Proboscidea (Mammalia) from the Upper Miocene of Crevillente (Alicante, Spain)

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The fossil Proboscidea from the Spanish Turolian (Upper Miocene) sites of Crevillente 2 (MN11) and Crevillente 15 and 16 (MN12) are described. The mastodont from Crevillente 2 is assigned to *Tetralophodon* cf. *longirostris* 'grandincisivoid form', recognised for the first time in the Iberian Peninsula, and that from Crevillente 16 to *Tetralophodon longirostris*. The Deinotheriidae from Crevillente 2 and Crevillente 15 are identified as *Deinotherium giganteum* and *Deinotherium* sp., respectively. The status of '*Mastodon*' *grandincisivus* and the 'grandincisivoid forms' of *Gomphotherium* and *Tetralophodon* are discussed.

Contents

Introduction

Many vertebrate sites are known in the continental Neogene of the area of Crevillente (province of Alicante, Spain) from a stratigraphic interval that covers the entire Turolian (Montenat, 1973; Bruijn *et al.*, 1975; Freudenthal *et al.*, 1991a; Montoya, 1994; Alfaro *et al.*, 1995; Montoya & Alberdi, 1995; Martín Suárez & Freudenthal, 1998). Some of these localities have yielded rich micromammal assemblages, but only three of them, Crevillente 2, 15 and 16, contain macromammal remains and only the first one can be considered as a rich macrovertebrate site. Figures 1 and 2 show the geographic and stratigraphic location of the three localities.

Crevillente 2 shows a rich association of both micro- and macromammals, and belongs to the lower Turolian. According to the biozonation proposed for the area of Crevillente by Martín Suárez & Freudenthal (1998), this site is included in the *sondaari* biozone. In addition, Crevillente 2 has been designated as the reference locality for zone MN11 (Mein, 1990, 1999; Bruijn *et al.*, 1992). Different aspects in the study of the mammals from Crevillente 2 have been approached in numerous papers, among them Montenat & Crusafont (1970), Montenat (1973), Alberdi (1974), Bruijn *et al.* (1975), Alcalá *et al.* (1987), Alberdi & Montoya (1988), Cerdeño (1989), Alcalá & Montoya (1990), Freudenthal *et al.* (1991b, 1998), Montoya & Morales (1991), Made *et al.* (1992),

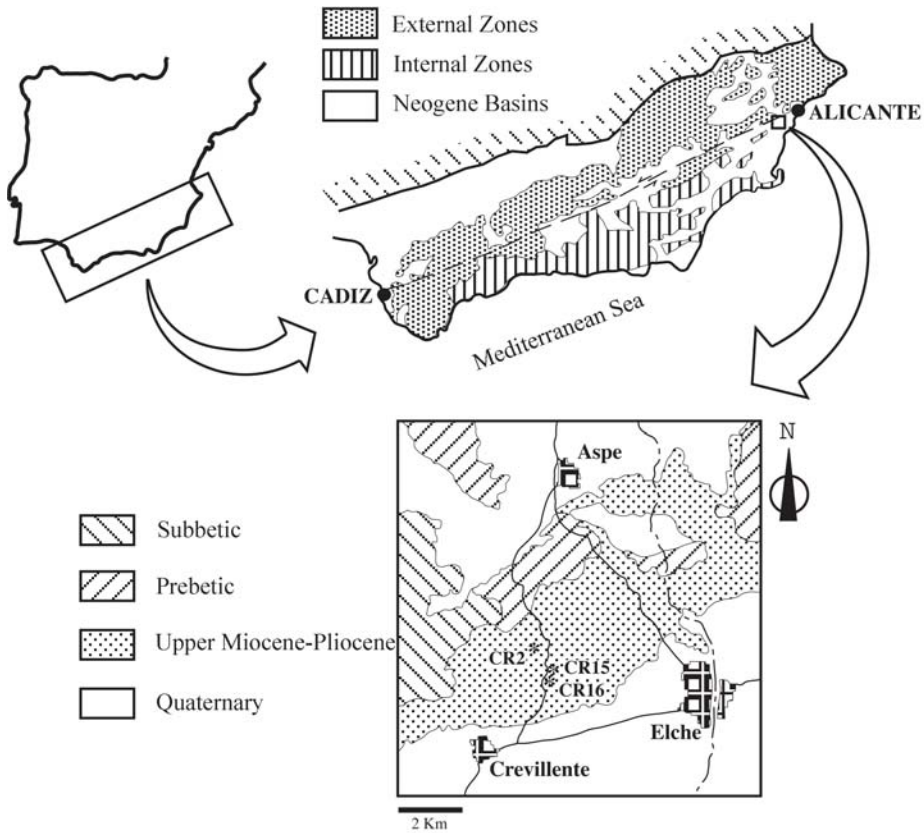


Fig 1. Geographical location and geological context of the macrommamal sites from Crevillente.

Martín Suárez & Freudenthal (1993, 1998), Montoya (1990, 1993, 1994, 1997), Azanza & Montoya (1995), Momparler (1996), Weers & Montoya (1996), Azanza (2000), Montoya *et al.* (2001) and Salesa *et al*. (in press). Crevillente 2 is the type locality for two taxa, *Neocricetodon occidentalis* (Aguilar, 1982) and *Lucentia iberica* Azanza & Montoya, 1995.

Crevillente 15 and 16 are stratigraphically and geographically very close, and have provided similar macromammal assemblages. Crevillente 15 is very rich in middle Turolian micromammals (MN12) and is included in the *turoliensis* biozone of Martín Suárez & Freudenthal (1998). This site is the type locality of *Apocricetus plinii* (Freudenthal *et al*., 1991a). Crevillente 16 has not been sampled for microvertebrates. The macromammals from Crevillente 15 and 16 have been studied in Made *et al*. (1992), Montoya (1994) and Montoya & Alberdi (1995). The micromamals from Crevillente 15 have been analysed by Freudenthal *et al.* (1991b, 1998) and Martín Suárez & Freudenthal (1993, 1998). Martín Suárez *et al*. (2001) recently made a palaeoecologic study of the area of Crevillente during the Turolian based on rodent assemblages.

The vertebrate lists of the three sites, based on the papers cited above, unpublished information and the present study, can be established as follows: —

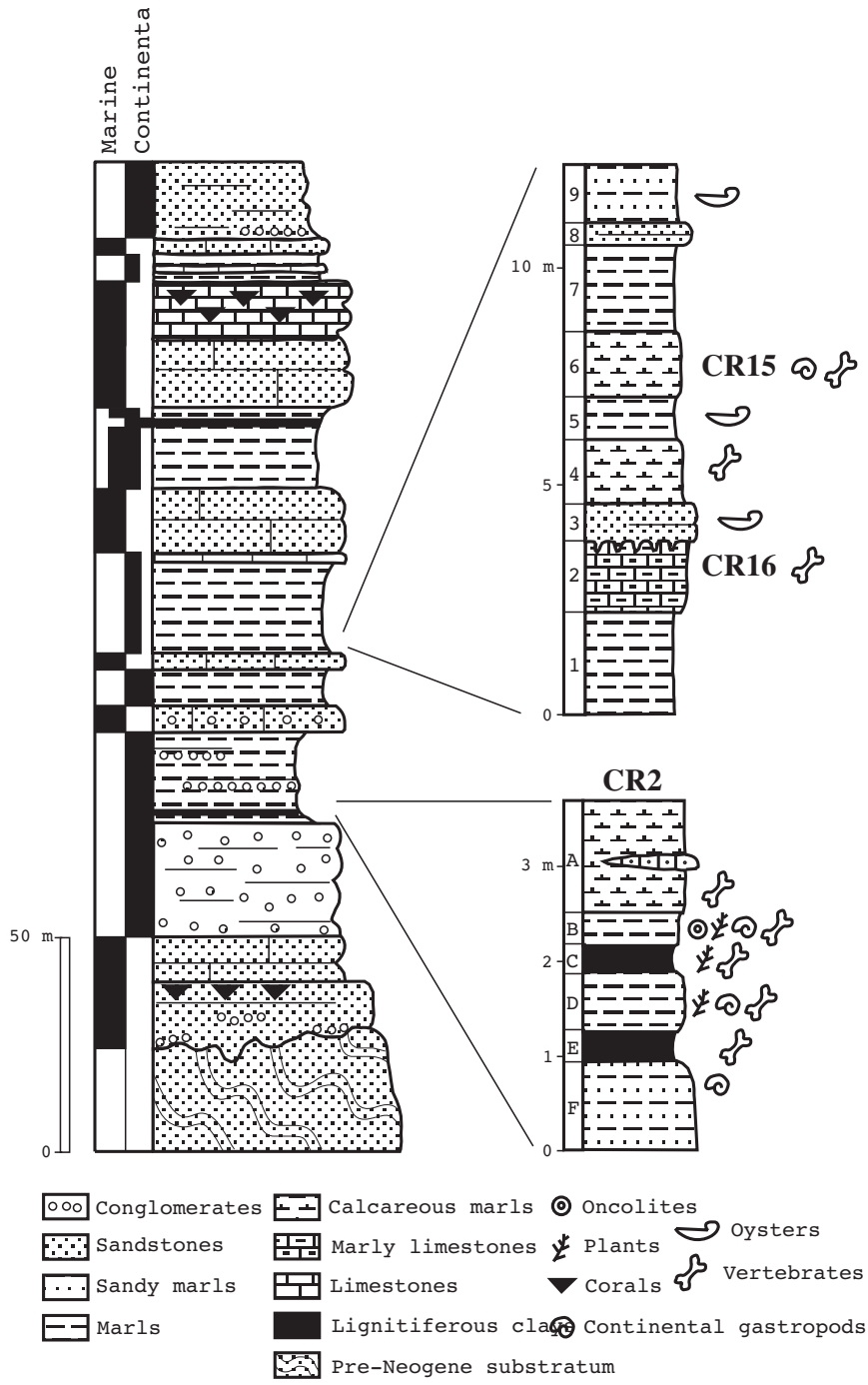


Fig. 2. Stratigraphic position of the macromammal sites from Crevillente. General sequence modified from de Bruijn *et al*. (1975).

1. Crevillente 2: *Rana perezi*, Eusuchia indet., Anguidae indet., *Ophisaurus* sp., *Lacerta* sp., *Dracaenosaurus* sp., *Vipera* sp., cf. *Naja* sp., *Cheirogaster* sp., *Testudo* sp., Anatidae indet., *Occitanomys sondaari*, *Apodemus lugdunensis*, *Apodemus* sp., *Huerzelerimys vireti*, *Hispanomys peralensis*, *Neocricetodon occidentalis*, *Cricetulodon bugesiensis*, *Eliomys truci*, *Muscardinus* sp., *Heteroxerus grivensis*, aff. *Aragoxerus* sp., *Hystrix parvae*, *Desmanella* sp., *Postpalerinaceus* cf. *vireti*, *Galerix iberica*, *Prolagus crusafonti*, *Indarctos atticus*, *Indarctos* cf. *vireti*, *Promephitis* sp., Viverridae indet., *Plioviverrops guerini*, *Adcrocuta eximia*, *Paramachairodus ogygia*, *Machairodus aphanistus*, *Microstonyx major*, *Dorcatherium naui*, *Lucentia iberica*, Muntiacinae indet., *Birgerbohlinia schaubi*, *Tragoportax gaudryi*, *Hipparion mediterraneum*, *Lartetotherium schleiermacheri*, *Deinotherium giganteum*, *Tetralophodon* cf. *longirostris* 'grandincisivoid form'.
2. Crevillente 15: Eusuchia indet., Ophidia indet., *Testudo* sp., *Hispanomys adroveri*, *Hispanomys* sp., *Neocricetodon* sp., *Apocricetus plinii*, *Apodemus barbarae*, *Occitanomys adroveri*, *Huerzelerimys turoliensis*, *Atlantoxerus adroveri*, *Spermophilinus turolensis*., *Muscardinus* sp., *Eliomys truci*, Soricidae indet., *Galerix iberica*, Talpidae indet., *Prolagus crusafonti*, cf. *Lycyaena* sp., *Paramachairodus* cf. *orientalis*, *Microstonyx major*, Cervidae indet., *Tragoportax gaudryi*, cf. *Hispanodorcas* sp., *Hipparion concudense* cf. *aguirrei*, *Lartetotherium schleiermacheri*, *Deinotherium* sp., cf. *Tetralophodon* sp.
3. Crevillente 16: Ophidia indet., *Testudo* sp., *Paramachairodus* cf. *orientalis*, *Machairodus* cf. *giganteus*, *Microstonyx major*, Cervidae indet., *Tragoportax gaudryi*, cf. *Hispanodorcas* sp., *Hipparion concudense* cf. *aguirrei*, *Tetralophodon longirostris*.

The proboscidean remains recovered from these three sites in the prospections and excavations carried out from 1985 to 1988 by the Universitat de València, the Museo Nacional de Ciencias Naturales de Madrid and the Museu Històric Municipal de Novelda, are described hereafter. In Crevillente 2, the mastodont remains come from beds A and D, and the remains of *Deinotherium* come from bed B (Fig. 2). The material studied in this work is stored in the following Spanish collections: MCNV - Museo de Ciencias Naturales de Valencia; MGUV - Museu de Geologia de la Universitat de València; MHMN - Museu Històric Municipal de Novelda (Alicante); MNCN - Museo Nacional de Ciencias Naturales (Madrid); and MPE - Museo Paleontológico de Elche (Alicante).

Systematic palaeontology

All the measurements are given in mm.

Order Proboscidea Illiger, 1811
Incertae familiae
Genus *Tetralophodon* Falconer, 1857
Tetralophodon cf. *longirostris* (Kaup, 1832) 'grandincisivoid form'

Pls. 1-6; Pl. 7, figs. 1, 2.

Studied material — Crevillente 2 (MN11), Bed D: mandible with the M_3 and the left lower tusk, MPE CR2-M279, CR2-M280, CR2-M281; femur, MCNV CR2-915 (fragment, with the distal end); big cuneiform, MGUV CR2-A82; first phalanx, MGUV

CR2-A83, MNCN CR2 not numbered; third phalanx: MGUV CR2 not numbered (incomplete); juvenile incisor: MGUV CR2-M418 (apical fragment).

Crevillente 2 (MN11), Bed A: M^3, MHMN CR2-S-58, CR2-S-59 (both incomplete); fragment of right mandible with the M_3, MHMN CR2-80-S; left M_3, MCNV CR2-77-S; M_2, MHMN CR2-78-S, CR2-79-S.

All specimens from bed D were found associated and belong to a single individual (here called 'individual 1'), except for the fragment of an upper tusk (CR2-M418), which was found far from the rest of specimens and belongs to a juvenile. The remains from bed A were also found associated and belong to a single individual (here called 'individual 2').

Description and measurements — The apical fragment of an upper tusk (CR2-M418) is strongly corroded by the action of roots and humic acids. Its section is suboval and there is no trace of enamel. Its small size (length 112 mm, section 30 × 27 mm) indicates that it belongs to a juvenile individual (Pl. 4, fig. 4).

'Individual 1' (dimensions in Tables 1, 2) — The jaw lacks the ascending branches and is composed of various fragments that fit together. The fragmented condition of the specimen and a substantial deformation of the symphysis explains the deficiencies of the photographic reconstruction (Pl. 3, figs. 1, 2).

The degree of wear of the M_3 indicates that, besides the upper and lower tusks, this animal had functional M_2 and M_3. An alveolus for the M_2, filled with sedimentary rock, can still be observed.

The symphysis is nearly complete, but very deformed. It is wide in the anterior part and bent downwards, becomes narrower in the middle zone and wider again in the posterior part. It is roughly 640 mm in length. Table 1 shows the measurements taken, following the model of Tassy (1985, fig. 99B).

The left lower tusk, the only one preserved, consists of two fragments that fit the rest of the tusk that comes out of the symphysis. It is large and shows a wear bevel surface (Pl. 3, fig. 5) and a diverging trajectory (Pl. 3, fig. 1) that is, apparently, more pronounced because of the symphysis deformation. It protrudes 640 or 650 mm, but, because of the broken symphysis, the observed value is 710 mm. Subrounded in transverse section, with the labial wall more convex than the lingual one and the dorso-ventral diameter larger than the transverse. The maximum diameter is obliquely placed (Pl. 3, fig. 3). Near the alveolus there is a dorsal keel that diminishes towards the apex (Fig. 3, j1-3). The maximum dimensions, located in the middle zone, are 104 × 87 mm, and the maximum circumference is 305 mm.

Table 1. Dimensions of the mastodont jaw ('individual 1') from Crevillente 2 . The numbers in parentheses refer to the measurements by Tassy (1985, fig. 99B).

Symphysis length (2)	640
Horizontal branch thickness (7)	137
Posterior symphysal width (9)	250
Anterior symphysal width (10)	260
Smallest symphysal width (12)	200
Largest horizontal branch height (16)	160
Symphysal rostrum height (19)	130

Table 2. Dimensions of the M_3 (CR2-M280, CR2-M281) of the mastodont from Crevillente 2 ('individual 1'). The numbers 1 to 7 refer to the seven lophids.

	length	width 1	width 2	width 3	width 4	width 5	width 6	width 7	talonid width
right M_3	227	71	76	84	84	81	74	62	44
left M_3	227.3	75	77	80	81.6	80	73	62	50

The M_3 (CR2-M280 and CR2-M281) are large, with seven lophids and a strong monotuberculate talonid (Pls. 1, 2). Except for the talonid, the whole specimen is abraded, with wear figures only in the first four lophids; the first two lophids have trefoiled ectoconids, not joined to the wear figures of the entoconids. The enamel is thick and there is anancoidy in the middle zone lophids. This characteristic is more pronounced in the right tooth than in the left one. The dimensions of these specimens are given in Table 2.

The fragment of strongly deformed femur (CR2-915) represents roughly two thirds of the total length of the specimen and preserves the distal end with the articular condyles (Pl. 4, fig. 1). The fragment is 655 mm in length, the minimum width of the diaphysis is 180 mm and the maximum width of the distal end is 260 mm.

'Individual 2' (dimensions in Table 3) — The M_2 (CR2-78-S, CR2-79-S) are large (although only the right one is complete), with four lophids and a bituberculate talonid that could be considered nearly a half lophid if it were not yet affected by the contact with the M_3 (Pl. 5, figs. 1, 2). The wear reaches even the talonid with only a wear figure in the first two lophs. The cusps of the first lophid are transversally aligned. The second and third lophids show an oblique arrangement and the fourth, an angular one. No anancoidy is observed. Both specimens preserve their roots.

The M_3 (CR2-80-S, CR2-77-S) are large, with seven lophids and a monotuberculate talonid bent over the preceding lophid (Pl. 5, fig. 3; Pl. 6). The right specimen is included in a mandibular fragment and fits perfectly with the M_2, but because of the deformation of the jaw the series becomes wrongly oriented. The anterior crest is strong. The wear is moderate and trefoils the first two ectoconids. Third ectoconid slightly worn. The first four lophids have bituberculate ecto- and entoconids; in the fifth and sixth lophids ectoconids are bituberculate and entoconids monotuberculate; in the seventh, both entoconids and ectoconids are monocuspidated. Simple general morphology, without anancoidy. Labial cingulum starting from the second valley. Enamel crenulate and rough.

Table 3. Dimensions of the M_2 (CR2-78-S, CR2-79-S), M_3 (CR2-77-S, CR2-80-S) and M^3 (CR2-S-58, CR2-S-59) of the mastodont from Crevillente 2 ('individual 2'). The numbers 1 to 7 refer to the seven lophs/ids.

	length	width 1	width 2	width 3	width 4	width 5	width 6	width 7
M_2	133	63	65.4	69.5	70			
	135	(60)	(63)	(66)	68.5			
M_3	241	83	84	87	85	71.5	59	51
	235	77	80	82.7	(82)	74	65.3	55
M^3	(218)			(93)	91.5	90	(82)	
				90	92.5	93	(80.3)	

The M^3 (CR2-S-58, CR2-S-59) are not complete (Pl. 7, figs. 1, 2). The left one is the best preserved, and has 6 lophs and a talon with four large cusps semicircularly arranged. The wear affects the whole molar except for the talon. There are trefoiled wear figures in the first two lophs and in the third entocone. In the posterior walls of entocones and ectocones are additional tubercles, therefore there is a high total number of cusps. Enamel thick and rough. Rests of cement in the last valleys. Lingual cingulum preserved only starting from the fourth loph, with large cusps that penetrate into the valleys. No anancoidy is observed.

The morphology of the M^3 is somewhat more complex than that of the M_3. However, all the mastodont remains from bed A, which is relatively poor in fossils, were found associated, and therefore we assume that all the teeth belong to the same single individual ('individual 2').

Discussion — The mandible size, the length of its symphysis, the development and section of the lower tusks, the dimensions of the M_3 and the correlation of the sedimentary rocks (lower Turolian, MN 11 zone) preclude the assignment of the mastodont from Crevillente 2 to trilophodont taxa (Mazo 1977, 1996). Numerous authors, including Schlesinger (1917), Lehmann (1950), Mottl (1969), Mazo (1977) and Tobien (1978), accepted that the tetralophodont form *Tetralophodon longirostris* evolved from the trilophodont *Gomphotherium angustidens*. Tassy (1985, 1990) did not agree with this hypothesis; in his opinion, *G. angustidens* has more autopomorphies than *T. longirostris*.

Besides the typical *Tetralophodon longirostris* Kaup, Schlesinger (1917, 1922) defined a second tetralophodont taxon from some localities in Europe and Asia, which was named *Mastodon (Bunolophodon) grandincisivus*, because of the big size of the lower tusk in the type specimen from Maragha (Iran). The diagnostic features of this second taxon, according to Osborn (1936), are the following; skull shortening, high cranial cavity, extreme growth of the mandibular symphysis, loss of the enamel band in the I^2 (which is lyre-shaped), I_2 strongly developed, reduction of the molar series, increase of the tetralophodoncy, lack of premolars and reduction of the additional cusps of the molars. In contrast, the characteristics given by Tobien (1973, 1978) for this taxon are the large body size, large upper and lower tusks, lower tusks much protruding from the symphysis and large, structurally complex, molars with frequent cement deposits.

Schlesinger (1917) included within *Mastodon (Bunolophodon) grandincisivus* a pyriform lower tusk from Maragha (Iran); two upper tusks, a lower tusk, and the upper and lower M3 of an individual from Kertch (Crimea), described by Pavlow (1903) as *Mastodon* cf. *longirostris*; the upper and lower tusks and M3 from Pestszentlörincz (Hungary); and some large isolated molars from Germany and Austria. Subsequently, Bakalov & Nikolov (1962) described a mandible with tusks, associated to the upper tusks and M^3, from Orjachovo (Bulgaria), included by Tobien (1978) in *grandincisivus*. Gaziry (1976) assigned some fragments of upper and lower tusks from Anatolia and Thrace to *Tetralophodon grandincisivus*.

The morphology of the lower tusks are essential to the discussion of *grandincisivus*. The drawings of Pavlow (1903) and the revision of these specimens by Tobien (1978) showed that the tusks from Maragha and Kertch had concentric layers of dentine in their structure. Internally there is something very similar to the dentine cones typical of the platybelodonts *sensu stricto*. The tusks from Pestszentlörincz also have tubular

Table 4. Dimensions of the lower tusk (CR2-M279) of the mastodont from Crevillente 2 ('individual 1'), compared with those of some Eurasian '*Mastodon grandincisivus*'.

I_2	Maragha	Kertch	Pestszentl.	Orjachovo	Crevillente 2
Fragment length		1400	1610		
Protrusion					640-650
Largest diameter	175	180	195	164	104
				185	

dentine according to Tassy (1985, p. 788). We have found no data about the dentine of the tusks from Orjachovo.

In Table 4, the length and maximum diameter of the lower tusk from Crevillente 2 are compared with the dimensions of specimens from Maragha, Kertch, Pestszentlörincz and Orjachovo. These data should be evaluated taking into account the section and the situation of the maximum diameter. In Figure 3 the section of the I_2 from Maragha, Kertch and Pestszentlörincz (data from Tobien, 1978, figs. 4, 5; Tassy, 1985, fig. 227) are compared with that of the I_2 from Crevillente. There are great differences and, whereas the maximum diameter is transversal in the specimens from central and eastern Europe, it is dorso-ventral in the specimen from Crevillente 2. Moreover, the tusk here studied has a dorsal keel and a lingual sulcus. In this respect, the observation by Tobien (1978, p. 182) indicates that, although Bakalov & Nikolov (1962) drew the Orjachovo tusk with a quite flattened section, the diameter values show a rather rounded or oval section.

The presence of tubular dentine in the lower tusks from Maragha, Kertch and Pestszentlörincz supports the hypothesis of Tobien (1978), accepted by Tassy (1985, 1990, 1996), that this group of mastodonts is related to the Amebelodontinae. Lower tusks such as those from these sites have very little or nothing to do with those from Crevillente 2. Instead, the morphology of tusks like the one here described, with a suboval section and a dorso-ventral maximum diameter, is more close to that of some European *Tetralophodon longirostris*. It is, for example, comparable to the morphology of a lower tusk from the Vallesian (MN-10) of Lyon Croix-Rousse (Fig. 3), whose maximum diameter, according to the drawing of Lortet & Chantre (1878, pl. 16) is 78 mm (Tassy, 1977, fig. 283, Q2).

In Spain, the lower tusks of *T. longirostris* are scarce. The specimen from the Vallesian of Polinyà (Barcelona) described by Alberdi (1971) shows a long mandibular symphysis (length 520 mm) with almost parallel tusks that protrude approximately

Table 5. Dimensions of the lower tusk (CR2-M279) of the mastodont from Crevillente 2 ('individual 1'), compared with those of some European and North African *Tetralophodon longirostris*.

I_2	Polinyà	Lyon	Bersmersheim	Gross-Weifendorf	Djebel Semenne	Crevillente 2
Fragment length				410		
				365		
Protrusion	300		700			640-650
Largest diameter	62	78	61	76	116	104
				82		

300 mm from the symphysis, with oval section and short dorsal wear facet. Its maximum diameter is 62 mm (Table 5). We do not agree with Tobien (1978) who considered this individual as an advanced *Gomphotherium angustidens*.

Among the abundant remains of *Tetralophodon longirostris* from the Vallesian of Bermersheim (Germany), from a locality near Eppelsheim, Klähn (1931) documented a specimen he named *Mastodon longirostris* form *gigantorostris* (Tobien, 1978, pl. 19, fig. 17). The left tusk, that seems not to have been in contact with the right one, protrudes 700 mm, has a maximum diameter of 61 mm and a pyriform section. The specimens from Eppelsheim, Bermersheim and Steinheim, although all assigned to *T. longirostris*, show a great variability in the deflexion of the mandibular symphysis and different degrees of structural complexity in the intermediate molars.

The section in the zone near the alveolus of other lower tusks could be compared with that of the tusk described herein, like those of a *Tetralophodon longirostris* from the Vallesian of Gross-Weiffendorf (Germany) (Fig. 3) studied by Steininger (1965). The maximum diameter of these tusks diverges dorsally considerably more than in the specimen from Crevillente 2.

A fragment of a mandibular symphysis from the Vallesian of Djebel Semenne (Tunisia), assigned by Bergonioux & Crouzel (1956, fig. 2) to *T. longirostris*, shows tusks of pyriform section with a dorso-lingual sulcus and a maximum dorso-ventral diameter of 116 mm. These characteristics are very close to those of the tusk from Crevillente 2, although the dorso-lingual sulcus is more pronounced in the specimen from Djebel Semenne (Fig. 3). This individual was assigned by Tobien (1978) to a small *grandincisivus* or to a *Tetralophodon* cf. *longirostris* with grandincisivoid characteristics, and by Tassy (1999) to cf. *Stegotetrabelodon*. Bergounioux & Crouzel (1956) erroneously interpreted these specimens as upper tusks; therefore, their figure seems inverted when compared with that of Tobien (1978) who interpreted them correctly.

In Figure 3 the sections of the tusk from Crevillente 2, and of homologous specimens from Djebel Semenne (Bergounioux & Crouzel, 1956), Lyon Croix-Rousse (Lortet & Chantre, 1878), Steinheim (Tassy, 1985) and Gross-Weifendorf (Steininger, 1965), are compared. Considering both the section and the dimensions, the tusk from Crevillente seems to be especially related to those from Djebel Semenne (Tunisia) and Lyon Croix-Rousse (France), although this latter, of unknown original anatomical position, shows a clearly smaller size. Figure 4, modified from Tobien (1978, fig. 12), shows the metrical similarity of the material from Crevillente and Djebel Semenne, and the differences with regard to the remains of *grandincisivus* from Maragha, Pestszentlörincz, Kertch and Orjachovo. The analysis of numerous tusks included in *Tetralophodon grandincisivus* displays a heterogeneity which is difficult to accept.

Also among trilophodont forms attributed to *G. angustidens*, specimens have been cited with grandincisivoid characteristics (Mottl, 1970). According to Tobien (1978), an example is the remains from the upper Aragonian Spanish site of Monte de la Abadesa (Burgos), stored in the Museo GeoMinero (Madrid). Besides postcranial remains, this locality yielded some M_2 and M_3 associated with apical fragments of lower tusks determined by Badillo (1952) as *Mastodon longirostris* and by Zbyszewski (1954) as *Serridentinus hispanicus*. Bergounioux & Crouzel (1958) created the new taxon *Geisotodon hispanicus* for these specimens. The M_2 from Monte de la Abadesa has three lophids, a developed talonid and a size of roughly 145 $\times$ 84 mm; the M_3 show five lophids and a

talonid measuring 225 × 90 mm and 227 × 90 mm. The apical fragments of tusks have a pyriform section, 85.3 × 62 mm in size, although it is difficult to determine whether the maximum diameter was oblique or transversal.

The same site delivered a palate, a mandible and a fragment of an upper tusk of a juvenile specimen (Bergounioux & Crouzel, 1958, figs. 6-9, pls. 60-62). The upper and lower M1 have three lophs/lophids and a talon/talonid, and the M_2, included in the mandible, show three lophids and a talonid that can be interpreted as a fourth lophid. However, the fragment of upper tusk has a lateral enamel band, which is not compatible with the diagnostic characteristics of *Tetralophodon*.

Tobien (1978) considered that the remains from Monte de la Abadesa described by Badillo (1952), probably belong to a 'grandincisivoid' individual of *Gomphotherium angustidens*. We agree (Mazo, 1977) that these remains could be included in *Gomphotherium*, without excluding their possible inclusion in some form related to primitive platybelodonts, as suggested by Tassy (1977, 1996).

As for the cheek teeth, the 'individual 1' from Crevillente 2 has the M_3 in anatomical position, as commented above. Since we have the M_2 and the upper and lower M3 of a second specimen ('individual 2'), a combined analysis was made. Comparing dimensions (Table 3; Fig. 5), the M_2 of 'individual 2' from Crevillente (133 × 70 mm and 135 × 68.5 mm) are close to the M_2 of the type mandible of *T. longirostris* (135 × 68 mm). Nevertheless, the M_3 of the type specimen (189 × 68 mm plus five lophids and talonid) is smaller than the three M_3 from Crevillente 2 (227.3 × 81.6 mm and 227 × 84 mm in 'individual 1,' 241 × 87 mm in 'individual 2').

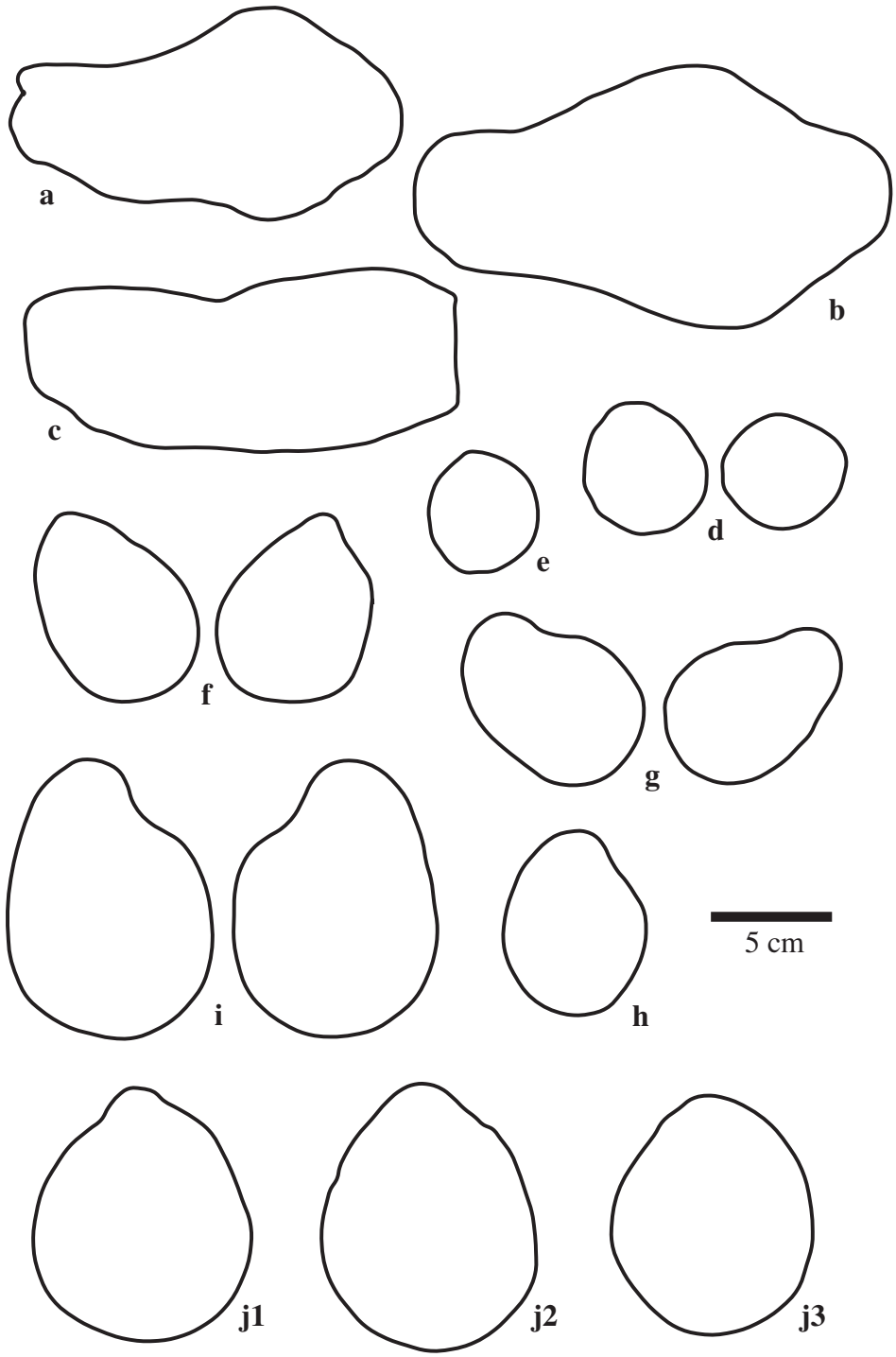
Figure 5 is a length-width scatter diagram comparing the complete M_2 of the 'individual 2' from Crevillente 2 with the typical M_2 of *T. longirostris* and with various grandincisivoid specimens of *Tetralophodon* from central Europe. The M_2 from Crevillente 2 and the grandincisivoid specimens fall within the field of typical *T. longirostris*.

Figures 6 and 7 are scatter diagrams where the lower and upper M3 of the two individuals from Crevillente 2 are compared with other homologous elements of *T. longirostris*, *T.* cf. *longirostris* 'grandincisivoid form' and '*Mastodon grandincisivus*' from central and eastern Europe. The length values of the M_3 from Crevillente 2 are within the maximum values of the scatter area of the typical *T. longirostris*, whereas their width values are relatively low. The M^3 show dimensions close to those of the typical '*grandincisivus*'.

Data for the comparison of postcranial remains are scarce. The femur of the adult specimen of *Tetralophodon longirostris* from Polinyà (Barcelona, Spain), described by Alberdi (1971), is 950 mm long and its distal end is 213 mm wide, whereas that of the specimen from Crevillente 2 is 260 mm. Like the teeth, the postcranial remains from Crevillente 2 belong to a large individual.

The systematic and phylogenetic position of '*Mastodon grandincisivus*' and of the

Fig. 3. Lower tusk sections (posterior view) of '*Mastodon*' *grandincisivus* from Maragha (a), Pestszentlörincz (b) and Kertch (c), *Gomphotherium steinheimensis* from Steinheim (d, e), *Gomphotherium angustidens* (grandincisivoid specimen) from Monte de la Abadesa (f), and *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Gross-Weiffendorf (g), Lyon Croix-Rousse (h), Djebel Semenne (i) and Crevillente 2 (j1-3). j1, proximal section; j2, medial section; j3, distal section. Figures 'a, b, c, d, e, g, h' from Tassy (1985, figs. 227, 283); figure 'i' from Bergounioux & Crouzel (1956). ▶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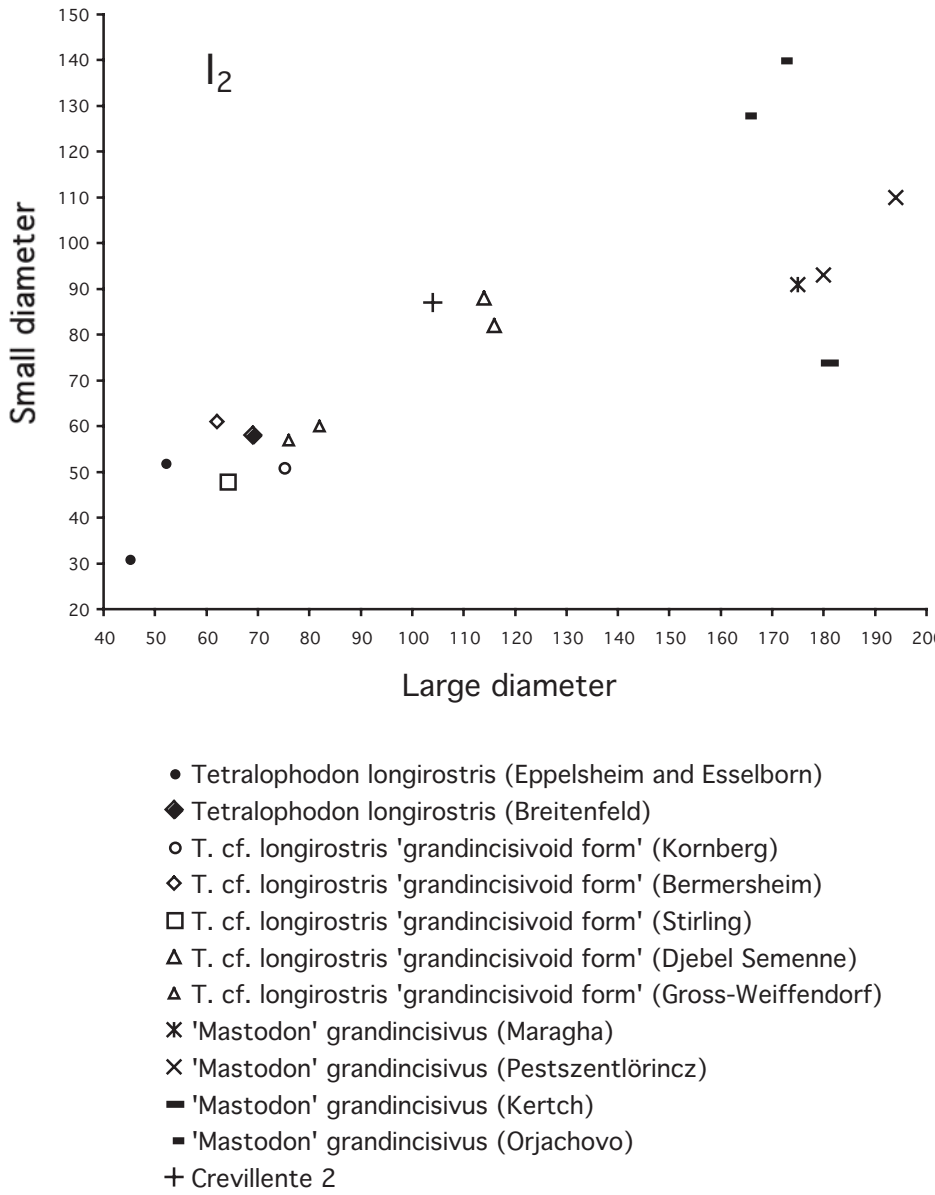

Fig. 4. Scatter diagram of the lower tusks of *Tetralophodon longirostris*, *Tetralophodon* cf. *longirostris* 'grandincisivoid form' and '*Mastodon*' *grandincisivus*. Data, in part, from Tobien (1978).

so-called 'grandincisivoid forms' is not very clear (Kalb *et al*., 1996; Göhlich, 1999). Tobien (1978) included '*M. grandincisivus*' of the Turolian of western Europe, Near East and North Africa in the genus *Stegotetrabelodon* Petrocchi, 1941. This possible relationship is a controversial theme. An exhaustive discussion can be consulted in Tassy (1999). The cladistic analysis made by Tassy (1985), Tassy & Darlu (1986, 1987) and

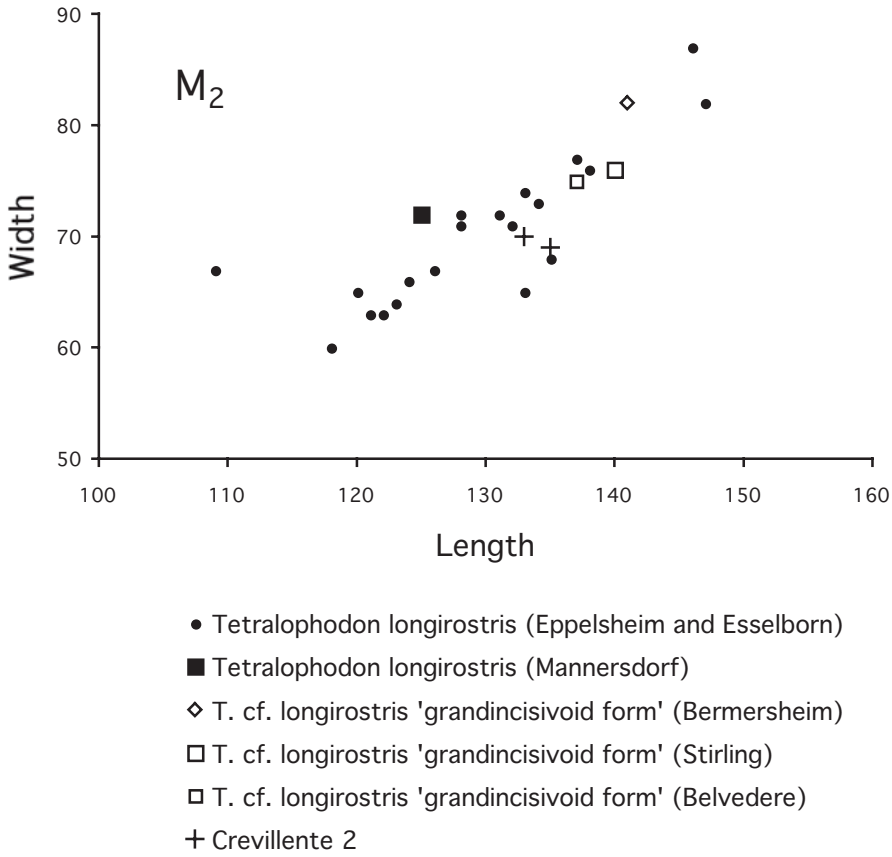

Fig. 5. Scatter diagram of the M_2 of *Tetralophodon longirostris* and *Tetralophodon* cf. *longirostris* 'grandincisivoid form'. Data, in part, from Tobien (1978).

Kalb *et al*. (1996) do not support the inclusion of *Mastodon* (*Bunolophodon*) Schlesinger in *Stegotetrabelodon*.

The specimens from Crevillente 2 do not fit several of the diagnostic characters of the genus *Stegotetrabelodon*, as given by Maglio (1973) and revised by Gaziry (1987). The lower tusk from Crevillente 2 is metrically situated near the ones from Djebel Semene, assigned by Tassy (1999) to cf. *Stegotetrabelodon*, and far from those from Abu Dhabi, which were considered by Tassy (1999) to be a stegotetrabelodontine. It is important to take into account that even the primitive forms of *Stegotetrabelodon* differ from the other mastodonts in that their upper and lower M3 have no cusps with trefoiled wear figures in their distal lobes. Instead, they have transverse rows of cusps of equal height that resemble the lamellae of the elephants. The molars from Crevillente do not have the distal cusps resembling lamellae, another difference, in addition to incisor morphology, with *Stegotetrabelodon*.

According to the analysis of Tassy & Darlu (1986, 1987) and Tassy (1990), the 'grandincisivoid forms' seem to be more related to *Tetralophodon* than to any other taxon. The revision of Kalb *et al*. (1996) considered '*Mastodon grandincisivus*' as a sister

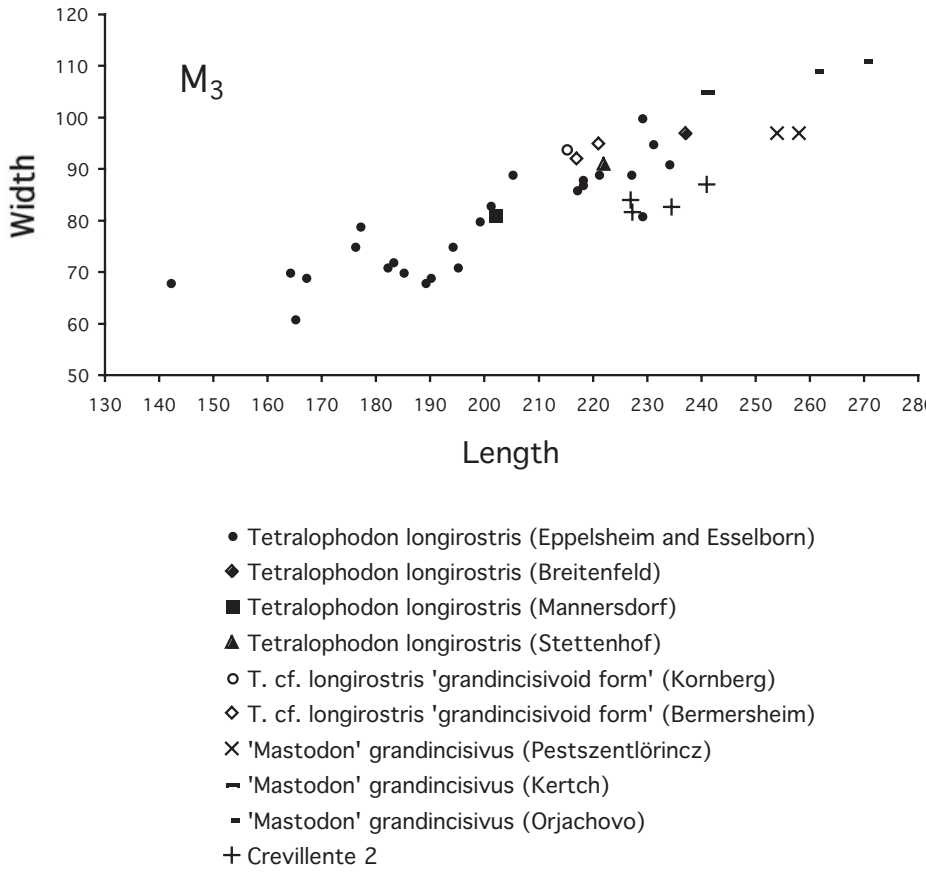

Fig. 6. Scatter diagram of the M_3 of *Tetralophodon longirostris*, *Tetralophodon* cf. *longirostris* 'grandincisivoid form' and '*Mastodon*' *grandincisivus*. Data, in part, from Tobien (1978).

group of the clade comprising *Tetralophodon*, *Paratetralophodon*, *Anancus*, *Stegolophodon*, *Stegotetrabelodon*, *Stegodibelodon*, *Stegodon* and Elephantinae. In addition the Tobien's (1978) 'grandincisivoid forms,' assigned either to *Gomphotherium* or *Tetralophodon*, but considered of uncertain affinity by Kalb *et al*. (1996), should be considered here.

We support Tassy (1999), who suggested that the name *grandincisivus* should only be applied to specimens associated with lower tusks showing tubular dentine, strong protrusion, large size, pyriform section and oblique or transversal maximum diameter. If the dentine is arranged in concentric layers, the dimensions are not so extreme and the section is oval or rounded with a dorso-ventral maximum diameter, specimens should rather be included in *Tetralophodon* cf. *longirostris*, in Tobien's (1978) *Tetralophodon* 'grandincisivoid form'. Because of the aforementioned reasons we assign the remains of the mastodont from Crevillente 2 to *Tetralophodon* cf. *longirostris* 'grandincisivoid form'.

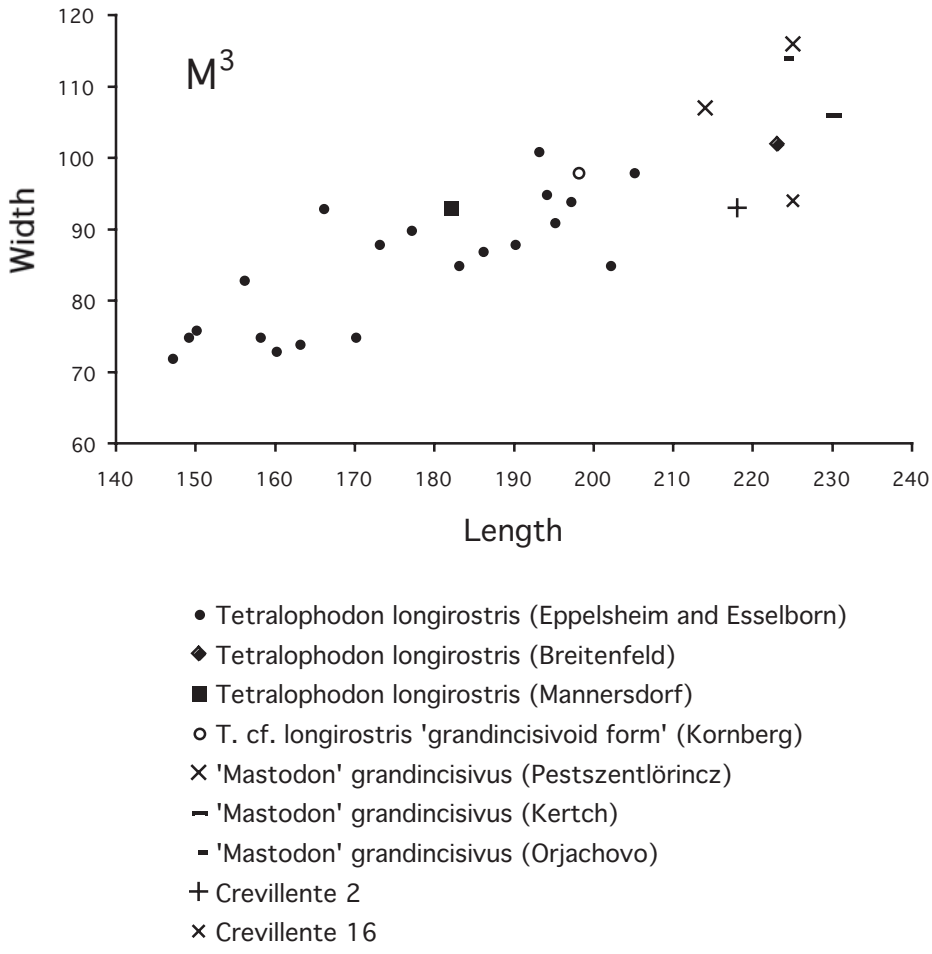

Fig. 7. Scatter diagram of the M3 of *Tetralophodon longirostris*, *Tetralophodon* cf. *longirostris* 'grandincisivoid form' and '*Mastodon*' *grandincisivus*. Data, in part, from Tobien (1978).

Tetralophodon longirostris (Kaup 1832)

Pl. 7, fig. 3.

Diagnosis — See Kaup (1832, p. 628), emended by Osborn (1936, p. 356).

Studied material — Crevillente 16 (MN12); posterior half of a right M^3, MGUV CR16-25 (figured by Montoya & Alberdi, 1995); left M^3, MGUV CR16-26. Both specimens were found together and belong to the same individual

Description — Left M^3 complete, with six lophs and talon with three small crenulations pointing forwards. Strong recurrent crest. Moderate wear that trefoils first loph and second entocone; second ectocone with elongate wear figure. Other lophs slightly

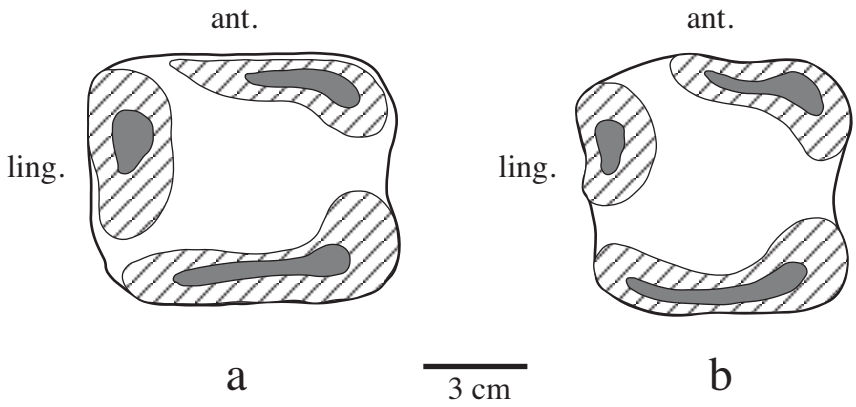

Fig. 8. Disposition of the roots in right P^4 of *Deinotherium giganteum*. (a) Specimen A.Mo.40 from Montredon (Tobien, 1988, fig. 2). (b) Specimen CR2-530 from Crevillente 2.

abraded. Morphology simple. Third, fourth and fifth entocones slightly ahead of ectocones. Small ledges between ectocones. Measurements in Table 6.

Discussion — The M^3 from Crevillente 16 is morphologically simple, with a low number of cusps, and the entocones are slightly ahead of the ectocones. Therefore, it differs considerably from the complex M^3 from Crevillente 2. The length of this third molar clearly exceeds that of the typical *Tetralophodon longirostris* from central Europe and is close to that of the mastodont from Breitenfeld, Styria (Austria), described by Mottl (1969) and Tobien (1978) as a large *T. longirostris* (Fig. 7). Apart from the size, there are no reasons to assign the remains from Crevillente 16 to a 'grandincisivoid form' like that from Crevillente 2; consequently we include them in *Tetralophodon longirostris*.

cf. *Tetralophodon* sp.

Studied material — Crevillente 15 (MN12); indeterminate fragments of teeth, MGUV not numbered.

Discussion — Only fragments of a dental crown of a bunodont mastodont have been recovered from this site which do not allow a more precise taxonomic identification. These remains have been attributed to cf. *Tetralophodon* sp. because of the high homogeneity among the macromammal assemblages from Crevillente 15 and 16, and

Table 6. Dimensions of the M^3 (CR16-26) of *Tetralophodon longirostris* from Crevillente 16. The numbers 1 to 6 refer to the six lophs.

	length	width 1	width 2	width 3	width 4	width 5	width 6
left M^3	225	90	94	92	88.5	79	76.5
right M^3					91	(81)	76.3

the age of both sites. That makes the presence of a bunodont mastodont belonging to another genus most unlikely.

Suborder Deinotherioidea Osborn, 1921
Family Deinotheriidae Bonaparte, 1845
Genus *Deinotherium* Kaup, 1829
***Deinotherium giganteum* Kaup, 1829**
Pl. 8, figs. 1, 2.

Diagnosis - See Tobien (1988).

Studied material — Crevillente 2 (MN11), Bed B; right P^4, MGUV CR2-530; right D^4, MGUV CR2-849.

Description — P^4 (CR2-530) is a large, very worn and eroded tooth (Pl. 8, fig. 1). Only some rests of enamel are preserved in the crown. There is a longitudinal crest, thus the morphology does not correspond to parallel lophodont crests. Three roots are preserved; the first is transversally elongate and located in the posterior edge of the tooth, the second one anterolabial and less elongate than the former, and the third in the lingual side, displaced forward.

The D^4 (CR2-849) tooth is poorly preserved (Pl. 8, fig. 2). Its crown, with a rectangular outline, has only scarce rests of enamel corresponding to two of the three original lophs. The roots are partially preserved. Measurements in Table 7

Discussion — In spite of the high degree of wear of both elements, some morphological characteristics together with the large size of the specimens make it possible to assign them to *Deinotherium*, a genus widely represented in the Miocene of the Iberian Peninsula. In CR2-530, the morphology and arrangement of the roots perfectly match those figured by Tobien (1988, fig. 2) for the right P^4 of *Deinotherium giganteum* from the French site of Montredon (Fig. 8). The scarce observations that can be made about the shape of the crown also suggest that it is a P^4.

The morphology of CR2-849, with an elongate crown composed of three lophs, is shared in *Deinotherium* by both the upper and lower D4 and M1. The aspect of the roots and the relatively reduced dimensions of this specimen, as well as its trapezoidal outline, indicate that it is probably a D^4.

Table 7. Dimensions of the P^4 (CR2-530) and D^4 (CR2-849) of *Deinotherium giganteum* from Crevillente 2, compared with those from Montredon (Tobien, 1988), Cerecinos de Campos, Sant Quirze, Hostalets de Pierola (upper levels) and Terral d'En Maties (Bergounioux & Crouzel, 1962).

D. giganteum		Montredon min.	med.	max.	n	Cerecinos de Campos	Sant Quirze	Upper Hostalets	T. d'En Maties	Crevillente 2
P^4	length	63.1	71.0	78.0	16	64	69 66		73	73.3
	width	71.0	81.1	90.2	16	62	73 72		80	> 68
D^4	length		70.3		1			62		72.3 ca
	width		50.5		1			53		52.5 ca

The dimensions of the elements from Crevillente 2 (Table 7) are very close to those of the abundant sample of *Deinotherium giganteum* from Montredon (France) (Tobien, 1988), and generally slightly larger than the homologous elements of this species from other Spanish sites (Bergounioux & Crouzel, 1962). Therefore, the remains from Crevillente 2 are attributed to *Deinotherium giganteum* Kaup, 1829, a species represented in Europe from the Middle Miocene to the Lower Pliocene.

The first occurrence of the family Deinotheriidae in the Spanish fossil record is in the lower Aragonian from La Artesilla (Azanza *et al.*, 1993). In the Vallés-Penedés, Bergounioux & Crouzel (1962) described the small form *D. bavaricum* from the sites near the locality of El Papiol, where Crusafont *et al.* (1955) had previously cited *D. cuvieri*. The large form *D. giganteum* is recorded from the upper Aragonian (zone MN7-8). The sites of Cerro del Otero (Palencia) and La Cistérniga (Valladolid) (Hernández Pacheco & Dantín, 1915), Fuensaldaña (Valladolid), Cerecinos de Campos (Zamora), Castrillo de Villavega (Palencia), as well as the Catalonian sites of Can Valls (Masquefa), Sant Quirze and the lower beds of Hostalets de Pierola, all cited by Bergounioux & Crouzel (1962), belong to this age.

Deinotherium giganteum, sometimes cited as *D. laevius*, is also found in the Vallesian. Thus, it occurs in the Catalonian sites of Can Llobateres, La Tarumba I (Viladecavalls), Sant Miquel del Taudell, La Bisbal (cited by Bergounioux & Crouzel, 1962), Caldes de Montbuí, Sabadell, Polinyà (Alberdi, 1974), upper levels of Hostalets de Pierola (Crusafont, 1952), El Firal (Golpe, 1981) and Terrassa (Santafé *et al.*, 1979), as well as in the Aragonese site of Pedregueras (Alberdi, 1974). In the Turolian, besides Crevillente 2 and Crevillente 15, *Deinotherium giganteum* is found in Piera (Crusafont, 1952), Alfacar (Bergounioux & Crouzel, 1959), Terral d'En Maties (Bergounioux & Crouzel, 1962), Las Pedrizas (Adrover, 1963) and Concud (Alcalá, 1994). *Deinotherium* has not been found in Spanish sites younger than the Late Turolian. The presence in Crevillente 2 of at least two individuals of *Deinotherium giganteum*, together with *Dorcatherium naui*, is in agreement with the existence of humid environmental conditions inferred for the lower part of the Turolian in the area of Crevillente, according to the model proposed by Martín Suárez *et al*. (2001).

***Deinotherium* sp.**

Pl. 8, fig. 3.

Studied material — Crevillente 15 (MN12); fragment of the crown of an indeterminate tooth, MGUV CR15-72.

Discussion — On the premise of the enamel thickness and especially of the morphology of the strongly crenulated edge, this specimen can only correspond to an unworn fragment of loph(id) of a deinothere tooth. The remain is so fragmentary that it must be determined as *Deinotherium* sp., although the Turolian age of the site indicates that it is probably a *Deinotherium giganteum*.

Conclusions

In the Upper Miocene of Crevillente (Alicante) two types of proboscideans have been found, mastodonts and deinotheres. The mastodonts from Crevillente 2 (MN11)

(at least three individuals) are assigned to *Tetralophodon* cf. *longirostris* 'grandincisivoid form' and those from Crevillente 16 (MN12) (one individual) to *Tetralophodon longirostris*. The deinotheres from Crevillente 2 and Crevillente 15 are, respectively, identified as *Deinotherium giganteum* and *Deinotherium* sp.

The comparison of the mastodonts from Crevillente 2 with specimens determined as *Tetralophodon longirostris*, '*Mastodon' grandincisivus* and 'grandincisivoid forms' of *Gomphotherium* and *Tetralophodon*, leads us to consider as '*M.*' *grandicisivus* only those individuals associated with lower tusks that have tubular dentine, strong protrusion, large size and pyriform section with oblique or transversal maximum diameter. Alternately, specimens associated with large lower tusks that have the dentine arranged in concentric layers and oval or subrounded section with dorso-ventral maximum diameter are included in Tobien's (1978) 'grandincisivoid forms', that can belong either to *Gomphotherium* or to *Tetralophodon*. This is the first time that a mastodont with large lower tusks of rounded section associated with M_3 that have seven lophids with anancoidy has been described from Spain. This demonstrates the difficulty of correctly interpreting isolated cheek teeth. The systematic and phylogenetic position of '*Mastodon*' *grandincisivus*, and of the 'grandincisivoid forms' is obscure. Tobien (1978) and Tassy (1985, 1990, 1996) considered that '*grandincisivus*' *sensu stricto* could be related to the Amebelodontinae.

The tusk from Crevillente 2 is quite similar to the lower tusks from Djebel Semenne (Tunisia) attributed to *T. longirostris* by Bergounioux & Crouzel (1956). The most similar section among the European specimens is that of a lower tusk of *T. longirostris* from Lyon Croix-Rousse (MN10) figured by Lortet & Chantre (1878), although the latter is somewhat smaller than those from Tunisia and Crevillente. The presence of *Deinotherium* in Crevillente 2 (together with *Dorcatherium*) and in Crevillente 15 supports the hypothesis that there were humid environmental conditions in this area, at least in the lower part of the Turolian (Martín Suárez *et al.*, 2001).

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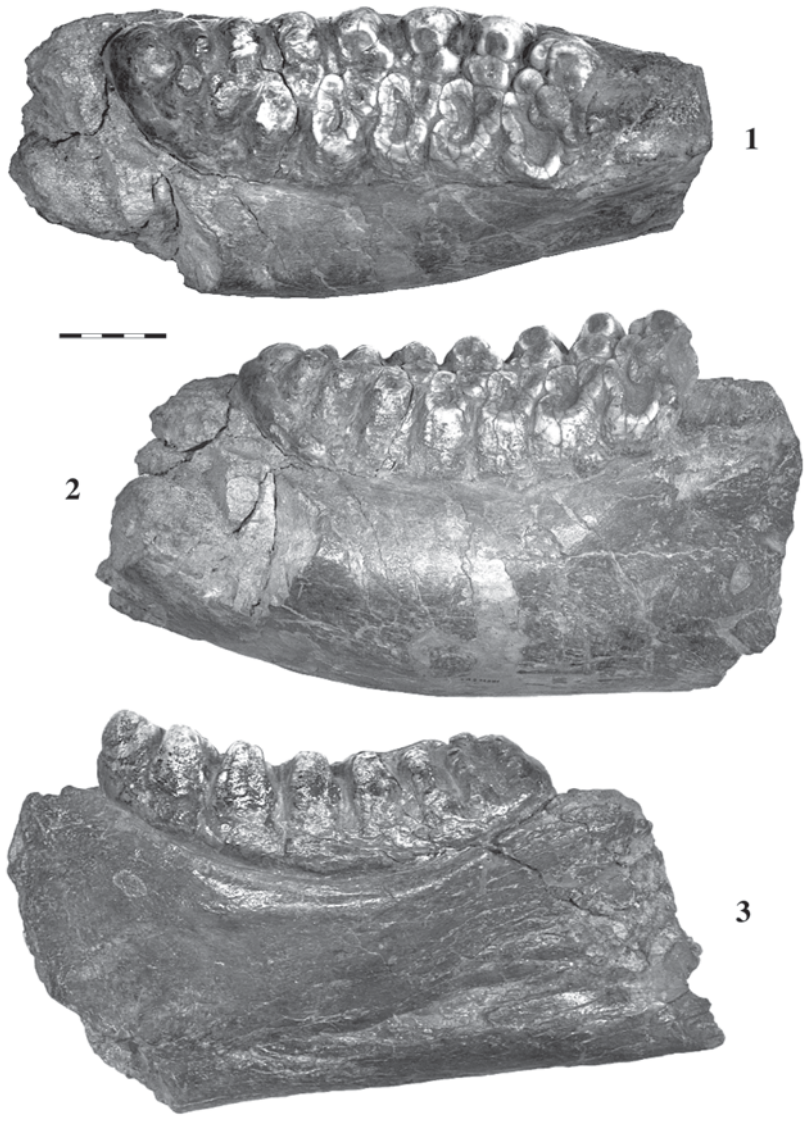

Plate 1

Right M_3 (CR2-M281) of the 'individual 1' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2. Scale bar represents 50 mm.
Fig. 1. Occlusal view.
Fig. 2. Labial view.
Fig. 3. Lingual view.

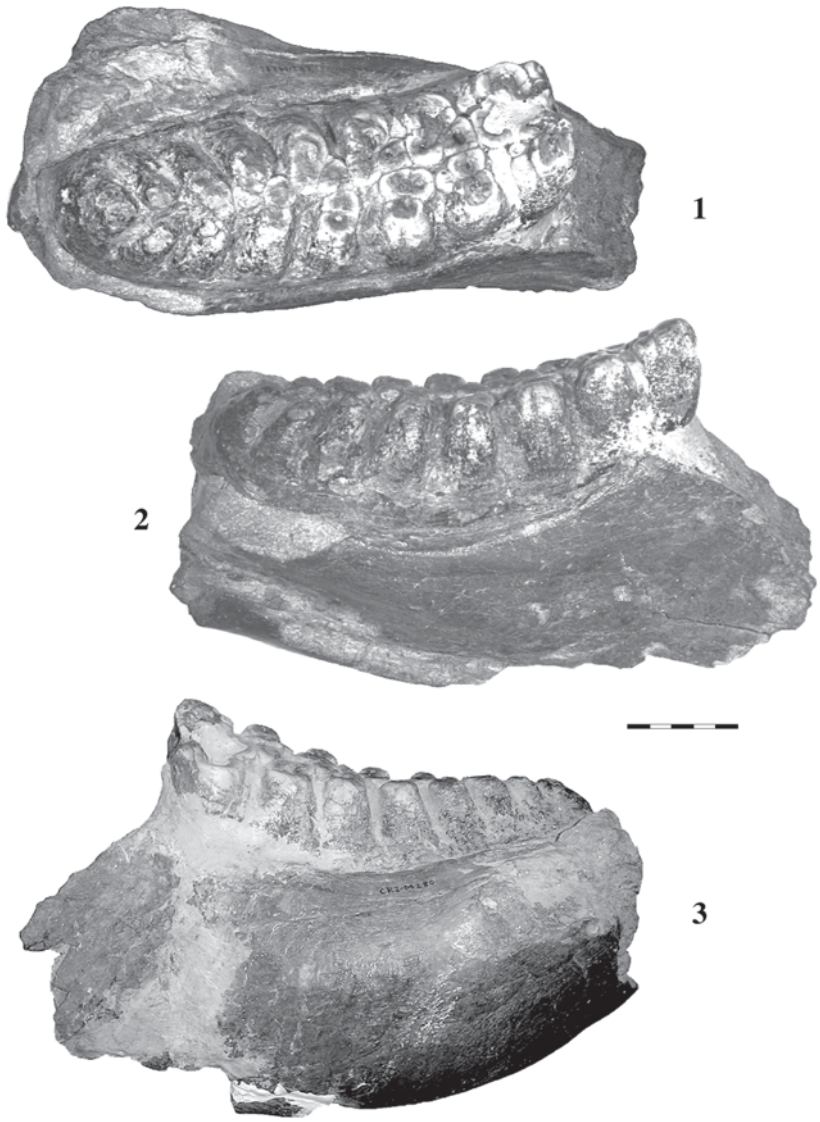

Plate 2

Left M_3 (CR2-M280) of the 'individual 1' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2. Scale bar represents 50 mm.
Fig. 1. Occlusal view.
Fig. 2. Lingual view.
Fig. 3. Labial view.

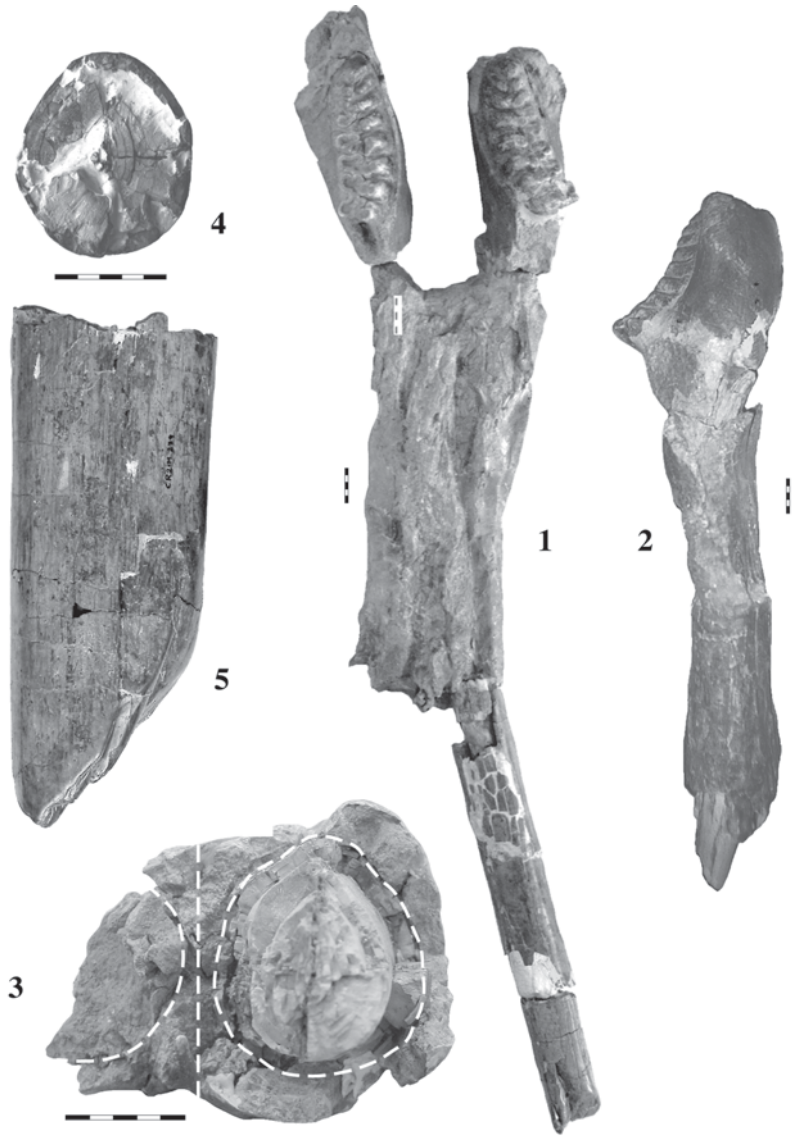

Plate 3

'Individual 1' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2. Scale bar represents 50 mm.

Fig. 1. Mandible with the M_3 and the left lower incisor (CR2-M279, M280, M281), occlusal view.

Fig. 2. Left hemimandible and symphysis (CR2-M280), labial view.

Fig 3. Anterior view of the mandibular symphysis. Broken line indicates the sagittal plane and the incisors outline.

Fig. 4. Section, in dorso-ventral position, of the apical fragment of the left incisor (CR2-M279), proximal view.

Fig. 5. Apical fragment of the left incisor (CR2-M279), lingual view.

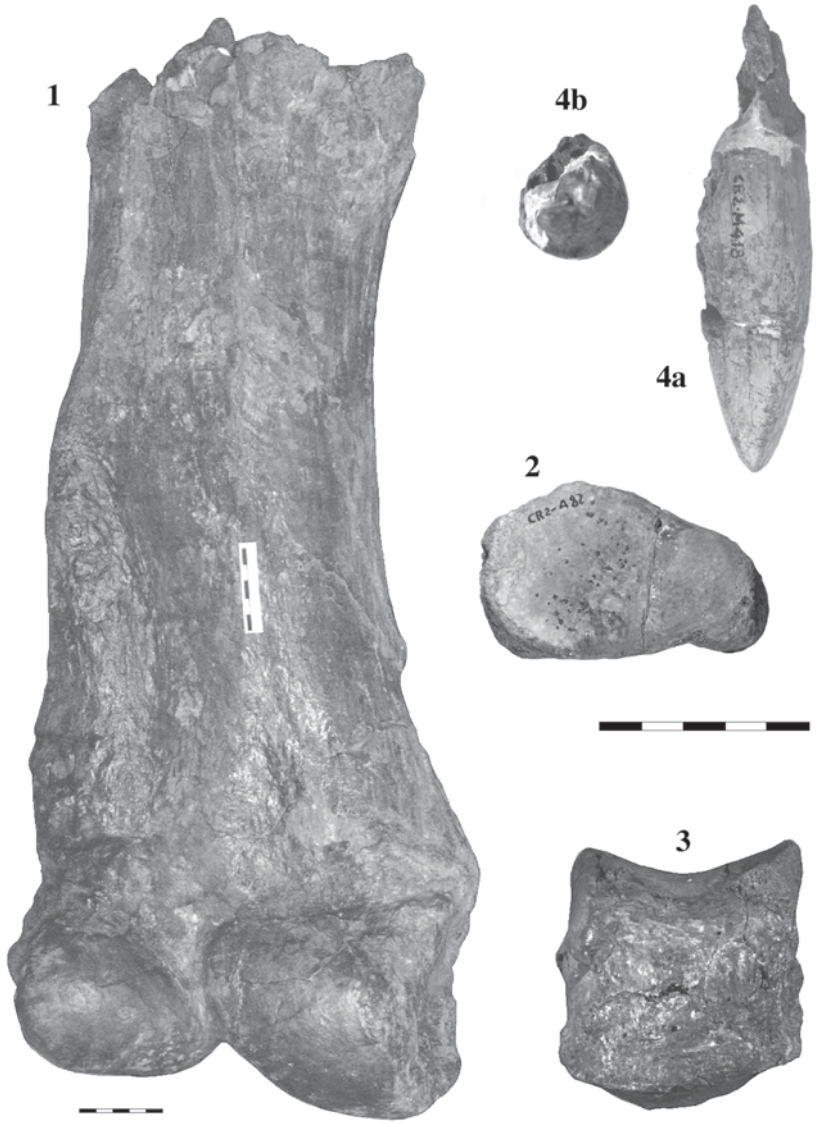

Plate 4

Figs. 1-3. 'Individual 1' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2.
Fig. 1. Incomplete femur (CR2-915), posterior view (note small scale bar).
Fig. 2. Big cuneiform (CR2-A82), proximal view.
Fig. 3. First phalanx (CR2-A83), dorsal view.

Fig. 4. Apical fragment of the juvenile incisor of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2 (CR2-M418) (a) Section in dorso-ventral position. (b) Lateral view.

Scale bars represents 50 mm.

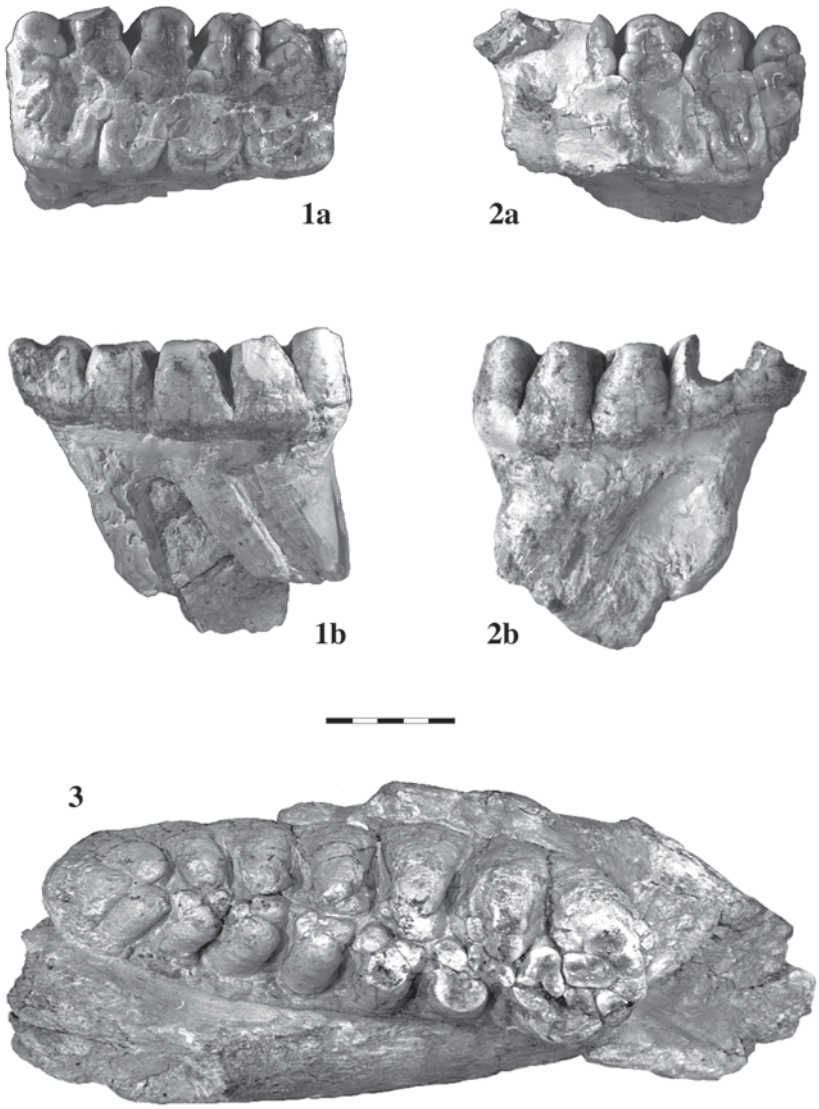

Plate 5

'Individual 2' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2. Scale bar represents 50 mm.
Fig. 1. Right M_2 (CR2-79-S). (a) Occlusal view. (b) Lingual view.
Fig. 2. Left M_2 (CR2-78-S). (a) Occlusal view. (b) Lingual view.
Fig. 3. Right mandible fragment with M_3 (CR2-80-S), occlusal view.

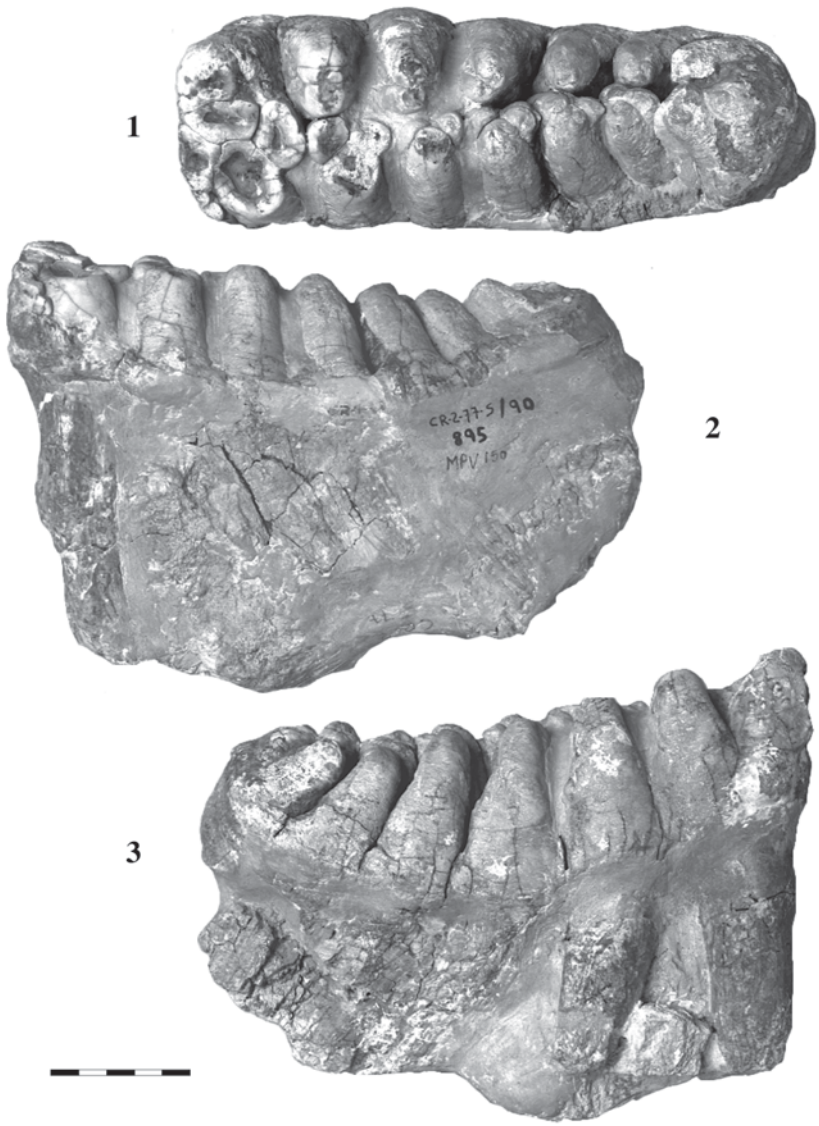

Plate 6

Left M_3 (CR2-77-S) of the 'Individual 2' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2. Scale bar represents 50 mm.
Fig. 1. Occlusal view.
Fig. 2. Labial view.
Fig. 3. Lingual view.

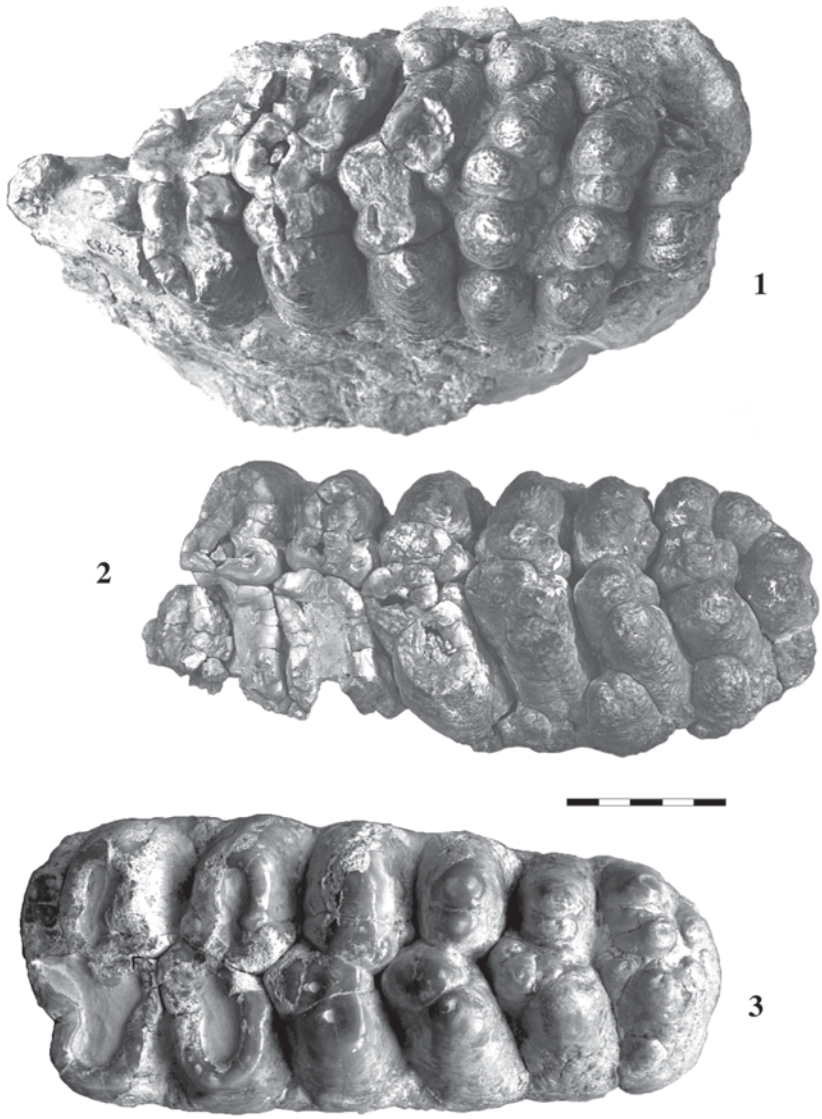

Plate 7

Figs. 1-2. 'Individual 2' of *Tetralophodon* cf. *longirostris* 'grandincisivoid form' from Crevillente 2.
Fig. 1. Rigth M^3 (CR2-S-59), occlusal view.
Fig. 2. Left M^3 (CR2-S-58), occlusal view.

Fig. 3. *Tetralophodon longirostris* from Crevillente 16. Left M^3 (CR16-26), occlusal view.

Scale bar represents 50 mm.

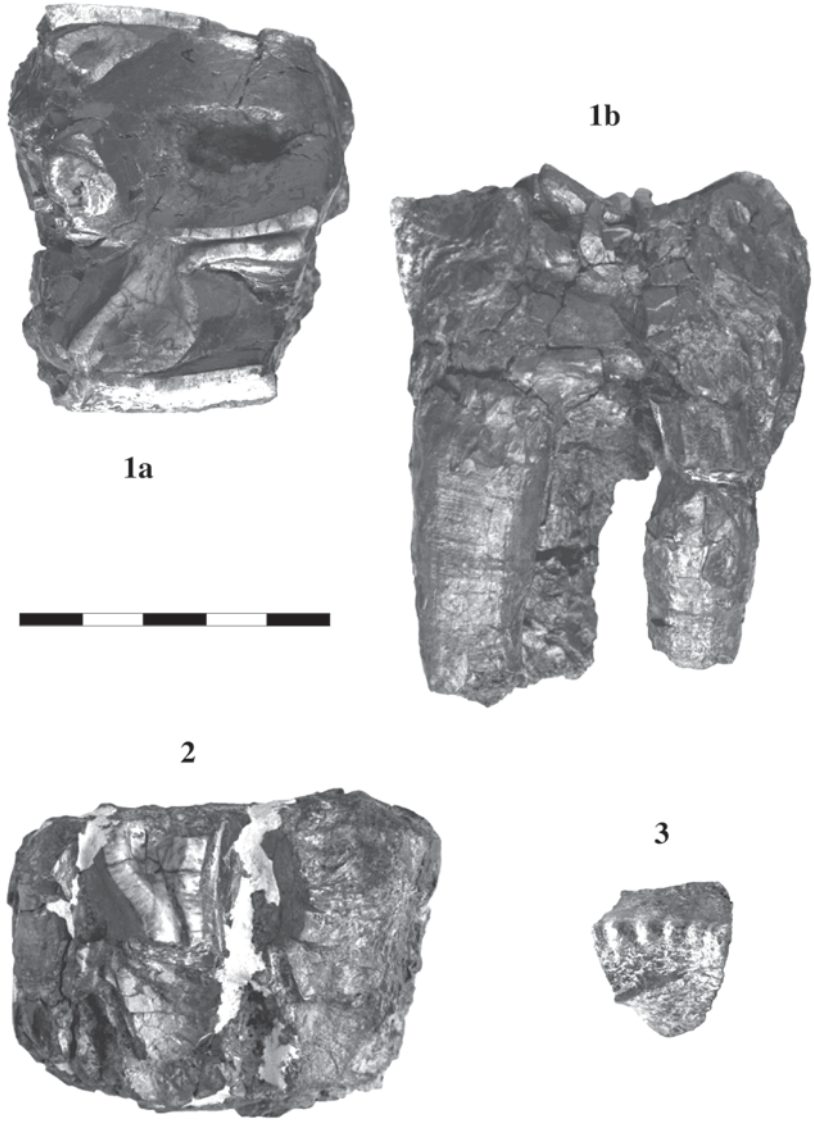

Plate 8

Figs. 1-2. *Deinotherium giganteum* from Crevillente 2.
1: Right P^4 (CR2-530). (a) Occlusal view. (b) Labial view.
2: Right D^4 (CR2-849), occlusal view.

Fig. 3. *Deinotherium* sp. from Crevillente 15. Crown fragment of an indeterminate tooth (CR15-72).

Scale bar represents 50 mm.