

***Mitilanotherium inexpectatum* (Giraffidae, Mammalia) from Huélago (Lower Pleistocene; Guadix-Baza basin, Granada, Spain) - observations on a peculiar biogeographic pattern**

Mitilanotherium inexpectatum (Giraffidae, Mammalia) de Huélago
(Pleistoceno Inferior; Cuenca de Guadix-Baza, Granada, España) –
observaciones acerca de una pauta biogeográfica peculiar

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ABSTRACT

Giraffid fossils from the lowermost Pleistocene (MN17) locality Huélago (Guadix-Baza Basin, Granada, Spain) are described and assigned to *Mitilanotherium inexpectatum* Samson & Radulesco (1966). The remains are compared to giraffid material from the Pliocene and younger. The known geographic distribution of this giraffid is disjunct; it is found in Spain and in an area stretching from Rumania and Greece to Tadjikistan, but not in central Europe. The oldest record is from the Upper Pliocene (MN16) of Turkey and the youngest is from the Lower Pleistocene of Greece (with an estimated age of about 1.2 Ma). Shortly after 2.6 Ma it may have dispersed to Spain, where it may have lived as much as half a million years. The dispersal did not leave a fossil record in the area between SE Europe and Spain. The same occurred with dispersals of other mammals in the Early, Middle and Late Miocene, Pliocene and Pleistocene. These species that show this pattern are interpreted to be adapted to open or arid environments. Their dispersals across Europe to Spain may have occurred during short periods of atypical environmental conditions and thus did not leave an easily detectable fossil record.

Keywords: *Mitilanotherium*, Giraffidae, Pleistocene, biogeography, Strait of Gibraltar

RESUMEN

Los fósiles de jirafas del Pleistoceno basal (MN 17) de la localidad de Huélago (Cuenca de Guadix-Baza, Granada, Spain) son descritos y asignados a *Mitilanotherium inexpectatum* Samson & Radulesco (1966). Los restos fósiles son comparados con jiráfidos del Plioceno, y formas más recientes. La distribución geográfica conocida muestra que es disyunta; encontrándose en España y en un área que se extiende de Rumania y Grecia a Tadjikistan, pero no en Europa central. El registro más antiguo procede del Plioceno Superior (MN 16) de Turquía y el más reciente del Pleistoceno inferior de Grecia (con una edad estimada de ca. 1, 2 Ma). Poco después de los 2,6 Ma la especie pudo haberse dispersado a España, donde como mucho pudo haber durado medio millón de años. Esta dispersión no dejó evidencias en el registro fósil en el área comprendida entre el SE de Europa y España. Lo mismo sucede con la dispersión de otros mamíferos en el Mioceno basal, medio y final, Plioceno y Pleistoceno. Las especies que muestran este patrón se interpretan como adaptadas a ambientes abiertos y áridos. Su dispersión a través de Europa a España pudo haber ocurrido durante periodos cortos de condiciones ambientales atípicas y en consecuencia no dejaron un registro fósil fácilmente detectable.

Palabras clave: *Mitilanotherium*, Giraffidae, Pleistoceno, biogeografía, Estrecho de Gibraltar

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Introduction

Giraffids have an interesting biogeographic history, that reflects some 20 millions of years of geographic and environmental changes in the Old World. Giraffidae are first known from the latest Early Miocene (MN3 equivalent; MN units after De Bruijn *et al.*, 1992, ages of MN units after Agustí *et al.*, 2001) of Africa, the Middle Miocene (MN 4 equivalent) of the Indian Subcontinent and from MN3-4 in Kazakhstan (Harris *et al.*, 2010; Barry & Flynn, 1990; Vislobokova, 1997) and only a little later (MN5, early MN6) they are known from Greece and Turkey (De Bonis *et al.*, 1997; Gentry, 1990). Not much later they also appeared in the north of China (Godina, 1979). From MN9 onwards giraffids appear in western Europe, where they are principally found in Spain (Nieto *et al.*, 1997). During the Late Miocene giraffids were very wide spread and diverse, while during the Early Pliocene they became rare in Eurasia (e.g. Godina, 1979), but remained diverse in Africa (Harris, 1991; Harris *et al.*, 2010). In Spain, the last giraffids are Sivetheriinae from the earliest Pliocene (MN14). In the area around the Black Sea, giraffids are found again in Late Pliocene - Early Pleistocene localities. The latest Eurasian giraffids are either the more robust Sivetheriinae or they generally assigned to *Mitilanotherium*, its synonyms *Macedonitherium* and *Sogdianotherium*, or to *Palaeotragus* (e.g. De Vos *et al.*, 2002; Titov, 2008). During the Pleistocene, giraffids became increasingly restricted to Africa, where they survive with two species.

Given this paleogeographic history, the appearance of Giraffinae in the Early Pleistocene of Spain would thus be unexpected. However, Nieto *et al.* (1997) cited a giraffine from the locality Huélago Carretera and Arribas *et al.* (2001) briefly discussed a giraffid from Fonelas, which they assigned to cf. *Mitilanotherium* sp. The material was described in more detail by Garrido & Arribas (2008), who assigned it to *Mitilanotherium* sp. The Plio-Pleistocene is particularly well known in France and Italy and no giraffids have been found there, nor in Germany, so that the known distribution of this giraffe is disjunct. Kostopoulos & Athanassiou (2005) raised the question whether the Spanish material represents an African immigrant in the Iberian Peninsula (migrating across the Strait of Gibraltar?), while Harris *et al.* (2010) suggested that *Mitilanotherium* might be present in North Africa. It is the aim of the present paper to describe

the giraffid material from Huélago and compare it to the relevant African material in order to classify the material and discuss biogeography.

The locality of Huélago

Huélago is a locality in the Guadix-Baza Basin in the north of the province of Granada in southern Spain. The geology of the basin and sedimentology and fauna from this and some other localities in the area were described in detail in a monograph (Alberdi & Bonadonna, 1989). The faunal list as given in this monograph includes: Testudinae indet., Soricidae indet., Talpidae indet., *Apodemus* sp., *Stephanomys* cf. *balcellsii*, *Castillomys crusafonti crusafonti*, *Mimomys* aff. *plioacaenicus*, *Mimomys cappetai*, *Mimomys* cf. *reidi*, *Prolagus* sp., cf. *Orcytolagus* sp., *Castor* sp., cf. *Mammuthus meridionalis*, *Equus stenonis livenzovensis*, *Dicerorhinus* cf. *etruscus*, *Leptobos* cf. *elatus*, *Gazella borbonica*, *Gazellospira torticornis*, Ovi-bovini indet. (cf. *Hesperidoceras merlae*), *Croizetoceros ramosus*, Cervidae indet. (medium size), *Eucladoceros* cf. *senezensis*.

The oldest record in western Europe of *Equus*, *Mammuthus* and *Eucladoceros* is in sediments with normally polarized palaeomagnetism of the Gauss and an age of around 2.6 Ma, as is the case in El Rincón-1 (Alberdi *et al.*, 1997). The last occurrence of *Gazella* is in a group of localities that have the three taxa mentioned above, but lack the important new appearance of *Canis*, which is first recorded in localities that are assumed to be around 2.1 Ma old, like Senèze (Heintz *et al.*, 1974; Sardella *et al.*, 1998). Together with other localities with *Equus*, *Mammuthus* and *Eucladoceros* and with *Gazella*, Huélago is placed in MN17, or the unit of Saint Vallier and has an age of between some 2.6 and 2.1 Ma.

Classification of the Plio-Pleistocene Giraffidae

There are two predominant trends in the evolution of the limb bones in the Giraffidae. One group tends to have robust limb bones, which is especially well seen in the metapodials. These are classified as Sivetheriinae and in the Plio-Pleistocene they are represented by *Sivatherium*. Another group tends to have long and slender and even extremely long and

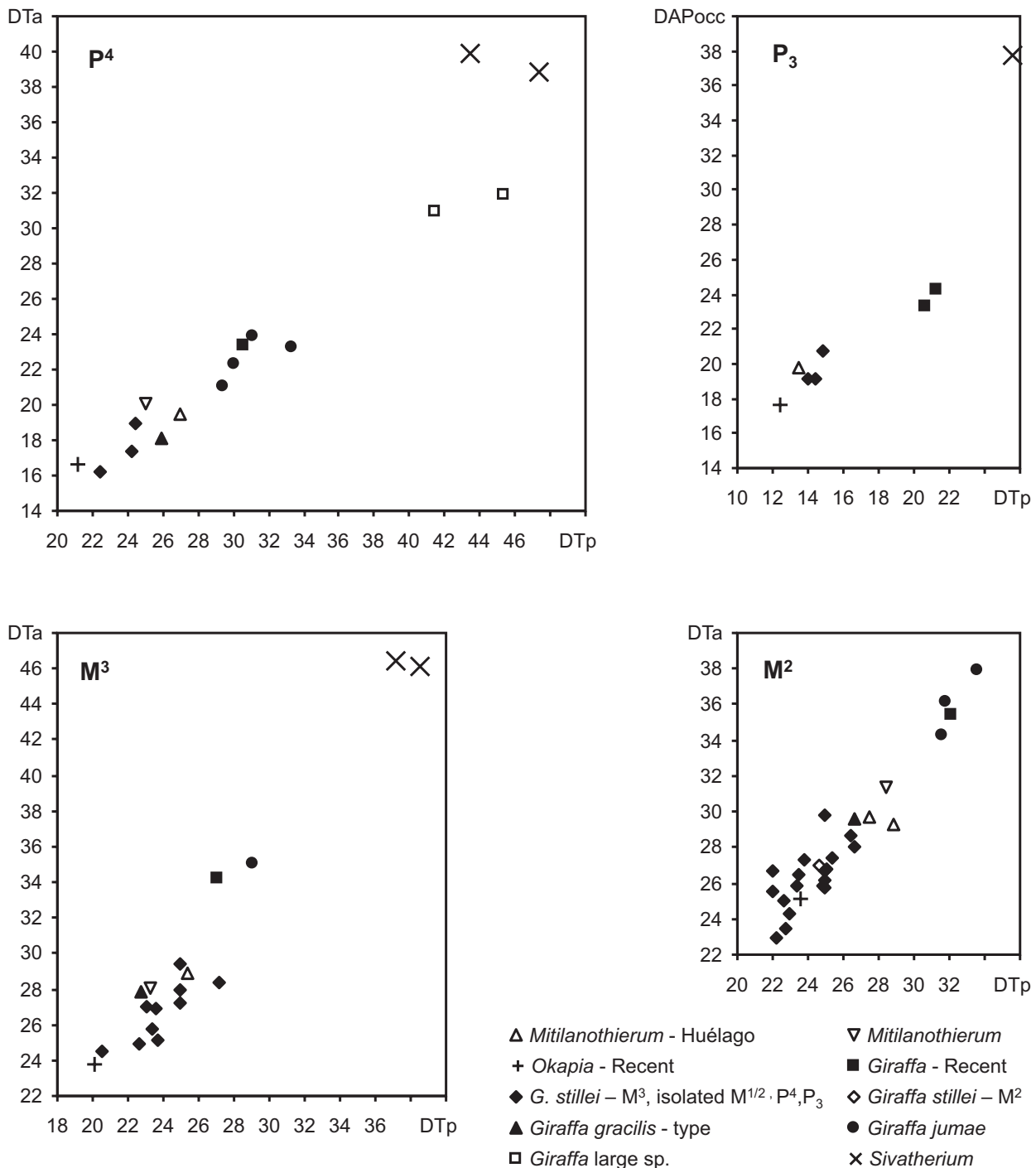


Fig. 1.—Bivariate diagrams of the cheek teeth of *Mitlanotherium* from Huélago (MNCN) and from Dafnero (AUT), recent *Okapia johnstoni* (MNCN), recent *Giraffa camelopardalis* (MNCN, IVAU), *Giraffa stillei* from “Serengeti” (collections described by Dietrich, (1942); MNB), the type material of *Giraffa gracilis* from Omo (MNHN), *Giraffa jumae* from “Serengeti” (MNB), a large *Giraffa* from “Serengeti” (MNB), and *Sivatherium* from “Serengeti” (MNB). In a single tooth row the three upper molars are very close in size and, as a consequence, plain size does not help to identify molar position. Isolated M³ are recognized by a relatively narrow second lobe and the lack of a posterior wear facet. Isolated M¹ and M² are more difficult to separate. For *Giraffa jumae* one of the three specimens is an isolated molar, of which the attribution to M² could be doubted, for *Giraffa stillei* all specimens are isolated, save for one, which is indicated with a different symbol. The P⁴ from Huélago is damaged and the DAP indicated is possibly somewhat too small.

slender limb bones. These are either classified as the two subfamilies Palaeotraginae and Giraffinae, or as a single subfamily, Giraffinae, with the two tribes Giraffini and Palaeotragini. While the attribution of *Giraffa* and *Palaeotragus* is clear, *Okapia* and *Mitilanootherium* have been placed by different authors in either of these tribes or subfamilies, and *Okapia* even in a subfamily of its own.

Various fossil species of *Giraffa* have been described from East Africa: *G. pygmaea*, *G. stillei*, *G. gracilis*, *G. jumae*, and there is the recent *G. camelopardalis* (Dietrich, 1942, Arambourg, 1948, Leakey, *et al*, 1965, Harris, 1991). There are some taxonomic problems and it seems better to discuss these before, than making comparisons of the Huélago specimens to all different species and samples. Harris (1991) was of the opinion that there are three fossil species with different sizes: *G. pygmaea* Harris, 1976; *G. stillei* Dietrich, 1942 (= *G. gracilis* Arambourg, 1948), and *G. jumae* Leakey, 1965. Dietrich (1942) figured many specimens from different localities in the Serengeti, but did not give the measurements of the individual specimens. In his material (MNB), three clearly separated size groups of *Giraffa* can be recognized (Figures 1-2). The largest species may have been confused with *Sivatherium*, but differs clearly in morphology. The smallest species is *G. stillei* and is represented by much material. In Figures 1 and 2, *G. pygmaea* plots in the middle and *G. gracilis* in the upper range of *G. stillei*. All this material might belong to the latter species. Material from Koobi Fora assigned by Harris (1991) to *G. jumae* either plots with *G. stillei* or with the medium sized *Giraffa* from “Serengeti” (Figure 2). *G. jumae* is a relatively large species, close in size to *G. camelopardalis* (Leakey *et al.*, 1965). We assume that the middle sized material from “Serengeti” and Koobi Fora belongs to that species.

Dietrich (1942) described *Giraffa stillei* as a species of *Okapia*, because of its brachydonty and morphology, though he declined to describe the morphology, because he considered it so similar to that of *Okapia*. Harris transferred it to *Giraffa* (Harris, 1976a, 1991). Hampe (2001) insisted in an attribution to *Okapia* and provided a morphological feature in the D_3 to support this. There are many differences between the species “*stillei*” and *O. johnstoni*, and these differences tend to be similarities to the two species of *Giraffa* from the Serengeti, but not always with *G. camelopardalis*. We refrain here from taking part in the debate on the affinities of

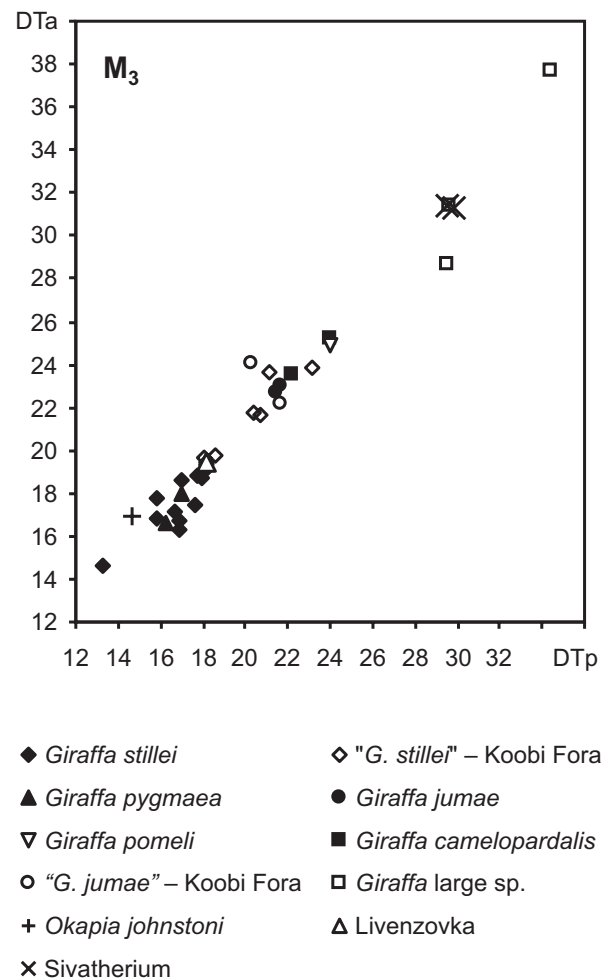


Fig. 2.—Bivariate diagram of the lower third molar (M_3) of: *Giraffa stillei* from “Serengeti” (MNB), “*Giraffa stillei*” from Koobi Fora (Harris, (1991)), “*Giraffa pygmaea*” from Koobi Fora (Harris, (1991)), *Giraffa jumae* from “Serengeti” (MNB), *Giraffa pomeli* type material from Ain Hanech (MNHN), recent *Giraffa camelopardalis* (MNCN, IVAU), “*Giraffa jumae*” from Koobi Fora (Harris, (1991)), *Giraffa large sp.* from “Serengeti” (MNB), recent *Okapia johnstoni* (MNCN), “*Palaeotragus (Yuurlovia) priasovicus*” from Livenzovka (RRM), and *Sivatherium* from “Serengeti” (MNB).

“*stillei*”, but treat it as *Giraffa* in the morphological comparisons.

Most authors who studied *Mitilanootherium* classified it in the Palaeotraginae (or Palaeotragini within the Giraffinae) (Sickenberg, 1967; Sharapov, 1974; Godina & Baygusheva, 1986; Solounias, 2007; Garrido & Arribas, 2008) and we follow this classification. *Macedonitherium* and *Sogdianotherium* are now considered to be synonyms of *Mitilanootherium*; some authors believe *M. martinii* to be a synonym of *M. inexpectatum*, while others maintain it provision-

ally as a separate species (De Vos *et al.*, 2002; Kostopoulos & Athanassiou, 2005; Garrido & Arribas, 2008). The latter species is the type species of *Mitilanothereum* and was described from the Early Pleistocene of Rumania (Samson & Radulescu, 1966).

Arambourg (1979) named *Giraffa? pomeli* on the basis of material from Ain Hanech and included also specimens from Ain Brimba, but expressed doubts as to whether the species could be a late survivor of the genus *Palaeotragus*. Geraads (1981) assigned material from Tighenif (Ternifine) to the same species, noted the short metatarsal and expressed also doubts as to the generic affinities. More recently, Harris *et al.* (2010) suggested that the species could be a late survivor of the Palaeotraginae and belong to *Mitilanothereum*. Geraads (1986) assigned two teeth from Ubeidiya to Giraffidae gen. et sp. indet., and noted similarities of one of the specimens to a tooth from Tighenif, he previously assigned to "*Giraffa*" *pomeli* (Geraads, 1981) and suggested that the teeth might belong to the Palaeotraginae. This material is of a middle sized giraffe comparable to *G. camelopardalis* and *G. jumae* and may well belong to a single species, which we here indicate as *Giraffa? pomeli*.

Collections

The material described here is kept in the Museo Nacional de Ciencias Naturales in Madrid. Where in this text reference is made to material studied for comparison, the collection is indicated by its abbreviation.

- AUT Aristotle University of Thessaloniki.
- GSM Georgian State Museum, Tbilisi.
- MNCN Museo Nacional de Ciencias Naturales, Madrid.
- MNHN Muséum National d'Histoire Naturelle, Paris.
- NHCV Natural History Collection of Vrísssa (Lesbos, Greece).
- NUA National and Kapodistrian University of Athens.
- RRM Rostov Regional Museum, Rostov-on-Don.
- TUC Technische Universität Clausthal, Insitut für Geologie und Paläontologie

Measurements and nomenclature

All measurements are given in mm. They are indicated as: DAPbas = antero-posterior diameter or length, measured at the base of the crown; DAPocc = antero-posterior diameter or length, measured at the occlusal surface; DTa = transverse diameter of the anterior lobe; DTp = transverse diameter of the posterior lobe.

In the descriptions, common dental nomenclature is used, and occasionally a more precise nomenclature for certain morphological elements (Van der Made, 1996).

Systematic description

- Family Giraffidae Gray, 1821
- Subfamily Giraffinae Gray, 1821
- Tribe Palaeotragini Pilgrim, 1911
- Genus *Mitilanothereum* Samson & Radulesco 1966

Synonymy

- Macedonitherium* Sickenberg, 1967.
- Sogdianotherium* Sharapov, 1974.

Mitilanothereum inexpectatum Samson & Radulesco, 1966

Synonymy

- 1966 *Mitilanothereum inexpectatum*, n. sp. - Samson & Radulesco: 589-594; Fig. 1.
- 1967 *Macedonitherium martinii* nov. gen. nov. spec. - Sickenberg: 314-330; Pl. 1, fig. 1; Pl. 2, figs. 1-5.
- 1971 *Macedonitherium* - Sickenberg & Tobien: 60.
- 1974 *Sogdianotherium kuruksaense* n. gen. n. sp. - Sharapov: 517-521, Figs 1-2.
- 1975 *Macedonitherium martinii* - Becker-Platen, Sickenberg & Tobien: 43.
- ?1986 *Palaeotragus (Yuorlovia) priasovicus* n.sp. - Godina & Baygusheva: 68-72, Fig. 1 a-i.
- 1986 *Macedonitherium martinii* Sickenberg - Godina & Baygusheva: 72.
- 1986 *Mitilanothereum inexpectatum* Samson et Radulescu - Godina & Baygusheva: 72.
- 1986 *Sogdianotherium kuruksaense* Sharapov, 1974 - Sharapov: 163-171, Figs. 48-51.
- 1986 *Macedonitherium martinii* - Van der Meulen & Van Kolfshoten: Fig. 3.
- 1988 *Macedonitherium martinii* SICKENBERG, 1967 - Steensma: 228-231, 234, Fig. 77, Pl. 10, figs 1-3.
- 1988 Palaeotraginae gen. et sp. indet. - Steensma: 231-233, Pl. 10, fig. 4.
- ?1988 Giraffidae gen. et sp. indet. - Steensma: 233-234, Pl. 10, fig. 5.
- 1988 *Mitilanothereum inexpectatum* - Steensma: 234, Tab. 40.
- 1996 cf. *Macedonitherium martinii* SICKENBERG, 1967 - Athanassiou: 95-105, 332, Fig. 43.
- 1996 *Mitilanothereum inexpectatum* - Athanassiou: 99-105.
- 1996 *Mitilanothereum martinii* (Sickenberg, 1967) - Kostopoulos: 44-61, Pl. 1, figs. 1-4.
- 1997 Giraffinae indet. - Nieto *et al.*: 137-138.
- 2001 Giraffidae cf. *Mitilanothereum* sp. - Arribas *et al.*: 17 & 22-23; Plate 2, fig. 2.

- 2002 *Mitilanothereum* cf. *inexpectatum* Samson & Radulesco, 1966 - De Vos *et al.*: 45-47.
- 2005 *Mitilanothereum inexpectatum* SAMSON & RADULESO, 1966 - Kostopoulos & Athanassiou: 186-188.
- 2005 *Mitilanothereum martinii* (SICKENBERG, 1967) - Kostopoulos & Athanassiou: 186-188, Figs 8-9.
- 2005 *M. kuruksaense* - Kostopoulos & Athanassiou: 188.
- ?2005 *Palaeotragus priasovicus* - Kostopoulos & Athanassiou: 187-188.
- ?2007 *Palaeotragus* sp. - Lordkipanidze *et al.*: Supplementary information 3-4, Table S1.
- 2008 *Mitilanothereum* sp. - Garrido & Arribas: 397-411, Figs 1-4, 8.
- 2008 *Mitilanothereum martinii* - Garrido & Arribas: 397-411, Fig. 7.
- ?2008 *Palaeotragus (Yurlovina) priasovicus* Godina et Baigusheva, 1985 - Titov: 147-150, 229-230, Figs. 66-67, Pl. 10, figs 1-2, Pl. 11, figs. 1-6.

Material

HC92, 8	left P ₃	DAPocc = 19.8; DAPbas = 19.5; DTa = 12.6; DTp = 13.5
HC85, B-18	right M ²	DAPocc = 30.8; DAPbas = 28.9; DTa = 29.7; DTp = 27.5
HC85, C-37	right M ³	DAPocc = 28.7; DAPbas = 25.8; DTa = 28.9; DTp = 25.4
HC85, C-38	left M ²	DAPocc = 30.7; DAPbas = 30.0; DTa = 29.3; DTp = 28.8
HC85, C-36	right P ⁴	DAPocc > 20.0; DAPbas = 18.2; DT = 24.9
HC85, C-37	right P ⁴	DAPocc ≥ 18.9; DAPbas = 18.1; DT = —

Description and comparison

Both M² (Figure 3, figs 1 & 4) have the same structure. The teeth are selenodont. The paracone and metacone and their crests form a continuous buccal wall, but the surface of the second lobe sticks out more buccally. The buccal side of the protocone has a clear vertical ridge (protoexocrista), but in the buccal surface of the metacone is nearly flat. The mesostyle is well developed, but does not become much larger towards its base, and the parastyle is even more developed, while the metastyle is the weakest, which is moreover partially worn by contact with the M³. The protocone has two crests forming a crescent shape. The posterior one (the protoendocrista) ends close to the mesostyle, but without reaching the buccal wall of the tooth, while the anterior one (protoprecrista) fuses with the parastyle. The metaconule (or tetracone) is also crescent shaped and its anterior crest (tetraprecrista) approaches the buccal wall of the tooth (near the end of the parapostcrista), without really connecting. The posterior crest (tetrapostcrista) ends close to the buccal wall on the posterior side of the tooth. The anterior fossa is open posteriorly and the posterior fossa is open both anteriorly and posteriorly. The enamel is coarsely rugose. The crowns are worn, but were probably not very high.

The morphology of the M² from Huélago is unlike in bovids, where the crests of the lingual cusps fuse to the buccal wall of the tooth, so that the fossas are closed. The height of the crowns must have been far less than in bovids, possibly excepting the most primitive and early species. There is no well developed cingulum or interlobular collumn on the lingual side, which is unlike in cervids. This tooth morphology occurs in Giraffidae. The M² from Huélago are close in size to the specimen from Dafneró and are clearly larger than in *Okapia*, only slightly larger than in *Giraffa gracilis* and *Giraffa stillei*, but clearly smaller than *Giraffa jumae* and *Giraffa camelopardalis* (Figure 3). *Giraffa stillei* (Figure 3, fig. 11) and the other species of *Giraffa* tend to have the anterior and posterior crests of the lingual cusps with additional crests or folds of the enamel in the fossas, the relief on the buccal wall is much more pronounced and a buccal cingulum tends to be more developed, the mesostyle becomes much wider near the base, the crowns were probably lower and the fusion of the posterior crest of the paracone and the anterior crest of the metacone occurs much lower and even in worn molars the buccal wall may be interrupted here. *Mitilanothereum* from Dafneró (NUA) has a morphology that is similar to the specimens from Huélago.

The M³ (Figure 3, fig. 3) has an anterior wear facet that fits a posterior wear facet on the right M², suggesting that both teeth belong to the same individual. The structure is similar to that of the M², but the second lobe is narrower. Due to lesser wear, the anterior crest of the protocone (protoprecrista) is not yet fused to the parastyle and the anterior fossa opens on the anterior side of the tooth. The anterior crest of the metaconule (tetraprecrista) is directed antero-buccally and ends well anterior of the middle of the tooth (unlike in the M², where it ends close to the middle).

In the M³, the same morphological differences between the material from Huélago and *Giraffa* are noted as in the M². Again, *Mitilanothereum* from Dafneró (NUA) has a similar morphology and is close in size (Figure 3).

The P⁴ (Figure 3, figs. 5 & 6) is selenodont, low crowned and has coarsely rugose enamel, like the molars. The paracone is very well marked on the buccal side of the tooth (paraexocrista). This is the part of the tooth that protrudes most buccally, whereas the anterior and posterior styles are not particularly well developed. The protocone is crescent shaped and the anterior crest (protoprecrista) becomes very low and thin before reaching the buccal side of the tooth, leaving the fossa open on the anterior side of the tooth, though with much wear the fossa would be closed. Seen from the buccal side, the tooth is not very a-symmetrical.

In the P⁴ of bovids and cervids, the anterior and posterior styles reach further buccally than the base of the paracone, while in giraffids it is common (but not universal) that the paracone protrudes more. A fossa that opens anteriorly is unlike in bovids and cervids. Seen from the buccal side, the P⁴ of bovids and cervids tend to be markedly a-symmetrical. The relief on the buccal side is much less than in *Giraffa stillei* (Figure 3, figs 10 & 12) and other *Giraffa*, and the styles are less developed and the crescent shape of the protocone is more developed. *Mitilanothereum* from Dafneró (NUA) has a P⁴ with a similar morphology (open fossa, large paraexocrista, small buccal styles) and is close in size (Figure 3). A specimen of *Mitilanothereum* from Libakos (TUC) is not included in Figure 2, because of damage, but is close in size to the specimens from Huélago and Dafneró.

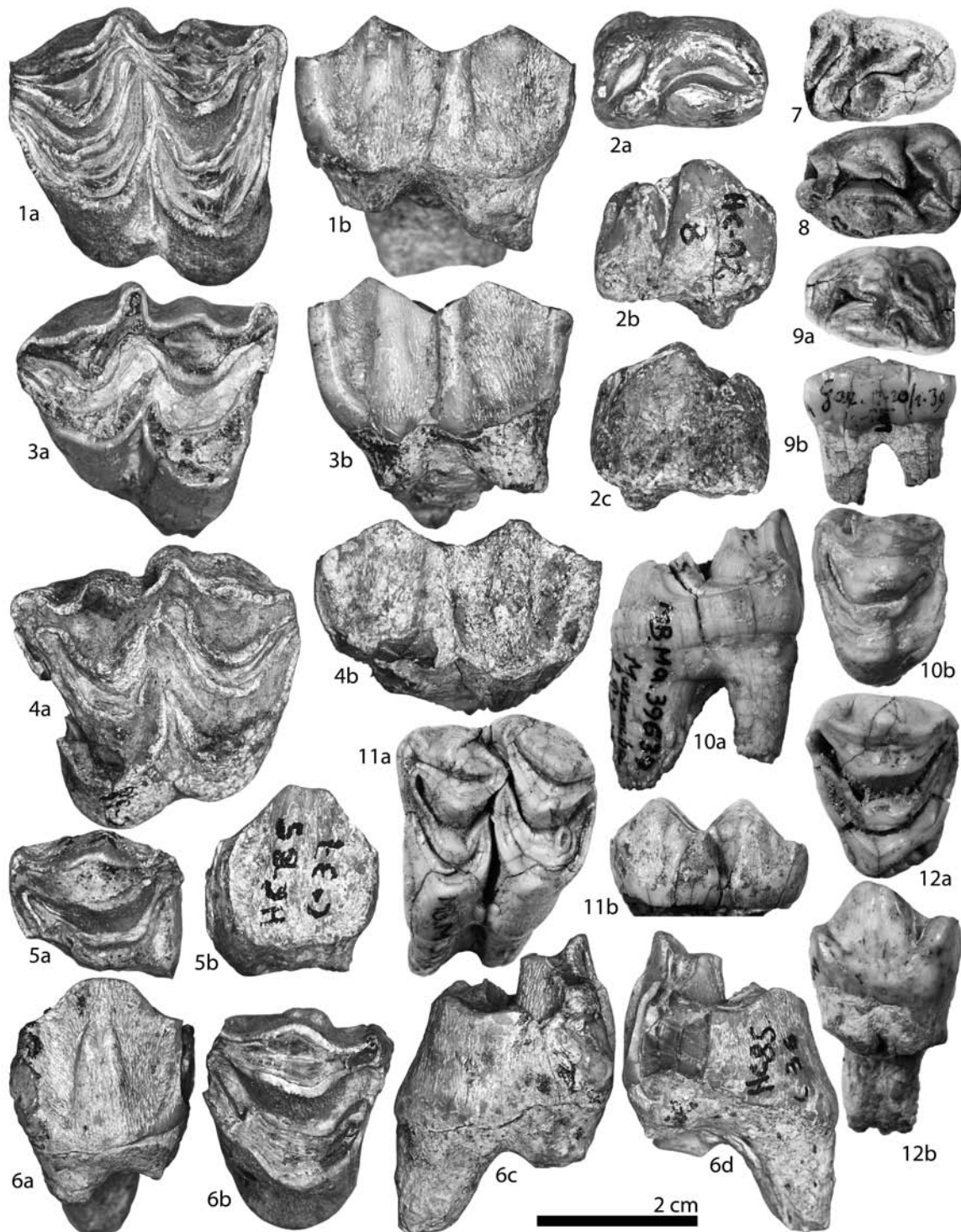


Fig. 3.— *Mitilanotherium inexpectatum* from Huélago (MNCN): 1) HC85, B-18 - right M², occlusal (a) and buccal (b) views. 2) HC92, 8 - left P_{3/4} (P₃?), occlusal (a), lingual (b) and buccal (c) views. 3) HC85, C-37 - right M³, occlusal (a) and buccal (b) views. 4) HC85, C-38 - left M⁴ (M²?), occlusal (a) and buccal (b) views. 5) HC85, C-37 - right P⁴, occlusal (a) and buccal (b) views. 6) HC85, C-36 - right P⁴, buccal (a), occlusal (b), posterior (c) and anterior (d) views; *Giraffa stillei* from "Serengeti": 7) MB.Ma 39728 - left P₃ from Deturi East, occlusal view. 8) MB.Ma 39074 - right P₃ from Garussi, occlusal view. 9) MB.Ma 39734 - right P₃ from Garussi, occlusal view (a), lingual view (b). 10) MB.Ma 39623 - left P⁴ from the Vogelfluss area, posterior (a) and occlusal (b) views. 11) MB.Ma 39784 - left M^{1/2} from the Vogelfluss area, occlusal (a) and buccal (b) views. 12) MB.Ma 39639 - left P⁴ from Maramba west, occlusal (a) and buccal (b) views.

The P_3 (Figure 3, fig. 2) is a small tooth, too small to occlude with the P^4 and therefore it is a P_3 and not a P_4 . Like the previously described teeth it is selenodont. The protocone has simple anterior and posterior crests, that are not bifurcated. By its posterior crest, it is connected to the entoconid, but it is not connected to the hypoconid. The anterior extreme of the anterior crest meets and fuses to the anterior crest of the metaconid. There is no transverse connection between protoconid and metaconid. The anterior fossid opens posteriorly on the lingual wall of the tooth. The hypoconid has a posterior crest reaching the lingual side of the tooth. Anteriorly the hypoconid connects with the posterior crest of the protoconid, but this occurs well below its tip.

Given that the tooth is a P_3 and not a P_4 , its large metaconid would be uncommon in cervids and bovids, but is normal in giraffids. The lack of a transverse connection between protoconid and metaconid is also common in giraffids. The specimen from Huélago differs from *Giraffa stillei* (Figure 3, figs 7-9) and other species of *Giraffa* in that: the cusps and crests appear to be more slender and higher, the anterior crest of the metaconid reaches further anterior, and the anterior crest of the protoconid is not curved fully lingually at its anterior end. As with the previously described teeth, the specimen has a size close to *Giraffa stillei* (Figure 3). The premolars of *Giraffa camelopardalis* tend to be relatively wider than those of the other species, including the species from Huélago. No P_3 of *Mitilanotherium* has been described yet, so a comparison cannot be made.

Discussion

As appears from the description the dentition from Huélago has the following characters, which are typical of the family Giraffidae: crests of the lingual cusps of the upper cheek teeth often fail to fuse to the buccal wall of the tooth, low crowns, strongly crenelated enamel, P^4 symmetrical in buccal view, the lack of a transverse connection of the metaconid and protoconid in the P_3 .

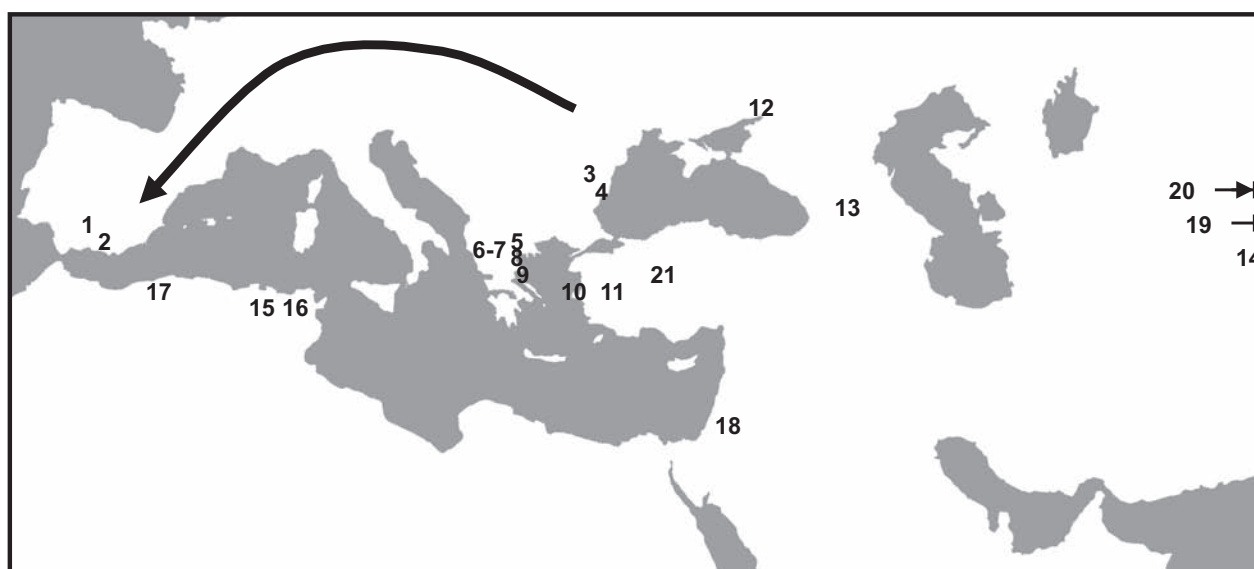
Sivatherium is a large form (Figures 2 & 3), larger than the giraffe from Huélago, and is more hypsodont than the other giraffids. The material from Huélago is smaller than *Giraffa jumae*, *G. camelopardalis* and the large *Giraffa*, but it is close in size to *G. stillei*. In the description, numerous morphological differences between the material from Huélago and *Giraffa*, and in particular *Giraffa stillei*, are mentioned. Due to the scarcity of the material morphological comparisons with *Giraffa? pomeli* are limited, but the M_3 from Ain Hanech is in the upper range of the middle sized giraffes, such as *G. jumae* and *G. camelopardalis* (Figure 2) and is much larger than *Mitilanotherium inexpectatum*, which is in the upper range of the small sized giraffes (Figure 1). Also the material from Tighenif is middle sized. If

Giraffa? pomeli turns out to belong to *Mitilanotherium* (or another palaeotragine), it is likely to belong to a different and larger species than the species of Huélago.

The material from Huélago differs from *Okapia johnstoni* in the shape of the P_3 , with a flat metaconid with pronounced anterior and posterior crests, closing the anterior fossid anteriorly, whereas the *Okapia* in the MNCN (no. 5226) has a P_3 with a rounded and backwards placed metaconid, that leaves the fossid wide open anteriorly. The morphology of the P_3 from Huélago is close to that of the Early Pliocene *Palaeotragus microdon* (Bohlin, 1926, Pl. 3, fig. 4), though the variability in this tooth is high (Bohlin, 1926; Morales & Soria, 1981).

As noted above, the upper dentition from Huélago has many similarities to a maxilla from Dafneró attributed to *Mitilanotherium martinii* (Athanasios, 1996; Kostopoulos, 1996; Kostopoulos & Athanasios, 2005), but also with the upper dentition of the type of *Sogdianotherium kuruksaense* from the Early Pleistocene of Kuruksai (Sharapov, 1974, 1986). Both are included here in *M. inexpectatum*, which occurs in a number of localities (see synonymy and Figures 4 & 5), but is never represented by abundant material. In fact differences in size and morphology are small, and at present these differences can be explained by individual variability so that there is no firm ground to recognize more than a single species. We assign the material from Huélago to *Mitilanotherium inexpectatum* Samson & Radulesco, 1966.

Palaeotragus priasovicus Godina & Baygusheva, 1985 is based on material from Livenzovka. The authors noted already similarities with *Mitilanotherium inexpectatum*, and suggested that the latter species might belong to *Palaeotragus*. The generic identity is indeed a general question which needs to be addressed. A direct comparison of the teeth of *P. priasovicus* with the specimens from Huélago cannot be made, since there are no common elements. However the M_3 from Livenzovka is in the upper ranges of *G. stillei* (Figure 2) and suggests thus an animal of similar size as *Mitilanotherium inexpectatum*. This is confirmed by the comparable limb bones. These giraffids are rare and it is unexpected to find in the same area and time two species of the same size of which no morphological differences are known. *Palaeotragus* was also cited from Dmanisi (Lordkipanidze *et al.*, 2007).



<i>Mitlanotherium inexpectatum</i>		<i>Giraffa? pomeli</i>	<i>Palaeotragus</i> sp.
1 Huélago	8 Vólax	15 Tighenif (Ternifine)	19 Esekartan
2 Fonelas	9 Seskló	16 Ain Hanech	20 Beregovaya
3 Fîntîna lui Mitilan	10 Vathera	17 Ain Brimba	
4 Valea Grăunceanului	11 Gülyazı	18 Ubeidiya	
5 Dafneró 1	12 Livenzovka		
6 Libakos	13 Dmanisi	<i>Giraffa jumae</i>	
7 Q-Profil	14 Kuruksai	21 Çalta	

Fig. 4.—Geographic position of the localities with *Mitlanotherium inexpectatum*, *Giraffa? pomeli*, the latest *Palaeotragus* and of a locality with *Giraffa jumae* outside Africa.

The distribution of *Mitlanotherium* in a wider biogeographic context

Present evidence suggests that *Mitlanotherium inexpectatum* was restricted to Kazakhstan, Russia, Georgia, Anatolia, Greece, Rumania on the one hand and Spain on the other (Figure 4). Qiu *et al.* (1999) exhaustively listed the Chinese Pleistocene mammals and indicated their general stratigraphic distribution, but do not mention Giraffidae, which suggests that *Mitlanotherium* did not extend its range into eastern Asia. It is probably the disjunct distribution of *Mitlanotherium*, that lead Kostopoulos & Athanassiou (2005) to suggest that the Spanish giraffid might be a descendant of an African species, rather than the same species as *Mitlanotherium inexpectatum*, which is present in SE Europe.

This remark makes sense only if one thinks of a dispersal across the Strait of Gibraltar, especially if it is combined with the suggestion of Harris *et al.* (2010) that the North African *Giraffa? pomeli* belongs to *Mitlanotherium*. Therefore it is not only necessary to discuss morphology and phylogenetic relationships, but also certain general aspects of long distance dispersal.

Figure 5 gives the approximate stratigraphic position of the localities. Libakos and the nearby “Q-Profil” have *Hippopotamus* and thus could be younger than about 1.2 Ma. It should be noted that claims for European *Hippopotamus* older than 1.2 Ma are not universally accepted. The bulk of the localities belong to MN17. It is noteworthy that several new arrivals, including that of *Canis*, suggest that Fonelas belongs to a younger faunal unit

than Huélago, suggesting a prolonged presence of *Mitilanothereium* in Spain, possibly even over 0.5 Ma. The locality of Gülyazi is the oldest, since it has *Hipparion*, but no *Equus* (Van der Meulen & Van Kolfschoten, 1986), and thus belongs to MN16.

Figures 4 and 5 give also the temporal distribution of the material attributed to *Giraffa? pomeli*. The temporal range is similar to that of *M. inexpectatum*. Above it was concluded already that the material from Huélago belongs to a different species than *G.? pomeli*, but this does not exclude the possibility that it is a descendant of the latter. If *G.? pomeli* would be a palaeotragine and the Spanish giraffe would be a descendant of *G.? pomeli*, that crossed the Strait of Gibraltar, there would be a remarkable convergence with *M. inexpectatum* in that it dwarfed exactly to the same size. This model requires thus the explanation of a dispersal and a convergent evolution, whereas in the model in which the Spanish giraffid is the same species as in SE Europe, only a dispersal has to be explained. The latter model is thus more parsimonious.

From the description and comparison of the material, it is clear that the Spanish material is different from *Giraffa*, including *Giraffa stillei*, and *Okapia*, so these do not provide links to Africa. Dispersals across the Strait of Gibraltar are easily evoked to “solve” a biogeographic problem. However, the study of insular faunas helps to establish the capacities of different types of mammals to cross sea barriers, and this suggests that but few species may have been able to cross the Strait of Gibraltar during the Early Pleistocene (Van der Made, 2005). Also from this point of view it seems justified to assume that the Spanish giraffids did not cross the Strait of Gibraltar.

Where could *Mitilanothereium inexpectatum* have originated? Apart from *Mitilanothereium*, the latest Palaeotraginae belong to the genus *Palaeotragus* and are from the Early and Middle Pliocene of Asia (Godina, 1979; Sotnikova *et al.*, 1997; Vislobokova, 2008; Figure 5) and from the latest Miocene of Africa (Harris *et al.*, 2010). Palaeotraginae became rare in the Pliocene, though there is a poor but continuous record in Asia, while in Africa there is a hiatus of a duration of 2 Ma or more (Figure 5). With the present data, it seems thus more likely that *Mitilanothereium* originated in Asia, and if *Giraffa? pomeli* is a Palaeotragine, or even a *Mitilanothereium*, it also might have originated in Asia.

How to explain that *M. inexpectatum* dispersed from SE Europe to Spain, without leaving a fossil record in the intermediate areas?

The disjunct distribution pattern of *Mitilanothereium*, with Spain being isolated from the rest of the area of distribution, is repeated in other giraffids. For instance in *Decennatherium*, which is found in Spain in Los Valles de Fuentidueña, Nombrevilla, Matillas and La Roma 2 (MN9-10) and in Greece and Turkey in Ravin des Zouaves, Vathylakkos 3, Ravin x, Pikermi, Samos, Veles and Kayadibi (Montoya & Morales, 1991), but not in the intermediate areas. It is also the case in the Turolian bovids *Protoryx*, *Palaeoryx* and *Hispanodorcas* (Van der Made *et al.*, 2006). The Early Miocene giraffoids *Teruelia* and *Lorancameryx* arrived probably by dispersal in Spain, since there is no anterior giraffoid record there, and did not leave a fossil record in central Europe or France (Morales *et al.*, 1993; Moyà Solà, 1987). The rhinoceros *Hispanotherium* appeared in Spain in MN5, but is also found in Turkey and northern China (Antoine, 2002; Deng, 2003). The palaeochoerid *Schizochocerus* was present in SE Europe and Anatolia from MN6 to MN9 or MN10 and appeared early in MN10 in Spain (Van der Made, 1997, 2010a). Outside Africa, *Theropithecus* is known from Spain, the Indian Subcontinent and probably from Israel (Belmaker, 2003), while the occurrence in Italy is under discussion (Hughes *et al.*, 2008). The distribution pattern of this monkey suggests a dispersal from the Middle East through Europe, where it may have left no fossil record, to Spain. This list of taxa with the same disjunct distribution is far from exhaustive and shows that the case of *Mitilanothereium* is not unique.

In those cases where dental or locomotory adaptations can be studied, they suggest that the taxa with these distributions lived in arid or open environments, they are found with other fossil taxa that have such adaptations and when close living relatives are known, these live in such environments. The palaeodistributions of all these taxa coincide with the present arid or open environments.

From the beginning of their history giraffids tend to be larger than other contemporary ruminants. Their large size (and in many cases their long legs) allow them to cover large distances, which in turn allows them to forage far away from drinking water; whereas wildebeest and zebra forage up to 15-20 km away from drinking water, giraffes do this 30-35 km away (Western, 1975). Giraffids tend

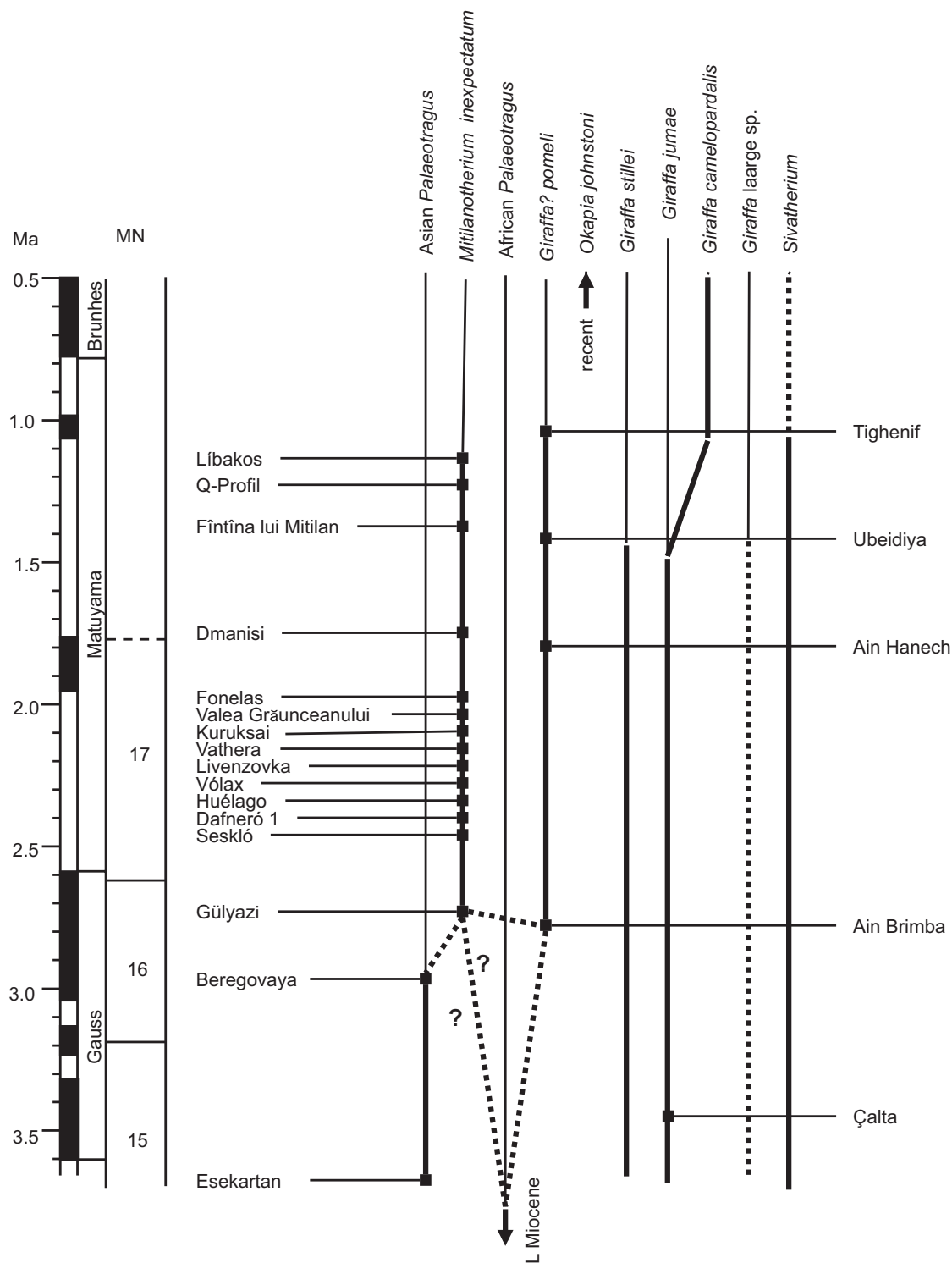


Fig. 5.—Approximate ages of the localities with *Mitilanotherium inexpectatum* and *Giraffa? pomeli* and of a locality with *Giraffa jumae* outside Africa, as well as the temporal ranges of the giraffids mentioned in the text. The left part of the figure gives the time scale in millions of years (Ma) and the ages of the MN units after Agustí *et al.* (2001). The ages of the North African localities were extensively discussed by Sahnouni & Van der Made (2009). The position of Esekartan is placed on paleomagnetism (Sotnikova *et al.* 1997) and of Beregovaya on biostratigraphy (Vislobokova, 2008). *Okapia johnstoni* is only known as a living species and the last African *Palaeotragus* are Late Miocene (both outside the graph). Solid squares indicate presence of taxa in the localities and open squares indicate possible presence (aff., cf. or ?).

to be browsers and save for the Sivatheriinae, they have relatively long legs, which give them access to food at heights that are not accessible to other ungulates. In arid environments, where drinking water and food are sparsely distributed, giraffids have an advantage over smaller ruminants.

The distribution of the giraffoidea seems very much restricted to areas that at present are arid or have more or less open landscapes. The same was observed for Camelidae (Van der Made *et al.*, 2002) and a similar phenomenon was noted for the distributions of animals that need humid or closed environments, such as Talpidae, Tapiridae, Cervidae, Castoridae and *Anchitherium* (Van der Made, 1992, 2010b). These long-standing biogeographic patterns suggest that the arid belt that at present stretches from the Sahara over the Middle East to arid central Asia, existed at least from early Middle Miocene onwards, though probably not always with the extend and same degree of aridity. Mid-latitude Europe may have had more humid or closed environments, limiting the distribution of taxa adapted to dry or closed environments. Some of these, after being limited during millions of years, finally dispersed from SE Europe into Europe (Van der Made & Mateos, 2010). Spain is peculiar in that it is more arid than the rest of western and central Europe and disconnected from the other arid areas. This is seen also in the giraffoid record, giraffoids are known from Spain and the area around the Black Sea, but tend to be rare in the area in between.

So if the giraffids and other mammals with disjunct distributions in Spain and SE Europe, were adapted to arid or open environments, how did they get through a large part of Europe where apparently humid or closed environments were dominant, without leaving a fossil record?. A possible answer to that question is that climatic changes may have caused very short periods of slightly more favorable conditions for these animals in central Europe. The idea is similar, but not identical to the Traffic Light Model of Vrba (1995), who proposed that the time lag between rising temperatures and rising sea level after a glaciation might create short term conditions favoring out of Africa and into Eurasia. Some situation resulting from a time lag between two processes, most likely climatic change and its vegetational response, and inherently of geologically very short duration, may have been the cause for the dispersals of SE European species to Spain, that did not leave a fossil record in the intermediate areas. Such conditions of very short dura-

tion may have allowed these taxa to live in larger parts of Europe, where they usually did not live. Moreover, the conditions may have been not optimal, resulting in lesser population densities than in optimal conditions. The short duration and lower population densities may have resulted in an apparent lack of fossil record of mammals, explaining why no fossils are found in central Europe of animals like *Lorancameryx*, *Hispanotherium*, *Protoryx*, *Decennatherium* and *Mitilanootherium*, which must have moved through this area in order to reach Spain.

From 2.7-2.5 Ma onward, the 40 ka obliquity Milankovich cycle had a stronger effect on the climate of mid- and high latitudes (Shackleton, 1995; deMenocal, 1995), resulting in the first major glaciations on the Northern hemisphere. This had a major effect on flora and fauna, leading to extinctions in Europe of plants like *Magnolia* and animals like *Tapirus*. Another type of effect is that many long distance dispersals occurred: *Equus* spread from America into the Old World, *Mammuthus* spread into mid-latitudes. Biogeography changed: deer and lagomorphs entered the Indian Subcontinent, where they were previously absent (Colbert, 1935; Hussain *et al.*, 1992). *Mitilanootherium* appeared some time after this in Spain. It is possible that its dispersal is related to environmental change due to glacial cycles.

After a glaciation, temperatures rise rapidly, but the recolonisation of mid-latitude Europe by trees out of their southern refuge areas lags behind. For instance, Eemian pollen profiles start with herbs and show a sequence of different tree species arriving, resulting in a sequence of periods with different vegetation. These periods have durations on the scale of a thousand years. The chance of finding a fossil fauna of exactly such a period, which moreover contains identifiable remains of a rare species, is small.

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