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

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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 Tadzhikistan, 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 occured 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

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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 Brujin *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 widespread 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 Sivatheriinae 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 Sivatheriinae or they generally assigned to Mitilianotherium, its synonyms Macedonitherium and Sogdianotherium, or to Palaeocerotidae (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 giraffe from the locality Huélago Carretera and Arribas *et al.* (2001) briefly discussed a giraffid from Fonelas, which they assigned to *Mitilianotherium* sp. The material was described in more detail by Garrido & Arribas (2008), who assigned it to *Mitilianotherium* 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 *Mitilianotherium* 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: Testudinidae indet., Soricidae indet., Talpidae indet., Apodemus sp., Stephanomys cf. balcellsi, Castillomys crusanfonti crusanfonti, Mimomys aff. ploicaenicus, Mimomys cappaet, Mimomys cf. reidi, Prolagus sp., cf. Orcytolagus sp, Castor sp., cf. Mammutthus meridionalis, Equus stenonis livenzovensis, Dicerorhinus cf. etruscus, Leptobos cf. elatus, Gazella borbonica, Gazelllospira torticornis, Ovibovini indet. (cf. Hesperidoceras merlae), Croizetocros ramosus, Cervidae indet. (medium size), Eucladoceros cf. senezensis.

The oldest record in western Europe of *Equus, Mammutthus* 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-I (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, Mammutthus* 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 Sivatheriinae 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 *Mitilanotherium* 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 *Mitilanotherium* 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 D1 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 “*stillei*”, but treat it as *Giraffa* in the morphological comparisons.

Most authors who studied *Mitilanotherium* classified it in the Palaeotraginae (or Palaeotragini within the Giraffinae) (Sickenberg, 1967; Sharapov, 1974; Godina & Bagushcheva, 1986; Solounias, 2007; Garído & Arribas, 2008) and we follow this classification. *Macedonitherium* and *Sogdianotherium* are now considered to be synonyms of *Mitilanotherium*; some authors believe *M. martini* to be a synonym of *M. inexpectatum*, while others maintain it provision-
ally as a separate species (De Vos et al., 2002; Kostopoulos & Athanassiu, 2005; Garrido & Arribas, 2008). The latter species is the type species of *Mitilanotherium* and was described from the Early Pleistocene of Rumania (Samson & Radulesco, 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 *Mitilanotherium*. 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** Aristote 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 Vríssia (Lesbos, Greece).
- **NUA** National and Kapodistrian University of Athens.
- **RRM** Rostov Regional Museum, Rostov-on-Don.
- **TUC** Technische Universität Clausthal, Institut 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 diametre of the anterior lobe; DTP = transverse diametre 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 *Mitilanotherium* Samson & Radulesco 1966

**Synonymy**

*Mitilanotherium inexpectatum* Samson & Radulesco, 1966

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The protocone has two crests forming a cresent 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 parastyle (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 M\textsuperscript{2} 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 M\textsuperscript{2} from Huélago are close in size to the specimen from Dafnéró and are clearly larger than in Okapia, only slightly larger than in Giraffa gracilis 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. Mitilanotherium from Dafnéró (NUA) has a morphology that is similar to the specimens from Huélago.

The M\textsuperscript{3} (Figure 3, fig. 3) has an anterior wear facet that fits a posterior wear facet on the right M\textsuperscript{2}, suggesting that both teeth belong to the same individual. The structure is similar to that of the M\textsuperscript{2}, 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 metacone (tetraprecrista) is directed antero-buccally and ends well anterior of the middle of the tooth (unlike in the M\textsuperscript{2}, where it ends close to the middle).

In the M\textsuperscript{3}, the same morphological differences between the material from Huélago and Giraffa are noted as in the M\textsuperscript{2}. Again, Mitilanotherium from Dafnéró (NUA) has a similar morphology and is close in size (Figure 3).

The P\textsuperscript{4} (Figure 3, figs. 5 & 6) is seléndont, 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 P\textsuperscript{4} 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 P\textsuperscript{4} 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. Mitilanotherium from Dafnéró (NUA) has a P\textsuperscript{4} with a similar morphology (open fossa, large paraexocrista, small buccal styles) and is close in size (Figure 3). A specimen of Mitilanotherium from Libakos (TUC) is not included in Figure 2, because of damage, but is close in size to the specimens from Huélago and Dafnéró.
Mitilanotherium inexpectatum (Giraffidae, Mammalia) from Huélago

Fig. 3.— Mitilanotherium inexpectatum from Huélago (MNCN): 1) HC85, B-18 - right M₂, occlusal (a) and buccal (b) views. 2) HC92, 8 - left P₃ (P₇), occlusal (a), lingual (b) and buccal (c) views. 3) HC85, C-37 - right M₂, occlusal (a) and buccal (b) views. 4) HC85, C-38 - left M₂ (M₇), occlusal (a) and buccal (b) views. 5) HC85, C-37 - right P₇, 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” (MNB): 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 M₁₀ 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 P3 (Figure 3, fig. 2) is a small tooth, too small to occlude with the P4 and therefore it is a P3, not a P4. Like the previously described teeth it is selodont. 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 P3, and not a P4, 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 P3 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, P3 symmetrical in buccal view, the lack of a transverse connection of the metaconid and protoconid in the P3.

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 M3 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 Tíffen 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 P3, 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 P3 with a rounded and backwards placed metaconid, that leaves the fossid wide open anteriorly. The morphology of the P3 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 (Athanassiou, 1996; Kostopoulos, 1996; Kostopoulos & Athanassiou, 2005), but also with the upper dentition of the type of Sogdianotherium kuruskaense 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 M3 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).
The distribution of Mitlanothenium in a wider biogeographic context

Present evidence suggests that Mitlanothenium 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 Mitlanothenium did not extend its range into eastern Asia. It is probably the disjunct distribution of Mitlanothenium, 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 Mitlanothenium 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 Mitlanothenium. 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 Hippotamus 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 *Mitilanotherium* 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 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 *Mitilanotherium inexpectatum* have originated? Apart from *Mitilanotherium*, 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 *Mitilanotherium* originated in Asia, and if *Giraffa pomeli* is a Palaeotragine, or even a *Mitilanotherium*, 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 *Mitilanotherium*, 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, Vathykkos 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 *Hispanodraco* (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 *Schizochoerus* 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 *Mitilanotherium* 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
Mitilanotherium inexpectatum (Giraffidae, Mammalia) from Huélago

Fig. 5.—Approximate ages of the localities with Mitilanotherium inexpectatum and Giraffa? pomelii 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 Sahnooui & Van der Made (2009). The position of Esekertan 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 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 duration 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 Mitilanothereum, 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, Mammutthus spread into mid-latitudes. Biogeography changed: deer and lagomorphs entered the Indian Subcontinent, where they were previously absent (Colbert, 1935; Hussain et al., 1992). Mitilanothereum 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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