent
C. Symphysis and lower tusks	0, long, tusks present 1, more or less shortened, down-curved, tusks present 2, short, tusks absent (at least in usual adults)
D. Molar trefoils	0, single 1, variably incipient double trefoils 2, double trefoils
E. Molar lophs (and lophids)	0, $\frac{4-4 \frac{1}{2}}{4 \frac{1}{2}-5}$ 1, $\frac{4 \frac{1}{2}-5}{5-5 \frac{1}{2}}$ 2, $\frac{5-5 \frac{1}{2}}{5 \frac{1}{2}-6}$ or more
F. Shape of skull	0, intermediate or gomphotherioid 1, short, high or elephantoid; long, low

too poorly known and its ancestral status still uncertain. *Gomphotherium* is certainly a primitive mastodont, on the whole, and is probably in or near the ancestry of this whole group, whether or not that ancestry passed through *Protanancus*. Early *Gomphotherium* is therefore used as a base, its characters scored as zero. All true *Anancus* is already divergent from any New World forms and is not here considered. Scoring of characters in the New World forms depends on some undemonstrated assumptions as to evolutionary sequence and is to that extent uncertain and hypothetical. Perhaps the most dubious point is whether the lower symphysis and tusks of the New World Anancinae passed through a rhynchothere-like stage. We ad-

Application of these scores to the relevant genera is shown in table 13.

These characters are not all independent. It is, for instance, reasonably sure that the shape of the skull is influenced by the shape of the tusks. There are various other deficiencies and uncertainties, and of course different scoring weights could be assigned no more arbitrarily. As is evident on other grounds as well, *Gomphotherium* and *Rhynchotherium* are poorly distinguished, and the four other genera could all be derived from one or the other of those genera or from both in sequence. As far as these characters go, *Haplo-mastodon* could have given rise to *Notiomastodon* (conditionally, depending on the real status of the enameled tusks) and to *Stego-*

TABLE 13
SCORING OF PRIMITIVE AND ADVANCED CHARACTERS IN SOME MASTODONTS
(For explanation of scoring scale, see text.)

Genus	Character Scores						Total Score	Total as Per Cent of Maximum (10)
	A	B	C	D	E	F		
<i>Gomphotherium</i>	0	0	0	0	0	0	0	0
<i>Rhynchotherium</i>	0	0	1	0	0	0?	1	10
<i>Haplomastodon</i>	1	1	2	1	1	0	6	60
<i>Cuvieronius</i>	1	0	2	1	1	1	6	60
<i>Notiomastodon</i>	1	0 (or 1?)	2	2	2	1?	8 (or 9?)	80 (or 90?)
<i>Stegomastodon</i>	1	2 (or 1?)	2	2	2	1	10 (or 9?)	100 (or 90?)

mastodon, but not to *Cuvieronius*. *Notiomastodon* could have given rise to (or with the afore-mentioned condition could even be synonymous with) *Stegomastodon*. *Cuvieronius* probably could not have arisen from or have given rise to any of the other three genera. Those inferences, reasonable but quite uncertain, reflect the impression that led Hoffstetter to place *Cuvieronius* in one subfamily and the other three genera together in another subfamily. It must, however, be noted that the known species of the four genera are in part contemporaneous and in any case do not form a sequence confirming the structurally possible ancestral-descendent relationships.

Even if *Haplomastodon* proved to be a little-modified survivor of forms phylogenetically near *Stegomastodon*, it does have considerable resemblance to *Cuvieronius* and could be collaterally nearer to the latter. The whole picture again suggests most strongly that the three well-established genera, and perhaps *Notiomastodon* as a fourth, have advanced separately and to different degrees along somewhat diverging pathways. The interest of the scoring is in showing how far, comparatively, each has advanced and also in providing incidentally a succinct and lucid generic key to the group.

ADDENDUM

HOFFSTETTER (1955) has published a detailed, adverse criticism of our short preliminary abstract of conclusions (Simpson and Paula Couto, 1955). His objections seem to us to have been largely answered before they were made, and we have not felt it necessary to alter preceding parts of this manuscript as a result of his paper. The basis for our views is now published, and any detailed reply to Hoffstetter, whose excellent earlier work we took as a point of departure, is obviated. Just two points should be briefly mentioned because they relate to differences between the brief abstract reviewed by Hoffstetter and the present complete and final version.

The Portuguese, but not the English, version of our abstract said that the variable presence or absence of transverse foramina in atlas and axis is "*sem qualquer expressão taxonômica*." Hoffstetter took this to mean that we refuse "*toute signification taxinomique à un caractère lorsque celui-ci est variable*." Our abstract was perhaps not sufficiently explicit as to the fuller conclusions then already expressed in our manuscript and now published without change. First, no difference in incidence of these variant characters has yet been demonstrated between Brazilian and Ecuadorian populations; second, a difference in average incidence, if demonstrated, would be a taxonomic distinction at some level; third, that distinction would in all probability be subspecific or lower, so would not be likely to modify the specific synonymy here pro-

posed. A detailed reconsideration of the statistical probabilities involved and their most likely biological significance has been made, and it confirms us in these conclusions.

In our abstract we retained the subfamily Cuvieroninae and referred *Haplomastodon* to it. Hoffstetter insists on his earlier opinion that *Haplomastodon* is much more closely related to *Stegomastodon* and belongs in the Anancinae as opposed to the Cuvieroninae. (Whether *Stegomastodon* itself would belong in the Anancinae in a classification so split as to give *Cuvieronius* subfamily status is a difficult question that might be raised in that context.) After writing our abstract, but before receipt of Hoffstetter's criticism, we modified our manuscript, provisionally proposing suppression of the subfamily Cuvieroninae. In our present view, on grounds already discussed, *Stegomastodon*, *Haplomastodon*, and *Cuvieronius* are tentatively considered terminal members of three divergent lineages within one broader group. *Haplomastodon* is to some extent intermediate between *Stegomastodon* and *Cuvieronius*. Further argument as to the exact shading of resemblance or affinity to one or the other would be quite subjective and futile at present.

We want to emphasize our great appreciation of Hoffstetter's fine work on the Ecuadorian Pleistocene fauna. It makes a giant stride forward in our understanding of South American faunas and of the mammals in general.

SUMMARY

1. A LARGE COLLECTION, mainly of isolated molars, from Águas do Araxá, Brazil, seems to represent a single population within a species identified as *Haplomastodon waringi*. The variation, described in some detail, is far greater than has hitherto usually been taken into consideration in the diagnosis of supposed species of mastodonts.

2. Mastodonts have been found at many localities scattered throughout Brazil. A few specimens are anomalous, but the great majority belong to, or are at least inseparable from, *H. waringi* on the basis of known characters.

3. Ecuadorian *Haplomastodon* is not at present specifically separable from *H. waringi*, and neither in Brazil nor in Ecuador is there good evidence of the presence of more than one species (or subgenus).

4. The only species and genera that now seem to be clearly distinct among South

American mastodonts are *Cuvieronius hyodon*, *Haplomastodon waringi*, and *Stegomastodon platensis*. All these names have numerous synonyms. The species *Stegomastodon superbus* and the genus and species *Notiomastodon ornatus* are also tentatively listed as distinct, but are of doubtful status.

5. *Haplomastodon* is believed to be about as closely related to *Cuvieronius* as to *Stegomastodon*.

6. All the South American mastodonts seem to represent end terms of divergence within a single broad stock. *Cuvieronius*, *Stegomastodon*, and probably also *Haplomastodon* were already differentiated before they spread from North America to South America. The North American *Rhynchotherium* may belong to the same complex. All may ultimately have arisen from early Old World Anancinae, and all are tentatively referred to that subfamily.

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PLATES 1-23

PLATE 1

Restorations of heads of three South American mastodonts, by Ibsen
de Gusmão Câmara

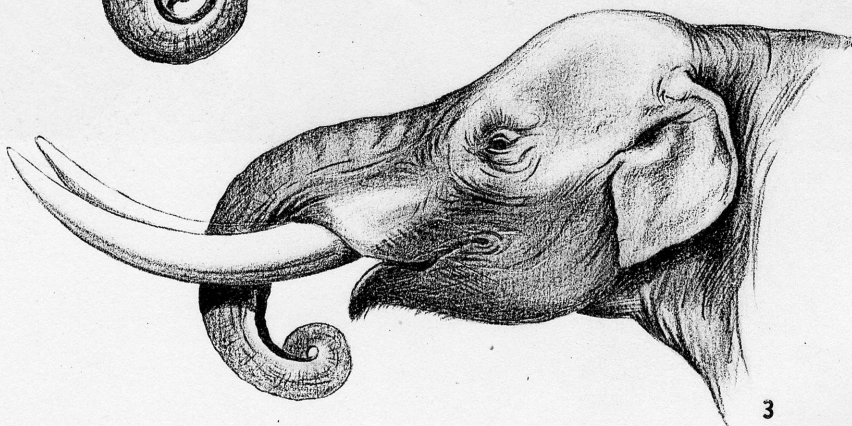
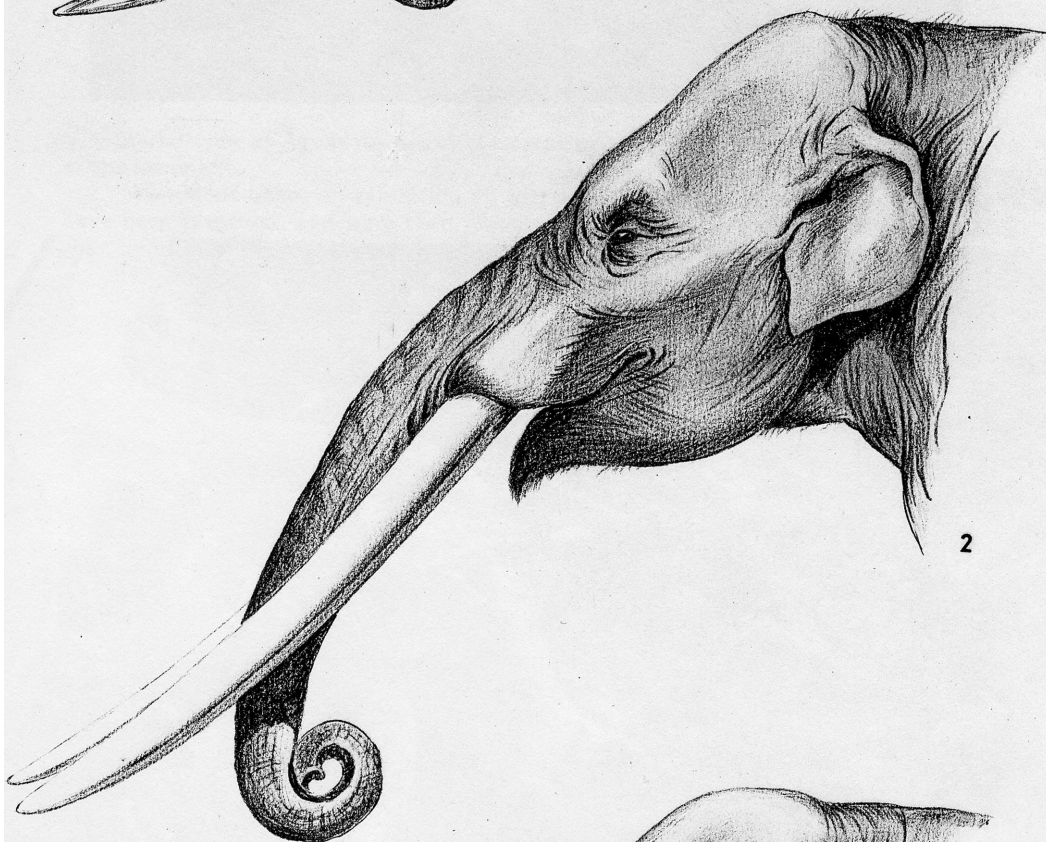
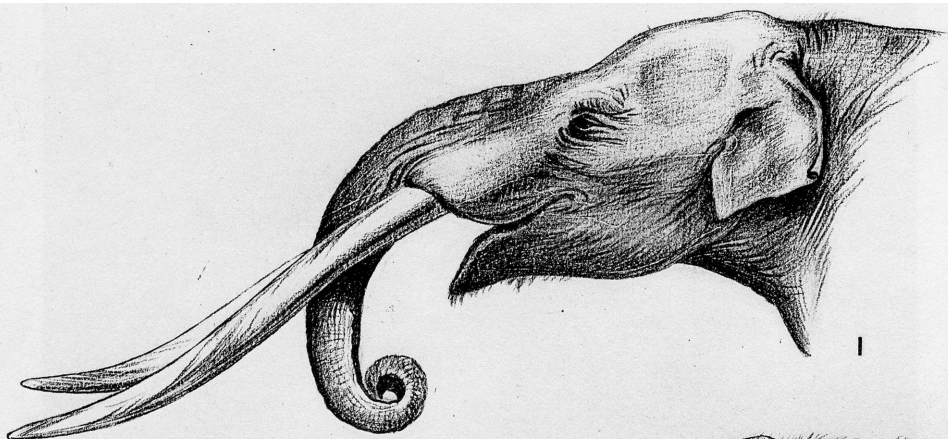
1. *Cuvieronius hyodon*, based on a photograph of A.M.N.H. No. 26984, with tusks modified.

2. *Stegomastodon superbus*, based on Cabrera's (1929) drawing of M.L.P. No. 8-1.

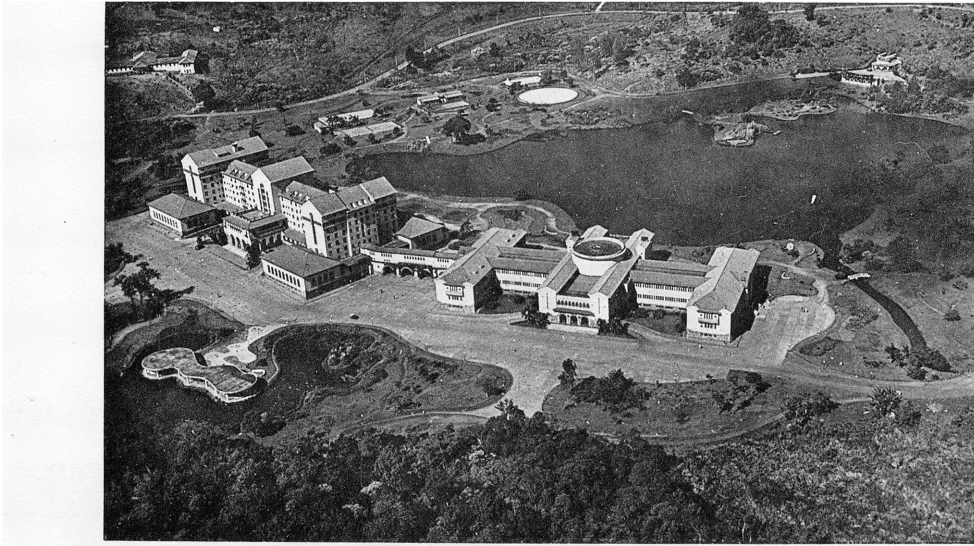
3. *Haplomastodon waringi*, based on Spillmann's photograph (published in Osborn, 1936) of his "*Bunolophodon ayorae*," a skull formerly in the Museo de la Universidad Central de Quito, Ecuador.

All three individuals are adult and probably male. The distinctly different head shapes of *Cuvieronius* and *Stegomastodon* and the more or less intermediate shape of the head of *Haplomastodon* are well shown.

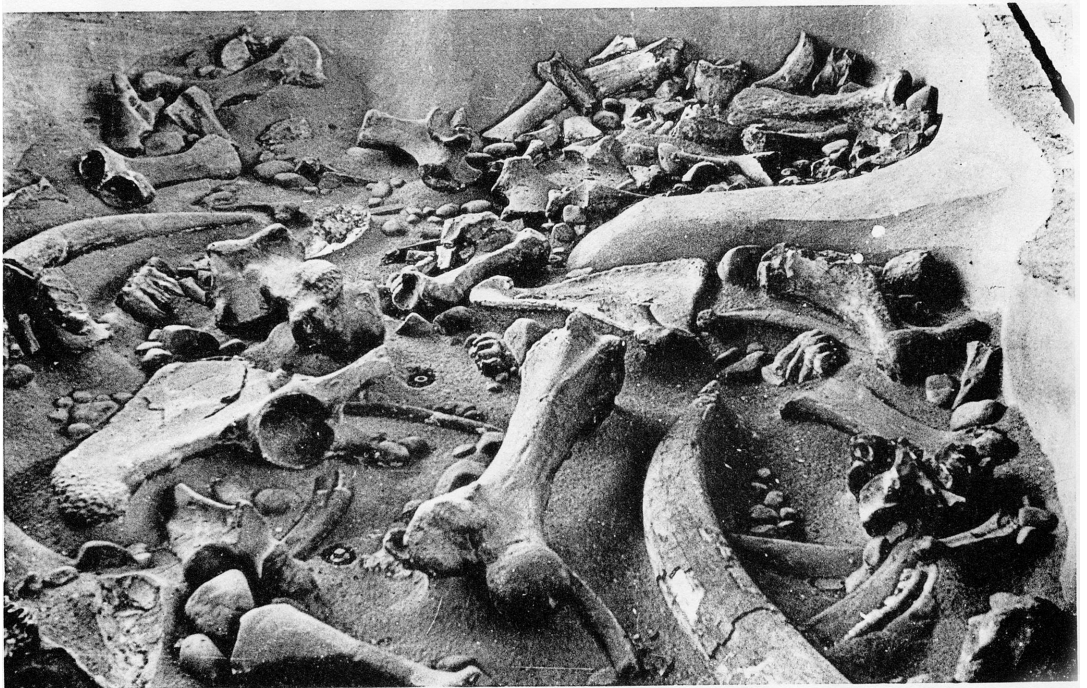
All $\times 1/18$.



I. Camara
1936



1



2

PLATE 2

1. Aerial view of Águas do Araxá. The mastodont locality is covered by the pavilion at the lower left.
2. Mastodont bones on exhibition at Águas do Araxá. The specimens here displayed have been prepared, and were then placed on a concrete base at the place where they were found.

PLATE 3

Mastodont remains *in situ* at Águas do Araxá. Same as 2 of plate 2, but the photograph was taken from a higher angle and from the right side of the deposit as seen in 2 of plate 2.



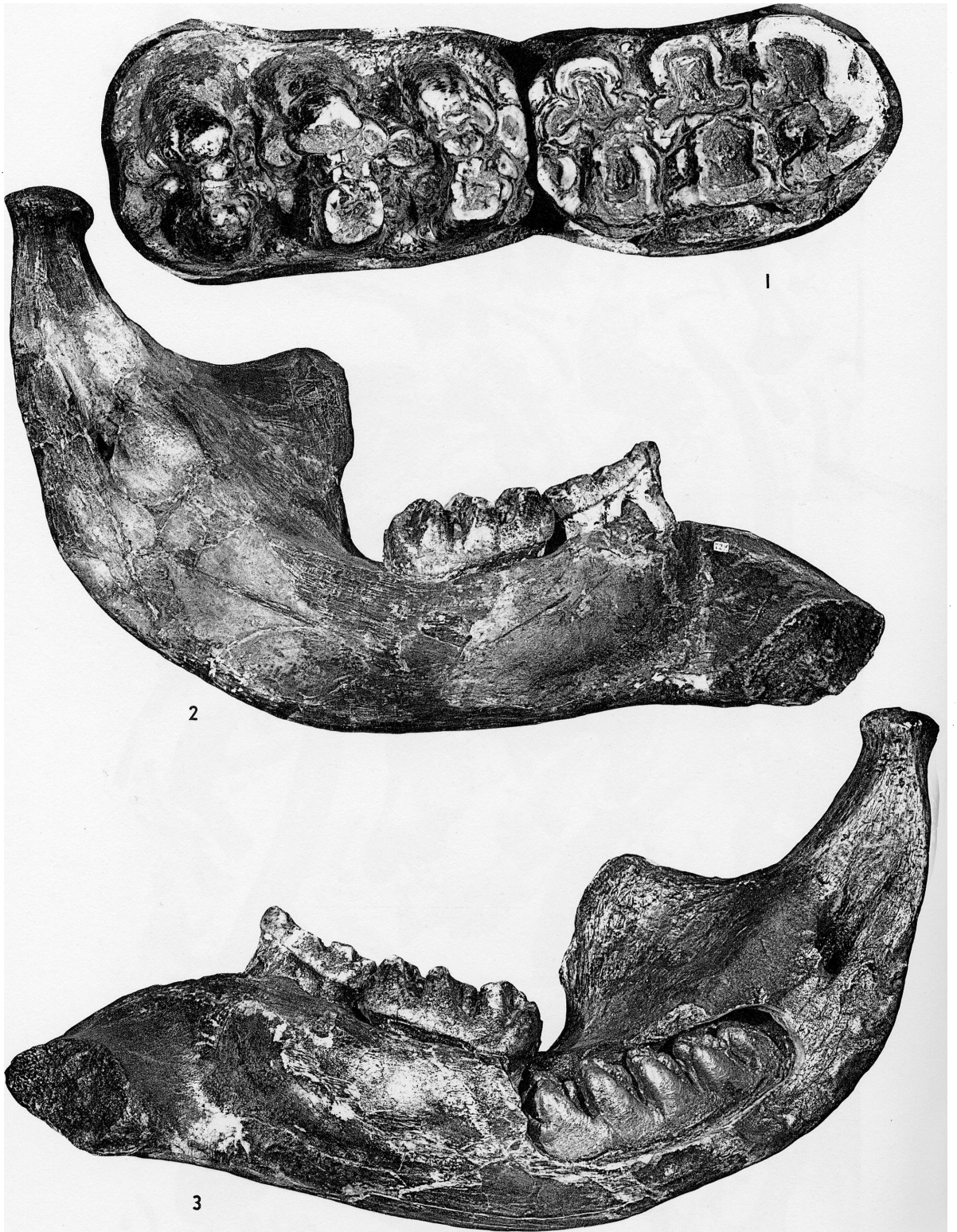


PLATE 4

Haplomastodon waringi (Holland), D.G.M. No. 72M, from Águas do Araxá

1. Left M_{1-2} , crown view. Length, 234 mm.
2. Left lower jaw showing M_{1-2} .
3. Right lower jaw showing M_{1-2} in place and unerupted M_3 .

PLATE 5

Haplomastodon waringi (Holland)

1. D.G.M. No. 72M, from Águas do Araxá, unerupted M_3 , removed from jaw, crown view. Length, 222 mm.
 2. Lower jaw with right M_3 and left M_3 in place, dorsal view. Length of right M_3 , 220 mm.; of left M_3 , 197 mm.
 3. Left M_3 from the jaw shown in 2, crown view.
 4. Right M_3 , crown view. Length, 200 mm.
- 2-4 are *in situ* at Águas do Araxá.

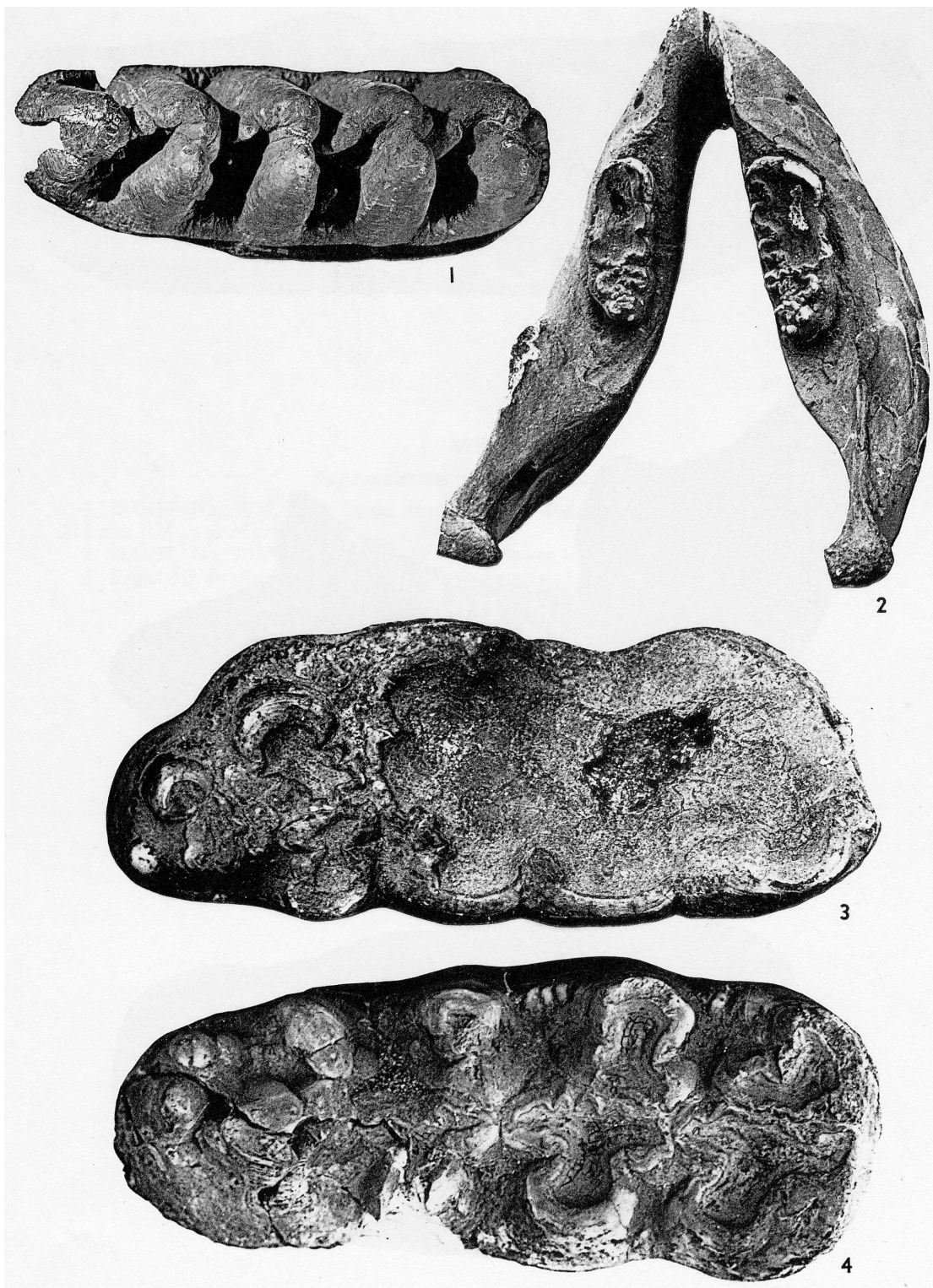




PLATE 6

Haplomastodon waringi (Holland)

1. D.G.M. No. 70M, from Águas do Araxá, left M_{2-3} , crown view. Length of M_{2-3} , 274 mm.? M_{2-3} , or M_3 alone?
2. D.G.M. No. 70M, from Águas do Araxá, lower left jaw with M_{2-3} , lingual view.
3. Right M^3 , *in situ* at Águas do Araxá, crown view. Length, 189 mm.

PLATE 7

Haplomastodon waringi (Holland), right lower jaw, *in situ* at Águas do Araxá

1. M_{1-2} and unerupted M_3 . Length of M_3 , 130 mm.
2. Right M_{1-2} , crown view.
3. Right, unerupted M_3 , crown view. Length, *ca.* 220 mm.



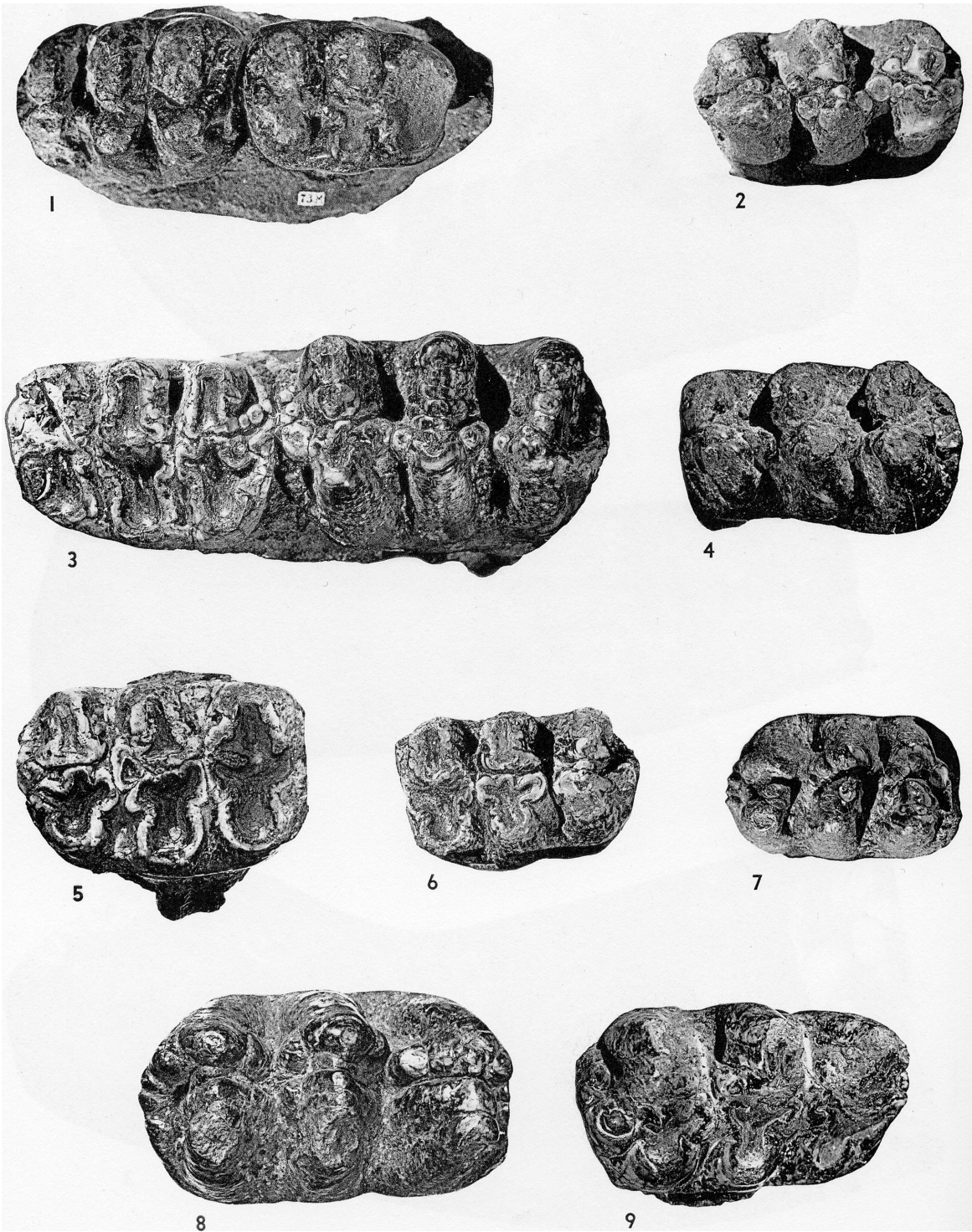


PLATE 8

Haplomastodon waringi (Holland)

1. D.G.M. No. 73M, right dm^4-M^1 , crown view. Length of dm^4 , 79 mm.; of M^1 , 98 mm.
 2. D.G.M. No. 98M, right M_1 , crown view. Length, 110 mm.
 3. D.G.M. No. 74M, left M_{1-2} , crown view. $\times 15/37$.
 4. D.G.M. No. 89M, left M_1 , crown view. Length, 107 mm.
 5. A.M.N.H. No. 45981, right M^1 , crown view. Approximately $\times \frac{1}{2}$.
 6. D.G.M. No. 91M, left M^1 , crown view. Length, 101 mm.
 7. D.G.M. No. 111M, right M^2 , crown view. Length, 132 mm.
 8. A.M.N.H. No. 45980, right M^2 , crown view. Approximately $\times \frac{1}{2}$.
 9. D.G.M. No. 104M, right M^2 , crown view. Length, 128 mm.
- All are from Águas do Araxá.

PLATE 9

Haplomastodon waringi (Holland)

1. A.M.N.H. No. 45977, left M_2 , crown view. Approximately $\times \frac{1}{2}$.
 2. D.G.M. No. 75M, right M_2 , crown view. Length, 145 mm.
 3. D.G.M. No. 112M, left M_2 , crown view. Length, 148 mm.
 4. D.G.M. No. 97M, left M_2 , crown view. Length, 124 mm.
 5. A.M.N.H. No. 45978, right M_2 , crown view. Approximately $\times \frac{1}{2}$.
 6. D.G.M. No. 106M, right M^3 , crown view. Length, 129 mm.
 7. U.M.G. No. LB-15, left M^3 , crown view. Length, 198 mm.
- All are from Águas do Araxá.

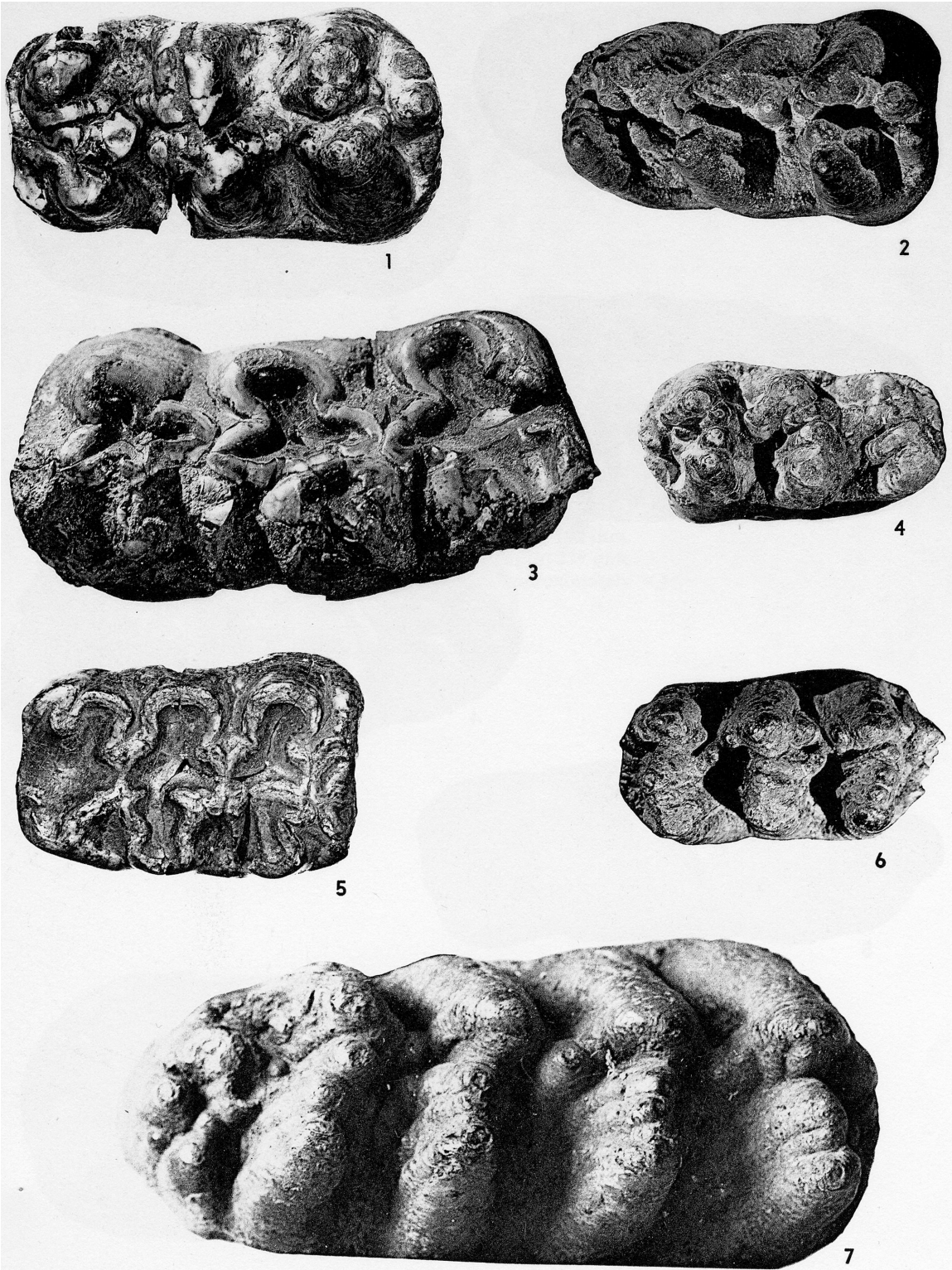




PLATE 10

Hapломastodon waringi (Holland)

1. D.G.M. No. 126M, right M^3 , crown view. Length, 176 mm.
 2. D.G.M. No. 117M, right M^3 , crown view. Approximately $\times 9/26$.
 3. D.G.M. No. 116M, left M^3 , crown view. Length, 216 mm.
 4. D.G.M. No. 128M, left M^3 , crown view. Length, 192 mm.
 5. D.G.M. No. 60M, right M_3 , crown view. Length, 239 mm.
 6. A.M.N.H. No. 45979, left M^3 , crown view. Approximately $\times \frac{1}{2}$.
- All are from Águas do Araxá.

PLATE 11

Haplomastodon waringi (Holland)

1. A.M.N.H. No. 45976, right M_3 , crown view. Length, 230 mm.
 2. D.G.M. No. 131M, right M_3 , crown view. Length, 200 mm.
 3. D.G.M. No. 71M, right M_3 , crown view. Approximately $\times 7/24$.
 4. D.G.M. No. 132M, left M_3 , crown view. Length, 223 mm.
 5. D.G.M. No. 133M, left M_3 , crown view. Length, 196 mm.
- All are from Águas do Araxá.





PLATE 12

Haplomaston waringi (Holland), D.G.M. No. 144M, from Águas do Araxá, atlas

1. Anterior view. $\times 9/20$.

2. Posterior view. $\times 9/20$.

The transverse foramina are present on both sides.

PLATE 13

Haplomastodon waringi (Holland), D.G.M. No. 144M, from Águas do Araxá, atlas

1. Ventral view.
2. Dorsal view.
3. Lateral view.

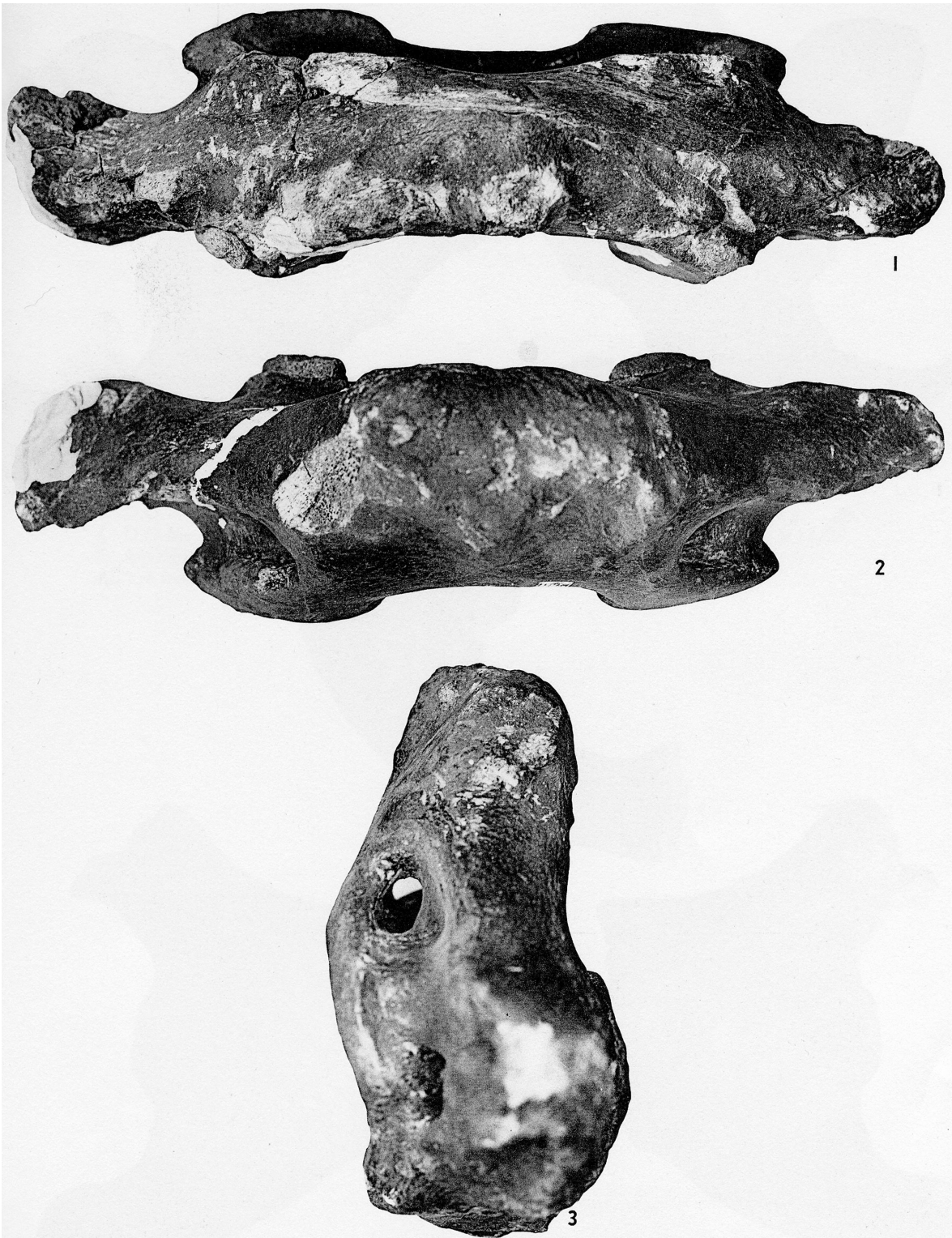




PLATE 14

Haplomastodon waringi (Holland)

1. D.G.M. No. 394M, half atlas, posterior view, transverse foramen absent. Approximately $\times \frac{1}{2}$.
 2. Anterior view of specimen shown in 1. Approximately $\times \frac{1}{2}$.
 3. D.G.M. No. 393M, half atlas, posterior view, transverse foramen absent. $\times \frac{1}{2}$.
 4. D.G.M. No. 395M, half atlas, posterior view, transverse foramen present. $\times 12/29$.
 5. Anterior view of specimen shown in 4. $\times 12/29$.
- All are from Águas do Araxá.

PLATE 15

Hapломastodon waringi (Holland), D.G.M. No. 145M, from Águas do Araxá, axis

1. Anterior view. $\times 7/17$.
2. Right lateral view. $\times 6/17$.
3. Posterior view. $\times 3/7$.





PLATE 16

1. *Haplomastodon waringi* (Holland), left femur, *in situ* at Águas do Araxá, posterior view. Length, 1060 mm.

2, 3. *Haplomastodon waringi* (Holland), left ulna, *in situ* at Águas do Araxá. 2. Anterior view. 3. External view. No scale.

4. *Haplomastodon* cf. *warangi*, D.G.M. No. 423, from Rio Araguari, Amapá, right M², crown view. Length, 135 mm.

5. *Haplomastodon* cf. *warangi*, U.S.P. No. 2538, from the upper Juruá River, Amazonas, right M₃, crown view. Length, 182 mm.

PLATE 17

Haplomastodon waringi (Holland)

1. U.S.P. No. 3-1201, from Monte Alto, Bahia, posterior part of right M_3 , crown view. Length of the part preserved, 142 mm.
2. Lund collection, Copenhagen, juvenile skull from Lagoa Santa, Minas Geraes, right side view, with dp^2 - dp^3 . Length of dp^2 , 34 mm.; of dp^3 , 56.5 mm.
3. Anterior view of the skull shown in 2.
4. Palatal view of the skull shown in 2, with right and left dp^2 - dp^3 .





PLATE 18

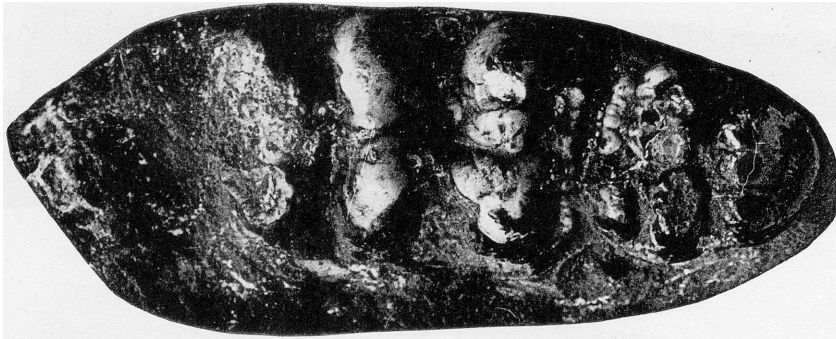
Haplomastodon waringi (Holland), H. V. Walter collection, juvenile skull from
the Lapa do Caetano da Cerca Grande, Minas Geraes

1. Anterior view.
2. Palatal view. Length of right dm^2 , 32 mm.; of dm^3 , *ca.* 56 mm.
3. Right side view showing dm^2 - dm^3 .
4. Left side view showing dm^2 - dm^3 . Length of dm^2 , 33 mm.; of dm^3 , 55 mm.

PLATE 19

Haplomastodon waringi (Holland), H. V. Walter collection

1. Right dm^2 - dm^3 of juvenile skull from the Lapa do Caetano da Cerca Grande, Minas Geraes, crown view. Length of dm^2 , 32 mm.; of dm^3 , *ca.* 56 mm.
2. Left dm^2 - dm^3 of same skull as shown in 1, crown view. Length of dm^2 , 33 mm.; of dm^3 , 55 mm.
3. Isolated left M^3 , from Lapa do Borges, Minas Geraes, crown view. Length, 172 mm.



1



2



3

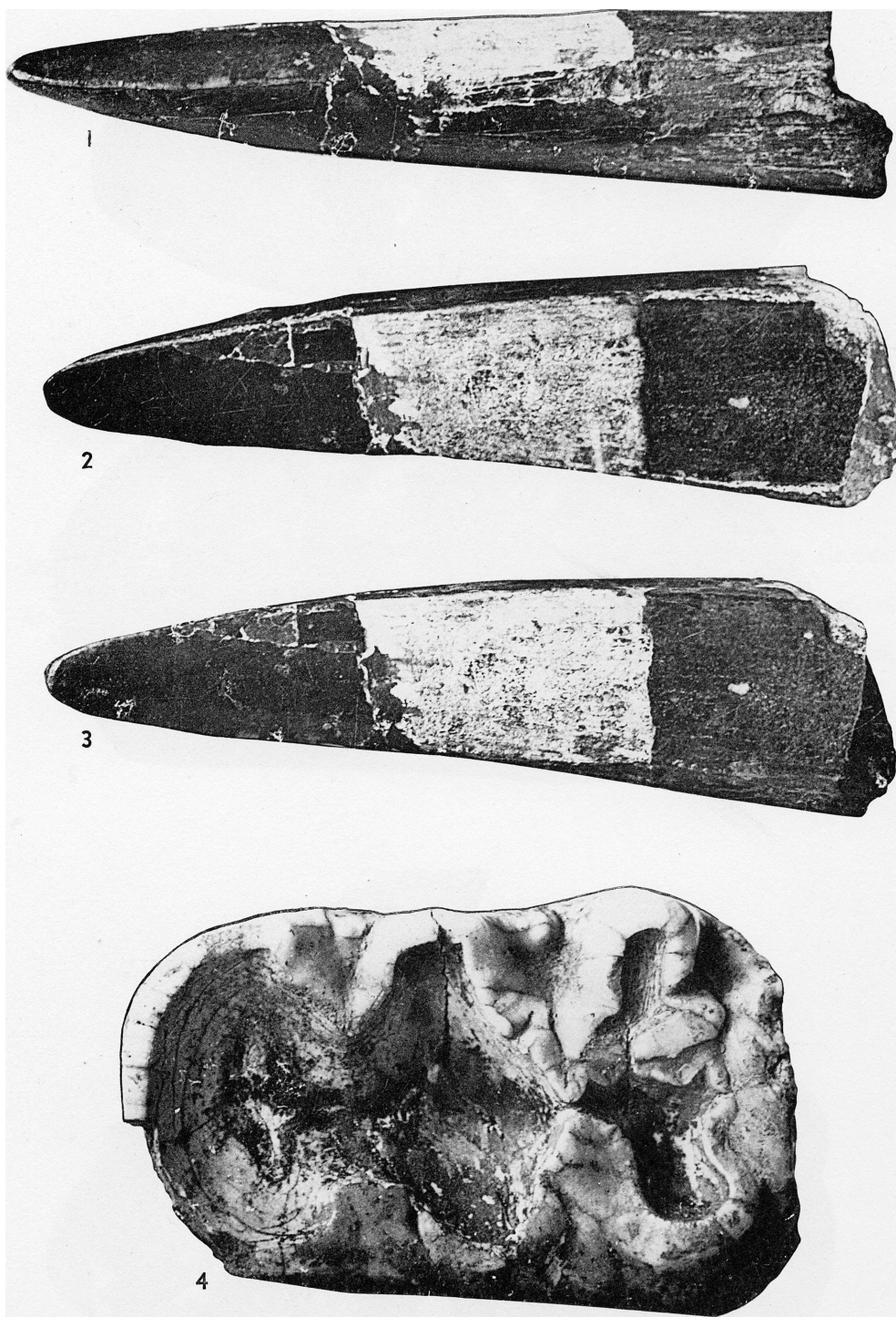


PLATE 20

1-3. Genus and species uncertain, possibly an unusual *Haplomastodon*, U.M.G. No. LB-1, incomplete tusk with very slightly spiral enamel band. Length of the enamel band from the tip to the broken proximal end, 240 mm.

4. *Haplomastodon waringi* (Holland), U.M.G. No. LB-6, left M_2 , crown view. Length of the second lophid, *ca.* 128 mm.; of the third lophid, 85 mm.

All are from Lapa do Borges, Minas Geraes.

PLATE 21

Haplomastodon waringi?

1. U.M.G. No. LB-7, broken dm_4 or possibly M_1 , crown view. Width on the second lophid, 57 mm.
 2. U.M.G. No. LB-12, right mandible with the posterior end of M_2 and *situs* of M_3 . M_3 was lost during life, with some bone dissolution and secondary deposition. No scale.
 3. Lateral view of specimen shown in 2. No scale.
- All are from Lapa do Borges, Minas Geraes.





PLATE 22

1. *Stegomastodon?* sp., U.S.P. No. 3-1238, from Araxá (?), somewhat water-worn left M^3 , crown view. Length, 175 mm.
2. *Haplomastodon* cf. *waringi*, in the University of São Paulo, incomplete right M_2 , from Águas da Prata, São Paulo, crown view. Length, ca. 130 mm.
3. Lingual view of specimen shown in 2.
4. *Stegomastodon?* sp., in the Museu Júlio de Castilhos, Porto Alegre, Rio Grande do Sul, isolated left M_2 from Barra do Ouro. ~~municipio~~ of Osório, Rio Grande do Sul, crown view. No scale.

PLATE 23

1. *Haplomastodon waringi* (Holland), type, C.M. No. 11033, from Pedra Vermelha, Bahia, molar fragment with posttrite cone, crown view. Approximately $\times \frac{1}{2}$.
2. Lateral view of specimen shown in 1.
3. *Haplomastodon waringi* (Holland), type, C.M. No. 11033, from Pedra Vermelha, Bahia, tip of tusk. Approximately $\times \frac{1}{2}$.
4. *Stegomastodon platensis* (Ameghino), M.A.C.N. No. 12046, from Rio Caracraña, Province of Buenos Aires, Argentina, juvenile skull, right side view. $\times \frac{1}{3}$.
5. Left side view of specimen shown in 4.

