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Els Casots (Subirats, Catalonia), a key site for the Miocene vertebrate record of Southwestern Europe

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ABSTRACT

Els Casots is one of the richest fossil vertebrate sites of the Vallès-Penedès Basin (Catalonia, Spain). It was discovered in 1989 and excavated briefly during the 1990s, resulting in the recovery of thousands of remains and the erection of several new mammal species. Excavations resumed in 2018 and continue to date. Here we provide updated results regarding the age, stratigraphy, biota and palaeoenvironment of the site. The age of the site is well constrained to ~15.9 Ma thanks to recent bio- and magnetostratigraphic data, thus coinciding with the onset of the Miocene Climatic Optimum (MCO). The stratigraphic succession at the site area indicates lacustrine to palustrine environments with cyclically oscillating water level. There are several fossiliferous layers that have yielded a vertebrate fauna comprising up to 74 different vertebrate species including amphibians, reptiles, birds and mostly mammals. The finding of several articulated partial skeletons indicate that the site records an autochthonous to parautochthonous assemblage. The abundance and completeness of the vertebrate remains together with a well-constrained age and detailed stratigraphic and palaeoenvironmental data, make els Casots a key site for understanding wetland ecosystems in southern Europe during the MCO.

KEYWORDS: Miocene Climatic Optimum, fossil vertebrates, taphonomy, palaeoenvironment, Vallès-Penedès Basin, Spain

Introduction and historical overview

The Early to Middle Miocene transition was a crucial period marked by important climatic and faunal changes. The former notably comprise the Miocene Climatic Optimum (MCO), the warmest interval since the late Eocene, which peaked between ~17–15 Ma (Zachos et al. 2001). This interrupted the long-term Cenozoic cooling trend and Antarctic ice-sheet build up (Shevenell et al. 2008; Foster et al. 2012), resulting in estimated mid-latitude atmospheric temperatures 5–7° C warmer than today (Steinthorsdottir et al. 2021). The MCO coincided with a series of faunal dispersals, such as those of modern cricetid rodents or bovids which —contrary to earlier Miocene dispersals (e.g., those between Africa and Eurasia)— were not facilitated by new continental connections. During the Miocene these newcomers would replace older groups of Palaeogene origin and 'modernise' the mammal faunas. This time interval is well represented in several Spanish basins, such as the Calatayud-Montalbán Basin (Aragon; Van der Meulen et al. 2012; García-Paredes et al. 2016), the Magro Basin (Valencia; Ruiz Sánchez et al. 2003), the Ribesalbes-Alcora Basin (Valencia, Crespo et al. 2019) or the Bardenas Reales (Navarra) in the Ebro Basin (Suárez-Hernando 2017). However, their record mostly consists of microvertebrates, larger mammals being generally scarce. By contrast, the Vallès-Penedès Basin (Catalonia) presents a rich record for the Early/Middle Miocene transition that includes several sites that have yielded both large and small vertebrates. Amongst these, els Casots stands out as one of the richest sites of the whole basin, including thousands of specimens, often exceptionally complete.

Els Casots (note that the correct toponym according to the Cartographical and Geological Institute of Catalonia is 'els Casots', with 'els' not capitalized) pertains to the municipality of Subirats (l'Alt Penedès), less than 40 km away from Barcelona. During the late 19th century, several short-lived lignite mines were active near els Casots and eventually the workers found a few fossil bones and teeth that were handled to the priest and geologist

Jaume Almera, from the Geological Museum of the Barcelona Seminary. These stand out amongst the earliest finds of fossil vertebrates in Catalonia. Almera entrusted their identification to well-known vertebrate palaeontologists of his time, such as Charles Depéret and Albert Gaudry, who ascribed them to rhinoceroses, ruminants and rodents (Almera 1898). When the mines closed no further findings were reported and eventually those given to Almera were lost or destroyed in 1936, at the beginning of the Spanish Civil War. Later, the renowned palaeontologist Miquel Crusafont, founder of the Institut de Paleontologia de Sabadell (IPS, predecessor of the Institut Català de Paleontologia Miquel Crusafont, ICP), and his collaborators surveyed the mine surroundings and only found some fossil plants but not vertebrates (Crusafont et al. 1955). Finally, in 1989 Toni Adell, an amateur fossil hunter found several bones on the surface of a vineyard close to the ancient mines (Figure 1a) and these were reported to S.M.S from the IPS (Moyà-Solà and Rius Font 1993). Systematic excavations followed between 1989 and 1993, resulting in the recovery of more than 3,000 macrovertebrate remains from different fossiliferous levels (Moyà-Solà and Rius Font 1993). In addition, samples from some levels were screen-washed and yielded hundreds of identifiable micromammal teeth. All the recovered fossils were deposited at the ICP and most of them have been prepared. In 1995, the site was acquired by the municipality of Subirats and protected as cultural heritage by the Catalan government. However, excavations were interrupted in 1994, mostly because the discovery or re-excavation of major sites in the same area (e.g., Can Llobateres) required the limited funding and personnel available.

Nevertheless, the study of the fauna continued during the 1990s, mostly focusing on artiodactyls. New species such as the listriodontine suid *Eurolistriodon adelli* (Pickford and Moyà-Solà, 1995) or the palaeomerycid *Ampelomeryx ginsburgi* Duranthon et al., 1995 were erected based on material from els Casots. In the 21st century taxonomic studies expanded to consider crocodylians, rodents and small carnivorans, amongst others (see below). Yet, there are relatively few works devoted to the biota from els Casots and none summarising the characteristics and significance of the site. In 2018, after more than 20 years of inactivity, the ICP resumed fieldwork at els Casots. Yearly campaigns are currently conducted, and these include not only systematic excavation, but also geological survey and sampling to provide further insights on the age and palaeoenvironment of the site. Furthermore, several actions, such as building permanent structures to shelter main excavation areas (Figure 1b), have been undertaken by the Subirats municipality and the site is open for touristic visits upon request. Here we present an overview of the els Casots site, its geology, age, biota and palaeoenvironment based on our latest data.

Geological setting

Els Casots is located at the southern margin of the Vallès-Penedès Basin (VPB), an elongated half-graben sub-parallel to the Catalan coastline and bounded by the Catalan Coastal Ranges (Figure 2a), that was formed during the opening of the Western Mediterranean by the late Oligocene (Roca et al. 1999; Cabrera et al. 2004). The VPB sedimentary record covers most of the Miocene (from about 20 to 7 Ma) and is mainly continental except for relatively brief marine episodes that occurred during the late Burdigalian (Early Miocene), Langhian and early Serravallian (Middle Miocene), and Tortonian (Late Miocene; Casanovas-Vilar et al. 2016). Early to early Middle Miocene continental alluvial deposits interdigitate and are finally overlain by shallow to deep marine (bay, shelf) and transitional deposits (fan deltas and minor deltas, shoreline systems and saline lagoons) ranging in age from late Burdigalian to Langhian. The continental, transitional and marine facies are stacked in transgressive–regressive sequences that attained their maximum spreading and depth in the basin during the Langhian sea-level high stand.

In general, the Early to early Middle Miocene (Ramblian to early Aragonian mammal ages) terrestrial vertebrate record of the VPB is comparatively poorer than later intervals (late Aragonian and Vallesian mammal ages; Casanovas-Vilar et al. 2016). This interval is recorded by the sequences of the Lower Continental Units, a lithostratigraphical unit that crops out near the southern basin margins and at the Llobregat and Anoia river valleys. This assemblage includes intensely red alluvial fan facies sourced from the surrounding reliefs and minor cyclically arranged alluvial-shallow lacustrine units of various ages (Cabrera Pérez 1981a; Cabrera et al. 1991; de Gibert and Casanovas-Vilar 2011; Casanovas-Vilar et al. 2011, 2016). The younger alluvial-lacustrine assemblage (Subirats alluvial-lacustrine unit; Agustí and Cabrera 1980; Cabrera Pérez 1981a, 1981b) includes the site of els Casots as well as other rich fossil sites such as les Cases de la Valenciana (Crusafont et al. 1955; Jovells-Vaqué et al. 2018), Can Julià and Can Martí Vell (Crusafont et al. 1955; Agustí and Cabrera 1980; Agustí 1983). This unit unconformably overlays directly the Mesozoic basement (Cabrera Pérez 1979, 1981a, 1981b) and extends a few kilometres along the present southern basin margin between the municipalities of Gelida and Subirats (Figure 2). Els Casots is located in a continental to transitional sequence developed in an extensional faulted zone that affected both the Mesozoic basement and the Miocene cover.

Structure, stratigraphy and age of the succession

Structure and arrangement of the basement

The pre-Miocene basement at the area of els Casots consists of Mesozoic, mainly Early Cretaceous, marine carbonates (Figure 2b). To determine the basement arrangement, geophysical prospection using ERT (Electrical Resistivity Tomography) methods was conducted at the site area to infer the thickness of Miocene sediments and preliminarily study the basement morphology. ERT data were collected along two intersecting sections (Figure 2b), and they encompassed three ERT profiles. Geoelectrical results are presented along two sections built from the 2D models obtained from the ERT profiles (Figure 3). Geoelectrical section 1 (Figure 3a) shows a preferential stratified behaviour with an alternate of conductive and resistive layers gently dipping to the centre of the section. It also presents three segments (A, B, and C) where this stratification is not complete. A similar behaviour is recognized in section 2 (Figure 3b), with a horizontal stratification and an abrupt change in segment D.

The interpretation of section 1 is based on the information provided by two core samples (CS-A and CS-B, see following section and Figure 4) taken next to the section (see Figure 2b). The Cretaceous basement is identified as the bottom resistive layer (Figure 3, in blue), while the different conductive and resistive layers in the Miocene cover can be associated with the clayey and carbonate sequences described in the cores. Regions A, B, and C (Figure 3a) may be interpreted as three fractured zones affected by minor normal faults dipping to the N. In Section 2 (Figure 3b), basement identification is not straightforward because this section runs along the fractured zone B. However, this section does not present E-W changes in resistivity except in region D, which coincides with the location of the inferred NE-SW fault (Figure 2b).

Attending to the geological and geophysical data, the pre-Miocene basement at els Casots area consists of Mesozoic (mainly Early Cretaceous) marine carbonates, which make up the present surrounding reliefs. During the Early to Middle Miocene these rocks constituted a weathered, eroded and karstified palaeorelief later affected by NE-SW and NNE-SSW faults related to extensional processes in the area.

Miocene stratigraphy

The overall stratigraphy of the Subirats alluvial-lacustrine unit at els Casots has been previously described (Cabrera Pérez 1979, 1981a, 1981b). The lithological succession in the area nearby the fossil site was further studied by means of geological core sampling next to the excavation area (core CS-A; Figure 2b) and at the point of maximum thickness of Miocene sediments as inferred from ERT results (core CS-B; Figure 2b).

Core CS-B (Figure 4) reached the Mesozoic basement at 36 m of depth. A 4 m-thick deposit of clast- to matrix-supported scree breccias overlay the karstified Cretaceous basement. The often large (up to several cm in diameter) clasts are made of Cretaceous carbonates and show little rounding or are clearly subangular to angular, thus indicating that they derived from in situ substrate fragmentation. The matrix consists of mudstone that grades upwards from ochre/reddish to greenish grey due to reductive conditions associated to the lacustrine flooding. Grey mudstone including outsized limestone granules and clasts overlay the clast dominated lowermost deposits. Similar deposits overlay the basement in the surrounding outcrops (Figure 2b) and include plant, gastropod and vertebrate fossils, badly broken macrovertebrate remains and abundant micromammals (Cal Sutxet site; Jovells-Vaqué and Casanovas-Vilar 2021). The lowermost breccia unit is of variable thickness because it overlaid the pre-existing palaeorelief. This breccia unit is overlain by a 25 m-thick, cyclically-arranged mudstone/limestone succession that at the bottom includes thin (mm to dm thick) sub-bituminous coal deposits. Cycles often include a lower dark, organic matter rich term that grades upwards to grey-bluish massive mudstones with minor, scattered millimetric siderite-like ferruginous nodules. The upper part of the cycles is a carbonate term that includes a variety of bioclastic- to micrite-dominated limestones (grainstones, wackestones and mudstones) that range from a few centimetres to a maximum of a couple of meters thick (Figure 4). The carbonate facies include bioclastic laminae made up of accumulations of ostracods, charophytes and micrite-coated algal filaments. Very thin tufa-like carbonates also occur (Cabrera Pérez 1979). Thin ferruginous laminae are associated to some of the bioclastic facies. Both carbonates and siliciclastic mudstones may include abundant plant fragments and freshwater gastropod shells or casts. This lacustrine/marshy lacustrine succession has yielded abundant vertebrate fossils in the excavated area (Figure 5).

The lacustrine succession ends rather abruptly and in core CS-B grades along the uppermost 5 m into intensely reddish and mottled silts and sandstones topped by carbonate-rich pedogenic to palustrine facies (Figure 4). These palustrine facies crop out W of Cal Sutxet farmhouse (Figure 2b) and are rich in internal moulds of terrestrial gastropods but are devoid of vertebrate fossils. They are overlain by red mudstones and green/grey sandstones that record subaerial distal channelized alluvial fan facies. The continental deposits are in turn overlain by an oyster coquina and a bioclastic quartzarenite, which marks the early Langhian transgressive surface in this sector. The Langhian marine transgression and high-stand marine facies in the area record successive episodes of deposition of bioturbated sandstones overlain by grey marine bay-shelf mudstones and marls and some episodes of minor reef construction (Bessedik and Cabrera 1985; Agustí et al. 1990; Domènech et al. 2011; Casanovas-Vilar et al. 2016).

Age

Els Casots has been generally correlated to European Neogene Mammal (MN) unit MN4, which corresponds to the early Aragonian, latest Early Miocene (e.g., Agustí et al. 1990; Agustí and Llenas 1993; Duranthon et al. 1995; Pickford and Moyà-Solà 1995; Casanovas-Vilar et al. 2011a, 2011b, 2016; Jovells-Vaqué et al. 2017a). Such correlation was mostly based on the rodent fauna, which includes the early modern cricetids *Megacricetodon primitivus* and *Democricetodon hispanicus* together with the eomyid *Ligerimys ellipticus*.

However, recent studies indicate that els Casots should indeed be correlated to MN5 (Jovells-Vaqué and Casanovas-Vilar 2021). The MN4/MN5 boundary was previously defined by the extinction of the eomyid genus *Ligerimys* (e.g., Mein 1999; Kälin and Kempf 2009), which turned out to be a diachronic event in Western Europe, with the last Iberian species, *L. ellipticus*, persisting for about 0.5 million years after the extinction of the last central European species, *Ligerimys florancei* (Van der Meulen et al. 2012). However, the extinction of *L. florancei* is synchronous in both areas (~16.4 Ma), so this has been proposed as the diagnostic criterion for the definition of the MN4/MN5 boundary (Hilgen et al. 2012; Van der Meulen et al. 2012). At els Casots, only *L. ellipticus* is present (and in low numbers), suggesting a correlation to early Aragonian subzone Cb (16.15–15.94 Ma; see Van der Meulen et al. 2012), corresponding to the earliest MN5, the beginning of the Middle Miocene.

Cores CS-A and CS-B were sampled for palaeomagnetism at an average interval of 0.35 cm, collecting 57 samples from core CS-A and 78 samples from core CS-B, and additional oriented samples were taken from the fossil site on surface and the overlying, non-lacustrine sediments, up to the Langhian oyster coquina (Figure 2). Bedding dip, when observable in the cores, was taken as a reference for the orientation of palaeomagnetic samples. Both stepwise alternating field (AF) and thermal (TH) demagnetization was applied to all samples, providing comparable results. A viscous component was demagnetized at temperatures below 200º C and peak AF of 10 mT. Above this range, a stable characteristic remanent magnetization (ChRM) could be determined up to temperatures of 450º C and peak AF of 60 mT. The ChRM was ranked as Quality 1 when a linear decay was observed until complete demagnetization. As the samples from cores lacked azimuthal orientation, the polarity determination relied only on the inclination of the ChRM, positive (downwards) inclination representing normal polarity and vice versa. For caution, ChRM components yielding low inclinations (reference palaeomagnetic inclination at the site is 60º) were not considered as reliable and were ranked as Quality 2. A complementary quality check applied was the coherency of the angular relationship between the viscous and the ChRM components. Since the viscous component mostly conform to the north-directed present-day field, a reversed polarity ChRM should be roughly antiparallel to the viscous component, while a normal polarity ChRM should tend to align with the viscous component. ChRM directions meeting this condition were included in Quality 1.

Best quality results were obtained from core CS-B, with 66 samples (88%) ranked as Quality 1, compared to 25 (44%) samples of Quality 1 from CS-A. The whole series shows reverse polarity except for a normal interval determined at a depth between 12–15 m in CS-A, but not confirmed in CS-B, which yielded a palaeomagnetic signal of higher quality. Therefore, we consider this interval of normal magnetization from CS-A possibly resulted from a secondary magnetization process, unrelated with the time of deposition. Two additional normal magnetization intervals in CS-B are very thin, marked only by one sample, and were not considered relevant for correlation purposes. As already exposed, the rodent assemblage indicates a correlation to early Aragonian subzone Cb, which in the Calatayud-Montalbán Basin spans the whole normal polarity geomagnetic chron C5Cn.1n and the earliest part of the inverse polarity chron C5Br (Van der Meulen et al. 2012). Considering these data, the dominantly reverse polarity interval recorded in the cores is best correlated to chron C5Br (15.974–15.160 Ma; boundaries after Ogg 2020). Coupled with the aforementioned correlation to Aragonian subzone Cb (16.15 – 15.94 Ma; Van der Meulen et al. 2012), this results in an estimated age of ~15.9 Ma for the site of els Casots.

Excavated area and taphonomic remarks

The fossiliferous area of els Casots is huge, comprising all the fields around the farmhouses of Cal Solà and Cal Sutxet, but only a small area of about 6,200 m^2 is protected (Figures 1, 2b). For the moment being, a small surface of just 400 m^2 has been excavated, most of it during the 1990s field campaigns. Detailed stratigraphic information from the different excavated sectors (or 'spots') was recorded during the 1990s field campaigns and up to 13 stratigraphic levels (labelled A to M) were distinguished from surface to bottom (Figure 5). These represent a ~2 m thick succession consisting of mostly greyish to ochre mudstones, with occasional thin black mudstone layers. A thin layer of reddish carbonates (L) crops out at the base of the excavated sections. Mudstones are often laterally discontinuous and of variable thickness within the site area. They are rich in mollusc shell fragments and may include plant remains (mostly wood). Carbonate nodules are abundant in some levels.

Although all levels have yielded macrovertebrate fossils, level E turned out to be the most productive in the 1990s campaigns. Field campaigns since 2018 have focused on the excavation of level J, a bone bed that has yielded partially articulated specimens (Figures 6b–d, 7). Furthermore, well-preserved carnivoran coprolites and numerous wood fragments have been found at level J. Taphonomic information was recorded during both recent and older field campaigns. Macrovertebrate remains occur in high concentrations in all the excavated area laying subhorizontally, parallel to stratigraphy, and do not show signs of transport. Therefore, although detailed taphonomic analyses have yet to be conducted, we interpret that the biota from els Casots represents an autochthonous to parautochthonous assemblage. Lithostatic pressure has resulted in extensive crushing and deformation of many remains. For example, the holotype cranium of the suid *Eurolistriodon adelli* (IPS9096; Pickford and Moyà-Solà 1995: figs. 1–2) is so flattened dorsoventrally that it measures less than 5 cm in thickness. Almost all the fossils recovered during the 1990s have been prepared for study, but only a few of the most relevant specimens (such as articulated skeletons and crania) found in the new excavations are prepared.

Microvertebrates were recovered during the 1990s field campaigns after screen-washing sediment samples from three different levels (CS-72, CS-73 and CS-74, certainly equivalent to excavation level D; Figure 5) and yielded hundreds of identifiable dental remains, mostly belonging to rodents (Agustí and Llenas 1993). During the new field campaigns large amounts of sediment have been screen-washed from layers K, J and M resulting in the recovery of thousands of microvertebrate remains, which include a diverse palaeoherpetological assemblage, some bird remains and numerous rodent, lagomorph and insectivoran cheek teeth. Even if only a small part of this collection has been prepared for study and is considered here, as shown in the following sections, the amount of new information is so relevant that els Casots can be already considered a key locality for the Miocene vertebrate record of Southwestern Europe.

Biota and palaeoenvironment

Flora and invertebrates

Crusafont et al. (1955) reported a single palm leaf found near the abandoned coal mines next to els Casots. Poorly preserved leaf fragments of helophytic plants, i.e., reeds and sedges (e.g., *Typha*) and wood fragments have been recovered during the recent excavations. Sediment samples next to the excavation area have been screen-washed and yielded gyrogonites which are currently under study. The charophyte assemblage is dominated by *Chara* cf. *vulgaris* and *Chara molassica* var. *notata*. Extant *C. vulgaris* inhabits various kinds of freshwater environments, ranging from small eutrophic temporary ponds to mesotrophic lakes and rivers. Core samples from the site area (see above) were also analysed in search for palynomorphs, but without success. Invertebrates are represented at the site by fragments of ostracod carapaces, mollusc shell fragments (such as freshwater gastropods) and, in the non-lacustrine upper layers, by moulds of terrestrial gastropods. Rare benthic foraminifera (i.e., *Ammonia* sp.) also occur in the assemblage and were probably transported from nearby marine settings.

Non-mammalian vertebrates

Highly fragmentary fish dental remains have been recovered by means of screen-washing but have neither been prepared nor studied. The herpetofauna is especially diverse, including up to 24 different species (Table 1), and the available collection has increased significantly after the latest field campaigns. Amphibians include anurans and urodeles, the latter represented by just a single humerus. Anurans are more abundant, but most of the recovered remains do not allow for a confident taxonomic attribution. Based on ilial morphology, at least three different genera are present: the discoglossine alytid *Latonia* (already known from the roughly coeval site of Sant Mamet and other younger sites in the VPB; Villa et al. 2019a), the bufonid *Bufotes* (gr. *viridis*), and the ranid *Pelophylax*.

Chelonian fossils include scarce remains of the geoemydid *Ptychogaster* as well as a few disarticulated shell plates and some phalanges attributed to the medium-sized tortoise *Testudo*. The lack of diagnostic shell parts precludes an assignment to the subgenus rank for both taxa (Luján et al. 2014a, 2016). The most abundant and complete chelonian material, comprising both shell and postcranial remains, belongs to giant tortoises of the genus *Titanochelon*. The epiplastron resembles that of *Titanochelon richardi,* common in Middle to Late Miocene (MN6–MN10) sites of the VPB (Luján et al. 2014b). Squamates are by far the most diverse group in the palaeoherpetological assemblage. Gekkotans are represented by very few bones, while lacertids, whose identification is often difficult if not impossible based on isolated and fragmentary bones, are represented by at least a non-amblyodont form together with a slightly-amblyodont one (cf. *Amblyolacerta* sp.). A scincoid is also present, based on the tooth morphology of few fragmentary dentigerous elements. Several remains of non-*Anguis* anguines were recovered, especially osteoderms and vertebrae. A single fragment of an indeterminate dentigerous bone with an *Ophisaurus*-like dentition as well as at least one trunk vertebra morphologically similar to those of *Pseudopus* has been recovered. A few vertebrae and isolated teeth possibly belong to varanid lizards. Two small amphisbaenian premaxillae can be referred to a member of the western clade of *Blanus* owing to the flat morphology of their anterior outline in lateral view (Bolet et al., 2014; Villa et al. 2019b). Snakes, in turn, are mainly identified based on vertebral morphology. The most abundant taxon is a pythonid, but an indeterminate scolecophidian, an erycine boid, at least one "colubrine" (sensu Szyndlar 1991), and possibly two viperids (a large and a smaller one) are present.

Small-sized crocodylians are extremely abundant at the site, being represented by countless isolated plates, osteoderms and teeth, as well as by complete skulls. During the 2021 field campaign a complete articulated skeleton was unearthed and is currently under study. Cranial remains recovered during the 1990s field campaigns were described in detail by Díaz Aráez et al. (2017) and assigned to the diplocynodontid *Diplocynodon ratelii*. This represents the youngest record of the genus in the Iberian Peninsula.

Avian remains are rare, and most can be attributed to a medium-sized diurnal raptor showing some morphological similarities with the extant *Circaetus*. There is also evidence of a larger eagle (cf. *Aquila* sp.), an unknown nocturnal raptor (Strigidae indet.) of the size of an eagle owl, and the well-known peafowl *Miophasianus altus* and present in other sites of the VPB (Sánchez-Marco 2021).

Small mammals

Small mammals are incredibly abundant in all levels and are represented by isolated cheek teeth as well as mandibular and cranial material (Jovells-Vaqué et al. 2017b). However, only some rodent groups have been studied in detail. Els Casots records one of the latest occurrences in the Iberian Peninsula (see Furió et al. 2012) of the small marsupial *Amphiperatherium frequens*, represented by a few isolated teeth. Chiropterans are similarly rare, just a couple of molars of a small-sized taxon have been found to date. Most of the recovered eulipotyphlan remains belong to the small-sized erinaceid *Galerix symeonidisi*. Other insectivorans include the heterosoricid *Heterosorex neumayrianus*, represented by just one fissident upper incisor, a few teeth belonging to the tiny soricid *Paenelimnoecus* cf. *truyolsi*, and two unicuspids with rather strong cingula that may belong to the dimylid *Plesiodimylus*. The insectivoran assemblage is somewhat poorer than that of older sites (MN3–MN4) of the same basin, which usually record up to six different species (Van den Hoek Ostende et al. 2020). Lagomorphs are represented by the ochotonid *Lagopsis*, common in Early and Middle Miocene sites of the VPB (López Martínez 1989).

Rodents display a remarkable diversity of ground squirrels (Sciuridae) including both xerins (*Atlantoxerus idubedensis*, *Heteroxerus rubricati*) and marmotins (*Csakvaromys besana*), which were described by Aldana Carrasco (1991, 1992). Cricetids and glirids stand out as the most abundant rodents. The former, which were thoroughly described by Jovells-Vaqué et al. (2017a) and Jovells-Vaqué and Casanovas-Vilar (2021), include *Megacricetodon primitivus* and three *Democricetodon* species: *De. hispanicus,* which is the most abundant; *De. gracilis*, represented by a few small specimens; and a larger indeterminate species recorded by a single lower first molar. Interestingly, *De. hispanicus* persists for longer in the VPB than in the Calatayud-Montalbán Basin (the type area of the Aragonian; east-central Spain), where it is last recorded at 16.63 Ma (Van der Meulen et al. 2003, 2012).

Democricetodon gracilis, on the other hand, indicates faunal affinities with Central Europe, whereas it is absent in inner Iberian basins (Jovells-Vaqué and Casanovas-Vilar 2021). Glirids have only been preliminarily studied (Agustí and Llenas 1993), but up to nine different species have been identified. Many of these are characterised by their simplified dental pattern –such as *Peridyromys murinus*, *Pseudodryomys ibericus* and the three species of *Simplomys* (*S. simplicidens*, *S. robustus*, *S. julii*)– which is generally thought to reflect a preference for open and arid environments (de Bruijn and Van der Meulen 1982; Van der Meulen and Daams 1992; Van Dam 2006). *Simplomys simplicidens* and *De. hispanicus* stand out as the most abundant rodents. The remaining glirids comprise presumably arboreal species with more complex dental patterns (De Bruijn and Van der Meulen 1982; Van der Meulen and Daams 1992; Van Dam 2006), namely *Bransatoglis* sp., *Glirudinus modestus*, *Microdyromys monspeliensis* and *Muscardinus* sp., which are generally scarce. Finally, eomyids are only represented by less than ten teeth (over more than 700 identifiable rodent teeth) of *Ligerimys ellipticus*. This endemic Iberian species represents the last survivor of the genus *Ligerimys*, which disappeared from central Spain at 15.93 Ma (Van der Meulen et al. 2012).

Large mammals

Carnivorans are diverse and comprise multiple families of caniforms and feliforms. Amongst the former, amphicyonids include two undescribed species of different size, the larger one being represented by an almost complete skeleton (Figure 7a). Hemycionids are represented by *Hemicyon stehlini*. Mustelids include the gulonin *Iberictis buloti*, the oldest member of the wolverine lineage, which is abundantly represented by dental and cranial material (Figure 6a; Valenciano et al. 2020). Other mustelids comprise *Paralutra* sp., represented by two mandibles, which was likely semiaquatic (Ginsburg 1999) as well as two distinct small-sized marten-like forms ("*Martes*" sp. 1 and 2). Feliforms include herpestids, hyaenids and felids.

Herpestids are represented by *Leptoplesictis aurelianesis*, for which only few, but remarkably complete, craniodental remains have been found at the site. Concerning hyaenids, only a single mandible tentatively attributed to *Protictitherium* has been recovered. Felids are better represented by abundant postcranial and dentognathic remains belonging to the lynx-sized "*Pseudaelurus*" *lorteti*. During the 2021 field campaign, a crushed complete skull was found and is currently under study.

Rhinocerotids stand out as one of the most abundant elements of the fauna, being recorded by *Dromoceratherium mirallesi*, which was originally described from the neighboring locality of Can Julià (Gelida, MN4) by Crusafont et al. (1955). This poorly known rhinoceros is generally included in *Plesiaceratherium* (Yan and Heissig 1986) but ongoing studies of the type material and additional remains from other VPB sites support the distinction of *Dromoceratherium* (Sanisidro et al. 2018). Further rhinocerotid remains include indeterminate juvenile mandibles (Figure 6c), isolated teeth, and postcranial elements pending detailed study but certainly belonging to another species. In contrast to rhinocerotids, equids are extremely rare at els Casots, being only represented by lower molar fragment assigned to *Anchitherium* sp. (Rotgers and Alba 2011).

Artiodactyls include the small cainotherid *Cainotherium miocaenicum*, a very common element in older (MN3–MN4) sites of the same basin (see Crusafont et al. 1955; Casanovas-Vilar et al. 2016), which is much rarer at els Casots, being represented by cranial and mandibular fragments. Concerning suoids, els Casots is the type locality of two species: a small "peccary-like" suoid, included in the family Palaeochoeridae (Van der Made 2020) or Siderochoeridae (Pickford 2017), and a larger listriodontine suid. The former is best represented by a crushed skull that is the holotype of *Choeromorus ibericus* (Pickford and Moyà-Solà 1994; Pickford 2017). Alternatively, Van der Made (2020) synonymized this species with *Choeromorus primus*, with the material from els Casots representing its last appearance datum. The listriodontine is assigned to *Eurolistriodon adelli*, a species originally described based on a skull with associated skeleton from els Casots (Pickford and Moyà-Solà 1995) that is alternatively included in *Bunolistriodon* by Van der Made (2020). However, cladistic analyses indicate that *Eurolistriodon* is the sister taxon of *Listriodon* s.l. (i.e., including *Bunolistriodon*; Orliac 2006; Orliac et al. 2010). Although *E. adelli* has been cited from multiple MN4 and MN5 localities (Van der Made 1997, 2020; Pickford and Morales 2003), in the VPB it is only known from els Casots.

Ruminant remains are very abundant, including pecoran and non-pecoran forms. Among the latter, the tragulid "*Dorcatherium*" *crassum*, which belongs to a stem group distinct from *Dorcatherium* s.s. (Sánchez et al. 2018), is represented by several dentognathic fragments (Alba et al. 2014). The pecoran fauna is diverse. Palaeomerycids are abundantly represented by *Ampelomeryx ginsburgi*, a species erected based on els Casots material (Duranthon et al. 1995). *Ampelomeryx ginsburgi* is abundantly represented by partial skeletons of various individuals (Figure 6b) including complete crania. It belongs to a palaeomerycid lineage characterised by possessing flattish non-pneumatised ossicones located over 'eyebrow' supraorbital projections, and flat forked occipital appendages (Sánchez et al. 2015). Lagomerycids are rare faunal elements in the VPB, and only a few specimens (assigned either to *Lagomeryx rutimeyeri* or *Lagomeryx pumilio*) have been recovered from Early Miocene sites (Crusafont et al. 1955). The few teeth from els Casots are referred to *L. rutimeyeri* because they are clearly larger than those of *L. pumilio*. Cervids are common and, although no protoantlers have been recovered, considering some similarities with the Sant Mamet material (referred by Crusafont et al. 1955 to *Procervulus dichotomus*), we tentatively ascribe the remains to *P.* cf. *dichotomus*. Together with palaeomerycids, bovids stand out as the most abundant ruminants at els Casots, being represented by profuse dental remains and even a partial skeleton of *Eotragus* (Figure 7b). The horn cores are small, short relative to their diameter, and show no evidence of torsion. All these traits, coupled with the moderately hypsodont teeth, justify an attribution to *Eotragus noyei*.

Proboscideans include both deinotheres and gomphotheres. The former are represented by a few cheek teeth assigned by Gasamans et al. (2021) to *Prodeinotherium* cf. *bavaricum*, a species characteristic of the early Middle Miocene (MN5–MN6) of Europe. Gomphothere remains are more common and include a partial skeleton uncovered during 2019 (Figure 6d) and additional cranial and dental material from the 1990s that is here assigned to *Gomphotherium* cf. *subtapiroideum* based on dental morphology.

Palaeoenvironment

Els Casots fossil site represents a shallow freshwater lacustrine-palustrine (Figure 8) environment as evidenced by the presence of charophytes, helophytic plants, ostracods, freshwater gastropods, fishes and various semiaquatic tetrapods. The latter include a diverse amphibian fauna, pond turtles (*Ptychogaster*), and abundant remains of small-bodied crocodylians (*Diplocynodon*). The mammal assemblage also includes the semiaquatic otter *Paralutra*, the aquophilous tragulid "*Dorcatherium*", and other taxa likely linked to wetlands. For example, palaeomerycids, abundantly represented by *Ampelomeryx*, generally are thought to be associated to boggy forests and would have fed on soft leaves and aquatic vegetation (Köhler 1993; DeMiguel et al. 2014). Concerning suoids, craniodental morphology suggests that *Choeromorus* species might have fed on swamp plants too (Pickford 2012). Stratigraphic data show cyclical fluctuations in the water level, probably related to climatic cycles.

The faunal list includes some megathermic taxa, such as crocodylians, giant tortoises, monitor lizards, pythonid and boid snakes. These indicate warm conditions associated with the MCO. The small mammal assemblage is overwhelmingly dominated by the cricetids

Democricetodon and *Megacricetodon* and the terrestrial glirid *Simplomys*. Considering that the site represents a certainly humid environment, the absence of beavers (castorids) is quite unexpected. The diversity of arboreal small mammals is surprisingly low, with only four dormice (glirid) species and no tree or flying squirrels. Insectivorous small mammals are also rare and only include four insectivorans and the marsupial *Amphiperatherium*. The number of arboreal and insectivorous small mammal species has been found to be positively correlated to precipitation and environmental humidity (Van Dam, 2006), so this may indicate that at els Casots more open and arid woodland environments occurred not far from the wetlands. The larger-bodied herbivores include only browsing species, many of them of small size (e.g., *Choeromorus*, *Lagomeryx*, *Procervulus*), which likely inhabited the more forested environments (Fortelius et al. 1996) surrounding water masses. The different signal provided by small and larger mammals may result from taphonomic bias. Whereas larger mammals represent a (para-)authothonous assemblage, birds of prey are commonly the main accumulation agents of small mammal remains, which would then provide a more regional signal. This palaeoenvironmental reconstruction is congruent with macrofloral (Sanz de Siria Catalán 1993, 2001) and palynologic (Bessedik and Cabrera 1985; Jiménez-Moreno and Suc 2007) data from nearby Langhian deposits from the Penedès area, which indicate tropical to subtropical environments with seasonal rainfall. Scattered forests rich in tropical elements developed at low altitudes near humid areas, whereas far away from the wetlands more open woodlands with herbs (Poaceae, Asteraceae) and leguminous trees (e.g., *Acacia*) defined the regional vegetation (Jiménez-Moreno and Suc 2007).

Conclusions

With up to 74 different vertebrate species represented by thousands of specimens, els Casots stands out as one of the richest early MN5 sites in Europe. It includes multiple fossiliferous layers, some of them bone beds, that have yielded remarkably complete remains, including partial skeletons. Recent field campaigns enable constraining its age combining bio- and magnetostratigraphic data to ~15.9 Ma (Aragonian subzone Cb, earliest MN5, Middle Miocene) and have also provided detailed insight on the stratigraphy of the site area and structure of the pre-Miocene basement. Sedimentologic, palaeobotanic and faunal data indicate that els Casots corresponds to an ancient freshwater lacustrine or palustrine environment that developed in a tropical-subtropical climate with rainfall seasonality. Vertebrate remains represent an autochthonous to parautochthonous assemblage, as evidenced by the partial articulation of several specimens. Many large mammals appear to have inhabited the forests surrounding the water masses, while small mammals provide evidence of drier woodlands further from the wetlands. Finally, it is noteworthy that the site dates to the onset of the Miocene Climatic Optimum and provides a unique opportunity to study wetland ecosystems from southern Europe during this exceptionally warm period.

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References

Agustí J. 1983. Roedores (Mammalia) del Mioceno Inferior de Can Martí Vell (Vallès-Penedès, Cataluña, España). Estud Geol. 39:417–430.

Agustí J, Cabrera L. 1980. Nuevos datos sobre la biozonación del Burdigaliense continental de la cuenca del Vallès-Penedès. Acta Geol Hisp. 15:81–84.

Agustí J, Cabrera L, Domènech R, Martinell J, Moyà-Solà S, Ortí F, de Porta J. 1990. Neogene of the Penedès area (Prelittoral Catalan Depression, NE Spain). Paleontol Evol. mem. espec. 2:187–207.

Agustí J, Llenas M. 1993. Los roedores del Mioceno Inferior de Els Casots (Vallés-Penedés). Nota preliminar. In: González Donoso, J.M., editor. Comunicaciones de Las IX Jornadas de Paleontología; Oct 28–30; Málaga: Universidad de Málaga, p. 70–72.

Alba DM, DeMiguel D, Morales J, Sánchez IM, Moyà-Solà S. 2014. New remains of *Dorcatherium crassum* (Artiodactyla: Tragulidae) from the Early Miocene (MN4) of Els Casots (Subirats, Vallès-Penedès Basin). C R Palevol. 13:73–86. doi:10.1016/j.crpv.2013.09.003

Aldana Carrasco EJ. 1991. Roedores esciuromorfos del Neógeno de Cataluña [dissertation]. Bellaterra: Universitat Autònoma de Barcelona.

Aldana Carrasco EJ. 1992. Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedès (Cataluña, España). Treb Mus Geol Barcelona. 2:69–97.

Almera J. 1898. Sobre la serie de mamíferos fósiles descubiertos en Cataluña. Mem Comun Real Acad Cienc Art Barcelona. 2:351–357.

Bessedik M, Cabrera L. 1985. Le couple récif-mangrove à Sant Pau d'Ordal (Vallès-Pénédès, Espagne), témoin du maximum transgressif en Méditerranée nord occidentale (Burdigalien supérieur - Langhien inférieur). Newsl Stratigr. 14:20–35. doi:10.1127/nos/14/1985/20

Blanchy G, Saneiyan S, Boyd J, McLachlan P, Binley A. 2020. ResIPy, an intuitive open source software for complex geoelectrical inversion/modelling. Comput Geosci. 137:104423. doi:10.1016/j.cageo.2020.104423

Bolet A, Delfino M, Fortuny J, Almécija S, Robles JM, Alba DM. 2014. An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards. PLoS ONE. 9:98082. doi:10.1371/journal.pone.0098082

Cabrera Pérez L. 1979. Estudio estratigráfico y sedimentológico de los depósitos continentales basales de la depresión del Vallès-Penedès [dissertation]. Barcelona: Universitat de Barcelona.

Cabrera Pérez L. 1981a. Estratigrafía y características sedimentológicas generales de las formaciones continentales del Mioceno inferior de la cuenca del Vallés Penedés (Barcelona, España). Estud Geol. 37:35–44.

Cabrera Pérez L. 1981b. Influencia de la tectónica en la sedimentación continental de la cuenca del Vallès-Penedès (provincia de Barcelona, España) durante el Mioceno inferior. Acta Geol Hisp. 16:163–169.

Cabrera L, Calvet F, Guimerà J, Permanyer A. 1991. El Registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de el Camp: organización secuencial y relaciones tectónica sedimentación. In: Colombo F, editor. I Congreso del Grupo Español del Terciario, Libro-Guía Excursión no. 4; Vic: Universitat de Barcelona, p. 1–132.

Cabrera L, Roca E, Garcés M, de Porta J. 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). In: Vera JA, editor. Geología de España. Madrid: Sociedad Geológica de España, Instituto Geológico y Minero de España; p. 569–573.

Casanovas-Vilar I, DeMiguel D, Galindo J, Robles JM, Garcés M, Cabrera L. 2011a. The continental Burdigalian (Early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). In: Pérez García A, Gascó F, Gasulla JM, Escaso F, editors. Viajando a mundos pretéritos. Morella: Ayuntamiento de Morella; p. 93–100.

Casanovas-Vilar I, Alba DM, Moyà-Solà S. 2011b. Parada 1. Panorámica general de la cuenca y yacimiento de els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior. Paleontol Evol. mem. espec. 6:81–88.

Casanovas-Vilar I, Madern A, Alba DM, Cabrera L, García-Paredes I, van den Hoek Ostende LW, DeMiguel D, Robles JM, Furió M, van Dam J, et al. 2016. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). C R Palevol. 15:791–812. doi:10.1016/j.crpv.2015.07.004

Crespo VD, Suárez-Hernando O, Murelaga X, Ruiz-Sánchez FJ, Montoya P. 2019. Early Miocene mammal assemblages from the Campisano ravine in the Ribesalbes-Alcora Basin (E Spain). J Iber Geol 45:181–194. doi:10.1007/s41513-018-0093-z

Crusafont M, Villalta JF de, Truyols J. 1955. El Burdigaliense continental de la cuenca del Vallés-Penedés. Mem Com Inst Geol. 12:3–272.

De Bruijn H, Van der Meulen AJ. 1982. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2. The Gliridae. Proc K Akad Van Wet. 85:485–524.

DeMiguel D, Azanza B, Morales J. 2014. Key innovations in ruminant evolution: a paleontological perspective. Integr Zool. 9:412–433. doi: 10.1111/1749-4877.12080

de Gibert JM, Casanovas-Vilar I. 2011. Contexto geológico del Mioceno de la cuenca del Vallès-Penedès. Paleontol Evol. mem. espec. 6:39–45.

Díaz Aráez JL, Delfino M, Luján ÀH, Fortuny J, Bernardini F, Alba DM. 2017. New remains of *Diplocynodon* (Crocodylia: Diplocynodontidae) from the Early Miocene of the Iberian Peninsula. C R Palevol. 16:12–26. doi:10.1016/j.crpv.2015.11.003

Domènech R, Martinell J, de Gibert JM. 2011. Registro paleontológico marino del Mioceno de la Cuenca del Vallès-Penedès. Paleontol Evol. mem. espec. 6:47–54.

Duranthon F, Moyà-Solà S, Astibia H, Köhler M. 1995. *Ampelomeryx ginsburgi* nov. gen., nov. sp. (Artiodactyla, Cervoidea) et la famille des Palaeomerycidae. C R Acad Sci Paris. 321:339–346.

Fortelius M, Van der Made J, Bernor RL. 1996. Middle and Late Miocene Suoidea of Central Europe and the Eastern Mediterranean: evolution, biogeography and paleoecology. In: Bernor RL, Fahlbusch V, Mittmann H-W, editors. The evolution of western Eurasian Neogene faunas. New York: Columbia University Press; p. 348–377.

Foster GL, Lear CH, Rae JWB. 2012. The evolution of pCO2, ice volume and climate during the middle Miocene. Earth Planet Sci Lett. 341–344:243–254. doi:10.1016/j.epsl.2012.06.007

Furió M, Ruiz-Sánchez FJ, Crespo VD, Freudenthal M, Montoya P. 2012. The southernmost Miocene occurrence of the last European herpetotheriid *Amphiperatherium frequens* (Metatheria, Mammalia). C R Palevol. 11:371–377. doi:10.1016/j.crpv.2012.01.004

García-Paredes I, Álvarez-Sierra MÁ, Van den Hoek Ostende LW, Hernández-Ballarín V, Hordijk K, López-Guerrero P, Oliver A, Peláez-Campomanes P. 2016. The Aragonian and Vallesian high-resolution micromammal succession from the Calatayud-Montalbán Basin (Aragón, Spain). C R Palevol. 15:781–789. doi:10.1016/j.crpv.2015.09.014

Gasamans N, Luján ÀH, Pons-Monjo G, Obradó P, Casanovas-Vilar I, Alba DM. 2021. The record of *Prodeinotherium* in the Iberian Peninsula: new data from the Vallès-Penedès Basin. J Mamm Evol. 28:647–660. doi:10.1007/s10914-021-09543-y

Ginsburg L. 1999. Order Carnivora. In: Rössner GE, Heissig K, editors. The Miocene land mammals of Europe. Munich: Verlag Dr. Friedrich Pfiel; p. 109–148.

Hilgen FJ, Lourens LJ, Van Dam JA. 2012. The Neogene Period. In: Gradstein FM, Ogg JG, Schmitz M, Ogg G, editors. The geologic time scale 2012. Amsterdam: Elsevier; p. 923–978. doi:10.1016/B978-0-444-59425-9.00029-9

Jiménez-Moreno G, Suc J-P. 2007. Middle Miocene latitudinal climatic gradient in Western Europe: Evidence from pollen records. Palaeogeogr Palaeoclimatol Palaeoecol. 253:208–225. doi:10.1016/j.palaeo.2007.03.040

Jovells-Vaqué S, Casanovas-Vilar I. 2021. Dispersal and early evolution of the first modern cricetid rodents in Western Europe: new data from the Vallès-Penedès Basin (Catalonia). C R Palevol. 20:401–439. doi:10.582/cr-palevol2021v20a22

Jovells-Vaqué S, García-Paredes I, Furió M, Angelone C, Ostende LWV den H, Barberà MB, DeMiguel D, Madurell-Malapeira J, Casanovas-Vilar I. 2018. Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain). Hist Biol. 30:404–421. doi:10.1080/08912963.2017.1317768

Jovells-Vaqué S, Ginestí M, Casanovas-Vilar I. 2017a. Cricetidae (Rodentia, Mammalia) from the early Miocene site of Els Casots (Vallès-Penedès Basin, Catalonia). Foss Impr. 73:141–154. doi:DOI 10.1515/if-2017-0007

Jovells-Vaqué S, Ginestí M, Casanovas-Vilar I. 2017b. First cranial material of *Democricetodon hispanicus* Freudenthal, 1967 (Rodenita, Cricetidae) from els Casots site (Vallès-Penedès Basin, Catalonia). Preliminary results. In: Barrios de Pedro S, Blanco Moreno C, de Celis A, Colmenar J, Cuesta E, García-Martínez D, Gascó F, Jacinto A, Malafaia E, Martín Jiménez M et al., editors. A glimpse of the past. Abstract book of the XV Encuentro de Jóvenes Investigadores en Paleontología/Encontro de Jovens Investigadores em Paleontologia; April 19– 22; Pombal, p. 223–226.

Kälin D, Kempf O. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrb Für Geol Paläontol Abh. 254:177–235. doi:10.1127/0077-7749/2009/0010

Köhler M. 1993. Skeleton and habitat of recent and fossil ruminants. Münch Geowiss Abh. 25:1–88.

López Martínez N. 1989. Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. Zaragoza: Diputación General de Aragón, Departamento de Cultura y Educación.

Luján ÀH, Alba DM, Fortuny J, Carmona R, Delfino M. 2014a. First cranial remains of *Cheirogaster richardi* (Testudines: Testudinidae) from the Late Miocene of Ecoparc de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula): taxonomic and phylogenetic implications. J Syst Palaeontol. 12:833–864. doi:10.1080/14772019.2013.863231

Luján ÀH, Delfino M, Casanovas-Vilar I, Alba DM. 2014b. Taxonomy of subgenus *Temnoclemmys* Bergounioux, 1958 (Testudines: Geoemydidae: Ptychogasterinae) based on new material from the Vallès-Penedès Basin. C R Paleovol. 13:277–295. doi: 10.1016/j.crpv.2013.11.004

Luján ÀH, Delfino M, Robles JM, Alba DM. 2016. A review of the Miocene tortoise *Testudo catalaunica* Bataller, 1926 and a revised phylogeny of extinct species of genus *Testudo* (Testudines: Testudinidae). Zool J Linn Soc. 178:312–342. doi: 10.1111/zoj.12414

Mein P. 1999. European Miocene mammal biochronology. In: Rössner GE, Heissig K, editors. The Miocene land mammals of Europe. Munich: Verlag Dr. Friedrich Pfiel; p. 25–38.

Moyà-Solà S, Rius Font L. 1993. El jaciment paleontològic dels Casots (Subirats, l'Alt Penedès). Tribuna d'Arqueologia 1991:7–12.

Ogg, JG. 2020. Geomagnetic polarity time scale. In: Grastein FM, Ogg JG, Schmitz MD, Ogg GM, editors. The geologic time scale 2020. Amsterdam: Elsevier; p. 159–192. https://doi.org./10.1016/B978-0-12-824360-2.00005-X

Orliac MJ. 2006. *Eurolistriodon tenarezensis*, sp. nov., from Montreal-Du-Gers (France): implications for the systematics of the European Listriodontinae (Suidae, Mammalia). J Vertebr Paleontol. 26:967–980. doi:10.1671/0272-4634(2006)26[967:ETSNFM]2.0.CO;2

Orliac MJ, Pierre-Olivier A, Ducrocq S. 2010. Phylogenetic relationships of the Suidae (Mammalia, Cetartiodactyla): new insights on the relationships within Suoidea. Zool Scr. 39:315–330. doi:10.1111/j.1463-6409.2010.00431.x

Pickford M. 2012. Les Suoidea (Artiodactyla) de Sansan : systématique, paléoécologie, biogéographie et biochronologieLes Suoidea (Artiodactyla) de Sansan : systématique, paléoécologie, biogéographie et biochronologie. In: Peigné S, Sen S, editors. Mammifères de Sansan. Paris: Publications Scientifiques du Muséum; p. 249–277.

Pickford M. 2017. Revision of "peccary-like" Suoidea (Artiodactyla: Mammalia) from the Neogene of the Old World. Münch Geowiss Abh A. 46:1–144.

Pickford M, Morales J. 2003. New Listriodontinae (Mammalia, Suidae) from Europe and a review of listriodont evolution, biostratigraphy and biogeography. Geodiversitas. 25:347–404.

Pickford M, Moyà-Solà S. 1994. *Taucanamo* (Suoidea, Tayassuidae) from the Middle Miocene (MN04a) of Els Casots, Barcelona, Spain. C R Acad Sci Paris. 319:1569–1575.

Pickford M, Moyà-Solà S. 1995. *Eurolistriodon* gen. nov., (Suoidea, Mammalia) from Els Casots, early middle Miocene, Spain. Proc Kon Ned Akad Wet. 98:343–360.

Roca E, Sans M, Cabrera L, Marzo M. 1999. Oligocene to Middle Miocene evolution of the central Catalan margin (northwestern Mediterranean). Tectonophysics. 315:209–229. doi:10.1016/S0040-1951(99)00289-9

Rotgers C, Alba DM. 2011. The genus *Anchitherium* (Equidae: Anchitheriinae) in the Vallès-Penedès Basin (Catalonia, Spain). In: Pérez García A, Gascó F, Gasulla JM, Escaso F, editors. Viajando a mundos pretéritos. Morella: Ayuntamiento de Morella; p. 347–354.

Ruiz Sánchez FJ, de Santiesteban Bové C, Lacomba Andueza JI. 2003. Nuevas faunas de roedores fósiles (Mammalia, Rodentia) de edad Aragoniense inferior y medio en la série del Barranco de Morteral (cuenca del Río Magro, prov. de Valencia, España). Col Paleontol. vol. ext. 1:579–594.

Sánchez IM, Cantalapiedra JL, Ríos M, Quiralte V, Morales J. 2015. Systematics and evolution of the Miocene three-horned palaeomerycid ruminants (Mammalia, Cetartiodactyla). PLoS ONE. 10:e0143034. doi:10.1371/journal.pone.0143034

Sánchez IM, Morales J, Cantalapiedra JL, Quiralte V, Pickford M. 2018. Preliminary phylogenetic analysis of the Tragulidae (Mammalia, Cetartiodactyla, Ruminantia) from Arrisdrift: implications for the African Miocene tragulids. Commun Geol Surv Namib. 19:110–120.

Sánchez-Marco A. 2021. Old and new fossil birds from the Spanish Miocene. J Iber Geol. 47:697–712. doi:10.1007/s41513-021-00178-9

Sanisidro Ó, DeMiguel D, Madurell-Malapeira J, Jovells-Vaqué S, Casanovas-Vilar I. 2018. Revalidation of the genus *Dromoceratherium* (Perissodactyla, Rhinocerotidae) and its key role within Rhinocerotinae. J Vertebr Paleontol. program and abstracts 2018:209.

Sanz de Siria Catalán A. 1993. Datos sobre la paleoclimatología y paleoecología del Neógeno del Vallès-Penedès según las macrofloras halladas en la cuenca y zonas próximas. Paleontol Evol. 26–27:281–289.

Sanz de Siria Catalán A. 2001. Flora y vegetación del Mioceno medio de la depresión del Vallès-Penedès. Paleontol Evol. 32–33:79–92.

Shevenell AE, Kennett JP, Lea DW. 2008. Middle Miocene ice sheet dynamics, deep-sea temperatures, and carbon cycling: A Southern Ocean perspective. Geochem Geophys Geosystems. 9:Q02006. doi:10.1029/2007GC001736

Steinthorsdottir M, Coxall HK, Boer AM de, Huber M, Barbolini N, Bradshaw CD, Burls NJ, Feakins SJ, Gasson E, Henderiks J, et al. 2021. The Miocene: the future of the past. Paleoceanogr Paleoclimatol. 36:e2020PA004037. doi:10.1029/2020PA004037

Suárez-Hernando O. 2017. Magnetobiocronología y Paleoecología del Mioceno inferior-medio en las Bardenas Reales de Navarra (cuenca del Ebro) [dissertation]. Leioa: Euskal Herriko Unibertsitatea.

Szyndlar Z. 1991. A review of Neogene and Quaternary snakes of central and eastern Europe. Part 1: Scolecophidia, Boidae, Colubrinae. Estud Geol. 47:103–126. doi:10.3989/egeol.91471-2412

Valenciano A, Abella J, Alba DM, Robles JM, Álvarez-Sierra MA, Morales J. 2020. New early Miocene material of *Iberictis,* the oldest member of the wolverine lineage (Carnivora, Mustelidae, Guloninae). J Mamm Evol. 27:73–93. doi:10.1007/s10914-018-9445-x

Van Dam JA. 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe. The use of small mammals as paleoprecipitation proxies. Paleogeogr Paleoclimatol Paleoecol. 238:190–218. doi:10.1016/j.palaeo.2006.03.025

Van den Hoek Ostende LW, Casanovas-Vilar I, Furió M. 2020. Stuck in the middle. A geographical appraisal of the oldest insectivores – and a marsupial – from the Vallès-Penedès

Basin (early Miocene, Catalonia, Spain). C R Palevol. 19:1–25. doi:10.5852/cr-palevol2020v19a1

Van der Made J. 1997. Los Suoidea de la Península Ibérica. In: Calvo JP, Morales J, editors. Avances en el conocimiento del Terciario ibérico. Madrid: Departamento de Geoquímica y Petrología, Universidad Complutense de Madrid; p. 109–112.

Van der Made J. 2020. The Suoidea from the Middle Miocene of Gračanica (Bugojno Basin, Bosnia and Herzegovina)—evolution, taxononomy, and biostratigraphy. Palaeobiodiversity Palaeoenvironments. 100:321–349. doi:10.1007/s12549-020-00420-9

Van der Meulen AJ, Daams R. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. Palaeogeogr Palaeoclimatol Palaeoecol. 93:227–253. doi:10.1016/0031-0182(92)90099-Q

Van der Meulen AJ, Pélaez-Campomanes P, Daams R. 2003. Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel basin (Zaragoza, Spain). Col Paleontol. vol. ext. 1:385–441.

Van der Meulen AJ, García-Paredes I, Álvarez Sierra MÁ, Van den Hoek Ostende LW, Hordijk K, Oliver A, Pélaez-Campomanes P. 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geol Acta. 10:159–179. doi:10.1344/105.000001710

Villa A, Delfino M, Luján ÀH, Almécija S, Alba DM. 2019a. First record of *Latonia gigantea* (Anura, Alytidae) from the Iberian Peninsula. Hist Biol. 31:371–382. doi:10.1080/08912963.2017.1371712

Villa A, Kirchner M, Alba DM, Bernardini F, Bolet A, Luján ÀH, Fortuny J, Hipsley CA, Müller J, Sindaco R et al. 2019b. Comparative cranial osteology of *Blanus* species (Squamata: Amphisbaenia). Zool J Linn Soc. 185:693–716. doi: 10.1093/zoolinnean/zly082

Yan D, Heissig K. 1986. Revision and autopodial morphology of the Chinese-European rhinocerotid genus *Plesiaceratherium* Young 1937. Zitteliana. 14:81–109.

Zachos JC, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science. 292:686–693. doi:10.1126/science.1059412

Figures

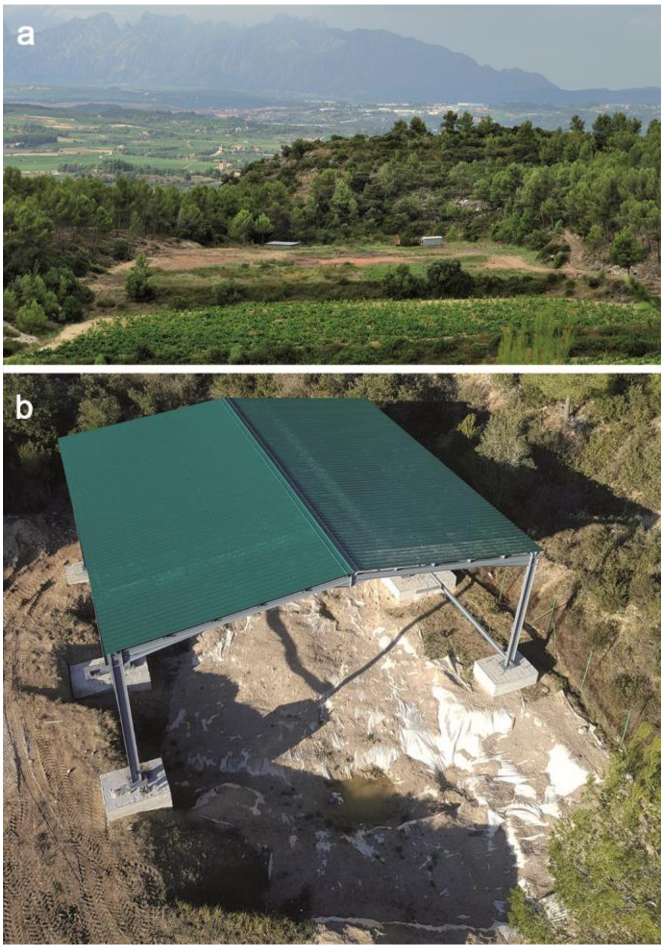

Figure 1. a, Panoramic view of the site of els Casots in 2011. Site perimeter is the deforested field behind the vineyards and corresponds to the hatched area in Figure 2. b, Excavated surface after the 2019 field campaign. A metal structure has been built over the main excavation area to protect the site from heavy rains and allow for guided touristic visits. Photograph courtesy of Ajuntament de Subirats.

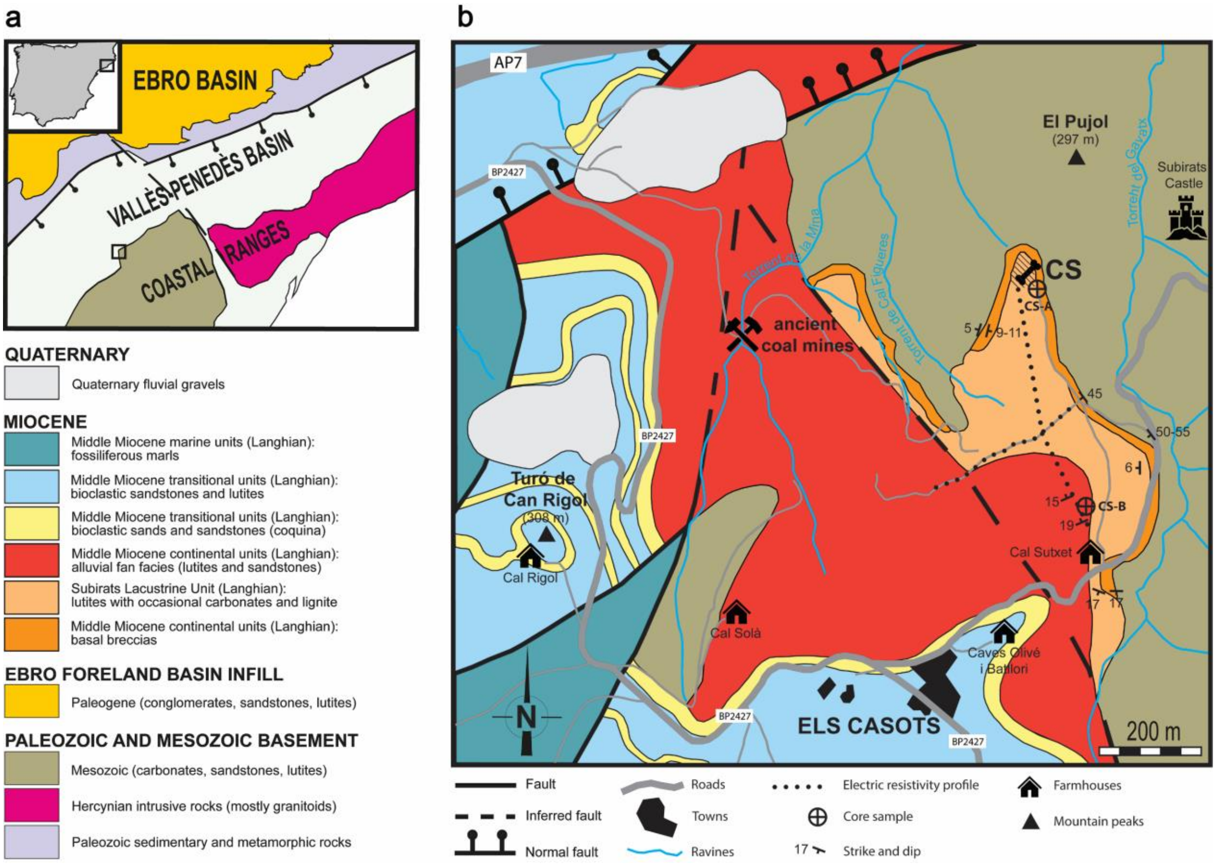

Figure 2. a, Geographical location and general geological context of the Vallès-Penedès Basin showing the location of the study area. b, Detailed geological map of the area around els Casots, showing the location of the fossil site, the electric resistivity profiles, and core samples. Observe the proximity of els Casots to the ancient coal mines as well as its situation directly overlying the Mesozoic basement. Also notice the close proximity of the site to the first Middle Miocene (Langhian) transitional and marine deposits.

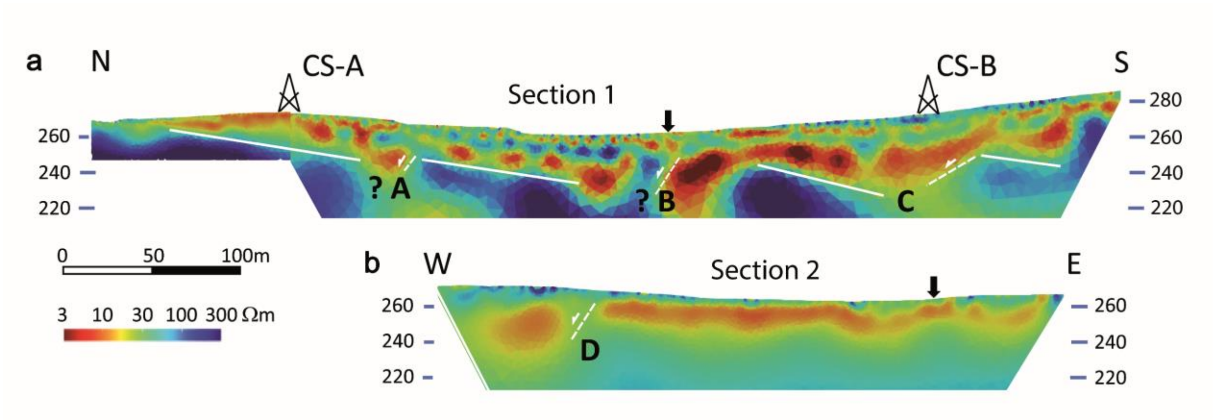

Figure 3. Geoelectric (ERT) sections 1 and 2. a, ERT section 1 is 585 m long with a direction S170, overlapping 34 m with two ERT profiles, one of 144 m long with an electrode spacing of 2 m, and the other of 475 m and 5 m of electrode spacing. b, ERT section 2 is 355 m with a direction N65 corresponding to a unique ERT profile with 5 m electrodes spacing. Data were acquired with a Syscal-Pro (Iris-Instruments), and the models were obtained with the ResIPy code (Blanchy et al. 2020). Locations of the drilled wells are projected in section 1. White lines show the expected contact between Miocene cover and the basement, whereas the black arrow indicates the point where both profiles intersect. Segments A–D represent resistivity changes interpreted as faulted zones (see text for interpretation). The vertical scale is the topographic elevation above sea level in meters. Section location is shown in Figure 2.

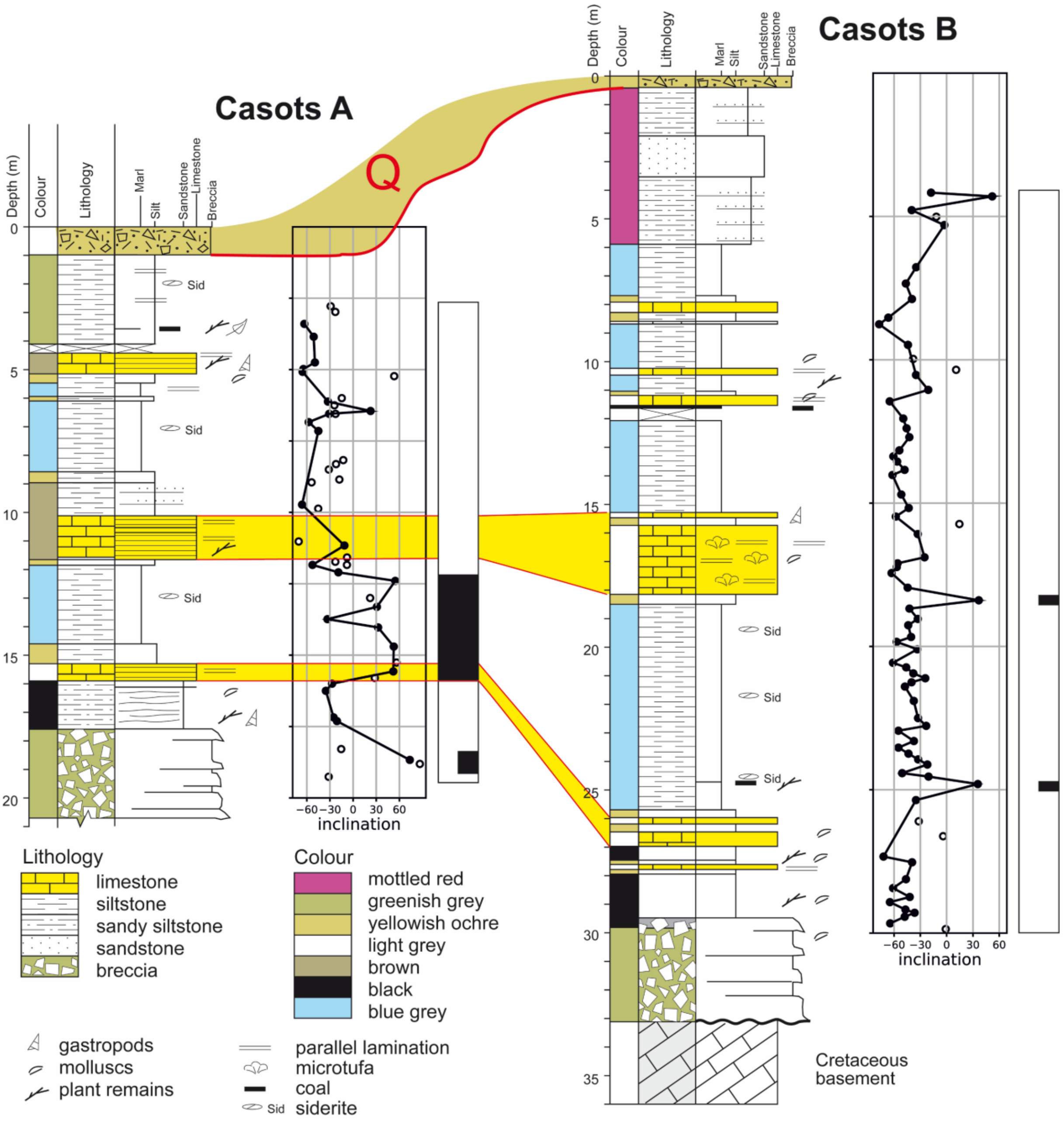

Figure 4. Stratigraphic logs of cores Casots A and B (see Figure 2b) and palaeomagnetic inclination from studied samples. Positive inclinations represent normal polarity (in black) and negative inclinations represent reverse polarity (white). Black circles indicate directions of best quality (Quality 1), while white circles indicate directions of lower quality (Quality 2, see text for explanation). Note the long reverse polarity interval in CS-B core.

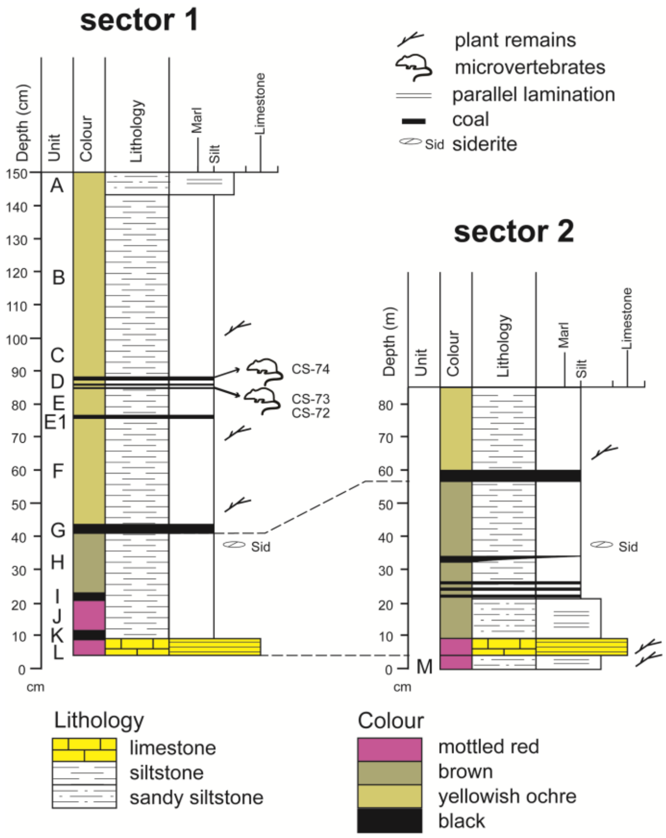

Figure 5. Detailed stratigraphic column of the excavation area (sectors 1 and 2). Capital letters refer to fossiliferous levels. In this sector, levels A–I were almost entirely excavated during the 1990s, so current excavations focus on levels J–M. The levels sampled for micromammals during the 1990s (CS-72, CS-73 and CS-74) are also indicated.

Figure 6. Some pictures of the recent field campaigns at els Casots. a, Almost complete mandible of *Iberictis buloti* (field number CS-150) recovered from level K in 2019. b, Part of a disarticulated hindlimb of *Ampelomeryx ginsburgi* (field number CS-77) recovered from level J in 2019. From left to right the long bones correspond to a metatarsal, a femur fragment and a tibia. c, Two juvenile hemimandibles of a rhinocerotid (field numbers CS-633 and CS-634) found in level K in 2021. d, Bone accumulation of different elements (mostly ribs and vertebrae) of *Gomphotherium* cf. *subtapiroideum* found in level K in 2019. A mandibular fragment with two molars can be observed in the upper left corner (field number CS-325). The whole accumulation of *Gomphotherium* bones covers a surface of 2 m^2.

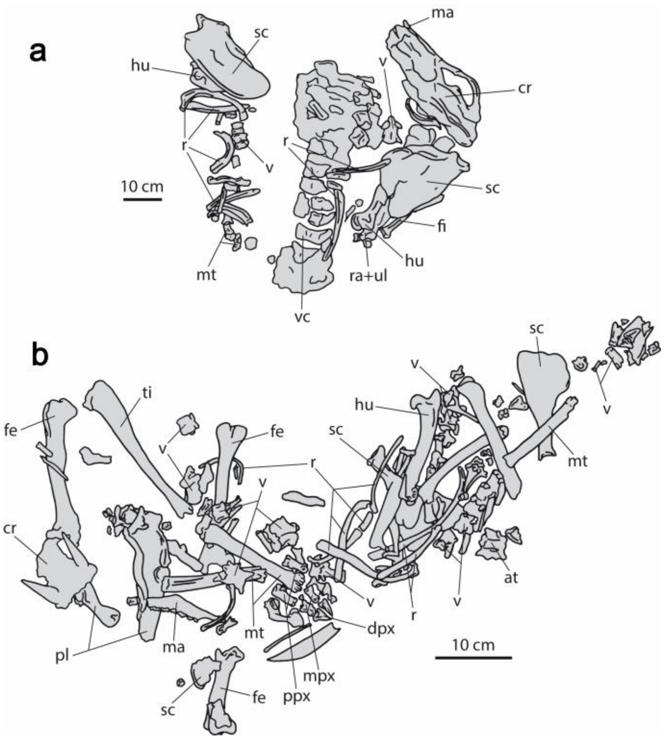

Figure 7. Excavation plans of two fossil accumulations excavated during the 1990s. a, Partial skeleton of Amphicyonidae sp. 1 (larger size) extracted during the 1993 campaign (collection number IPS11428). Observe the anatomical connection of some elements such as the vertebral column (vc) or the cranium and mandible (cr, ma). b, Bone accumulation of two different-sized juvenile ruminant individuals found during the 1994 campaign. The smallest, and more abundantly represented is *Eotragus noyei*. Although most elements are disarticulated, a few are in anatomical connection, such as vertebrae (v) and phalanges (ppx, mpx, dpx). Collection number for the cranial fragment (cr) of *E. noyei* is IPS11878. Orientation and exact position of the bone accumulations within the excavation area was not recorded. Anatomical abbreviations: at, atlas; cr, cranium; dpx, distal phalanx; fe, femur; fi, fibula; hu, humerus; ma, mandible; mpx, middle phalanx; mt, metapodial; pl, pelvis; ppx, proximal phalanx; r, rib; ra, radius; sc, scapula; ti, tibia; ul, ulna; v, vertebra; vc, vertebral column.

Figure 8. Reconstruction of the fauna and palaeoenvironment of els Casots. In the foreground the felid “*Pseudaelurus*” *lorteti* stares at a large amphycionid that has hunted an individual of the suid *Eurolistriodon adelli*. Behind them, three individuals of the palaeomerycid *Ampelomeryx ginsburgi* walk away. To their left and in the background, partly hidden behind a palm, there is the cervid *Procervulus* cf. *dichotomus*. The crocodylian *Diplocynodon ratelii* can be seen resting in the lake. In the background, a herd of *Gomphotherium* cf. *subtapiroideum* approaches the lake shore. Plant remains at els Casots are too fragmentary, so the reconstructed vegetation is based on that from contemporaneous nearby sites (see Sanz de

Síria Catalán 2001). Large plants include the palm *Sabal* and leguminous trees *Acacia* and *Mimosa*. Bushes in the foreground are *Caesalpinia* and *Cassia*, whereas reeds (*Typha*) grow abundantly on the lake shore. Palaeoart by Ó. Sanisidro, courtesy of Ajuntament de Subirats.

Table 1. Updated faunal list of the tetrapod assemblage from els Casots.

Class	**Order**	**Family**	**Taxonomic assignment**
Amphibia	Anura	Alytidae	*Latonia* sp.
		Bufonidae	*Bufotes* (group *viridis*) sp.
		Ranidae	*Pelophylax* sp.
	Urodela		Urodela indet.
Reptilia	Testudines	Testudinidae	*Titanochelon* sp.
			Testudo sp.
		Geoemydidae	*Ptychogaster* sp.
	Squamata		Gekkota indet.
		Lacertidae	cf. *Amblyolacerta* sp.
			Lacetidae indet.
			Scincoidea indet.
		Anguidae	cf. *Ophisaurus* sp.
			Pseudopus sp.
		Varanidae	cf. Varanidae indet.
		Blanidae	*Blanus* sp.
		Incertae sedis.	Scolecophidia indet.
		Boidae	Erycinae indet.
		Pythonidae	*Python* sp.
		Colubridae	“Colubrinae” indet.
		Viperidae	*Vipera* sp. (“Oriental vipers”) Viperidae sp. 2 (cf. “European vipers”)
	Crocodylia	Diplocynodontidae	*Diplocynodon ratelii*
Aves	Galliformes	Phasianidae	*Miophasianus altus*
	Falconiformes	Accipitridae	cf. *Circaetus* sp.
			cf. *Aquila* sp.
	Strigiformes	Strigidae	Strigidae indet.
Mammalia	Incertae sedis	Herpetotheriidae	*Amphiperatherium frequens*
	Chiroptera		Chiroptera indet.
	Eulipotyphla	Erinaceidae	*Galerix symeonidisi*
		Dimylidae	cf. *Plesiodimylus* sp.
		Heterosoricidae	*Heterosorex neumayrianus*
		Soricidae	*Paenelimnoecus* cf. *truyolsi*
	Lagomorpha	Ochotonidae	*Lagopsis* sp.
	Rodentia	Sciuridae	*Atlantoxerus idubedensis*
			Heteroxerus rubricati
			Palaeosciurus sp.
			Csakvaromys besana
		Gliridae	*Bransatoglis* sp.
			Glirudinus modestus
			Microdyromys monspeliensis
			Muscardinus sp.
			Peridyromys murinus

		Pseudodryomys ibericus
		Simplomys julii
		Simplomys robustus
		Simplomys simplicidens
	Eomyidae	*Ligerimys ellipticus*
	Cricetidae	*Democricetodon hispanicus*
		Democricetodon gracilis
		Democricetodon sp. 3
		Megacricetodon primitivus
Carnivora	Amphicyonidae	Amphicyonidae sp. 1
		Amphicyonidae sp. 2
	Hemicyonidae	*Hemicyon stehlini*
	Mustelidae	*Iberictis buloti*
		Paralutra sp.
		"*Martes*" sp. 1
		"*Martes*" sp. 2
	Herpestidae	*Leptoplesictis aurelianensis*
	Hyaenidae	cf. *Protictitherium* sp.
	Felidae	"*Pseudaelurus*" *lorteti*
Perissodactyla	Rhinocerotidae	*Dromoceratherium mirallesi*
		Rhinoceratidae sp. 2
	Equidae	*Anchitherium* sp.
Artiodactyla	Cainotheriidae	*Cainotherium miocaenicum*
	Siderochoeridae	*Choeromorus ibericus*
	Suidae	*Eurolistriodon adelli*
	Tragulidae	"*Dorcatherium*" *crassum*
	Palaeomerycidae	*Ampelomeryx ginsburgi*
	Lagomerycidae	*Lagomeryx rutimeyeri*
	Cervidae	*Procervulus* cf. *dichotomus*
	Bovidae	*Eotragus noyei*
Proboscidea	Deinotheriidae	*Prodeinotherium* cf. *bavaricum*
	Gomphotheriidae	*Gomphotherium* cf. *subtapiroideum*