Geologica Acta, Vol.10, Nº 1, March 2012, 1-17
DOI: 10.1344/105.000001702
Available online at www.geologica-acta.com

A new key locality for the Pliocene vertebrate record of Europe: the Camp dels Ninots maar (NE Spain)

B. GÓMEZ DE SOLER [1] [2] **G. CAMPENY VALL-LLOSERA** [1] [2] **J. VAN DER MADE** [3] **O. OMS** [4] **J. AGUSTÍ** [5] [1] [2]
R. SALA [2] [1] **H.-A. BLAIN** [1] [2] **F. BURJACHS** [5] [1] [2] **J. CLAUDE** [6] **S. GARCÍA CATALÁN** [1] [2] **D. RIBA** [1] [2] **R. ROSILLO** [7]

[1] **Institut Català de Paleoecologia Humana i Evolució Social (IPHES)**
C/ Escorxador s/n, 43003 Tarragona, Spain. Gómez de Soler E-mail: bgomez@iphes.cat Campeny E-mail: gcampeny@iphes.cat
Agustí E-mail: jordi.agusti@icrea.es Sala E-mail: robert.sala@urv.cat Blain E-mail: hablain@iphes.cat
García Catalán E-mail: sgarcia@prehistoria.urv.cat Riba E-mail: driba@iphes.cat

[2] **Àrea de Prehistòria, Universitat Rovira i Virgili (URV)**
Avinguda de Catalunya 35, 43002 Tarragona, Spain. Gómez de Soler E-mail: bgomez@iphes.cat Campeny E-mail: gcampeny@iphes.cat
Agustí E-mail: jordi.agusti@icrea.es Sala E-mail: robert.sala@urv.cat Blain E-mail: hablain@iphes.cat
Burjachs E-mail: francesc.burjachs@urv.cat García Catalán E-mail: sgarcia@prehistoria.urv.cat Riba E-mail: driba@iphes.cat

[3] **Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC**
José G. Abascal 2, 28006 Madrid, Spain. J. Van der Made E-mail: mcnjv538@mncn.csic.es

[4] **Departament de Geologia. Universitat Autònoma de Barcelona (UAB)**
Edifici C, Campus de la UAB 08193, Cerdanyola del Vallès, Spain. O. Oms E-mail: joseporiol.oms@uab.cat

[5] **ICREA Research Professor, Institut Català de Paleoecologia Humana i Evolució Social, Universitat Rovira i Virgili (URV)**
Plaça Imperial Tarraco 1, 43005 Tarragona, Spain. J. Agustí E-mail: jordi.agusti@icrea.es. F. Burjachs E-mail: francesc.burjachs@urv.cat

[6] **ISE-M, UMR5554 CNRS, Université de Montpellier 2**
cc64, 2 place Eugène Bataillon, 34095 Montpellier, cedex 5, France. J. Claude E-mail: julien.claude@univ-montp2.fr

[7] **Centre de Recerques Arqueològiques**
Carrer Ramon Llull, 15, 17455 Caldes de Malavella, Spain. R. Rosillo E-mail: rafelrosillo@gmail.com

ABSTRACT

A new Pliocene Konservat-Lagerstätte in north-eastern Spain is described here for the first time. It is referred to as Camp dels Ninots. The particular geological conditions of the site, which correspond to lacustrine sedimentation in a maar, made it ideal for the preservation of fossils. At present, five large mammal skeletons in anatomical connection have been recovered: three individuals of *Alephis tigneresi*, one of *Stephanorhinus jeanvireti* and one of *Tapirus arvernenis*, as well as isolated remains. A minimum of five individuals of the chelonian *Mauremys leprosa* have been recovered, some of them in anatomical connection. The rodent *Apodemus atavus*, the amphibians cf. *Pleurodeles* sp., *Lissotriton* aff. *helveticus* and *Pelophylax* cf. *perezi* and freshwater fishes (*Leuciscus* ?) complete the vertebrate assemblage uncovered up to the present time. The coexistence of *Stephanorhinus jeanvireti* and *Alephis tigneresi* suggests an age of about 3.2Ma for the Camp dels Ninots, near the MN15-MN16 transition. The Camp del Ninots fossil record enables one to extend the biogeographic range of some vertebrate taxa, such as *Stephanorhinus jeanvireti*, *Tapirus arvernensis* or *Mauremys leprosa* to the Iberian Peninsula. Taphonomic evidences of the skeletal remains indicates minimal (if any) weathering. Deposition at the lake bottom seems to have taken place in oxygen depleted layers. In this way, Camp dels Ninots is comparable to other remarkable maar sites such as Messel, the Eocene site situated in Germany.

KEYWORDS **Mammals. Chelonians. Amphibians. Pliocene. Konservat-Lagestätte. Maar.**

INTRODUCTION

Maars, lakes in volcanos, are ideal settings for the preservation of detailed palaeo-environmental records. Such lakes are relatively deep, protected from major erosion and may have anoxic bottom waters as meromictic lakes (Lutz and Kaulfuss, 2006). Therefore, they have a great potential for exceptionally well preserved fossils, such as in the case of the Eocene Fossil-Lagerstätten of Messel and Eckfeld (Germany), dated 50Ma and 45Ma, respectively (Franzen, 1977; Büchel, 1993; Neuffer et al., 1994; Mertz et al., 2000). Typically, a large representation of the whole biota is found, including vertebrates of several sizes (fishes, amphibians, reptiles, mammals, etc.), invertebrates (insects, etc.) and flora (both pollen and macroscopic remains). The successions of laminated sediments, usually found in such settings, provide detailed archives of palaeo-environmental change in terms of vegetation, climate, etc.

In the present paper, we give a detailed account for the first time of the new Pliocene maar site of Camp dels Ninots. The first studies in this area were carried out by Vidal (1882) who considered the sediments at this locality of lacustrine origin and Quaternary age. This interpretation was later followed by Bataller (1933), Llopis Lladó (1943) and Solé Sabarís (1946). The first fossil described from Camp dels Ninots was a fragmentary bone, which was assigned to the bovid *Leptobos* (Vicente, 1985). Several bones were found during the prospections of Vehí et al. (1999), who first interpreted the basin as a maar. In 2003 the Institut Català de Paleoecologia Humana i Evolució Social of the Universitat Rovira i Virgili (Tarragona) initiated a multidisciplinary research project that includes the study of the palaeontological and archaeological records of Plio-Pleistocene volcanic, lacustrine and fluvial deposits in the NE of the Iberian Peninsula. Subsequent excavations at Camp dels Ninots in the context of this project yielded articulated skeletons of large mammals and other vertebrates. The aim of this paper is to summarize the first geological and palaeontological results obtained for the study of this new site, to provide information about the vertebrate fauna and to contribute information concerning its age and palaeoenvironmental setting.

GEOLOGICAL SETTING

The palaeontological site of Camp dels Ninots (García Catalán et al., 2007; Gómez de Soler et al., 2008; Oms et al., 2008) derives its name from the presence of menilites with singular shapes resembling little “puppets” (“ninots”). The site is located in the town of Caldes de Malavella near the city of Girona in the La Selva Depression (Pous et al., 1990). This basin is bounded by Paleozoic rocks of the Catalan Coastal Ranges (Fig. 1A), and its morphology is controlled by two sets of faults oriented ENE-WSW and NW-SE. It is formed as a result of the distensive tectonics

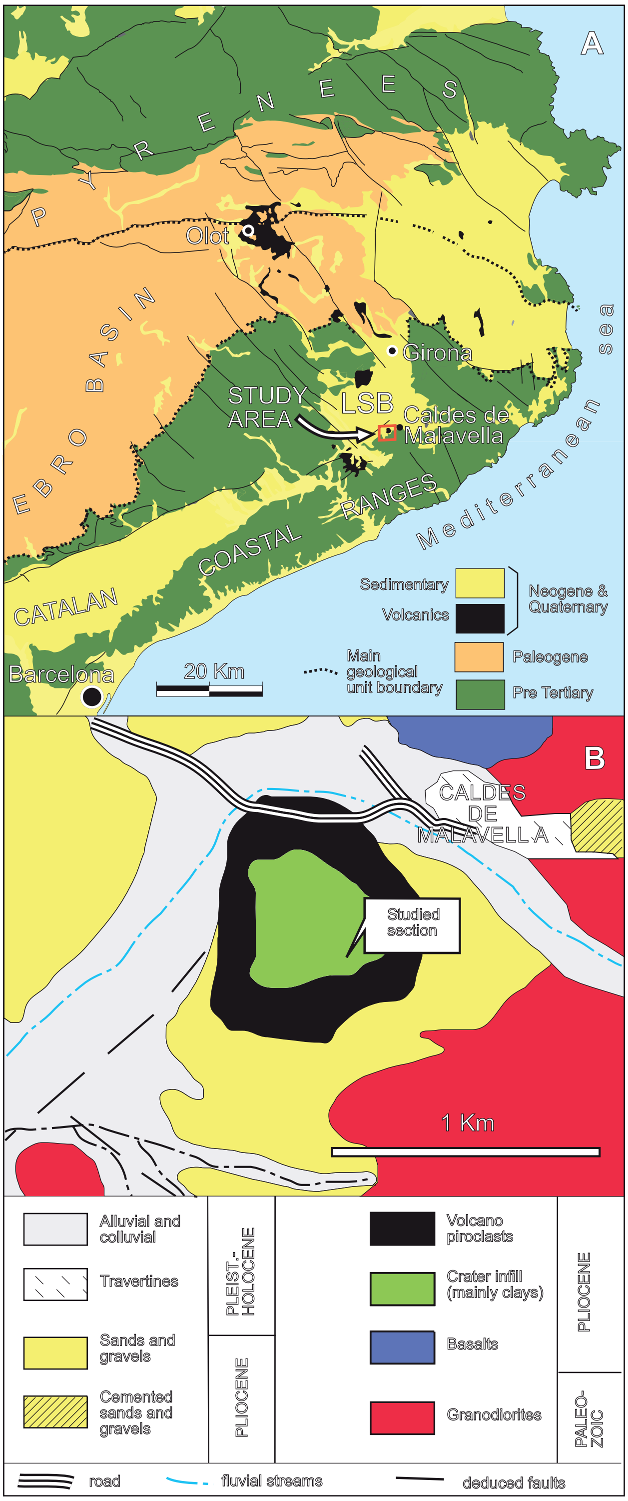

FIGURE 1 | Geology of the Camp dels Ninots Volcano. A) Location within the main geological units from NE Iberia. LSB: La Selva Basin. B) Detailed geology from the area and extension of the crater (modified from Vehí et al., 2005).

that affected the western Mediterranean for most of the Neogene and Quaternary (detailed geotectonic setting is presented in Roca, 1996; Roca et al., 1999; Tassone et al., 1994).

Several volcanic episodes occurred during the Neogene and thermalism shows that there is still important geothermal activity at the margins of the Selva Depression (Vehí et al., 2005). Volcanic activity took place mainly during the Pliocene (Donville, 1976) as part of the Catalan Volcanic Complex (Araña et al., 1983), which was active from 14Ma to 10,000 years BP in the NE of the Iberian Peninsula (Guardia, 1964). The La Selva volcanism is alkaline with a record of olivine-rich basaltic floods and volcanic cones with both explosive and non-explosive activity phases (see summary and references in Vehí et al., 1999). Volcanic rocks are found all around the basin margins, such as in the Crosa de Sant Dalmai volcano (Vilobí d'Onyar) or around Caldes de Malavella. Both basalt flood units (dated at 5Ma, Donville, 1976) and the Camp dels Ninots volcano are found in this latter area (Fig. 1B). This volcano was first identified by Vehí et al. (1999) who described and identified the Camp dels Ninots strata as lake sediments filling the crater. The new palaeontological data reported herein come from the lacustrine beds of this maar. According to substrate features, this volcano can be classified as a soft-substrate maar lake (Lorenz, 2000).

The sedimentary infill of the maar has been studied during several excavations, but the only available, relatively -thick section is the one of 8 metres at the Can Argilera excavation sector (Figs. 2, 3). There, we described the reference stratigraphic section for the Camp dels Ninots. From base to top (1 to 4), we observed four local units that can be partially found in smaller trenches dug in other parts of the maar (Fig. 2). Lowermost sediments of unit 1 are greyish clays, sandstones and diatomites. Unit 2 is broadly built up by greenish laminated clays with diatoms. Carbonates (that include dolomite and ankerite) are found in subunits 2.1, 2.2 and 2.4. Subunit 2.3 includes isolated, sandstones and no carbonates. In subunits 2.1 and 2.2, distinctive opal mineralizations are found (see Fig. 2). Unit 3 consists of around 1meter of reddish laminated clays of Quaternary age. In this unit, we found some archaeological remains, consisting exclusively of lithic industry. Finally, unit 4 consists of slope wash deposits of recent origin draping present day geomorphology.

Subunit 2.3 is the one that contains all articulated mammal skeletons and most palaeontological findings, including a large amount of plant remains (particularly tree leaves). In detail, this subunit is built up by greenish laminated clays with benthic diatoms. In this sediment, quartz is the dominant mineral, albite and microcline being also present. Regarding clay minerals, montmorillonite is the dominant one and illite can also be found. Despite the fact that lamination may be difficult to discern, local counts suggest that around a thousand laminae are likely to be present in this unit. The upper laminites are richer in silts and sandstones and the unit is capped by a fine-medium sandstone (basically built up of piroclast grains) with no fossil remains. Articulated skeletons of large mammals are found in three distinct stratigraphic levels (see Fig. 2, right).

It is generally observed that maar sediments are arranged in a typical vertical stratigraphic succession or lithozonation (Pirrung et al., 2003; Linder et al., 2006; among others). From base to top wall rock debris and pyroclasts decrease, while laminated silts and clays increase. According to this scheme, the materials studied at Camp dels Ninots would correspond to lithozone D in

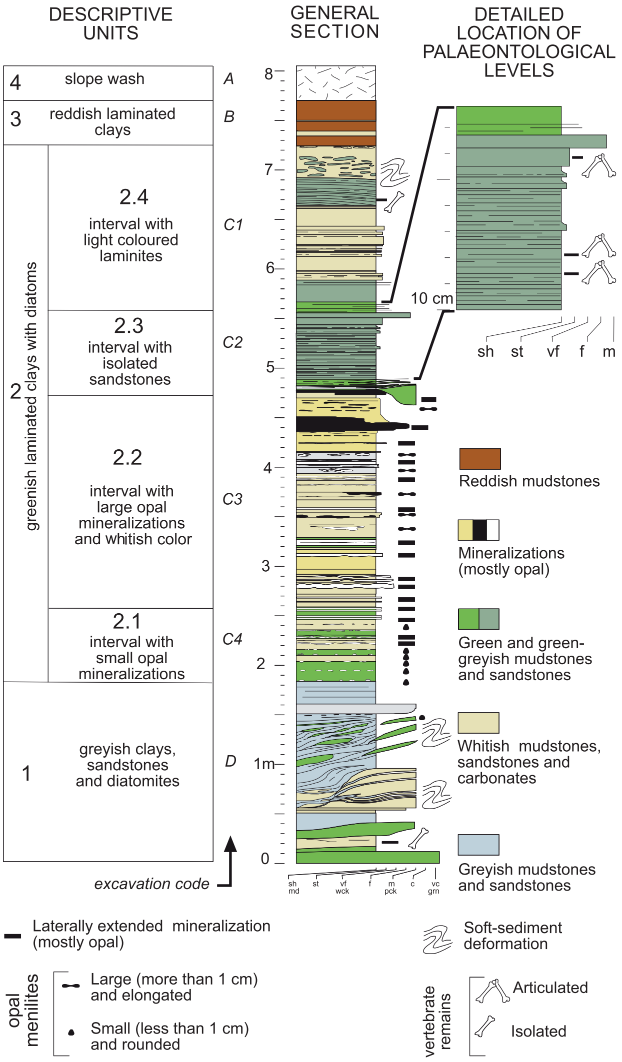

FIGURE 2 | Stratigraphic succession and units of the Camp dels Ninots crater infill at Can Argilera section (see location in Fig. 3).

the sense of Pirrung et al. (2003), which was defined as "laminated silt and clays with some turbidites and debris flow deposits".

Maar lake settings containing important fossil sites are well-known from the literature. Some outstanding examples are those from Messel (see references in Gruber and Micklich, 2007), Eckfeld (see references in Sachse, 2005) or Las Higueruelas (Martín-Serrano, 2009). Maar lake settings strata are common formed under anoxic conditions (such as sapropels) and they may even be related to palaeontological sites (Wuttke, 1992a). This is not the case for the studied section and site (Fig. 2), although data by Vehí et al. (1999) suggest that such sediments may be present in deeper parts of the lacustrine infill of the volcano. The general features (and stated lithozonation) of the studied strata, together with the marginal position close to the volcano border, indicate deposition in a proximal setting (see for example, Lorenz, 2000). Additionally, we observe no evidence of lake desiccation as it is found in palustrine settings such as las Higueruelas.

METHODOLOGY OF EXCAVATION AND SAMPLING

The Camp dels Ninots maar has an elliptic shape with maximum and minimum diameters of over 650 and 400 metres, respectively (Fig. 1B). This area was divided into several sectors for the organization of the fieldwork. Up to the present date, we have excavated small parts of four sectors (Can Argilera Sector, Can Pol Sector, Can Cateura Sector and Butano sector), defined by the limits of field ownership, where we made different pits searching the limits of the lake and the fossiliferous levels (Fig. 3).

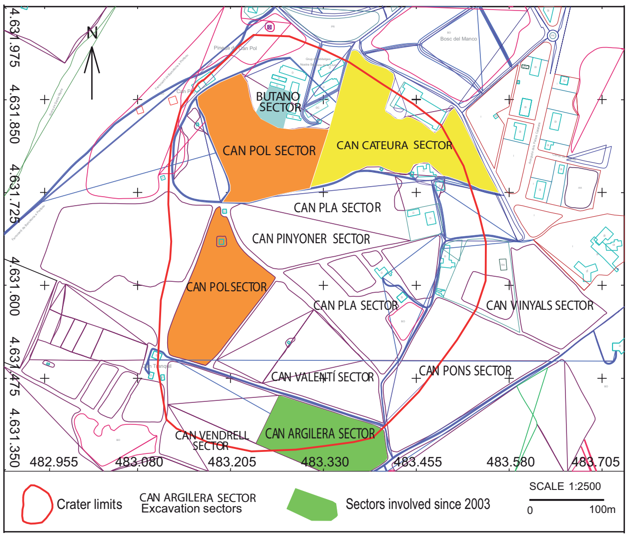

FIGURE 3 | Topographic map of the Camp dels Ninots area with the crater limits, the excavation sectors and the sectors involved since 2003.

These pits were first opened by a backhoe and then the fossil strata were manually excavated. The maximum depth of the pits was about 4 or 5 meters and their size ranged from 4m² to 100m² for those pits with fossil evidences. The fossiliferous strata are approximately 1m thick. Pits and fossil occurrences were positioned through the Universal Transverse Mercator (UTM). The recovery of the fossils started with the delimitation and excavation of the remains, which were drawn and their position in space was recorded using the reference grid that corresponds to their register code (name of the site by initials -CN-, year, sector, pit, excavation unit, square and number of register). The most damaged specimens were impregnated for their removal. When skeletons were found in connection, articulated elements that could not be taken out individually were taken out in blocks with polyurethane protection for its later excavation in the laboratory of the Institut Català de Paleoecologia Humana i Evolució Social (Gómez-Merino et al., 2009). In the case of well preserved remains in anatomical connexion, a cast was made *in situ*. Plant fossils were photographically documented in the field for a later taxonomical identification in the laboratory, first with a good description (Ash et al., 1999) and then using different manuals, or in this case, monographic plates for its classification (Sanz de Siria, 1987; Vicente, 1988; Barron, 1996; among others). Wood and fruit remains and some of the leaves were recovered in blocks with different technical systems (López-Polín et al., 2009).

Sediment samples were taken from each level for small vertebrate and pollen analysis. Microvertebrate fossils were recovered by the conventional screen-washing of the sediment samples, using superposed sieves with 2 and 0.5 millimeter meshes. A binocular microscope at low magnification was used to pick microfossils from the residues. Pollen was extracted from samples from different sectors (Can Pol, Can Argilera and Butano Sector) by using the protocol proposed by Goeury and Beaulieu (1979), slightly modified by the elimination of acetolysis according to Girard and Renault-Miskovsky (1969), and as to the protocol developed by Burjachs et al. (2003).

All the remains are provisionally stored in the collections of the Institut Català de Paleoecologia Humana i Evolució Social at Tarragona.

PALAEONTOLOGY

Up to now, the Camp dels Ninots vertebrate fossil record includes remains of freshwater fishes, amphibians, reptiles and mammals (Fig. 4). The taxa identified so far are: cyprinid fishes (*Leuciscus* ?), cf. *Pleurodeles* sp., *Lissotriton* aff. *helveticus*, *Pelophylax* cf. *perezi*, *Mauremys leprosa*, *Alephis tigneresi*, *Stephanorhinus jeanvireti*,

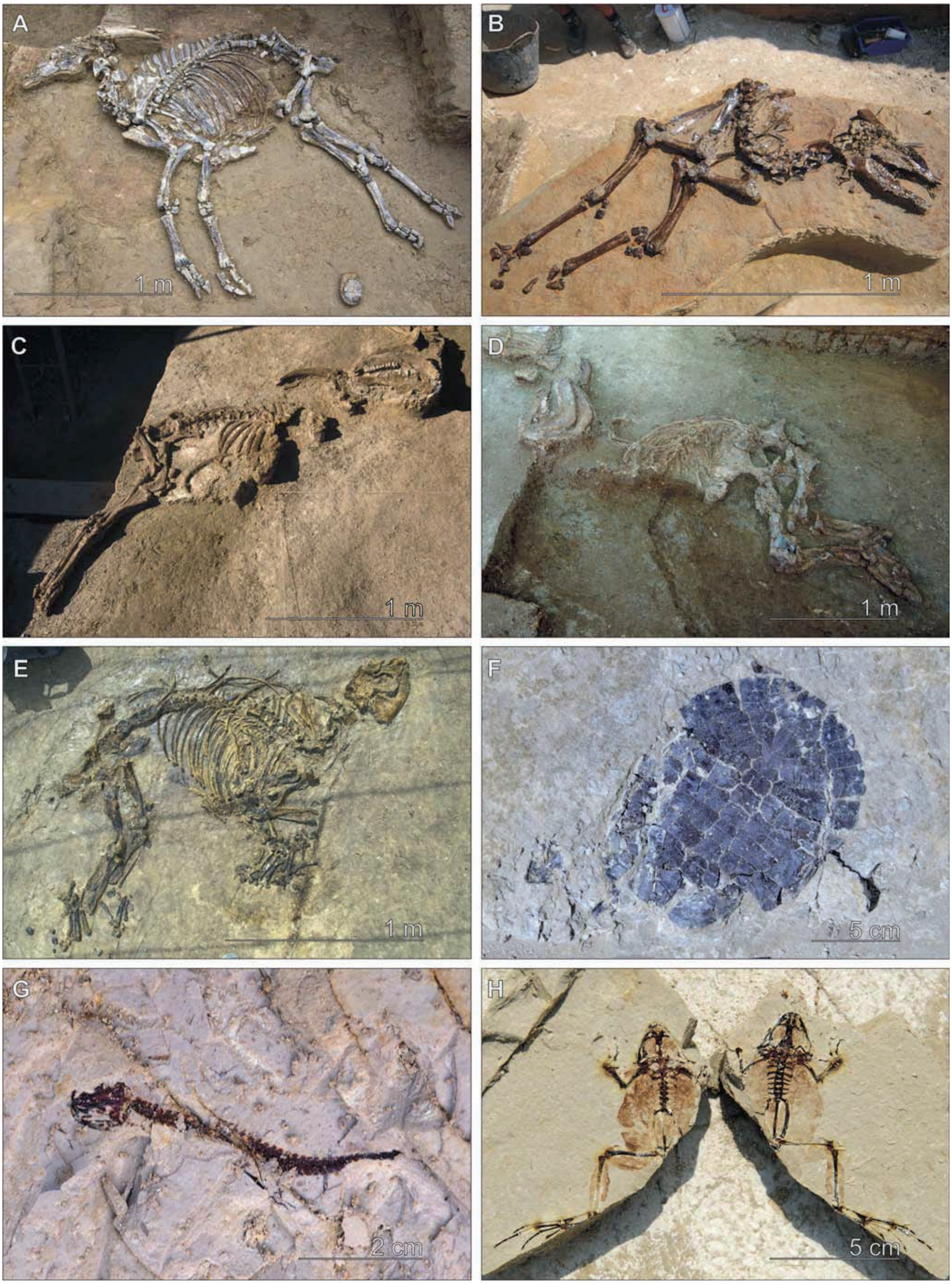

FIGURE 4 | A to C) Skeletons of *Alephis tigneresi* recovered in A) 2005 B) 2004 and C) 2006; the posterior and anterior limbs in B and C are not present because of a fault in the field. D) Skeleton of *Stephanorhinus jeanvireti* recovered in 2006; the anterior limbs are not present because of the same fault in the field. E) Skeleton of *Tapirus arvernensis* recovered in 2008. F) *Mauremys leprosa* recovered in 2008. G) Newt *Lissotriton* ? in anatomical connection recovered in 2005. H) Articulated frog skeleton *Pelophylax* cf. perezi recovered in 2008.

Tapirus arvernenis and *Apodemus atavus*. Freshwater fishes are still under study, but preliminar data allowed to recognize at least two or three forms of cyprinids. All the fossil remains have been localized in unit C2 except for a few isolated materials found in C1 and D units (see Fig. 2).

It is remarkable that not a single shell of invertebrate organism (gastropods, ostracods, bivalves etc.) was found despite the significant excavated surface and intensive sieving. This relatively unusual fact in lake sediments may reflect a strong taphonomical bias caused by abiotic processes such as selective dissolution. Maar lakes have generally acid to slightly basic waters (Varekamp et al., 2000, Marini et al., 2003), leading to calcite dissolution and silica precipitation.

Palaeobotanical studies are underway, primarily focusing on microremains, palynology and macroremains. Until now, palynological analysis of all excavated areas has not provided abundant microremains. Nevertheless, it has been possible to determine the presence of *Taxodiaceae*, *Picea, Pinus, Abies*, Cupressaceae, *Betula, Corylus/Myrica, Quercus, Olea/Phillyrea, Arbutus, Erica, Calluna, Ephedra*, Cistaceae, *Artemisia, Asphodelus*, Poaceae, Cyperaceae and *Typha-Sparganium* taxa; and various NPP's (*Gloeotrichia, Rivularia, Botryococcus, Spirogyra*, protists, fungi spores and microzooremains). On the other hand, large plant fossils, which are preserved as impressions in lacustrine clays, indicate a subtropical type of flora with lauroid leaves of evergreen trees (Fig. 5). In addition, some wood and fruit impressions were found (Fig. 5E, F).

Amphibia

Caudata

cf. *Pleurodeles* sp.

Material. 5 isolated vertebrae. Code: "CN"08. Can Argilera Sector. Pit 7/8. K24'.

Description and comparison. A large newt is represented by a few presacral vertebrae (centrum length >4mm). Vertebrae are opisthocoelous, elongated, with a long, high and thin neural spine and a highly vaulted neural arch. On our fossil material the prezygapophyses are linked posteriorly to the base of the dorsal costal process and not to the ventral costal process as described by Barroso-Ruiz and Bailon (2003) and Haller-Probst (1997). Such a characteristic has been seen on some modern specimens of *Pleurodeles waltl* coming from the amphibian and reptile collection at the Museo Nacional de Ciencias Naturales (Madrid, Spain). In lateral view, a large foramen opens on each side of the vertebra at the basis of prezygapophyses, whereas on the posterior half there are two or three smaller postero-lateral foramina. Fossil vertebrae morphology is concordant with an attribution to genus *Pleurodeles*. In the fossil record, the genus *Pleurodeles* is known since the Upper Miocene or Lower Pliocene of Rambla de Valdecebro III, Teruel, Spain (Sanchíz, 1977; Estes, 1981). The presence of *Pleurodeles* in Camp dels Ninots suggests a northernmost extension of the genus during the Pliocene. Current *Pleurodeles* lives in a great variety of habitats mainly under warm and dry climate (García-París et al., 2004). *Pleurodeles waltl* preferently frequents large water environments with a depth comprised between 2.5 and 10 meters and generally avoids streams with moderate or strong currents. This newt is mainly aquatic and if a water point is permanent, it remains in the water all year long.

Lissotriton aff. *helveticus* (Razoumosky, 1789)

Material. 4 isolated vertebrae, a femur, a humerus, and possibly an articulated specimen.

- Articulated specimen. Code: "CN"05. Can Argilera Sector. Pit 7/8. C2 unit'.
- Isolated material. Code: "CN"07. Butano Sector. Pit 2. C2 unit. R46'.

Description and comparison. A small-sized newt referred to *Lissotriton* aff. *helveticus* is represented in Camp dels Ninots by 4 presacral vertebrae (centrum length about 2mm), a femur and a humerus recovered by sieving-washing of the sediment. During the 2005 excavation a quasi-complete articulated skeleton was found, but unfortunately it could not be preserved (Fig. 4G). Vertebrae are characteristic of the genus *Lissotriton*: opisthocoelous, elongated, with a long, high, thin and posteriorly forked neural spine and a well vaulted neural arch. The ratio neural arch height/vertebra height is around 0.47. The subcentral foramina are large. The general morphology and size of the fossils matches well with that of the extant palmate newt *L. helveticus*, which is known since the late early Miocene of Béon 1 in France (Rage and Bailon, 2005).

The articulated skeleton (total length around 6 centimeters) is exposed in latero-dorsal view (Fig. 4G) and shows some derived characteristics of the family Salamandridae with the presence of a frontosquamosal arch and possibly fused premaxillae (reversed in *Pleurodeles*, *Tylototriton* and *Chioglossa*; Frost et al., 2006). The morphology of its presacral vertebrae seems to be concordant with the isolated vertebrae attributed to *Lissotriton*.

The palmate newt *Lissotriton helveticus* is currently well represented in areas with a humid and moderate climate (García-París et al., 2004). During its aquatic period, the species prefers shallow and still waters, generally with the presence of abundant aquatic vegetation and a dense lakeside vegetal cover. In Catalonia, this newt is found today in areas with a mean annual precipitation higher than 700 millimeters. It is the less aquatic of the Iberian newts and is present in the water from November to May.

Anura

Pelophylax cf. *perezi* (Seoane, 1885)

Material. 4 articulated specimens and an isolated humerus and a mandible.

-Articulated specimens. Codes: "CN"05. Can Argilera Sector. Pit 7/8. C2 unit. N23, 1', "CN"05. Can Argilera Sector. Pit 7/8. C2 unit. I18, 1', "CN"08. Can Argilera Sector. Pit 7/8. C2 unit. J26, 1', "CN"08. Can Argilera Sector. Pit 7/8. C2 unit. M23, 32'.

-Isolated material. Code: "CN"06. Butano Sector. Pit 2. C2 unit. S46'.

Description and comparison. Several articulated specimens recovered during the excavations of 2005 to 2008 (Fig. 4H) as well as a few isolated bones recovered by sieving-washing of the sediment, document the presence of a representative of the genus *Pelophylax*. On the articulated specimens, characteristics of the family can be observed: diplasiocoelous vertebral column, with short and non-imbricate neural arch, sacrum unfused with the urostyle that bears cylindrical sacral apophysis, bicondylar sacro-urostylar articulation, transverse processes of the urostyle lacking, absence of ribs, firmisternous sternum with ossified omosternum, premaxilla and maxilla teeth bearing. Features of the genus *Pelophylax* can also be recognized: higher dorsal crest on the ilial shaft and more open sacral apophysis (approximately 130°) than in genus *Rana*. Some discrete characteristics permit to establish a link between these fossils and the extant species *Pelophylax perezi* (Seoane, 1885), as the fourth toe length/snout-vent length ratio, the tibia length/snout-vent length ratio and the relative position of the vomers (Crochet et al., 1995). However, the head width/snout-vent length ratio is closer to *P. ridibunda* than *P. perezi* but this may be an artifact of a little compression during fossilization. The southern marsh frog (*P. perezi*) is currently the only representative of the genus in the Iberian Peninsula, where it is mentioned with doubt from isolated and fragmentary bones at least since the late Pliocene (Sanchíz, 1998; Blain, 2005). Therefore, its occurrence in the Pliocene of Camp dels Ninots may represent the earliest citation for this

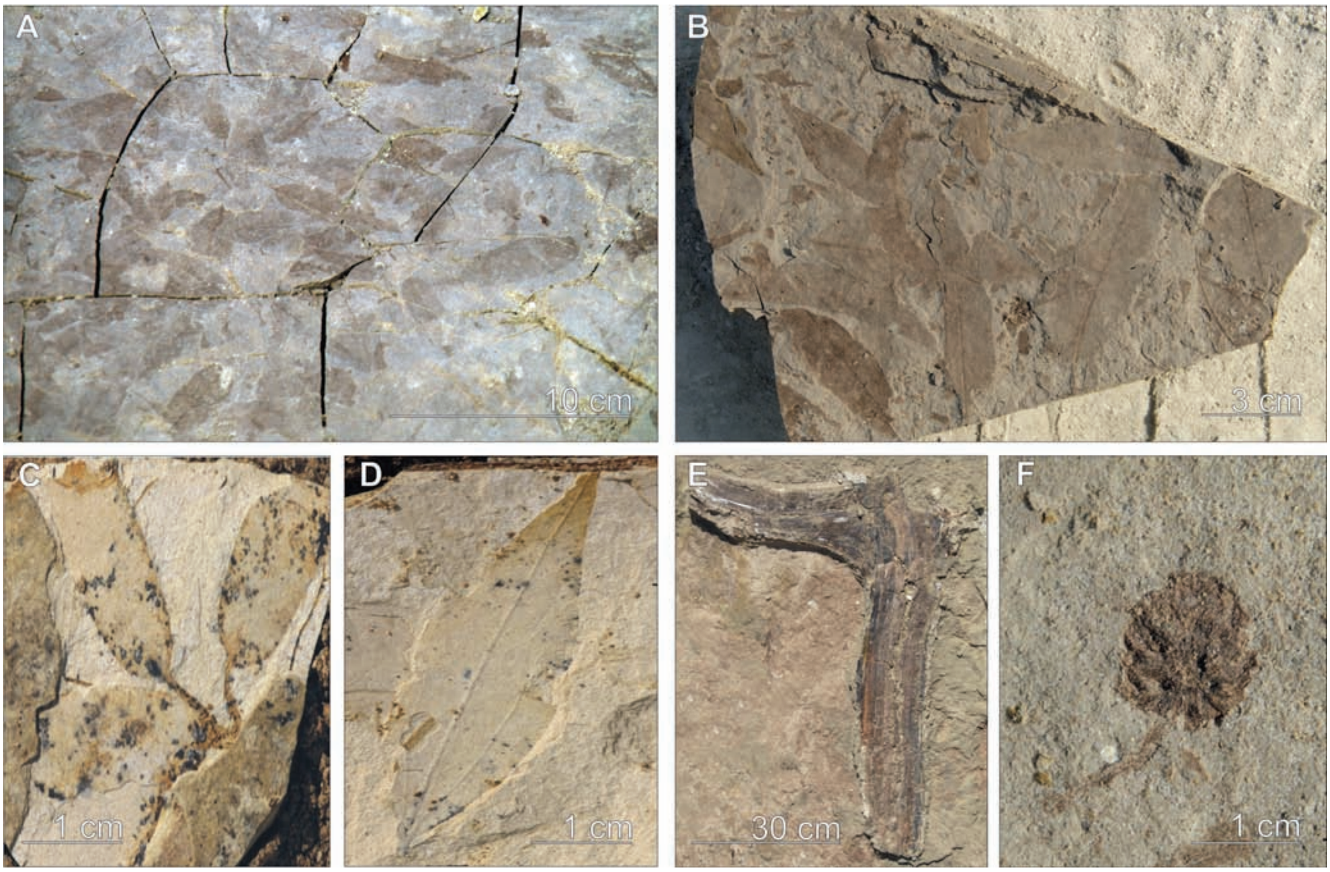

FIGURE 5 | A and B) Surface with plants fossils (lauroid leaves). C) *Quecus drymeja.* D) *Daphnogene polymorpha.* E) wood imprint. F) *Alnus* fruit.

species, although, according to molecular data, *P. perezi* is supposed to have split off from *P. saharica* at 5.4Ma, when the Straight of Gibraltar opened (García-París et al., 2004). *Pelophylax perezi* is a species that lives in most sunny aquatic environments, the presence of which only seems to be limited by the absence of permanent water (Llorente and Arano, 1997; García-París et al., 2004).

Testudines

Mauremys leprosa (Schweigger, 1812)

Material. Two complete articulated skeletons and some isolated material:

-Articulated skeletons. Codes: "CN"05, Can Argilera Sector, Pit 7/8, C2 unit, M22, 1', "CN"05, Can Argilera Sector, Pit 7/8, C2 unit, L24, 1' (Fig. 4F).

-Isolated material. Code: "CN"05, Can Argilera Sector, Pit 7/8, C2 unit, N25, 3; T23, 1; M22, 2-6'.

Description and comparison. Reptiles are represented at Camp dels Ninots by chelonians that can be referred to the species *Mauremys leprosa* (Schweigger, 1812), the so-called Mediterranean Pond Turtle (Fig. 4F). This species is recorded by partial and more complete shells, as well as axial, appendicular and skull bones. The material is often connected or sub-connected. At least five individuals are present. The estimated shell lengths vary from 12 to 25cm, the smaller specimen being a subadult, while larger specimens are adults. The shells are oval in shape and rather flat, with a smooth posterior margin. The bone arrangement, the anal notch, the wider than long pygal plate, and musk ducts in third and seventh peripheral plates allow to assign these specimens to the geoemydid family (Claude and Tong, 2004). Neurals are wide and predominantly anteriorly short sided, however one specimen exhibits a heptagonal third neural plate and a pentagonal fourth neural plate. The wide first vertebral scute reaching the second marginal scute, the rather wide and, in some cases, irregular neural series, the short anal scutes, the rather short bridge, the entoplastron partially covered by pectoral and gular scutes, and the weakly developed buttresses are diagnostic of the genus *Mauremys* (Claude et al., 2007). *Mauremys portisi* from the Pliocene of Italy differs from the new specimens found by the position of the humero-pectoral sulcus and by the shape of its vertebral scute. As in the living *Mauremys leprosa, M. rivulata,* and *M. caspica* and the fossil *M. gaudryi,* gulars are slightly pinched posteriorly, the third and fourth vertebral scute are rather rectangular and the first vertebral is anteriorly very wide. In Camp dels Ninots, the shorter humeral than anal scute, and the rather elongated cervical are characters that are found more often in *M. leprosa* than in *M. caspica* or *M. rivulata*. Specimens from Camp dels Ninots also differ from *M. rivulata* by their larger size. The smaller individual (subadult) does not show lateral keels and therefore, it differs from subadults of *M. caspica* and *rivulata* but resembles *M. leprosa*. *M. gaudryi* from the Pliocene of Perpignan is very similar to *M. leprosa* and differences may be smaller than intraspecific variation. However, the fossil specimen from Spain differs from the type material of *M. gaudryi* by its narrower first vertebral, the narrower cervical, and the shorter marginals and is therefore more similar to the living *M. leprosa*. Today, *Mauremys leprosa* lives in calm water streams, ponds, lakes or oxbows.

Mammalia

Artiodactyla

Alephis tigneresi Michaux, Aguilar, Calvet, Duvernois and Sudre, 1991

Material. Three articulated skeletons:

-Partial articulated skeletons. Codes: "CN"04, Can Argilera Sector, Pit 7/8, C2 unit, K19, 1 and 2; L20, 1-44; M20, 1-17; K20, 1-45; L21, 1-12 '(Fig. 4B), "CN"06, Butano Sector, Pit 2, C2 unit, O47, 1-21; P48, 1-16; N47, 1-8; O48, 1-3' (Fig 4C).

-Complete articulated skeleton. Code: "CN"05, Can Argilera Sector, Pit 7/8, C2 unit, M23, 1-31; M24, 1-35; M25, 1-38; N23, 1-7; N24, 1-44; N25, 1-27' (Fig. 4A).

Description and comparison. Three articulated skeletons were found (Figs. 4A-C) of a single species of bovid, larger than any non-bovine bovid known from Europe. The horn cores originate a little behind the orbit. They have an oval section and an anterior keel, they are directed backwards and are not much curved. This is unlike in *Bos* and *Bison*. The cheek teeth are smaller high crown and the molars have smaller interlobular columns than *Leptobos*, *Bos* and *Bison*. The limb bones are robust, like in *Parabos*, *Alephis* and *Leptobos*, but not as robust as in *Bos* and *Bison*. The limb bones are in the upper ranges of *Leptobos*, or larger. All characters studied in the specimens from Camp dels Ninots are similar to those of the genera *Parabos* and *Alephis*.

The genus *Parabos* was named by Arambourg and Piveteau (1929), while Gromolard (1981) named the genus *Alephis* for the species "*cordieri*", which was placed until then within *Parabos*, and claimed the former genus to belong to the Bovini and the latter to the Boselaphini. Geraads (1992) had a similar opinion, but Montoya et al. (2006) believed both genera to be closely related to the basal Bovini and transferred the species *P. cordieri* to the genus *Alephis*. In addition to the two genera, five species were named from Western and two from Eastern Europe (Gromolard, 1981; Morales, 1984; Michaux et al., 1991; Arambourg and Piveteau, 1929; Radulescu et al., 2003). There are probably more names than taxa which can be recognized on the basis of morphology and metrics. In a broad sense, the geologically younger material has longer and more flattened horn cores, which flare out more. The material from Camp dels Ninots has such morphology and is particularly similar to the type material of *Alephis tigneresi* Michaux, Aguilar, Calvet, Duvernois and Sudre, 1991.

Bovini tend to be specialised grazers, which is an adaptation to open landscapes. But *Parabos* and *Alephis* were less high crowned and lacked other adaptations to grazing. Their appearance in the fossil record is probably related to environmental change, but the lack of well developed adaptations to grazing, and the fact that they persisted in Europe when more evolved Bovini existed elsewhere, suggests that they were adapted to landscapes that were not very dry or open.

Perissodactyla

Tapirus arvernensis Croizet and Jobert, 1828

Material. one complete articulated skeleton. Code: “CN”08, Can Argilera Sector, Pit 7/8, C2 unit, F19, 1-3; G20, 1-53, H20, 1-44’ (Fig. 4E).

Description and comparison. The complete skeleton found (Fig. 4E) presents: mesaxonic foot structure with four robust metacarpals in the manus and three robust metatarsals in the pes, high placed reduced nasals, lophodont cheek teeth, molarized premolars, and a full set of incisors and canines. These are all characteristics of *Tapirus*. The specimen from Camp dels Ninots fits morphologically and metrically fits the species *Tapirus arvernensis* Croizet and Jobert, 1828 as described by Fejfar (1964) and Guérin and Eisenmann (1994).

Tapirus arvernensis is probably closely related to the living Malayan tapir, *Tapirus indicus* and thus, its ecology may have been similar. Tapirs eat principally fruits and leaves and are adapted to humid forests. It is believed that they went extinct in Europe because of increased seasonality, which limited the availability of their preferred food during part of the year (Made and Stefanovic, 2006). The abundance and geographic distribution of tapirs changed over time, presumably reflecting the distribution of favorable habitats and climate. The record at Camp dels Ninots is the southernmost record of *T. arvernensis* in SW Europe and one of the southernmost of the Tapiridae of the whole Neogene. This most probably reflects a climatic optimum of some kind, with the important variables being humidity, temperature and seasonality.

Stephanorhinus cf. *jeanvireti* (Guérin, 1972)

Material. Partial articulated skeleton. Code: “CN”06, Butano Sector, Pit 2, C2 unit, L45, 1-5; M45, 1-50; N45, 1-7; M46, 1-11, N46, 1-4’ (Fig. 4D).

Description and comparison. An articulated skeleton with partial skull and mandible, but without anterior limb bones indicates the presence of a rhinoceros. The mandibular symphysis does not show any indication of large or reduced incisors, suggesting that it belongs to one of the species of *Stephanorhinus* that are known from Europe, but not to the species “*megarhinus*”, which retains vestiges of the incisors. Guérin (1980, 1982a, b) placed these species in *Dicerorhinus*, but it is current usage to place them in *Stephanorhinus* (Heissig, 1996, 1999; Fortelius et al., 1993). The material from Camp dels Ninots belongs to a large species, larger than *Stephanorhinus etruscus* and *S. miguelcrusafonti*, and similar in size to the species *Stephanorhinus jeanvireti* (Guérin, 1972), which is defined on material from Vialette (Guérin, 1980; table 115).

Present day rhinoceroses are either grazers or browsers. The grazers (*Ceratotherium simum*) are hypsodont and the browsers are more brachydont (the remaining species). In addition the grazers tend to have overhanging occiputs (Zeuner, 1934). Occiput shape, the low crowned teeth and the lack of abundant cementum on the crowns suggests that *Stephanorhinus jeanvireti* was a browser. Its known geographical distribution suggests that it preferred the same habitats as tapirs.

Rodentia

Apodemus atavus Heller, 1936

Material. Two first upper molars (M1) and a maxilla without teeth.

-First upper molar (M1). Code: “CN”04, Can Argilera Sector, Pit 7/8, C2 unit, K20’.

-First upper molar (M1) and a maxilla without teeth. Code: “CN”08, Can Argilera Sector, Pit 7/8, C2 unit’.

Description and comparison. Small mammals are scarcely represented at Camp dels Ninots by two first upper molars of the murid *Apodemus atavus*. The upper M1 presents a large and rounded t1, which is placed posteriorly with respect to t2 and t3. The t3 is rounded, without any evidence of posterior spur. The connection between t6 and t9 is large and well established. The t7 is large and oval in shape, being connected to the posterior wall of the t4. The t12 is small, well separated from the t9. The low degree of stephanodonty of the upper M1 suggests that it belongs to an archaic population of this species. *Apodemus atavus* is a species widely distributed in the Pliocene and early Pleistocene of Europe, from Southern Spain to Georgia, throughout France, Germany and Hungary (Pasquier, 1974; Bachelet, 1990; Fejfar and Storch, 1990; Aguilar et al., 1991; Lordkipanidze et al., 2007).

DISCUSSION

Age and correlation

The mammals Neogene (MN) units form a biostratigraphical scale, based on mammals, for the European and North African Neogene (Mein, 1975; Bruijn et al., 1992; Agustí et al., 2001). Normal bio-zones have boundaries that are defined by the first or last occurrence of a specified taxon, but MN units are not defined by their boundaries, but by a reference locality and other fossil localities should be placed in an MN unit on the basis of the overall resemblance of their fauna to the reference fauna. The original publication on MN units consisted of a chart that provided, for each MN unit, the principal localities and the first and last occurrences as well as typical taxa (Mein, 1975). In a later publication, tables with principal localities of each MN unit, distribution of important genera, and faunal lists of the reference localities are given (Bruijn et al., 1992). In the latter, ranges of genera are generally given as if they ended abruptly at MN boundaries, even though it is stated that the transitions between MN units are gradual. Contrary to the idea of gradual transitions, Agustí et al. (2001) gave very precise ages for the boundaries of the MN units. There are contradictions between the accepted positions of localities and the accepted temporal or stratigraphic distribution of taxa from these localities, which are of relevance here, and need to be discussed or at least mentioned before we can discuss the age of Camp dels Ninots. Figure 6 shows the ages of relevant localities and the distribution of taxa.

According to Bruijn et al. (1992) "*Parabos*" (with quotation marks and apparently including also *Alephis*) is replaced by *Leptobos* at the MN15-16 transition. However, *Leptobos* is already cited from Layna (Pérez and Soria, 1990), which is placed in MN15 Bruijn et al. (1992), and *Parabos* and *Alephis* are still cited from MN16 (Gromolard, 1981; Radulesco et al., 2003). Gromolard (1981) cited *Parabos* from Sofia, a possible *Alephis* from Kislang and *Alephis* from Capenis, Virghis and Iaras, all placed in MN16. Kislang is a locality with problems of mixing, while in Sofia only *Parabos* and *Anancus* are cited, so that there is no fundament for MN16 age.

Radulesco et al. (2003) placed the Romanian localities with *"Parabos" athanasiui* in the top of MN14 (Beresti), MN15 (Malusteni, Capeni, Varghis) and the base of MN16 just above the Gilbert-Gauss boundary (Iaras 1). In the earlier MN tables Malusteni and Beresti were placed in MN16 (Mein, 1975), while later these localities were omited (Bruijn et al., 1992). According to Radulesco et al. (2003; table 1), Malusteni, Capeni and Iaras (Iaras 3?) have *Equus* (or *Plesippus/Allohippus stenonis*), while the latter locality has also *Eucladoceros* (though in the text on Iaras, p. 556, neither *Equus* nor *Eucladoceros* are mentioned). This would imply that *Equus* and *Eucladoceros* appeared in Romania in MN15 and MN16, while in other parts of Europe they appeared in MN16 or 17 and MN17 respectively (Bruijn et al., 1992; Agustí et al., 2001). On the one hand, if we placed these three localities in MN17, so that the first appearances of *Equus* and *Eucladoceros* are similar to those in other parts of Europe, the stratigraphic range of *Alephis/Parabos* would be extended upward. On the other hand, during all of the Neogene and Quaternary, there are examples of mammals appearing considerably earlier in SE Europe than in Western Europe (Made and Mateos, 2010). It is impossible to solve this problem now, but we should note that none of these localities has *Leptobos*, which in Western Europe replaced these bovids and that the faunal lists suggest the co-occurrence of *Parabos* (or *Alephis*) with taxa that appeared considerably later than *Leptobos*. Though *Parabos/Alephis* and *Leptobos* are never found in one locality, their temporal ranges may have overlapped.

According to Guérin (1980; 1982a, b) the species *Stephanorhinus miguelcrusafonti* is known from the late Ruscinian or faunal unit MN15, while *S. jeanvireti* is known from the earliest Villafranchian or MN16 and *S. etruscus* from the earliest Villafranchian till the earliest Middle Pleistocene (generic assignation here after Heissig, 1999). Although the range of *Dihoplus*? *megarhinus* (previously placed in *Dicerorhinus* or *Stephanorhinus*) is generally considered to be MN14-15 (Guérin, 1980, 1982a; Heissig, 1996), this species is found in Baccinello V3 and Arc-près-Gray (=Autrey) (Guérin, 1980; Heissig, 1996), localities which belong probably to MN13 (Made et al., 2006; Made and Stefanovic, 2006). It is also present in the locality of Hajnácka (Fejfar, 1964), a locality that is generally placed in MN16 (Bruijn et al., 1992).

The rhinoceros from Camp dels Ninots is probably *Stephanorhinus jeanvireti*, rather than *S. miguelcrusafonti* or *Dihoplus? megarhinus*. The age of Camp dels Ninots is thus comprised between the last appearance of *Parabos/Alephis*, MN15 or possibly in MN16, and the first appearance of *Stephanorhinus jeanvireti* in MN16, while the other species give less precise age indications. This suggests that Camp dels Ninots should be palced around the MN15-16 transition, or slightly later. Agustí et al. (2001) situated the MN15-16 boundary between the Kaena and Mammoth events, around 3.2Ma, while the MN16-17 transition was dated around 2.5Ma. In the context of the Spanish Pliocene large mammal succession, the extraordinary record of Camp dels Ninots is therefore situated between the well known sites of Layna (MN15; Pérez and Soria, 1990) and Villaroya (MN16; Villalta, 1952; Agustí and Oms, 2001).

Palaeobiogeography

The record in Camp dels Ninots is interestingly both geographically and chronologically close to the limits of distribution of the Tapiridae in this part of the world (Fig. 7). Being frugivores and folivores and being short legged with large lateral toes, tapirs are adapted and limited to humid and closed environments with a low degree of seasonality. Their distribution and abundance in time and space has fluctuated greatly, presumably reflecting the distribution of their favored habitat.

Tapiridae were already present in Europe during the Oligocene and earliest Miocene and in Spain, they are known from Cetina de Aragón (Zaragoza; Fig. 7A) and Valquemado (Cuenca) (Cerdeño and Ginsburg, 1988). Around the Early–Middle Miocene transition Tapiridae disappeared from Europe (as well as from America–this time is called the "tapir-vacuum"). The genus *Tapirus* probably originated in Asia and dispersed during the Middle Miocene into Europe, where it is represented by three to four middle and large sized species (Made and Stefanovic, 2006). The latest Aragonian and the Vallesian were a time when humid closed environments were widespread and seasonality was not very strong. At this time, tapirs were more abundant and widespread, reaching Spain, where the species *Tapirus priscus* is found in the localities El Firal (Seu de Urgell) and Can Llobateres and Can Ponsic II (Vallés Penedés) (Golpe-Posse and Crusafont Pairo, 1982; Made and Stefanovic, 2006). During the Vallesian Crisis, *Tapirus* went extinct in Europe, but the rare small Late Miocene tapir *Tapiriscus pannonicus* appeared, which is known from Spain from Camallera II (*Tapirus arvernensis* of Gómez-Alba, 1988). During the latest Miocene, there was a new peak in abundance, when the species *Tapirus arvernensis* appeared. This species lasted till the Late Pliocene, peaking again between some 3 and 4Ma ago and going extinct around 2.5Ma ago (Made and Stefanovic, 2006). The record from Camp dels Ninots belongs to this last phase.

Bovids of the type of *Parabos* and *Alephis* seems to be rare in the fossil record if we compared with other groups. Figure 7B shows all occurrences we could trace from the literature (without revision–revision might lead to the exclusion of some localities with poor remains). The temporal distribution and number of occurrences of this group is comparable to that of *Tapirus arvernensis*. However, its geographic distribution seems to be wider (e.g., southern Spain, southern Italy, Greece and Turkey) and the concentrations of the localities differ (in SE France, while the *Tapirus arvernensis* localities are concentrated in central Italy). This suggests that their optimal habitats were different. Probably, bovids tolerated more open or dry habitats.

Guérin (1980) listed 13 localities with *Stephanorhinus jeanvireti*, four in central and eastern France and seven in northern Italy. Figure 7C shows these localities as well as the other occurrences cited in the literature (without revision). The species is known from but few localities. The new finds extend the known range into Spain. Unlike the geographical distribution of *Parabos* and *Alephis*, the known distribution of *S. jeanvireti* does not extend beyond the ranges of the distribution of tapirs, suggesting that it may have preferred a similar habitat.

The current geographical range of *Mauremys leprosa* extends from the Iberian Peninsula to Northern Africa. It is known from the early Pliocene (Ruscinian) of Algeria (de Lapparent de Broin, 2000), but until now the oldest record of this species in Europe was in the Pleistocene. If one considers this species as distinct from *M. gaudryi* from Perpignan, the record from Camp dels Ninots extends considerably the range of this species to the north of the Mediterranean during the Pliocene.

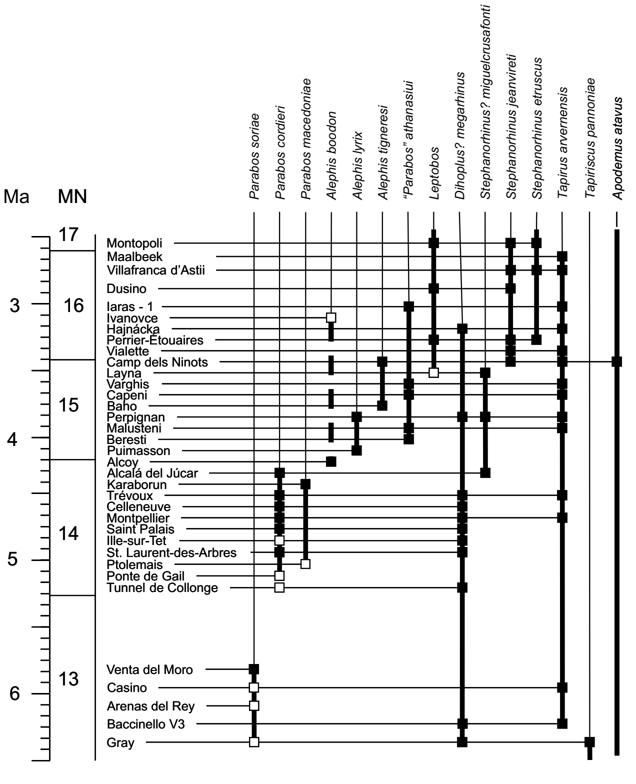

FIGURE 6 | The temporal distribution of the Bovidae *Parabos, Alephis* and the earliest *Leptobos*, selected Villafranchian Rhinocerotidae and *Tapirus* (largely based on Gromolard, 1981; Guérin, 1980; Radulescu et al., 2003; Mazo, 1997; Morales, 1984; Made and Stefanovic, 2006). Age in millions of years (Ma) and MN units (Mein, 1975; Bruijn et al., 1992) on the left. Solid squares indicate presence and open squares indicate a certain degree of doubt ("cf.", "aff." or "?"). Assignments by Gromolard (1981) based on just a fragment of a tooth or bone are generally indicated by open squares. No attempt was made to synonymize species or to correct assignments. The solid lines highlight the stratigraphic range as a result of the given occurrences.

Taphonomy

Detailed taphonomic studies have not yet been carried out at Camp dels Ninots, but some palaeontological and geological observations can assist preliminary hypotheses on taphonomic and preservation processes.

Horizontal scattering of both large and small vertebrates (and fossil record in general) at Camp dels Ninots seems to be the rule, and the finds are from distant areas such as Can Argilera and the Butano Sector (see Fig. 3) and from different levels of the sedimentary succession, though most complete skeletons as well as other fossils are from unit 2 (greenish laminated clays with diatoms) and in particular subunit 2.3 (interval with isolated sandstones). It is yet unclear whether such fossils belong to a single level (what could indicate a single mass mortality event) or are spread within the subunit (indicating several events or a period of enhanced preservation). Large vertebrate bones are generally found as complete skeletons in full anatomical connexion, but post-depositional processes (slumping, faulting, etc.) seem to have a significant role in carcass completeness. Large skeletons are found within fine grained sediments (mostly laminated mudstones), ruling out corpse transport by currents.

Large mammal bone preservation always belongs to "weathering stage 0" (Behrensmeyer, 1978), indicating minimal (if any) weathering. In all cases, body position seems to follow the same pattern: limbs are in a completely relaxing position lying on their side and in a parallel arrangement. This, together with the sedimentological observations made above, seems to indicate that large mammals sank to the bottom of the lake soon after death. Large mammal corpses were not scavenged, but sank undamaged to the bottom of the lake. This type of occurrence is also found in other maar sites such as Messel (Wuttke, 1992a).

Deposition at the lake bottom is (at least for some periods) likely to have taken place in oxygen depleted waters (being stratified, with hypolimnion), as evidenced by the fossilization of soft tissues and the absence of bioturbation. This setting resembles that of other maar lake sites such as that of Messel (Wuttke, 1992a, b).

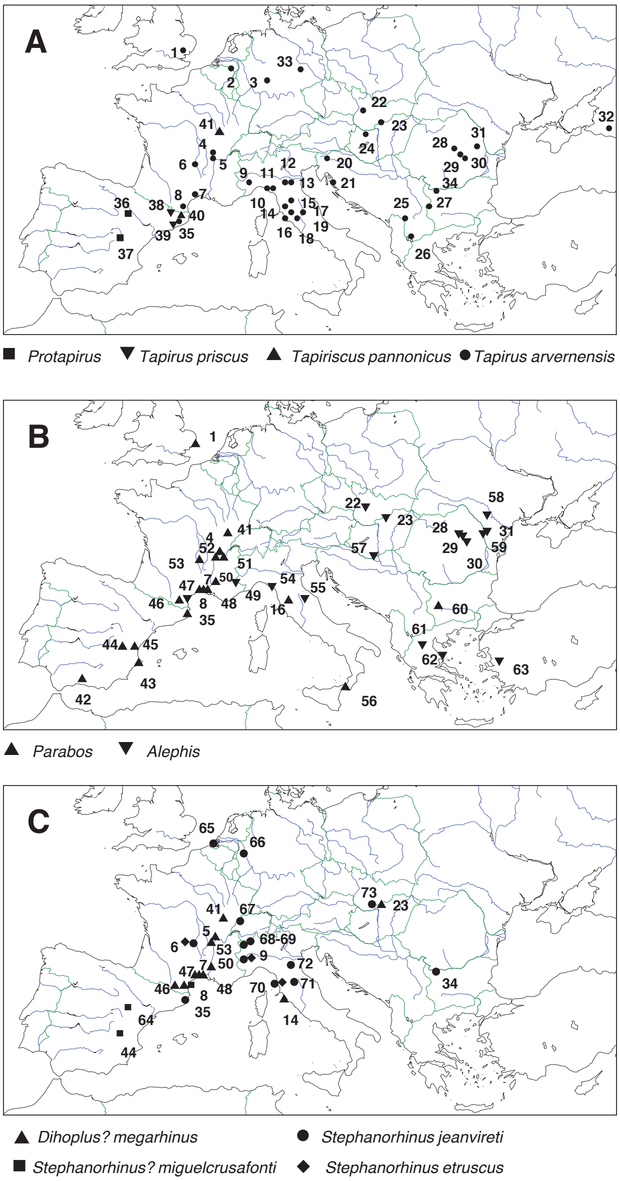

FIGURE 7 | Maps showing the distribution of taxa discussed in the text. A) *Tapirus arvernensis,* the Spanish localities with Tapiridae, and the youngest locality with *Tapiriscus* (after Van der Made and Stefanovic, 2006; additions from: Guérin, 1980; Spassov, 2005). B) *Parabos* and Alephis (after Gromolard, 1981; Morales, 1984; Mazo, 1997; Radulescu et al., 2003; Spassov, 2005; Cuscani Politi, 1979; Dallan, 1988). C) *Stephanorhinus jeanvireti* (after Guérin, 1980; additions from Lacombat and Mors, 2008; Holec, 1996; Bianucci et al., 2001; Campanino et al., 1994; Hooijer, 1981) and a selection of localities with other rhinoceroses mentioned in the text (after Guérin, 1980). Legend: 1) Red Crag; 2) Maalbeek; 3) Wölfersheim; 4) Changny (Tapirus), Autrey (*Tapirus, Parabos*); 5) Trévoux (*T, D), Mont Merle (T*); 6) Étouaires (*T, Sj, Se*), Le Coupet (*T*), Vialette (*T, Sj*); 7) Montpellier; 8) Perpignan; 9) Villafranca; 10) Val di Magra: Sarzanello, Ponzano-Magra; 11) Garfagnana: Barga, Pieve Fosciata; 12) Vignola; 13) Livergnana, Sasso di Glosina; 14) Casino; 15) Upper Valdarno: Gavile, Santa Barbara; 16) Baccinello V3; 17) Monticchiello; 18) Nera Montoro, Castel San Pietro; 19) Spoleto; 20) Sostanje; 21) Brebir; 22) Ivanovce; 23) Hajnácka; 24) Sütö; 25) Djonai; 26) Zivojno; 27) Hrabarsko; 28) Varghis (*T, A*), Araci-Fântâna Fagului (*T*); 29) Capeni; 30) Iaras 1 (*T, A*), Ilieni (*T, A*); 31) Malusteni; 32) Stavropol; 33) Sülzheim; 34) Musselievo; 35) Camp dels Ninots; 36) Cetina de Aragón; 37) Valquemado; 38) El Firal; 39) Can Llobateres, Can Ponsic I; 40) Camallera; 41) Gray (*Tp, P*), Vallay (*P*); 42) Arenas del Rey; 43) Alcoy; 44) Alcalá del Júcar; 45) Venta del Moro; 46) Ille-sur-Têt; 47) Saint Palais; 48) Celleneuve; 49) Puimasson; 50) St. Laurent-des-Arbres; 51) Jassans-Riottier; 52) Túnel de Collonges; 53) Pont-de-Gail; 54) Montecarlo; 55) Val di Pugna; 56) Gravitelli; 57) Kislang; 58) South Bessarabia; 59) Beresti; 60) Lozenets; 61) Ptolemais; 62) Karaboroun; 63) Esme-Manissa; 64) Layna; 65) Schelde; 66) Hambach; 67) Desnes–Vincent; 68) Dusino; 69) Roatto; 70) Montopoli (*Sj, Se*), Sienna (*Sj*); 71) Lower Valdarno, Capannoli; 72) Monte San Pietro, Pradalbino; 73) Nova Vieska.

CONCLUSIONS

In this paper we present the first results obtained from the study of a new Konservat-Lagerstätte site of Pliocene age, the Camp dels Ninots, putting particular emphasis on the new data on vertebrate fossils.

The vertebrate taxa identified until now are the bovid *Alephis tigneresi*, the rhinoceros *Stephanorhinus jeanvireti*, the tapir *Tapirus arvernenis*, the rodent *Apodemus atavus*, the turtle *Mauremys leprosa*, two newts, cf. *Pleurodeles* sp. and *Lissotriton* aff. *helveticus*, the frog *Pelophylax* cf. *perezi* and freshwater fishes (*Leuciscus* ?). There are also numerous plant remains but no invertebrate fossils. The large mammal association is suggestive of the transition of units MN15 and 16, and an age of about 3.2Ma.

Noteworthy is the presence of *Mauremys leprosa* and *Pelophylax perezi* in Camp dels Ninots, as they constitute the oldest record in Europe of these species, which were previously known only in the Pleistocene.

Tapirus arvernensis from Camp dels Ninots represents the southernmost occurrence in SW Europe and is also close to the southernmost record of several Miocene species of tapirs. The limits of distribution of tapirs and presumably of their preferred habitat (closed humid environments) reached Spain several times, suggesting some degree of stability of the distribution of these environments.

This exceptional site not only provides a unique chance to study the ecosystem of the area for this age, but also will contribute to better understand other significant maar lagerstätten sites such as Eckfeld or Messel (Eocene, Germany) and Las Higueruelas (Pliocene, Spain) among others.

We hope that future excavation campaigns will deliver more and better palaeontological and palaeobotanical material and geological information to enable us to get to know and understand the site better, as well as its taphonomy and its palaeoenvironment during the Pliocene.

ACKNOWLEDGMENTS

We thank the Montalat, Esteve Miquel and Cateura families and Repsol YPF, who gave permission to excavate on their fields, as well as all those who have participated in the fieldwork. The comments and changes carried out as a result of the revision process strongly contributed to improve the manuscript. The editorial work by L. Cabrera, X. Delclòs and J. M. de Gibert are highly appreciated. This paper has benefited from contributions from the Town Council of Caldes de Malavella, the Departament de Cultura i Mitjans de Comunicació de la Generalitat de Catalunya and the projects CGL2008-03881, CGL2009-7896 and CGL2009-12703-C03 (DGI, Ministerio de Ciencia e Inovación), and SGR2009-324 (Gencat). H.-A. Blain thanks J.E. González Fernández for access to the amphibian and reptile material of the Museo Nacional de Ciencias Naturales. D. Riba has a grant from Fundación Atapuerca. Our thanks to Charles Duke for revision of this article.

REFERENCES

Aguilar, J.P., Michaux, J., Bachelet, B., Calvet, M., Faillat, J.P., 1991. Les nouvelles faunes de rongeurs proches de la limite Mio-Pliocène en Roussillon. Palaeovertebrata, 20(4), 147-174.

Agustí, J., Oms, O., 2001. On the age of the last hipparionine faunas in western Europe. Paris, Comptes Rendus de l'Académie des Sciences, 332, 291-297.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth Science Reviews, 52, 247-260.

Arambourg, C., Piveteau, J., 1929. Les Vertébrés du Pontien de Salonique. Annales de Paléontologie, 18(2-3), 59-139, 3-14.

Araña, V., Aparicio, A., Martín Escorza, C., García Cacho, L., Ortíz, R., Vaquer, R., Barberi, F., Ferrara, G., Albert, J., Gassiot, X., 1983. El volcanismo neógeno-cuaternario de Cataluña: caracteres estructurales, petrológicos y geodinámicos. Acta Geológica Hispánica, 18, 1-17.

Ash, A., Ellis, B., Hickey, L.J., Jonson, K., Wilf, P., Wing, S., 1999. Manual of leaf architecture–morphological description and categorization of dicotyledonous and net-veined monocotyledoneous angiosperms. Washington, Smithsonian Institution, 65pp.

Bachelet, B., 1990. Muridae et Arvicolidae (Rodentia, mammalia) du Pliocène du sud de la France: systématique, évolution, biochronologie. Doctoral Thesis. Montpellier, Université de Montpellier, 180pp.

Barrón, E., 1996. Estudio tafonómico y análisis paleoecológico de la macro y microflora miocena de la cuenca de la Cerdaña. Doctoral Thesis. Madrid, Universidad Complutense de Madrid, 773pp.

Barroso-Ruiz, C., Bailon, S., 2003. Los anfibios y los reptiles del Pleistoceno superior de la Cueva del Boquete de Zafarraya. In: Barroso-Ruiz, C. (ed.). El Pleistoceno superior de la Cueva del Boquete de Zafarraya. Junta de Andalucía, Consejería de Cultura, Arqueología Monografías, 267-278.

Bataller, J.R., 1933. Condiciones geológicas de las aguas minerales de Cataluña. Barcelona, Laboratorio de Geología del Seminario de Barcelona, 8, 84pp.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology, 4, 150-162.

Bianucci, G., Mazza, P., Merola, D., Sarti G., Cascella, A., 2001. The early Pliocene mammal assemblage of Val di Pugna (Tuscany, Italy) in the light of calcareous planckton biostratigraphical data and paleoecological observations.

Rivista Italiana di Paleontologia e Stratigrafia, 107(3), 425-438.

Blain, H.-A., 2005. Contribution de la Paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. Doctoral Thesis. Paris, Muséum national d'Histoire naturelle, Institut de Paléontologie Humaine, 402pp.

Bruijn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., Heizmann, E., Mayhew, D.F., Van der Meulen, A.J., Schmidt-Kittler, N., Telles Antunes, M., 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters on Stratigraphy, 26(2-3), 65-118.

Büchel, G., 1993. Maars of the Westeifel, Germany. Lecture Notes in Earth Sciences, 49, 1-13.

Burjachs, F., López-Sáez, J.A., Iriarte, M.J., 2003. Metodología arqueopalinológica. In: Buxó, R., Piqué, R. (eds.). La recogida de muestras en arqueobotánica: objetivos y propuestas metodológicas. Barcelona, Museu d'Arqueologia de Catalunya, 11-18.

Campanino, F., Forno, M.G., Mottura, A., Ormezzano, D., Sala, B., 1994. *Sterphanorhinus jeanvireti* (Guérin) 1972 (Rhinocerotidae, Mammalia) from Roatto near Villafranca d'Asti, NW Italy. Revision of the specimen from Dusino. Torino, Bolletino del Museo Regionale di Scienze Naturali, 12(2), 439-499.

Cerdeño, E., Ginsburg, L., 1988. Les Tapiridae (Perissodactyla, Mammalia) de l'Oligocène et du Miocène Inférieur Européens. Annales de Paléontologie, 74(2), 71-96.

Claude J., Tong H., 2004. Early Eocene Testudinoid Turtles from Saint-Papoul, France, with Comments on the Origin of modern Testudinoidea. Oryctos, 5, 3-45.

Claude, J., Tong, H., Suteethorn, V., 2007. Turtles from the Late Eocene-Early Oligocene of the Krabi Basin (Thailand). Bulletin de la société géologique de France, Série 1, 178(4), 305-316.

Crochet, P.-A., Dubois, A., Ohler, A., Tunner, H., 1995. *Rana* (*Pelophylax*) *ridibunda* Pallas, 1771, *Rana* (*Pelophylax*) *perezi* Seoane, 1885 and their associated klepton (Amphibia, Anura): morphological diagnoses and description of a new taxon. Paris, Bulletin du Muséum national d'Histoire naturelle, 17(1-2), 11-30.

Cuscani Politi, P., 1979. Cranio di Parabos provineiente dalle formazioni plioceniche di Val di Pugna nei pressi di Siena (Toscana). Atti della Accademia dei Fisiocritici in Siena, 11, 265-278.

Dallan, L., 1988. Ritrovamento di *Alephis lyrix* nelle argille della serie lacustre du Montecarlo (Lucca) e considerazioni stratigrafiche dui depositi continentali dell'area tra el Monte Albano e il Monte Pisano. Tai Della Società Toscaza di Scienze Naturali Residente in Pisa, Memorie serie A, 95, 203-219.

Donville, B., 1976. Géologie néogène de la Catalogne orientale. Bulletin du Bureau de recherches géologiques et minières, 2(4), 177-210.

Estes, R., 1981. Gymnophiona, Caudata. In: Wellnhofer, P. (ed.). Handbuch der Paläoherpetologie, Part 2. München, Gustav Fischer Verlag, 15, 115pp.

Fortelius, M., Mazza, P., Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae) of the western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). Palaeontographia Italica, 40, 63-155.

Fejfar, O., 1964. The Lower-Villafranchian vertebrates from Hajnácka near Filákovo in southern Slovakia. Rozpravy, 30, 1-115.

Fejfar, O., Storch, G., 1990. Eine pliozäne (ober-ruscinische) Kleinsäugerfauna aus Gudersheim, Rheinhessen. I. Nagetiere: Mammalia, Rodentia. Senckenbergiana letahea, 71(1-2), 139-184.

Franzen, J.L., 1977. Urpferdchen und Krokodile-Messel vor 50 Millionen Jahren. Kleine Senckenberg-Reihe, 7, 1-36.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C., 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History, 297, 1-370.

García Catalán, S., Campeny, G., Gómez de Soler, B., Riba, D., 2007. Aportaciones preliminares al registro paleontológico de la depresión de la Selva: el yacimiento del Camp dels Ninots (Caldes de Malavella, Girona). In: Almécija, S., Casanovas-Vilar, I., Furió, M., Marmi, J., Vila, B. (eds.). Actas del III Encuentro de Jóvenes Investigadores en Paleontología. Sant Corneli (Cercs), 69-82.

García-París, M., Montori, A., Herrero, P., 2004. *Amphibia, Lissamphibia*. In: Ramos, M.A., Alba-Tercedor, J., Bellés, X., Gosálbez, J., Guerra, A., MacPherson, E., Serrano, J., Tamplado, J. (eds.). Fauna Ibérica, 24. Madrid, Consejo de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, 640pp.

Geraads, D., 1992. Phylogenetic analysis of the tribe Bovini (Mammalia: Artiodactyla). Zoological Journal of he Linnean Society, 104, 193-207.

Girard, M., Renault-Miskovsky, J., 1969. Nouvelles techniques de préparation en Palynologie appliqués à trois sédiments du Quaternaire final de l'Abri Cornille (Istres-Bouches du Rhône). Bulletin de l'Association française pour l'Étude du Quaternaire, 4, 275-284.

Goeury, C., Beaulieu, J.-L. de, 1979. À propos de la concentration du pollen à l'aide de la liqueur de Thoulet dans les sédiments minéraux. Pollen et Spores, XXI(1-2), 239-251.

Golpe-Posse, J.M., Crusafont-Paíro, M., 1982. Caracterización de *Tapirus priscus* Kaup en el Mioceno superior del Vallés-Penedés. Acta Geológica Hispánica, 17(1-2), 95-101.

Gómez de Soler, B., Campeny, G., Oms, O., García, S., Riba, D., Rosillo, R., Sala, R., 2008. El Camp dels Ninots. Intervencions arqueopaleontològiques del 2006 i 2007 (Caldes de Malavella, la Selva). L'Escala, IX Jornades d'Arqueologia de les Comarques Gironines, 13-23.

Gómez-Alba, J.A.S., 1988. Guía de Campo de los Fósiles de España y de Europa. Barcelona, Ediciones Omega S.A., 925pp.

Gómez-Merino, G., Ibáñez, N., Campeny, G., Gómez de Soler, B., 2009. Actuaciones de conservación-restauración y almacenaje de un cráneo de bóvido del yacimiento paleontológico del Camp dels Ninots (Caldes de Malavella, Girona). Presented at "I Consevation Workshop: Finding Global Solutions for Natural History Collections. In: Cancelo Fernández, C., Val Molina, S., Marigó Cortés, J., Celià Gelabert, L. (eds.). Sabadell, Servei de Publicacions de la Universitat Autònoma de Barcelona, 4 (Memòria especial), 201-210.

Gromolard, C., 1981. Les grands Bovidae (Mammalia, Artiodactyla) du Pliocène d'Europe occidentale, Biostratigraphie, Paléoneurologie, systématique, évolution, paléoécologie. Doctoral Thesis. Villeurbanne, Université Claude Bernard-Lyon I, 271pp.

Gruber, G., Micklich, N., 2007. Messel. Treasures of the Eocene. Darmstadt, Hessiches Landesmuseum Darmstadt, 159pp.

Guardia, P., 1964. Contribution à l'étude des volcans de la Province de Gerone et du paléomagnétisme de leurs coulées. Mém. du Diplôme d'Études Supérieures. París, Université de París, 56pp.

Guérin, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur en Europe occidentale. Comparaison avec les espèces actuelles. Lyon, Documents des Laboratoires de Géologie, 79(1-3), 1185pp.

Guérin, C., 1982a. Première biozonation du Pléistocène Européen, principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur d'Europe occidentale. Geobios, 15(4), 593-598.

Guérin, C., 1982b. Les Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur d'Europe occidentale comparés aux espèces actuelles: tendances évolutives et relations phylogénétiques. Geobios, 15(4), 599-605.

Guérin, C., Eisenmann, V., 1994. Les tapirs (Mammalia, Perissodactyla) du Miocene Supérieur d'Europe occidentale. Géobios, 27, 113-127.

Haller-Probst, M.S., 1997. Neues Salamandridenmaterial von süddeutschen Fundorten. Bayerische Staatssammlung für Palaeontologie und Historische Geologie Mitteilungen, 37, 53-73.

Heissig, K., 1996. The stratigraphical range of fossil rhinoceroses in the late Neogene of Europe and the Eastern Mediterranean. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.W. (eds.). The evolution of Western Eurasian Neogene Mammal Faunas. New York, Columbia University Press, 339-347.

Heissig, K., 1999. Family Rhinocerotidae. In: Rössner, G., Heissig, K. (eds.). The Miocene land mammals of Europe. München, Verlag Dr. Friedrich Pfeil, 175-188.

Holec, P., 1996. A Plio-Pleistocene large mammal fauna from Strekov and Nova Vieska, south Slovakia. Acta Zoologica Cracoviensia, 39(1), 219-222.

Hooijer, D.A., 1981. The first rhinocerotid of the Pretiglian "black bones" fauna from the Netherlands. Netherlands Journal of Zoology, 31(2), 472-475.

Lacombat, F., T. Mörs, 2008. The northernmost occurrence of the rare Late Pliocene rhinoceros *Stephanorhinus jeanvireti* (Mammalia, Perissodactyla). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 249(2), 157-165.

Lapparent de Broin, F. de, 2000. African Chelonians from the Jurassic to the Present. A preliminary catalog of the African fossil chelonians. Palaeontologia Africana, 36, 43-82.

Linder, H., Gabriel, G., Götze, H-J., Kaeppler, R., Suhr, P., 2006. Geophysical and geological investigation in the Upper Lusatia region (East Saxony). Zeitschrift der Deutschen Gesellschaft für Geowissenschaften, 157(3), 355-372.

López-Polín, L., Roubach, S., Gómez de Soler, B., Campeny, G., 2010. Prelimimary consolidation tests of fossil plant imprints form the Camp dels Ninots site (Caldes de Malavella, Girona, Spain). Presented at "I Consevation Workshop: Finding Global Solutions for Natural History Collections". In: Cancelo Fernández, C., Val Molina, S., Marigó Cortés, J., Celià Gelabert, L. (eds.). Sabadell, Servei de Publicacions de la Universitat Autònoma de Barcelona, 4 (Memòria especial), 233-239.

Llopis Lladó, N., 1943. Estudio hidrogeológico de los alrededores de Caldas de Malavella (Gerona). Speleon, II, 103-164.

Llorente, G.A., Arano, B., 1997. *Rana perezi*. In: Pleguezuelos, J.M., Martínez-Rica, J.P. (eds.). Distribución y Biogeografia de los anfibios y reptiles de España. Universidad de Granada, Monografias Revista Española de Herpetología, 3, 164-166.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de Léón, M., Zollikofer, C., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agustí, J., Kahlke, R., Kiladze, G., Martínez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. Nature, 449, 305-310.

Lorenz, V., 2000. Formation of maar-diatreme volcanoes. Terra Nostra, 6, 284-291.

Lutz, H., Kaulfuss, U., 2006. A dynamic model for the meromictic lake Eckfeld Maar (Middle Eocene, Germany). Zeitschrift der Deutschen Gesellschaft für Geowissenschaften, 157(3), 433-450.

Made, J. van der, Stefanovic, I., 2006. A small tapir from the Turolian of Kreka (Bosnia) and a discussion on the biogeography and stratigraphy of the Neogene tapirs. Monatsheften, Neues Jahrbuch für Geologie und Paläontologie, 240(2), 207-240.

Made, J. van der, Morales, J., Montoya, P., 2006. Late Miocene turnover in the Spanish mammal record in a wider context. Palaeogeography, Palaeoclimatology, Palaeoecology, 238, 228-246.

Made, J. van der, Mateos, I., 2010. Longstanding biogeographic patterns and the dispersal of early Homo out of Africa and into Europe. Quaternary International, 1223-1224, 195-200. doi 10.1016/j.quaint.2009.11.015.

Martín-Serrano, A., Vegas, J., García-Cortés, A., Galán, L., Gallardo-Millán, J.L., Martín-Alfageme, S., Rubio, F.M., Ibarra P.I., Granda, A., Pérez-González, A., García-Lobón, J.L., 2009. Morphotectonic setting of maar lakes in the Campo de Calatrava Volcanic Field (Central Spain, SW Europe). Sedimentary Geology, 222, 52-63.

Marini, L., Vetuschi Zuccolini, M., Saldi, G., 2003. The bimodal pH distribution of volcanic lake waters. Journal of Volcanology and Geothermal Research, 121, 83-98.

Mazo, A.V., 1997. El yacimiento Rusciniense de Alcalá del Júcar (Albacete). Estudios Geológicos, 53, 275-286.

Mein, P., 1975. Proposition de biozonation du Néogène méditerranéen à partir des mammifères. Madrid, Trabajos sobre Neógeno-Cuaternario, 4, 112p.

Mertz, D.F., Swisher, C.C., Franzen, J.L., Neuffer, F.O., Lutz, H., 2000. Numerical dating of the Eckfeld maar fossil site, Eifel, Germany: a calibration mark for the Eocene time scale. Naturwissenschaften, 87, 270-274.

Michaux, J., Aguilar, J.P, Calvet, M., Duvernois, M.P., Sudre, J., 1991. *Alephis tigneresi* nov. sp., un Bovidé nouveau du Pliocène du Roussillon. Geobios, 24(6), 735-745.

Montoya, P., Ginsburg, L., Alberdi, M.T, Van der Made, J., Morales, J., Soria, M.D., 2006. Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. Geodiversitas, 28(1), 137-173.

Morales, J., 1984. Venta del Moro: su macrofauna de mamíferos, y biostratigrafía continental del Mioceno Terminal mediterraneo, Madrid, Editorial de la Universidad Complutense de Madrid, 340pp.

Neuffer, F.O, Gruber, G., Lutz, H., (eds.), 1994. Fossillagerstätte Eckfelder Maar. Mainz, Mainzer Naturwiss Arch, Beiheft, 16, 222pp.

Oms, O., Gómez de Soler, B., Campeny, G., Sala, R., Agustí, J., Van der Made, J., Burjachs, F., 2008. Trapped inside a volcano: the fossil record at the maar site of el Camp dels Ninots (Pliocene, Catalonia). Oslo, August 6-14, 33rd International World Geological Congress (IGC). Symposia HPF-01 General contributions to paleontology and historical geology, Abstract CD-ROM, 69p.

Pasquier, L., 1974. Dynamique évolutive d´un sous-genre de Muridae *Apodemus* (*Sylvaemus*). Etude biométrique des caràcteres dentaires de populations fósiles et actuelles d'Europe occidentale. Doctoral Thesis. Montpellier, Université de Montpellier, 176pp.

Pérez, B., Soria, D., 1990. Análisis de las comunidades de mamíferos del Plioceno de Layna (Soria) y La Calera (Teruel). Paleontología y Evolució, 23, 231-238.

Pirrung, M., Fischer, C., Büchel, G., Gaupp, R., Lutz, H., Neuffer, F.-O., 2003. Lithofacies sucession of maar crater deposits in the Eifel area (Germany). Terra Nova, 15, 125-132.

Pous, J., Solé Sugrañes, L., Badiella, P., 1990. Estudio geoeléctrico de la depresión de La Selva (Girona). Acta Geológica Hispánica, 25(4), 261-269.

Radulescu, C., Samson, P.M, Petculescu, A., Stiuca, E., 2003. Pliocene large mammals of Romania. Coloquios de Paleontología, 1, 549-558.

Rage, J.-C., Bailon, S., 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). Geodiversitas, 27(3), 413-441.

Roca, E., 1996. La evolución geodinámica de la Cuenca Catalano-Balear y áreas adyacentes desde el Mesozoico hasta la actualidad. Acta Geológica Hispánica, 29(1), 3-25.

Roca, E., Sans, M., Cabrera, L., Marzo, M., 1999. Oligocene to Middle Miocene evolution of the central Catalan margin (northwestern Mediterranean). Tectonophysics, 315, 209-233.

Sachse, M., 2005. A remarkable fossiliferous mass flow deposit in the Eocene Eckfeld Maar (Germany)-sedimentological, taphonomical, and palaeoecological considerations. Facies, 51, 173-184.

Sanchíz, B., 1977. Nuevos anfibios del Neogeno y Cuaternario de Europa. Origen, desarollo y relaciones de la batrachofauna española. Doctoral Thesis. Madrid, Universidad Complutense de Madrid, 863pp.

Sanchíz, B., 1998. Salentia. In: Wellnhofer, P. (ed.). Handbuch der Paläoherpetologie, tome 4. München, Verlag Dr. Friedrich Pfeil, 275pp.

Sanz de Siria, A., 1987. Datos para el conocimiento de las floras pliocénicas de Cataluña. Paleontología y Evolució, 21, 295-303.

Solé Sabarís, L., 1946. Características hidrogeológicas de los manantiales carbónicos de Gerona llamados Fonts Picants. Anales del Instituto de Estudios Gerundenses, 1, 236-269.

Spassov, N., 2005. Brief review of the Pliocene ungulate fauna of Bulgaria. Quaternaire, 2, 201-212.

Tassone, A., Roca, E., Muñoz, J.A., Cabrera, L., Canals, M., 1994. Evolución del sector septentrional del margen continental catalán durante el Cenozoico. Acta Geologica Hispanica, 29(2-4), 3-37.

Varekamp, J.C., Pasternack, G.B., Rowe, G.L.Jr. 2000. Volcanic lake systematics II. Chemical constraints Journal of Volcanology and Geothermal Research, 97, 161-179.

Vehí, M., Pujadas, A., Roqué, C., Pallí, L., 1999. Un edifici volcànic inèdit a Caldes de Malavella (La Selva, Girona): el Volcà del Camp dels Ninots. Quaderns de la Selva, 11, 45-72.

Vehí, M., Bach, J., Roqué, C., Linares, R., 2005. Relationship between thermal ground-water and environmental genesis of wetlands: The case of the Prats de Sant Sebastià, northwestern Mediterranean margin. Journal of soil and water conservation, 60(6), 331-338.

Vicente, J., 1985. Troballa d'un *Leptobos* a Caldes de Malavella (La Selva). Societat d'Història Natural, Butlletí del Centre d'Estudis de la Natura del Barcelonès Nord, 1(1), 86-88.

Vicente, J., 1988. La flora fòssil de Montjuïc (Barcelona). Sèrie monogràfica, 1. Santa Coloma de Gramenet, Societat d'Història Natural, Institut d'Estudis de la Natura del Barcelonès Nord, 1-93.

Vidal, Ll.M., 1882. Estudio geológico de la estación termal de Caldas de Malavella (Gerona). Boletín de la Comisión del Mapa Geológico de España, 9, 65-91.

Villalta, J.F. de., 1952. Contribución al conocimiento de la fauna de mamíferos fósiles del Plioceno de Villaroya (Logroño). Boletín del Instituto Geológico y Minero de España, 64, 3-203.

Wuttke, M., 1992a. Death and burial of the vertebrates. In: Schaal, S., Ziegler, W. (eds.). Messel. An insight into the history of life and of the Earth. Oxford, Clarendon Press, 263-275.

Wuttke, M., 1992b. Conservation-dissolution transformation. On the behaviour of biogenic materials during fossilization. In: Schaal, S., Ziegler, W. (eds.). Messel. An insight into the history of life and of the Earth. Oxford, Clarendon Press, 263-275.

Zeuner, F., 1934. Die Beziehungen zwischen Schädelform und Lebensweise bei den rezenten und fossilen Nashörnern. Berichte der Naturforschende Gesellschaft, 34, 21-80.

Manuscript received April 2010;
revision accepted December 2010;