

TAXONOMIC REMARKS ON THE SOUTH AMERICAN MASTODONS REFERRED TO *HAPLOMASTODON* AND *CUVIERONIUS*

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ABSTRACT

New mastodon finds collected in the Province of Carchi (Northern Ecuador) give further evidence that in South America *Haplomastodon* and *Cuvieronius* are monospecific. Of all the specific names referred to the genus *Haplomastodon*, only *chimborazi* must be considered valid as it alone was based on significant diagnostic material. As far as the genus *Cuvieronius* is concerned a new type species, *Cuvieronius tarijensis*, is proposed as the type specimen of *Cuvieronius hyodon* likely belongs to *Haplomastodon*.

KEY WORDS : MAMMALIA, PROBOSCIDEA, PLEISTOCENE, ECUADOR.

RÉSUMÉ

Des nouvelles pièces de mastodonte recoltées dans la Province du Carchi, au Nord de l'Équateur, confirment qu'en Amérique du Sud les genres *Haplomastodon* et *Cuvieronius* sont monospécifiques. Tous les noms spécifiques proposés pour le genre *Haplomastodon*, avec la seule exception de *chimborazi*, ne sont pas valables parce qu'ils sont fondés sur des exemplaires qui n'ont pas d'importance diagnostique. En ce qui concerne le genre *Cuvieronius* une nouvelle espèce type, *Cuvieronius tarijensis*, est proposée parce que l'exemplaire type de l'espèce *Cuvieronius hyodon* appartient vraisemblablement au genre *Haplomastodon*.

MOTS-CLÉS : MAMMALIA, PROBOSCIDEA, PLÉISTOCÈNE, ÉQUATEUR.

In a preceding study of the mastodons of Ecuador (Ficcarelli *et al.* 1993) it was hypothesized, in accordance with Simpson and de Paula Couto (1957), that only one species of *Haplomastodon*, *H. waringi* (HOLLAND, 1920), lived in South America, and that all the species previously attributed to this genus should be considered to be synonymous. In September and October of 1992, a further excavation in the Quebrada Pistud site near Canton of Bolivar, in the Carchi Province (Northern Ecuador), yielded many mastodon remains including an almost complete skull.

The skull (MECN 82), an atlas (MECN 83), an axis (MECN 84) and most of the new finds belong to the same individual as the mandible (MECN 133), ulna (MECN 134), radius (MECN 210), and part of a manus (MECN 216, 217, 218,

219, 220, 221, and 183) described in the previous paper. The study of this almost complete individual provides the possibility to analyze all its most diagnostic characteristics, throwing light on the systematics of the genus *Haplomastodon*, and giving a better picture of the Pleistocene Ecuadorian mastodons.

Abbreviations of the institutions owning the specimens analyzed and figured in this paper are as follows :

A.M. : American Museum of Natural History, New York.

MECN : Museo Ecuatoriano de Ciencias Naturales, Quito.

M.N. : Museu Nacional, Rio de Janeiro.

MNHN : Musée National d'Histoire Naturelle, Paris.

MATERIALS STUDIED

Of the remains recovered, only the skull with tusks (MECN 82), the atlas (MECN 83), the axis (MECN 84), a distal end of juvenile tusk (MECN 258), and a fragment of a female or sub-adult male tusk (MECN 59) will be discussed here. All the other elements, including those from the pre-

vious expeditions (1987-1992), will be matter of a future monograph. The specimens listed above contribute substantially to our knowledge of the systematics of South American mastodons. Therefore we felt it was opportune to make some observations known, before the material is completely restored and ready for a definitive study.

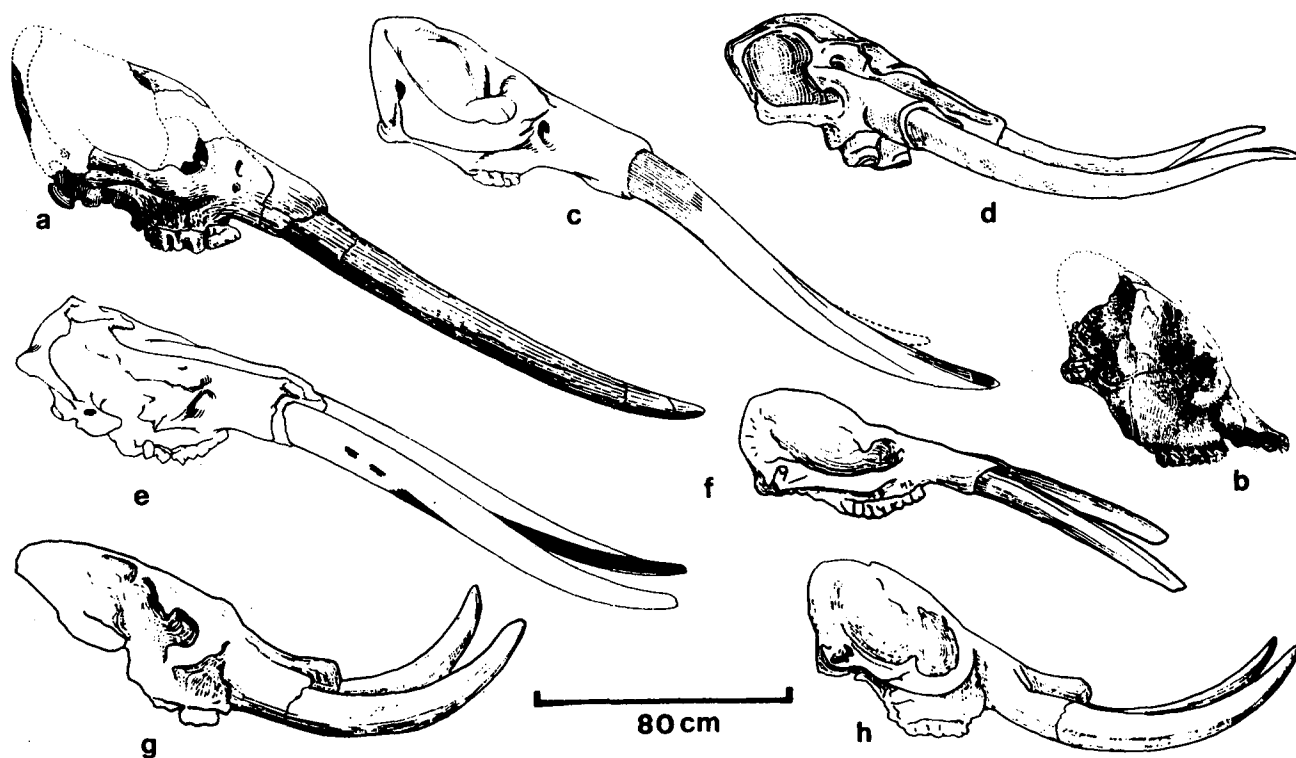


Figure 1 - Skulls of fully adult south american mastodons - lateral view. **a**, *Stegomastodon platensis*, from Arrecifes, Province of Buenos Aires, Argentina. Redrawn after Cabrera (1929, fig. 6 - rev.). Kept in the Museo de La Plata. **b**, *Stegomastodon* ? sp., from Paramo de lo Cucuy, Colombia. Redrawn after Boule & Thevenin (1920, fig. 32). Kept in the Musée National d'Histoire Naturelle of Paris. **c**, *Cuvieronius tarijensis* (= *Cuvieronius hyodon*), from Tarija, southern Bolivia. Redrawn after Osborn (1936, fig.507) from Boule & Thevenin (1920, pl. 1, fig. 1). Kept in the Musée National d'Histoire Naturelle of Paris. **d**, *Cuvieronius tarijensis* (= *Mastodon antium*), from Tarija, southern Bolivia. Redrawn after Osborn (1936, fig. 507) from Burmeister (1889, pl. 9, fig. 1 - rev.). Kept in the Museo Nacional Bernardino Rivadavia of Buenos Aires. **e**, *Cuvieronius tarijensis* (= *Mastodon andium*), from Tarija, southern Bolivia. Redrawn after Osborn (1936, fig.507) from Nordenskiöld (1903, pl. 1, fig. 1). Kept in the Stockholm Museum. **f**, *Cuvieronius tarijensis* (= *Cordillerion andium*), from Tarija, southern Bolivia. Drawn from OSBORN, (1936, fig. 532 A). Kept in the American Museum of Natural History of New York. **g**, *Haplomastodon chimborazi*, from Bolivar, Province of Carchi, northern Ecuador. Drawn from pl. 1, fig. 2. Kept in the Museo Ecuatoriano de Ciencias Naturales of Quito. **h**, *Haplomastodon chimborazi* (= *Bunolophodon ayorae*) from Punin, Province of Chimborazo, central Ecuador. Drawn from Spillmann (1931, fig. opposite pag. 68 - rev.). Destroyed by fire (1929) in the Museum of the Universidad Central of Quito. Crânes de mastodontes adultes de l'Amérique du Sud - Vue laterale. **a**, *Stegomastodon platensis*, de Arrecifes, Province de Buenos Aires, Argentine. Redessiné d'après Cabrera (1929, fig. 6 - inv.). Déposé dans le Museo de La Plata. **b**, *Stegomastodon* ? sp., de Paramo de lo Cucuy, Colombie. Redessiné d'après Boule & Thevenin (1920, fig. 32). Déposé dans le Musée National d'Histoire Naturelle de Paris. **c**, *Cuvieronius tarijensis* (= *Cuvieronius hyodon*), de Tarija, Bolivie du Sud. Redessiné d'après OSBORN (1936, fig. 507) sur Boule & Thevenin (1920, pl. 1, fig. 1). Déposé dans le Musée National d'Histoire Naturelle de Paris. **d**, *Cuvieronius tarijensis* (= *Mastodon antium*), de Tarija, Bolivie du Sud. Redessiné d'après Osborn (1936, fig. 507) sur Burmeister (1889, pl. 9, fig. 1 - inv.). Déposé dans le Museo Nacional Bernardino Rivadavia de Buenos Aires. **e**, *Cuvieronius tarijensis* (= *Mastodon andium*), de Tarija, Bolivie du Sud. Redessiné d'après Osborn (1936, fig. 507) sur Nordenskiöld (1903, pl. 1, fig. 1). Déposé dans le Musée de Stockholm. **f**, *Cuvieronius tarijensis* (= *Cordillerion andium*), de Tarija, Bolivie du Sud. Dessiné de Osborn (1936, fig. 532 A). Déposé dans l'American Museum of Natural History de New York. **g**, *Haplomastodon chimborazi*, de Bolivar, Province du Carchi, Equateur du Nord. Dessiné de pl. 1, fig. 2. Déposé dans le Museo Ecuatoriano de Ciencias Naturales de Quito. **h**, *Haplomastodon chimborazi* (= *Bunolophodon ayorae*), du Punin, Province du Chimborazo, Equateur central. Dessiné de Spillmann (1931, fig. opposée à page 68 - inv.). Détruit lors de l'incendie de 1929 dans le Musée de l'Universidad Central de Quito.

DESCRIPTION

The skull with right and left M2/-M3/ and both the tusks is from a young adult (Pl. 89, fig. 1) ; its neural region is deformed and slightly crushed. The skull has not yet been completely restored, and our observations are therefore limited to its tooth structure and to very general characteristics. The outline of the skull in lateral view and the general proportions of the same are very similar to the only undoubted adult skull of *Haplomastodon*, found to date, unfortunately destroyed by fire, figured by Proaño (1922) and Spillmann (1931). Our skull does not show any significant difference from those of *Cuvierionius* aside from the alveoles of the tusks which are less divergent (Fig. 1,2). The skull seems less elephant-like than in *Stegomastodon* but the comparison is not very reliable. In fact as Simpson & de Paula Couto (1957) put in evidence one of the two only at the present known adult skulls referred to *Stegomastodon* is from Columbia "that is far outside the really positively established range of *Stegomastodon* in South America and in a region where *Haplomastodon* would seem, *a priori*, somewhat more likely to occur" ; the other, from Argentina, is "heavily restored and the skull proportions are not really certain". However it is undoubted that, judging from the parts preserved, both the skull from Columbia and from Argentina show a more fore-and-aft compression and a greater elevation of the occiput (Fig. 1).

The tusks are enamel free, upcurved, and oval in cross section. The M2/ are trilophodont with simple trefoils. All molars show very few accessory conules in the valleys. The first and second lophes of M2/ and M3/ are normal to the main axes of the teeth ; the other lophes, in particular those of M3/, have a tendency to show a perceptible obliquity (Pl. 89, fig. 1). In the mandible (MECN 133) the first and second lophids of M/2 and M/3 show a pronounced obliquity, while in the other lophids the obliquity is less evident (Pl. 90, fig. 1).

The juvenile tusk (Pl. 89, fig. 3) bears an evident longitudinal band of enamel. The other tusk, from a female or sub-adult male (Pl. 89, fig. 4), shows a slight trace of torsion, but no evidence of an enamel band.

The atlas and the axis have clearly evident transverse foramina (Pl. 90, fig. 3-4).

DISCUSSION AND CONCLUSIONS

There is no doubt that our material belongs to the genus *Haplomastodon*. The finds confirm our earlier hypothesis, that there was only one species of *Haplomastodon* in Ecuador. In addition, they prove that the presence or absence of transverse foramina in the atlas and axis is a variable characteristic, which therefore has no taxonomic significance at the specific level, and even less at the generic level (Simpson & de Paula Couto

Skull MECN 82

Right tusk	L	= 870	Left tusk	L	= 880
	Max. Diam.	= 114		Max. Diam.	= 114
Right M2	L	= 132	Left M2	L	= 130
	W 2° loph.	= 86		W 2° loph. = 84	
Right M3	L	= 161	Left M3	L	= 163
	W 1° loph.	= 85		W 1° loph. = 84	

Atlas MECN 83

Maximum height	ca.235
Maximum width	ca.390
Height of neural canal	95
Width of anterior articular surface	210
Width of posterior articular surface	200

Axis MECN 84

Maximum height	ca.295
Maximum width	250
Height of neural canal	60
Width of anterior articular surface	205
Width of posterior articular surface	154

Measurements (in millimeters)

1957 ; Ficarelli *et al.* 1993). The skull and the two isolated tusks improve our knowledge of the mastodons of Ecuador.

All the recent Authors agree with the conclusions of Hoffstetter (1952) who recognized that the species *Cuvieronius hyodon* was present in the Cangahua deposits of Ecuador in addition to *Haplomastodon*. Hoffstetter attributed the following specimens to this species :

- the badly preserved M2/ examined by Cuvier (1806), which was found in the Cangahua horizons of the Imbabura Province (Pl. 89, fig. 5) that correlate with those which produced our samples, and which is considered by all researchers to be the type specimen of the species. The tooth is kept in the Musée d'Histoire Naturelle of Paris (MNHN AC 1738) ;
- an incomplete femur from the Quebrada Colorada of the Punín region (Chimborazo Province), kept in the Escuela Politécnica Nacional of Quito;
- two adult fragmentary tusks, a right one (Pl. 89, fig. 6) and a left one, with a well evident band of enamel and spiral torsion, an incomplete mandible with symphyseal region, an incomplete left mandibular ramus with M/2 and part of M/3, a fragment of left mandibular ramus with M/2, a fragment of left mandibular ramus with M/3, collected at Baños de Cuenca and kept in the Colegio Benigno Malo of Cuenca ;
- an approximately 15 cm. long fragment of juvenile tusk, subcircular in cross section, with an enamel band along its entire length and a slight spiral torsion, found at Guayallabamba, north of Quito. The specimen was divided into two parts, one of which was kept in the Colegio Militar Eloy Alfaro of Quito, and the other in the Universidad Central of Quito ;
- a tip of juvenile tusk, about 30 cm long, of unknown provenance ; it also has an enamel band and a spiral curve, and was preserved in the Universidad Central of Quito.

Only the M2/, femur, and the material preserved in the Colegio Benigno Malo of Cuenca, are available for study. The other finds have been lost.

Of all the material referred by Hoffstetter to *Cuvieronius* only the remains collected at Baños de Cuenca belong undoubtedly to this genus. In fact the enamel band and the spiral torsion of the tusks are perfectly similar to those of the specimens from Tarija in Bolivia, the most representative of this mastodon. *Fide* Dr. Salvador Idrovo M., Director of the Colegio Benigno Malo of Cuenca, all the material was collected in the same geological horizon. At present a detailed stratigraphic analysis of the deposit is wanting. It must be emphasized that, given our present knowledge, no tusk of *Cuvieronius* has been collected in the Cangahua deposits of Ecuador.

The other finds referred by Hoffstetter to *Cuvieronius* are not significant singly and could be ascribed indifferently either to *Haplomastodon* or *Cuvieronius*.

A comparison of the M2/ of the Bolivar *Haplomastodon* skull with the M2/ from Imbabura (Pl. 89, fig. 1,5) showed that the latter was slightly larger, but revealed no significant morphological differences. Since *Cuvieronius*, according to the literature, is, on the average, smaller than *Haplomastodon* also in dentition and no reliable find of *Cuvieronius* has been at present collected in the Cangahua deposits of Ecuador, we think that the tooth can indeed more likely be attributed to *Haplomastodon*. Therefore it follows that what is assumed to be the type specimen of *Cuvieronius hyodon* cannot be considered representative of the genus.

Also, the value of the greater or lesser obliquity of the loph and lophids as a means of distinguishing between *Cuvieronius* and *Haplomastodon* (HOFFSTETTER, 1952) pales, because the fields of variability of the characteristic overlap considerably between the two genera, especially with regard to the upper molars. As Simpson & de Paula Couto (1957) point out, the obliquity in *Haplomastodon* "when strongly developed is a distinction from the otherwise extremely similar molars of *Cuvieronius hyodon*. *Cuvieronius* does,

PLATE 89

- Fig. 1 - *Haplomastodon chimborazi* (PROAÑO, 1922) - Skull with M2/ and M3/. Quebrada Pistud, near Bolivar (Carchi). MECN 82. **a**, frontal view (x 1/12) ; **b**, palatal view (x 1/12) ; **c**, left M2/ (x 1/2).
- Fig. 2 - *Haplomastodon chimborazi* (PROAÑO, 1922) - Skull with mandible. Quebrada Pistud, near Bolivar (Carchi). MECN 82,133 (x 1/12).
- Fig. 3 - *Haplomastodon chimborazi* (PROAÑO, 1922). Distal end of juvenile tusk. Quebrada Pistud, near Bolivar (Carchi). MECN 258 (x 1/5).
- Fig. 4 - *Haplomastodon chimborazi* (PROAÑO, 1922). Fragment of a female or sub-adult male tusk. Quebrada Pistud, near Bolivar (Carchi). MECN 59 (x 1/5).
- Fig. 5 - *Haplomastodon chimborazi* (?) (PROAÑO, 1922) - Left M2/, ex *Cuvieronius hyodon* type. Near the Imbabura volcano (Imbabura). MNHN AC 1738 (x 1/2).
- Fig. 6 - *Cuvieronius tarijensis*. Right fragmentary tusk. Baños de Cuenca. Uncatalogued (x 1/5).



nevertheless, have a slight tendency to have lophs oblique in the same way, and the distinction is neither invariable or sharply diagnostic". They conclude that the molar structure "is virtually identical in *Haplomastodon* and *Cuvieronius* to such an extent that isolated teeth may be difficult, perhaps in some cases impossible to distinguish". We definitely agree with this conclusion.

The fact that a tusk with a slight trace of torsion makes part of our material (MECN 59) is not demonstrative of a presence of *Cuvieronius*. Simpson & De Paula Couto (1957), in their revision of the mastodon remains from Brazil, note that among the specimens from Araxa, "a nearly complete female or young, but not strictly juvenile, tusk (62 M)... 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". The authors conclude that these differences fall within the field of specific variability and attribute all the remains to *Haplomastodon waringi*. Furthermore Simpson & de Paula Couto (1957, fig. 7) referred the tusk collected by Castellanos (1948) at Sitio Laje Grande (Pernambuco, Brazil) and kept at the Museu Nacional of Rio de Janeiro (M.N. 56-V) to the same species. This tusk displays at the proximal end an enamel band and also a slight spiral torsion very much like that of the Araxa specimen. Castellanos had instead attributed it to a new species, *Notiomastodon vidali*. The same variability observed at Araxa is present in the material we collected. We hold, in agreement with Simpson & DE Paula Couto, that this variability reflects different ontogenetic stages and/or characteristics related to sexual dimorphism.

To end this discussion, we feel that no remains have yet been found that convincingly demonstrate the presence of *Cuvieronius* in the Canga-hua deposits of Ecuador. In addition, even though the problems related to the systematics of Ecuadorian mastodons have not yet been completely resolved, we tend to believe that *Haplomastodon*

was the only mastodon to live in the Country in the Late Pleistocene. Our conclusions are also supported by the fact that the most reliable representatives of *Cuvieronius* in South America (Tarija Formation, southern Bolivia) make part of a fauna of the early Middle Pleistocene. The Tarija Formation spans a time interval from about 1 My to about 0.7 My B.P. or perhaps a little less (Mac Fadden *et al.* 1983).

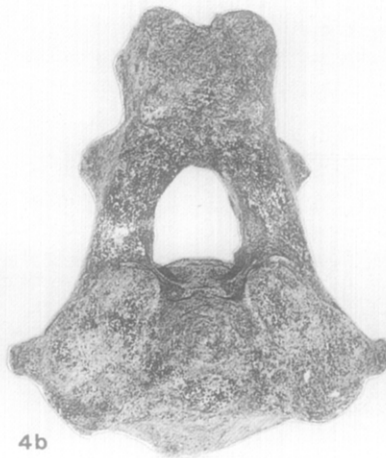
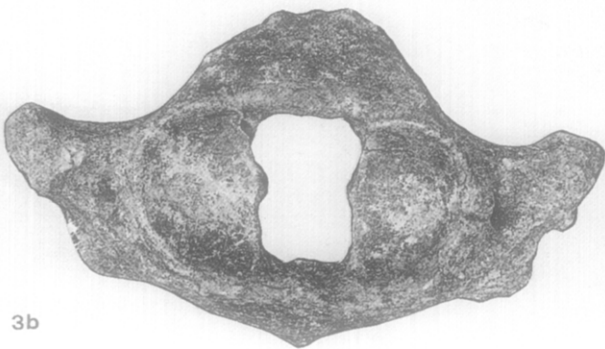
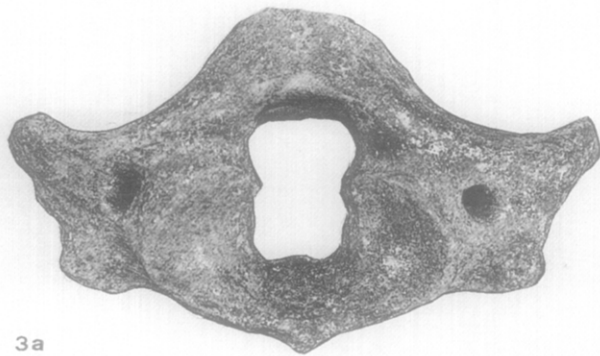
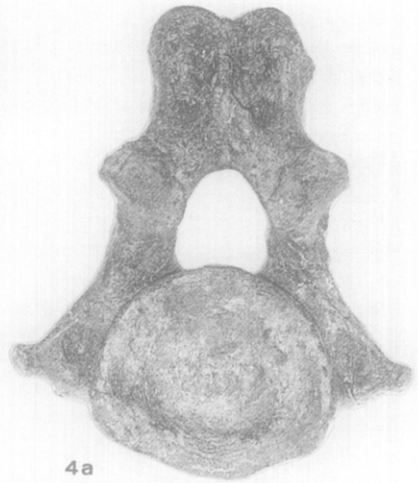
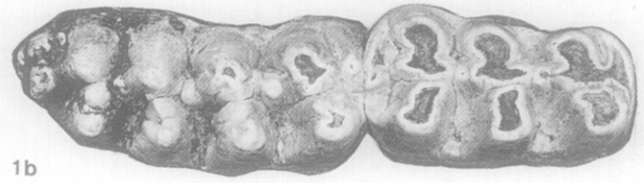
The picture that emerges after our finds is very clear, but at the same time becomes extremely confusing from a nomenclatural stand point, because of the numerous and at times unwarranted interpretations that have been given to the various South American mastodons.

The fact that the M2/ upon which the species *Cuvieronius hyodon* (FISCHER, 1814) was founded probably belongs to *Haplomastodon* completely reopens the problems of nomenclature of the South American mastodons, at both the generic and the specific level.

Osborn defined the genus *Cuvieronius* (1923) including species which have subsequently been attributed to *Stegomastodon* or *Haplomastodon*, and the genus *Cordillerion* (1926) where he clustered species which all subsequent authors, following Cabrera's (1929) classification, have referred to *Cuvieronius*. In his revision of the South American mastodons, Cabrera equated the genus *Cuvieronius* as defined by Osborn with the genus *Stegomastodon* and considered *Cuvieronius* senior synonym of *Cordillerion*. The conclusions of Cabrera have been based on two assumptions: first, of the synonymy between the species *hyodon* (= Cuvier's mastodon of the Cordillera, 1806; = Fischer's *Mastotherium hyodon*, 1814; = Cuvier's *Mastodon andium*, 1824; = Osborn's *Cordillerion andium*, 1926) and *humboldtii* (= Cuvier's humboldian mastodon, 1806; = Cuvier's *Mastodon humboldtii*, 1824; = Osborn's *Cuvieronius humboldtii*, 1923); and second, that the type teeth of these species, respectively the M/2 from Imbabura (MNHN AC 1738) and the M/1 or DP/4 from Concepcion in Chile or Ecuador (MNHN AC 1743), belong to the mastodons of the Andean re-

PLATE 90

- Fig. 1 - *Haplomastodon chimborazi* (PROAÑO, 1922) - Mandible with M/2 and M/3. Quebrada Pistud, near Bolivar (Carchi). MECN 133. **a**, (x 1/12); **b**, left M/2-M/3 (1/4); **c**, right M/2-M/3 (x 1/4).
 Fig. 2 - *Haplomastodon chimborazi* (PROAÑO, 1922). **a**, left M3/, **b**, right M3/, **c**, right M2/. Quebrada Pistud, near Bolivar (Carchi). MECN 82 (x 1/4).
 Fig. 3 - *Haplomastodon chimborazi* (PROAÑO, 1922) - Atlas. Quebrada Pistud, near Bolivar (Carchi). MECN 83. **a**, caudal view; **b**, cranial view (x 1/5).
 Fig. 4 - *Haplomastodon chimborazi* (PROAÑO, 1922) - Axis. Quebrada Pistud, near Bolivar (Carchi). MECN 84. **a**, caudal view; **b**, cranial view, **c**, detail of transverse foramen (x 1/5).



gions which were characterized, as adults, by tusks with a marked spiral torsion and a longitudinal band of enamel. The richest and most diagnostic specimens of these forms have been found at Tarija (Southern Bolivia), in deposits attributed to the Middle Pleistocene (Mac Fadden *et al.* 1983).

Our finds invalidate the second of these two assumptions, and thus reopen the discussion on the use of the name *Cuvieronius*. *Haplomastodon waringi* should really be considered junior synonym of *Cuvieronius hyodon* as the M2/ type of the latter likely belongs to *Haplomastodon*, and the generic term *Cordillerion* (OSBORN, 1926) should revive for those mastodons characterized by spirally curved tusks with longitudinal band of enamel in the adult phase. At this point there are two possibilities: either follow Cabrera's lead, because it is more parsimonious and is by now commonly accepted, or to reintroduce *Cordillerion*, as defined by Osborn, leaving out however the M2/ from Imbabura because of the points raised above. The DP4/ or M1/ from Concepcion could be included with reserve if it would be proved to come from Chile, where no finds of *Haplomastodon* were collected till now. In the last case what has since been attributed to *Haplomastodon* (HOFFSTETTER, SIMPSON & DE PAULA COUTO, BOUSTOS, and later authors) should be referred to *Cuvieronius*. All with the proper emendaments, because, as Cabrera mentioned and we have underlined, Osborn placed what should have been attributed to *Stegomastodon* in *Cuvieronius*. In this light *Haplomastodon* should be invalidated because junior synonym of *Cuvieronius*.

We deem more advisable to follow Cabrera's classification because it met the widest consensus among recent authors and because, as stated by Simpson & de Paula Couto (1957), "this usage may be less likely to be upset again by some other arbitrary application or interpretation of the Rules". Finally we conclude that only the generic names *Cuvieronius* and *Haplomastodon* must be considered valid for the mastodons under consideration here.

Since the truly significant characteristics that allow one to distinguish between *Haplomastodon* and *Cuvieronius* are those of the tusks, skulls and of the symphyseal region of the mandible, we feel that all the taxa which have been established only on the basis of the morphology of the molars are unreliable, because they are founded upon plesiomorphic characteristics. Therefore we feel that it would be best to invalidate all the specific names based only upon the molars. This also applies both to the species *warangi* (HOLLAND, 1920)

and to the species *hyodon* (FISCHER, 1814). The former was founded only on molars and on fragmentary material whose taxonomic significance is restricted, the latter on a M²/. Otherwise, if the species *hyodon* is considered valid, since it appears to belong to the monospecific genus *Haplomastodon*, it has priority over *warangi*.

We think that, among all the species attributed to *Haplomastodon* in the literature, only *Haplomastodon chimborazi* (PROAÑO, 1922) must be saved. In fact the Author erected the species on a complete skull with molars and tusks, a mandible with molars and on much of the post-cranial skeleton, collected in the Cangahua Formation of the Quebrada Chalán of Punín (Chimborazo Province, central Ecuador). Geological and paleontological considerations allow us to correlate the Cangahua horizon, where this material was collected, with that of our fossiliferous site.

Since the type material of this species was lost in the fire that destroyed much of the collection preserved at the Museum of the Universidad Central of Quito in 1929, we feel that the skull with mandible and the post-cranial skeleton belonging to the same individual, found in the Carchi Province, must be designated as neotype of *Haplomastodon chimborazi*. The remaining specimens of our sample, which is more complete and diagnostically significant than any other body of *Haplomastodon* remains found to date, have to be designated as paratypes.

With regards to the specific name of the only South American species referable to the genus *Cuvieronius*, none of the names introduced previously is free from pitfalls. About the species *hyodon* we have above come to the conclusion that it can indeed more likely be referred to *Haplomastodon*. The species *humboldtii* is not reliable for the reasons previously debated. The names *rhomboides* (RAFINESQUE, 1814), *humboldtianus* (RAFINESQUE, 1814), *cordillerarum* (DESMAREST, 1822) and *andium* (CUVIER, 1824) were based on the same teeth which represent the type material of the species *hyodon* and *humboldtii* and which are, as we said, diagnostically insignificant. The species *argentinus* (AMEGHINO, 1888), based upon a tusk with broad enamel band, should most likely be referred to *Notiomastodon*, as Osborn (1936) observed, or to *Stegomastodon*. The species *chilensis* and *bolivianus* (PHILIPPI, 1893) founded on fragments of mandible, do not permit to decide to which genus they may be referred, even if, judging from the figures reported in Osborn (1936; figs. 512 and 547 "figure" 2) and from the description of Boule & Thevenin (1920; p. 68), the latter species seems to

have a *Cuvieronius*-like symphyseal region. The species *tarijensis* (AMEGHINO, 1902) is improperly defined and is consequently a *nomen nudum*.

This overview shows that the situation is extremely confused, and the species must be adequately redefined. We feel that the best solution is to revive the term *tarijensis* and to erect the specimens from Tarija in Bolivia to type material because the most representative of *Cuvieronius* in South America. It consists of a rich collection of skulls, tusks, and post cranial skeletal elements, and its stratigraphic position is well known as a result of the research carried out over the past few years by North American workers.

As type material of the species we deem advisable to select the specimens of the Crequi-MONTFORT collection described and figured by Boule & Thevenin (1920), kept in the Musée National d'Histoire Naturelle of Paris, because they are well representative and were certainly collected in the same site. Finally, among this material, we suggest as holotype of the species *tarijensis* the skull with the right tusk, molars and mandible (MNHN TAR 1270) (Boule & Thevenin, 1920 ; pl. 1, figs. 1,2 ; pl. 2, figs. 1,6 ; pl. 3, fig. 1) and as paratypes all the other specimens of the collection. Moreover the presence in the collection of an atlas (MNHN TAR 802) with only one transverse foramen support what we hypothesized in a previous paper (Ficcarelli *et al.* 1993) "It is therefore reasonable to assume that the differentiated reduction of the transversal foramina in both the atlas and the axis, up to the obstruction of either or both, was a common, or at least not exceptional characteristic in the South American mastodon populations". We also proposed as topotypes the skull with tusks and mandible kept in the Museo Nacional Bernardino Rivadavia of Buenos Aires, described and figured by Burmeister (1889, pl. 9, fig. 1), the skulls with tusks, designated as male and female, kept in the Stockholm Museum, described and figured by Nordenskiöld (1903, pl. 1, fig. 1), the skull with tusks (A.M. 26984) figured by Osborn (1936, fig. 532 A) kept in the American Museum of Natural History of New York, collected by E.S. Riggs (Field Museum of Chicago expedition, 1926) and the skull with tusks and mandible kept in the Field Museum of Natural History of Chicago, figured by Osborn (1936, fig. 506).

The skull we collected in the Carchi Province and those from Tarija are very similar in shape ; and in the general features *Cuvieronius* and *Haplomastodon* are on terms of large familiarity (Fig. 1). The considerable resemblances between the

molars of the two genera, the greater age and higher plesiomorphy of the tusks and of the symphyseal region of the mandible of the former, support the hypothesis that *H. chimborazi* can be a direct descendant of the Tarija mastodon.

To end this discussion and to make a clearer picture of the situation, the most significant diagnostic characters and the synonymies both of the species *Haplomastodon chimborazi* and *Cuvieronius tarijensis* are reported in succession. The list does not include the specific names based on specimens not reliable from a taxonomic point of view. The specimens which can be reasonably assigned to the two species for stratigraphic position and geographic situation are reported with question mark.

Family GOMPHOTHERIIDAE Cabrera, 1929

Subfamily ANANCINAE Hay, 1922

Genus *Haplomastodon* HOFFSTETTER, 1950

HAPLOMASTODON CHIMBORAZI (PROAÑO, 1922)

Pl. 89, figs. 1-5 ; Pl. 90, figs. 1-4 ; Figs. 1g-h, 2b, 3a-c.

1806 - (?) Mastodonte des Cordilières Cuvier, p. 413.

1814 - (?) *Mastotherium hyodon* FISCHER, p. 341.

1814 - (?) *Mastodon rhomboides* RUFINESQUE, p. 183.

1824 - (?) *Mastodon Andium* CUVIER, p. 527.

1920 - *Mastodon Humboldti* BOULE & THEVENIN, p. 70.

1920 - (?) *Mastodon waringi* HOLLAND, p.229.

1922 - *Mastodon Chimborazi* PROAÑO, on an unnumbered page.

1931 - *Bunolophodon Ayorae* SPILLMANN, p. 67.

1931 - *Bunolophodon postremus* SPILLMANN, p. 73.

1952 - *Haplomastodon (Haplomastodon) chimborazi* HOFFSTETTER, p. 192.

1952 - *Haplomastodon (Aleamastodon) guayaensis* HOFFSTETTER, p. 208.

1952 - *Stegomastodon brasiliensis* HOFFSTETTER, p. 222.

1957 - *Haplomastodon waringi* SIMPSON & DE PAULA COUTO, p.171.

1962 - *Haplomastodon waringi* BUSTOS PARODI, p. 21.

1993 - *Haplomastodon waringi* FICCARELLI *et al.* p. 233.

Neotype - Skull (MECN 82), mandible (MECN 133), atlas (MECN 83), axis (MECN 84), and many other elements of the postcranial skeleton belonging to the same individual, kept in the Museo Ecuatoriano de Ciencias Naturales of Quito.

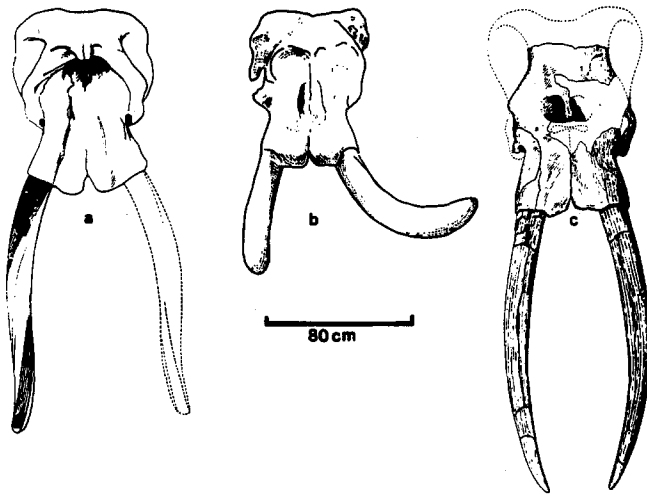


Figure 2 - Skulls of fully adult south american mastodons - dorsal view. **a**, *Cuvieronius tarijensis* (= *Mastodon andium*), from Tarija, southern Bolivia. Redrawn after Osborn (1936, fig. 507) from Boule & Thevenin (1920, pl. 2, fig. 1). Kept in the Musée National d'Histoire Naturelle of Paris. **b**, *Haplomastodon chimborazi*, from Bolivar, Province of Carchi, northern Ecuador. Drawn from pl. 1, fig. 1a. Kept in the Museo Ecuatoriano de Ciencias Naturales of Quito. **c**, *Stegomastodon platensis*, from Arrecifes, Province of Buenos Aires, Argentina. Redrawn after Cabrera (1929, fig. 7). Kept in the Museo de La Plata. *Crânes de Mastodontes adultes de l'Amérique du Sud - vue dorsale. a, Cuvieronius tarijensis* (= *Mastodon andium*), de Tarija, Bolivie du Sud. Redessiné d'après Osborn (1936, fig. 507) sur Boule & Thevenin (1920, pl. 2, fig. 1). Déposé dans le Musée National d'Histoire Naturelle de Paris. **b**, *Haplomastodon chimborazi*, de Bolivar, Province du Carchi, Equateur du Nord. Dessiné de pl. 1, fig. 1a. Déposé dans le Museo Ecuatoriano de Ciencias Naturales de Quito. **c**, *Stegomastodon platensis*, de Arrecifes, Province de Buenos Aires, Argentine. Redessiné d'après Cabrera (1929, fig. 7). Déposé dans le Musée de La Plata.

Paratypes - Three tusk fragments (MECN 59, 258, 162), kept in the Museo Ecuatoriano de Ciencias Naturales of Quito.

Type locality - Quebrada Pistud, near Bolivar Province of Carchi, northern Ecuador.

Geological horizon - Upper part of the Canga-hua Formation.

Known stratigraphic distribution - Late Pleistocene of Ecuador, most of tropical South America and temperate southwestern Brazil.

Diagnosis - The only currently defined species now recognized in the genus. Brevirostrine, bunolophodont. Skull depressed and elongate (Fig. 1). Alveoles of the tusks slightly divergent (Fig. 2). Enamel free, upward curving tusks oval in cross section. Juvenile tusks with evident longitudinal

band of enamel. In female or sub-adult male tusks with a slight trace of torsion with or without evidence of an enamel band. Trilophodont with simple trefoil. Molars either with very few accessory conules in the valleys, or structurally more complex, with better developed secondary conules and folds. First and second lophes of M2/ and M3/ normal to the main axes of the teeth. Other lophes, in particular those of M3/, with a tendency to show a perceptible obliquity. Lower molars with pronounced obliquity in the first and second lophids, less evident in the others ones. Atlas and axis either with well evident trasversal foramina or with the reduction up to the obstruction of one or both of the same.

Genus *Cuvieronius* OSBORN, 1923

CUVIERONIUS TARIJENSIS NOV. SP.

Pl. 89, fig. 6 ; Figs. 1c-f, 2a, 3f-m.

- 1806 - (?) *Mastodonte humboldtien* Cuvier, p. 413.
- 1814 - (?) *Mastotherium Humboldtii* FISCHER, p. 341.
- 1814 - (?) *Mastodon humboldtianus* RAFINESQUE, p. 183.
- 1818 - (?) *Mastodon Humboldtii* DESMAREST, p. 447.
- 1824 - (?) *Mastodon Humboldtii* CUVIER, p. 527.
- 1842 - (?) *Mastodon Andii* LAURILLARD in d'ORBIGNY, p. 144.
- 1893 - (?) *Mastodon bolivianus* PHILIPPI, p. 89.
- 1889 - *Mastodon antium* BURMEISTER, p. 1-65.
- 1903 - *Mastodon andium* NORDENSKIÖLD, p. 1-30.
- 1920 - *Mastodon andium* BOULE & THEVENIN, p. 17.
- 1936 - *Cordillerion andium* OSBORN (partim), p. 549.
- 1936 - (?) *Cordillerion bolivianus* OSBORN, p. 551.
- 1952 - *Cuvieronius hyodon* HOFFSTETTER (partim), p. 186.

Holotype - Skull with the right tusk, molars and mandible (MNHN TAR 1270) described and figured by Boule & Thevenin (1920), kept in the Musée National d'Histoire Naturelle of Paris.

Paratypes - All the specimens of the Crequi-Montfort collection described and figured by Boule & Thevenin (1920), kept in the Musée National d'Histoire Naturelle of Paris.

Topotypes - Skull with tusks and mandible kept in the Museo Nacional Bernardino Rivadavia of Buenos Aires (Burmeister 1889) ; skulls with tusks kept in the Stockholm Museum (Nordenskiöld 1903) ; skull with tusks kept in the American Museum of Natural History of New York (*in* Osborn 1936, fig. 532 A) ; skull with tusks and

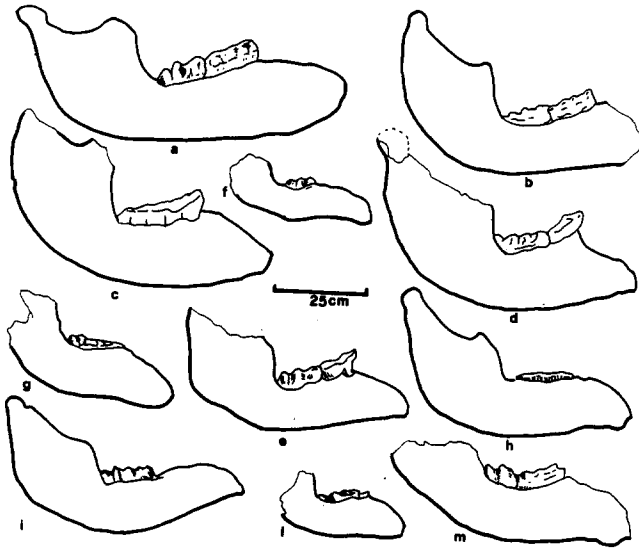


Figure 3 - Mandibles of south American mastodons - lateral view. **a**, *Haplomastodon chimborazi*, from Bolivar, Province of Carchi, northern Ecuador. Drawn from Ficarelli *et al.* (1993, pl. 1, fig. 3b). Kept in the Museo Ecuatoriano de Ciencias Naturales of Quito. **b**, *Haplomastodon chimborazi*, from Punin, Province of Chimborazo, central Ecuador. Drawn from Hoffstetter (1952, fig. 44A). Kept in the Escuela Politécnica Nacional of Quito. **c**, *Haplomastodon chimborazi*, from La Carolina, Province of Guayas, central Ecuador. Drawn from HOFFSTETTER (1952, fig. 54b). Kept in the Escuela Politécnica Nacional of Quito. **d**, *Stegomastodon platensis*, from Arrecifes, Province of Buenos Aires, Argentina. Drawn from Cabrera (1929, fig. 6 -rev.). Kept in the Museo de La Plata. **e**, *Cuvieronius tarijensis*, from Tarija, southern Bolivia. Drawn from Osborn (1936, fig. 532 A). Kept in the American Museum of Natural History of New York. **f-m**, *Cuvieronius tarijensis*, from Tarija, southern Bolivia. Drawn from Boule & Thevenin (1920, pl. 1, fig. 2 ; pl. 6, figs. 1-5 -rev.) kept in the Musée National d'Histoire Naturelle de Paris. *Mandibles de mastodontes de l'Amérique du Sud - vue laterale. a, Haplomastodon chimborazi, de Bolivar, Province du Carchi, Équateur du Nord. Dessiné de Ficarelli et al. (1993, pl. 1, fig. 3b). Déposé dans le Museo Ecuatoriano de Ciencias Naturales de Quito. b, Haplomastodon chimborazi, du Punin, Province du Chimborazo, Équateur central. Dessiné de Hoffstetter (1952, fig. 44A). Déposé dans l'Escuela Politécnica Nacional de Quito. c, Haplomastodon chimborazi, de La Carolina, Province du Guayas, Équateur central. Dessiné de Hoffstetter (1952, fig. 54 b). Déposé dans l'Escuela Politécnica Nacional de Quito. d, Stegomastodon platensis, de Arrecifes, Province de Buenos Aires, Argentine. Dessiné de Cabrera (1929, fig. 6 - inv.). Déposé dans le Museo de La Plata. e, Cuvieronius tarijensis, de Tarija, Bolivie du Sud. Dessiné de Osborn (1936, fig. 532 A). Déposé dans l'American Museum of Natural History of New York. f-m, Cuvieronius tarijensis, de Tarija, Bolivie du Sud. Dessiné de Boule & Thevenin (1920, pl. 1, fig. 2 ; pl. 6, figs. 1-5 - inv.). Déposé dans le Musée National d'Histoire Naturelle de Paris.*

mandible kept in the Field Museum of Natural History of Chicago (*in* Osborn 1936, fig. 506).

Etymology - From Tarija, southern Bolivia.

Type-locality - Tarija, southern Bolivia.

Geological horizon - Tarija Formation

Known stratigraphic distribution - Middle Pleistocene of the Andine region and adjacent lower regions to the south (Northern Chile). (?) Upper Pliocene-Pleistocene of Central America.

Diagnosis - Only surely valid species of the genus in South America. Brevirostrine, bunolophodont. Skull low and elongate (Fig. 1). Alveoles of the tusks divergent (Fig. 2). Symphyseal region of the mandible downturned (Fig. 3) and with possible presence, in the young individual, of traces of tusk alveoli (Boule & Thevenin 1920 ; pl. 5, fig. 1b). Tusks twisted in a long open spiral and with a spiral band of enamel persisting in the adults. Trilophodont with single trefoils. Molars structurally built as in *Haplomastodon* but with opposite cusps that show a somewhat lower mean tendency towards alternation in the first and second lophids of M/2 and M/3. Atlas and presumably also the axis either with well evident transversal foramina or with the reduction up to the obstruction of one or both of the same.

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