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Squamates, rodents, and birds from Holocene deposits of the Illa Grossa Island (Columbretes Islands, Castellón, Spain): an unexpected diverse assemblage

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ABSTRACT

The Columbretes Islands (eastern Spain) comprise a volcanic archipelago 50 km off the eastern Spanish coast. Illa Grossa is the main island of the archipelago. After the settlement of humans during the mid-19th century, strong modifications in biodiversity took place, including the reduction of the non-flying vertebrate fauna to a single taxon, *Podarcis liolepis atratus* (Boscá, 1916). The study of the fossils yielded at the COLT site (dated by AMC between 2780-2724 cal BP and 2600-2492 cal BP) from a loess deposit located at the south of Illa Grossa Island shows that this fauna was more diverse in the past. The assemblage was dominated by squamate reptiles, belonging to two lizards (*Chalcides bedriagai* (Boscá, 1880) and cf. *Podarcis* Wagler, 1830) and one snake (*Vipera* cf. *latastei* Boscá, 1878). The record in the late Holocene of Columbretes of *Vipera* cf. *latastei* settles the existing controversy about the identity of snakes in the archipelago. Regarding *Chalcides bedriagai*, this is the first record of its presence in the Columbretes Islands. Other faunal elements recovered from the site include at least six species of undetermined birds (passeriforms and procellariforms) and the anthropophilic *Mus* cf. *musculus* Linnaeus, 1758. The origin of the squamates taxa from Columbretes palaeontological site (COLT) is still unclear, but was probably related to the Late Pleistocene-Greenlandian (11 700 to 8300 BP, Early Holocene) sea transgression, natural passive colonization, and/or human introduction. We hypothesize implications for the conservation and management of the Natural Reserve.

KEY WORDS
Vipers,
conservation palaeobiology,
small vertebrates,
Mediterranean,
palaeoecology,
islets.

RÉSUMÉ

Squamates, rongeurs et oiseaux des dépôts holocènes de l'île Illa Grossa (îles Columbretes, Castellón, Espagne) : un assemblage diversifié inattendu.

Les îles Columbretes (Est de l'Espagne) constituent un archipel volcanique situé à 50 km de la côte est de l'Espagne. Illa Grossa est l'île principale de l'archipel. Après l'installation de la population humaine sur celle-ci au milieu du XIXe siècle, des importantes modifications de la biodiversité ont eu lieu, notamment la réduction de la faune vertébrée non volante dont un seul taxon persiste, *Podarcis liolepis atratus* (Boscá, 1916). L'étude des fossiles trouvés sur le site Columbretes (COLT) (daté par AMC entre 2780-2724 cal BP et 2600-2492 cal BP) dans un dépôt de lœss situé au sud de l'île Illa Grossa, montre que cette faune était plus diversifiée dans le passé. L'assemblage était dominé par des reptiles squamates, appartenant à deux lézards (*Chalcides bedriagai* (Boscá, 1880) et cf. *Podarcis* Wagler, 1830) et un serpent (*Vipera* cf. *latastei* Boscá, 1878). L'enregistrement à l'Holocène supérieur de Columbretes de *Vipera* cf. *latastei*, règle la controverse existante sur l'identité des serpents dans l'archipel. En ce qui concerne *Chalcides bedriagai*, il s'agit du premier signalement de sa présence dans les îles Columbretes. Les autres éléments de la faune vertébrée retrouvés sur le site comprennent, au moins, six espèces d'oiseaux indéterminés (passériformes et procellariformes) et l'anthropophile *Mus* cf. *musculus* Linnaeus, 1758. L'origine des taxons de squamates de COLT n'est toujours pas claire, mais elle est probablement liée à une transgression marine du Pléistocène supérieur (Groenlandien 11 700 à 8 300 BP, Holocène inférieur), une colonisation passive naturelle et/ou à une introduction par l'homme. Nous avons également émis des hypothèses sur les implications pour la conservation et la gestion de la réserve naturelle.

MOTS CLÉS
Vipères,
paléobiologie de la conservation,
petits vertébrés,
Méditerranée,
paléoécologie,
îlots.

INTRODUCTION

The Columbretes islands are a small volcanic archipelago close to the continental coast (50 km) in the western Mediterranean (Fig. 1A). This archipelago constitutes the emerged part of the Gulf of Valencia Volcanic Province (GVVP), extending 200 km NE-SW over the continental shelf between Tarragona and Valencia, mostly as submarine volcanoes. The GVVP is located on the western margin of the Valencia Through. This area, between the Pyrenean front and the Alboran sector, was affected by a rifting process developed after the Oligocene-Lower Miocene alpine orogenic stage (López-Ruiz *et al.* 2002). This led to the thinning of the crust that extends up to about 50 km on land in the Eastern sector of the Iberian Chain (Dañobeitia *et al.* 1992). This context is at odds with the idea of the Rhine-Rhône Rift spreading southwards. López-Ruiz *et al.* (2002) propose for this area a geodynamic model of the volcanism of the SE of Iberia with two phases. A first lower Oligocene-Miocene synorogenic phase linked to the genesis of the Valencia Trough, and a second terminal Miocene-Quaternary phase related to the functioning of the trans-Moroccan, Western Mediterranean, European Fault Zone (TMWMEFZ) that crosses the eastern sector of the Iberian Peninsula. Although, the origin of the archipelago has been dated, at least, between 0.8 and 0.3 My (Ancochea & Huertas 2021), the submarine structures associated to the volcanic field may be much younger, about 13 000 years old (Muñoz *et al.* 2005).

Traditionally, the archipelago is divided in four groups of islands, from north to south: Illa Grossa, Ferrera, Foradada and El Carallot (Fig. 1B). As Ancochea & Huertas (2020) and Huertas & Ancochea (2020) pointed out these groups do not correspond to a particular volcanic phase, and there are some islets than belong to a different phases (i.e., Ferrera group). Thus, there are recognised two alignments according to two strikes: a main N170° E direction (formed by more than seven volcanic centres of phonolitic composition and which, at present, appears as small islets) and a second direction, N55° E (which belongs to the two volcanic centres of basic composition, one of which is Illa Grossa) (Ancochea & Huertas 2020; Huertas & Ancochea 2020). Among them, the Illa Grossa group (Fig. 1C) would correspond to a magmatic outcrop older (0.7-0.8 My) than the other island groups (0.2-0.3 My) (Ancochea & Huertas 2021). Basanite and phonolite rocks mainly constituted the Illa Grossa island (Aparicio & García 1995). The current ring-shape of the Illa Grossa Island is the result of three successive emission centres (Ancoechea & Huertas 2020).

The name of the archipelago (Columbretes, from the latin word “coluber”, which derived in the Spanish word “culebra”, meaning “snake”) comes from the high density of snakes in the Illa Grossa Island. In fact, in the Antiquity, the island was called Ophiusa by the Ancient Greeks, and Colubraria by the Romans (Bernis 1968). The large number of snakes present on Illa Grossa prevented the human settlement on the island until the mid-19th century, when the construction of the lighthouse began. Starting from this point, in theory, human presence becomes apparent in the archipelago (Serrano Adell 1991), deeply altering its floral and faunal communities. Snakes were especially persecuted during this period, through direct hunting of specimens, the introduction of predators and, the burning of vegetation, until their total extinction on Illa Grossa Island, which affected the general biodiversity and has been related with the extirpation of the terrestrial gastropods *Theba pisana* (Müller, 1774) and *Potamias elegans* (Müller, 1774) (Robles 1991). The last reference of a living snake on the islands was in 1885 (Mestre *et al.* 2010). Despite the historical high density of snakes on the Illa Grossa Island, their taxonomic identity has remained unclear (Jiménez *et al.* 2002). Although most authors identified it as a viper (e.g. Castilla *et al.* 1991; van Damme & Castilla 1996; Brito 2017), no specimens or remains whose origin is unequivocally from the island have been preserved (Ruiz-Sánchez *et al.* 2019).

At present, the Columbretes Islands area is protected by various figures of the European and Spanish legislation due to their high natural heritage value (Special Protection Area and Site of Community Importance of the Natura 2000 network and Natural Reserve and Marine Reserve, among other). This archipelago also constitutes an important resting area for many birds during their pre- and post-nuptial migration routes between Europe and Africa (Mestre *et al.* 2010).

Humans are one of the main factors determining the current composition of biological communities in the Mediterranean region, and this is particularly evident in island faunas (Blondel & Aronson 1999; Corti *et al.* 1999). The study of these biocenosis and the disturbances produced by human colonization has been studied in the main insular areas in the Mediterranean, such as the Balearic Islands, Corsica, Sicily, Malta, Crete, and Cyprus (Seguí & Alcover 1999; Alcover 2000; Marra 2005; van der Geer *et al.* 2010). However, this kind of studies has been scarce on small islands (e.g. Cherry & Leppard 2017).

In 2005 a palaeontological survey of Illa Grossa was carried out to locate vertebrate fossil remains, in order to characterize the biological communities of the island prior to the human settlement, and to assess human impact in this area (Barnosky *et al.* 2017). As a result, the first palaeontological site of the island, named as Columbretes (COLT), was located in an extensive aeolian deposit in the southern part of Illa Grossa Island fossil remains of vertebrates and gastropods (Fig. 1C). In that area, Hernández-Pacheco & Asensio Amor (1966) reported the presence of numerous bones, although they identified them as belonging to rabbits, a species introduced by humans several times along the 19th century AC (Salvator 1895).

In the present work, the fossil remains of reptiles, birds, and rodents from the COLT site are studied within a radiocarbon dated deposit, thus providing new data about the palaeobiogeographical and palaeoecological context of the Columbretes islands in the time interval between 2 780 and 2 492 BP. For the first time, we have obtained snake remains unmistakably originating from the Columbretes archipelago. The conservation implications of these findings are also discussed.

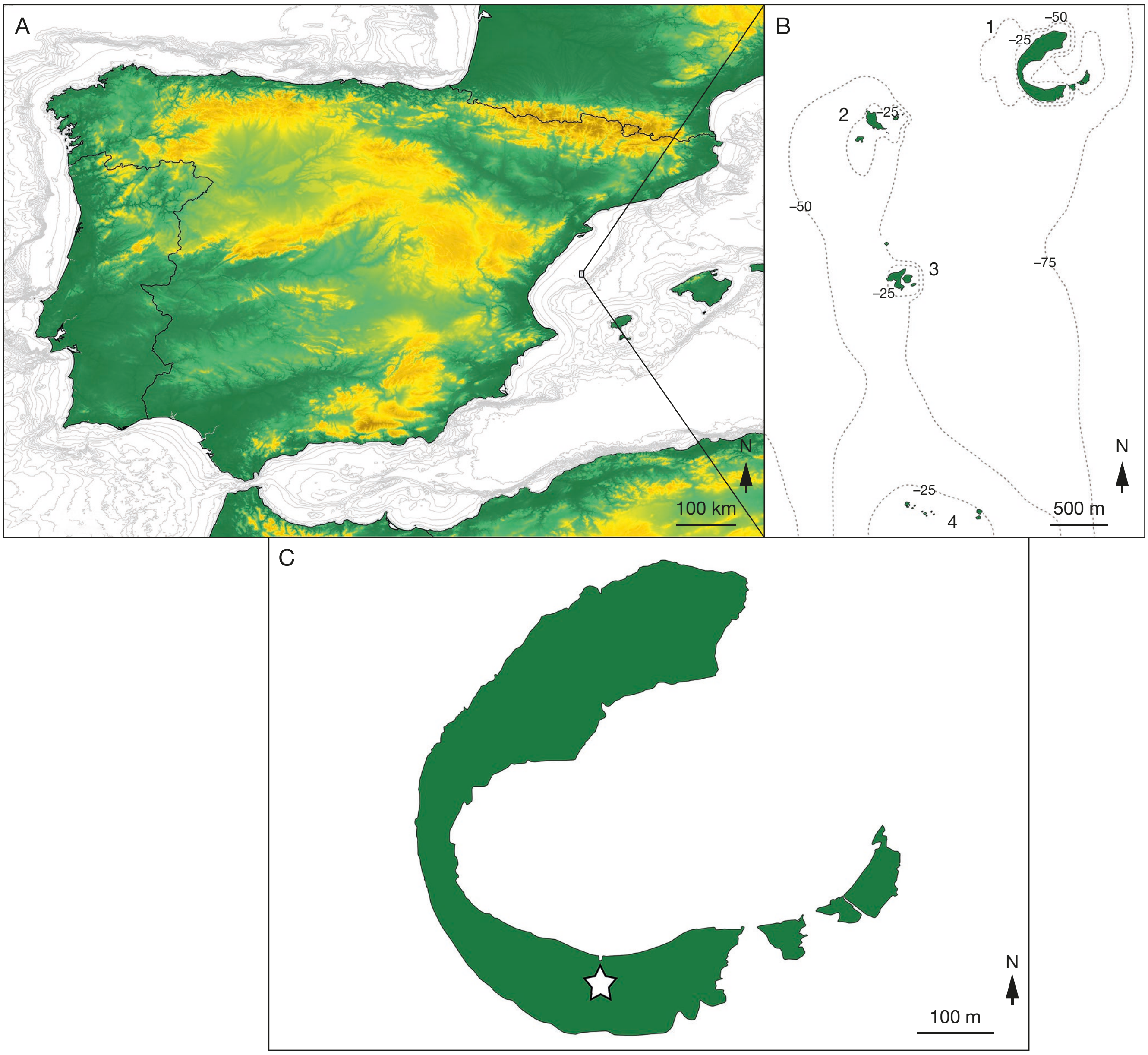

Fig. 1. — **A**, Location of Columbretes Islands in the western Mediterranean; **B**, location of Illa Grossa Island on the archipelago, Island's group: **1**, Illa Grossa group; **2**, Ferrera group; **3**, Foradada group; **4**, El Carallot group; **C**, location of the Columbretes palaeontological site (COLT) on Illa Grossa (**white star**).

GEOLOGICAL CONTEXT

The Illa Grossa Island is a circular structure open to the NE consisting of the emerged rim of a volcano with three SW to NE overlapping craters (Fig. 1C). It is composed of pyroclastic agglomerates, lapilli and ash (Vidal Romaní *et al.* 1972), in layers inclined both to the outside of the volcanic cone and to the inside of the crater. Most of the island has a relief with slopes and locally vertical cliffs (Las Covachas, Mascarat). Most of the materials are volcanic pyroclasts with the exception of a horizontal terrace between 26 and 36 metres above mean sea level. It is a horizontal sedimentary terrace described by Hernández-Pacheco & Asensio Amor (1966). This sedimentary terrace is 6 m thick and lies on lapilli and altered ashes. It consists of brown and yellowish silts, with traces of redeposited pyroclasts and levels of calcareous palaeosoils (Fig. 2). Hernández-Pacheco & Asensio Amor (1966) consider that the top of the fine grained materials of this terrace have a wind source. The paleontological remains studied in this paper have been sampled in this terrace, located 30 m high in the southern sector of the interior of the crater that forms the Puerto Tofiño. The sample has been extracted to a depth of 95 cm (Fig. 2).

MATERIAL AND METHODS

The material studied in the present work consists mainly of disarticulated elements collected during the 2005 palaeontological prospection campaign at Illa Grossa (Columbretes Islands, Spain). An amount of 40 kg of sediment was extracted in a first sampling, washed and sieved, yielding a small vertebrate collection of 239 identifiable remains. This material is stored at the Museu de la Universitat de València d'Història Natural (Burjassot, Spain), with the acronym COLT- (Columbretes). The sediment was water-screened using superimposed 1.5 and 0.5 mm-mesh screens. The fossils were processed, sorted and classified using a Leica MS5 binocular microscope. Measurements were taken on a Leica MZ75 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. Photographs were taken with a HITACHI 4800 scanning electron at the Servei Central de Suport a la Investigació Experimental (SCSIE) of the Universitat de València.

Squamata bones remains were assigned to different taxa following the criteria given by Szyndlar (1984), Barbadillo (1989), Bailon (1991), Barahona (1996), Barahona & Barbadillo (1997), Szyndlar & Rage (2002), Villa & Delfino (2019a) and Čerňanský *et al.* (2020). The obtained fossils were compared with the materials housed in the collections of dry skeletons of the Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas (MNCN-CSIC; Madrid, Spain), Muséum national d'Histoire naturelle (Paris, France), Gabinet de Fauna Quaternària of the Museu de Prehistòria de València (Valencia, Spain) and Departament de Botànica i Geologia from the Universitat de València (Burjassot, Spain). The osteological nomenclature follows Roček (1984), Szyndlar (1984), Bailon (1991), and Russell & Bauer (2008). We follow the taxonomic nomenclature of Speybroeck *et al.* (2020) for reptiles and Pasquier (1974) for mammals. All the measurements have been taken following Barahona (1996) and Barahona & Barbadillo (1997) for lacertids, Blain (2009) and Georgialis *et al.* (2021) for snakes and Pasquier (1974), Darviche & Orsini (1982) and Darviche *et al.* (2006) for mammals.

In order to identify the agent responsible of the fossil accumulation two preliminary taphonomical studies were carried out, one based on the small mammals and the other one only on the squamates fossils. In this sense, digestion marks on small mammal teeth (molars and incisors) have been studied based on the descriptive-systematic method developed by Andrews (1990) and Fernández-Jalvo *et al.* (2016). Regarding reptiles, the study has been based on vertebrae. The digestion marks were observed on the zygosphene, the prezygapophyseal process, condyles and the neural spine. We follow the categories of digestion established by Lebreton *et al.* (2020):

0, non digested;
1, diapophysis and/or parapophysis affected;
2, prezygapophyseal processes also affected;
3, condyle also affected;
4, loss of lamellar bone.

Two samples, one consisting of bone fragments (COLT-BONES) and the other of land snails remains (COLT-SNAILS), were selected for AMS radiocarbon dating and sent to the laboratory of Beta Analytic Inc. located in Miami (United States). COLT-SNAILS was pretreated with acid etch (diluted hydrogen chloride, HCl). For the extraction of the collagen, COLT-BONES was pretreated with alkali (sodium hydroxide, NaOH). The obtained ages were calibrated to calendar years (cal BC/AD) and calibrated radiocarbon years (cal BP). Calibration was calculated using one of the databases associated with the 2013 INTCAL program (Reimer *et al.* 2013).

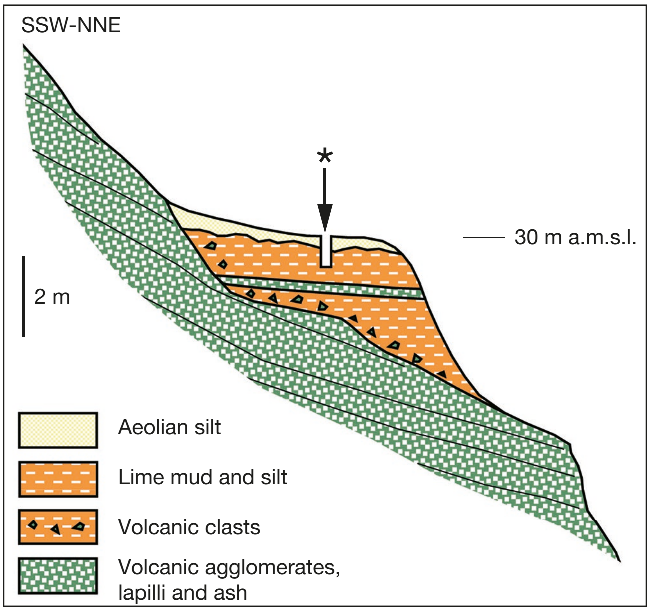

Fig. 2. — Lithostratigraphy of the sedimentary terrace and emplacement of the sample (**asterisk**). Abbreviation: **a.m.s.l.**, above mean sea level.

Abbreviations

c1	posterior accessory cusp;
cal BP	calibrated radiocarbon years before present;
CL	vertebral centrum length, measured ventrally and including the condyle;
CL/NAW	ratio between the centrum length and the minimum width of the neural arch;
COLT	Columbretes palaeontological site;
CTH	cotyle height;
CTW	cotyle width;
CTW/CTH	ratio between width and height of the cotyle;
CTW/NAW	ratio between cotyle width and the minimum width of the neural arch;
I	upper incisor;
L	length of the tooth;
M1	first upper molar;
M2	second upper molar;
m1	first lower molar;
m2	second lower molar;
MNCN-CSIC	Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas;
NAW	minimum width of the neural arch, measured at the maximum intrazygapohyseal constriction;
PO-PO	width of the external borders of the articular surfaces of the postzygapophysis;
PO-PO/NAW	ratio between the width of the external borders of the articular surfaces of the postzygapophysis and the minimum width of the neural arch;
PR-PR	width of the external borders of the articular surfaces of the prezygapophysis;
PR-PR/NAW	ratio between the width of the external borders of the articular surfaces of the prezygapophysis and the minimum width of the neural arch;

SCSIE	Servei Central de Suport a la Investigació Experimental;
W	width of the tooth;
t1, t7, tE	tubercles 1, 7 and E;
TL	total length;
ZW	zygosphene width;
ZW/NAW	ratio between the width of the zygosphene and the minimum width of the neural arch.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Laurenti, 1768
Order SQUAMATA Oppel, 1811
Family SCINCIDAE Oppel, 1811
Genus *Chalcides* Laurenti, 1768

Chalcides bedriagai (Boscá, 1880)
(Fig. 3A-H)

Gongylus ocellatus bedriagai Boscá, 1880: 50 (original description of the species, holotype designated).

Chalcides bedriagae – Boulenger 1887: 402 (current taxonomy established). — Salvador 1998: 152 (lectotype designed).

MATERIAL EXAMINED. — 1 right premaxilla (COLT-4); 4 right maxillae (COLT-7 and 8); 2 left maxillae (COLT-56); 1 left postfrontal (COLT-23); 2 right pterygoids (COLT-20 and 24); 3 right dentaries (COLT-1 and 9); 4 left dentaries (COLT-3 and 11); 11 dorsal vertebrae (COLT-12 and 13); 4 caudal vertebrae (COLT-14); 1 right coxal (COLT-45); 1 right femur (COLT-47).

DESCRIPTION

The preserved premaxilla (COLT-4) is the left one (Fig. 3A). This remain has three dental positions, but only two teeth are present. These are pleurodont, isodont, cylindrical, and monocuspid with a blunt apex. In frontal view, the posterodorsal process is short and leaf-shaped. No foramen is observable in the bone.

COLT-7 is the distal half of a right maxilla (Fig. 3B). Thus, only the posterior and prefrontal processes, although partially broken, are preserved. In labial view, the prefrontal process seems to be subpentagonal, with an anterior margin broken, a dorsal margin roughly subdivided in anterodorsal and posterolateral portions and a sigmoidal posterior margin. A dorsal corner and a posterodorsal corner are clearly visible. The labial surface of the bone is smooth and only one labial foramen is visible; however, the surface is highly damaged so an additional foramen might also be present. In lingual view, the maxilla bears pleurodont, isodont, cylindrical, and monocuspid teeth with a more or less blunt apex. The teeth show a more or less visible ornamentation, with delicate vertical striation limited ventrally by a transverse groove. The supradental shelf is arched and partially broken at the palatine process.

The postfrontal is Y-shaped (Fig. 3C). The anteromedial and anterolateral processes are short and pointed. Both processes have similar size; however, the anterolateral process is more robust than the anteromedial one. In ventral view, the ventral surface between these two processes is concave. On the medial margin, the insertion surface with the frontal and parietal is well marked, while on the lateral margin, the impression with the postorbital is less deep.

COLT-20 is the preserved anterior part of a right pterygoid (Fig. 3D). The quadrate (posterior), transverse (anterolateral) and palatine (anteromedial) processes are partially broken. However, the latter is subrectangular and shows a thicker area in the middle of its platform. The transverse process is subtriangular and has well marked impressions of the ectopterygoid on its dorsal surface. The pterygoid recess is deep and U-shaped. The basis of the quadrate process is broken, for this reason it is not possible to describe it. In lateral view, the transverse process presents a wide and short insertion surface of the pterygoideus muscle. No pterygoid teeth are present.

The dentaries bear pleurodont, isodonts, and cylindrical teeth with flattened or slightly concave lingual surfaces of the crowns and apices oriented in lingual direction (Fig. 3E). In labial view, the teeth appear monocuspid (a slightly pointed or blunt labial cuspid), but in lingual view, underneath the labial cuspid, a smaller lingual cuspid may be present. The *antrum intercristatum* is a generally well-marked groove located on one side and on the other, between these two cuspids. Every tooth apex shows a transversal groove, only some teeth show a vertical striation. The most complete dentaries (COLT-1 and COLT-3) are characterized by the presence of 17 dental positions (Fig. 3E). The width/height ratio for all the teeth equals 0.3 ($n = 31$; $\delta = 0.07$). The coronoid process is subtriangular, straight and posterodorsally projected. In labial view, this process does not show any impression of the coronoid on the wall of the dentary. The studied dentaries present four lingual foramina. In lingual view, the Meckelian groove is open in its whole length and narrower between the eighth-ninth dental position and the anterior end of the tooth row. The subdental shelf is slightly arched and the ventral margin of the dentary is straight.

The vertebrae are procoelous and longer than wide (vertebral centrum length (CL), $CL_{med} = 1.94$ mm; $n= 5$; $\sigma = 0.22$; $CL_{min} = 1.69$ mm; $CL_{max} = 2.23$ mm; minimum width of the neural arch, measured at the maximum intrazygapohyseal constriction (NAW), $NAW_{med} = 0.98$ mm; $n = 4$; $\sigma = 0.08$; $NAW_{min} = 0.86$ mm; $NAW_{max} = 1.05$ mm). In dorsal view, they show a few marked interzygapophyseal constrictions (Fig. 3F). The neural arch shows a rudimentary zygosphene-zygantrum articulation, *sensu* Hoffstetter (1969) and Hoffstetter & Gasc (1969), with two shorts lateral facets (zygosphene) but with a barely outlined posterior zygantrum. The neural spine runs along the entire length of the neural arch, finishing in a point that overtakes the posterior end of the postzygapophysis. In lateral view, the neural spine is low. The synapophyses are oval-shaped and slightly projected anteroposteriorly. In ventral view, the centrum is subcylindrical with its anterior part slightly wider than the posterior one. It shows neither haemal keel nor foramen, except in the case of one vertebra stored under the number COLT-13, which presents a pair of slightly marked large subcentral foramina. In anterior and posterior view, the condyle and cotyle are dorsoventrally flattened.

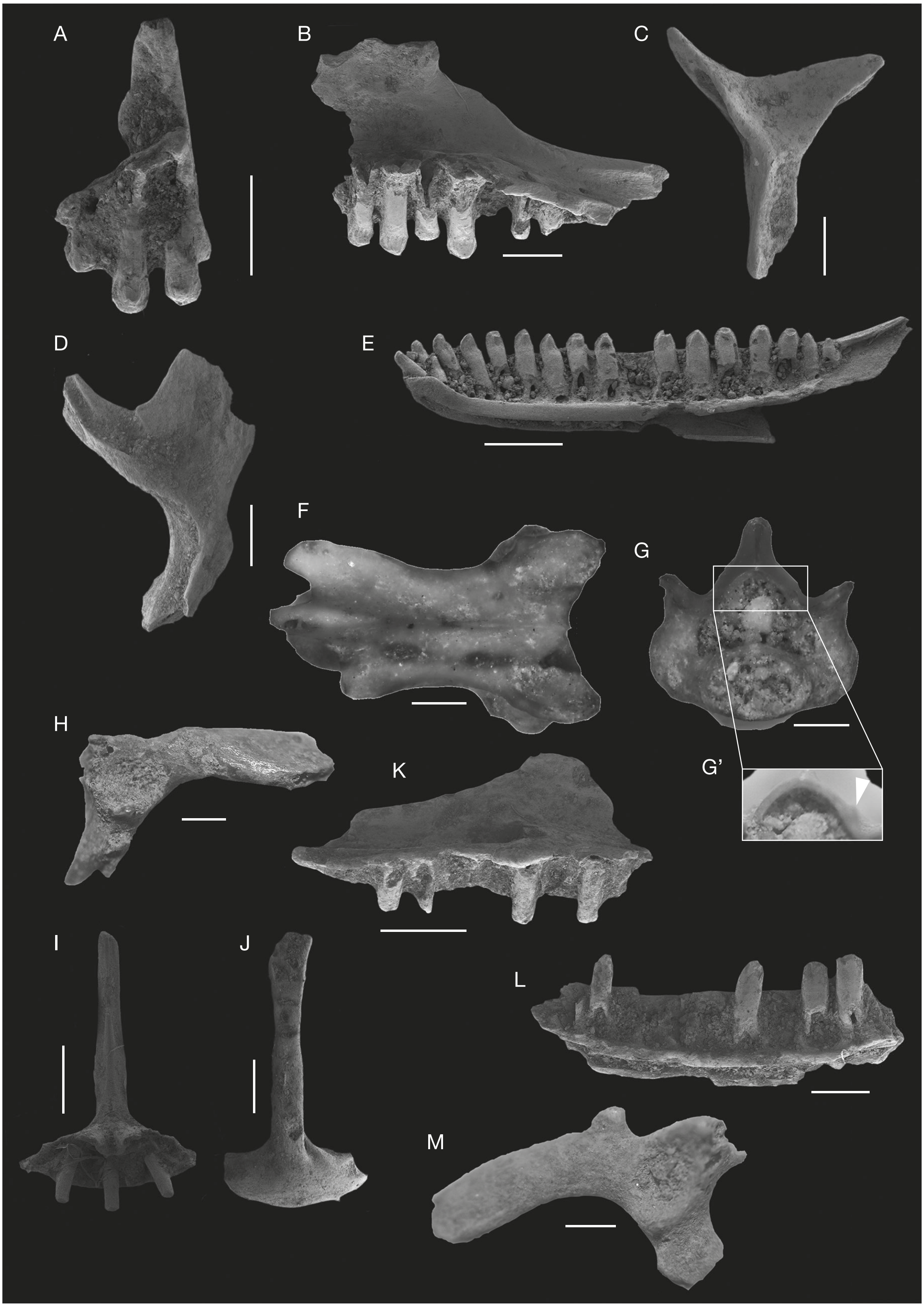

FIG. 3. — Squamates remains from COLT (Illa Grossa, Columbretes Island, Eastern Spain: **A**-**H**, *Chalcides bedriagai* (Boscá, 1880): **A**, left premaxilla (COLT-4), in lingual view; **B**, right maxilla (COLT-7), in lingual view; **C**, left postfrontal (COLT-23) in ventral view; **D**, right pterygoid (COLT-21) in dorsal view; **E**, right dentary (COLT-1) in lingual view; **F**, **G**, dorsal vertebra (COLT-12) in dorsal (**F**) and anterior (**G**) views; **H**, left coxal (COLT-44) in left lateral view; **I**-**M**, cf. *Podarcis* sp. Wagler, 1830: **I**, **J**, premaxilla in lingual (**I**) (COLT-43) and labial (**J**) (COLT-16) views; **K**, left maxilla (COLT-19) in lingual view; **L**, right dentary (COLT-25) in lingual view; **M**, right coxal (COLT-42) in right lateral view. The white **arrow** denotes the presence of the rudimentary zygosphene. Scale bars: 0.5 mm.

COLT-14 includes two vertebrae, which have a pair of dorsoventrally flattened transversal processes typical of caudal vertebrae (Bailon 1991).

COLT-45 is the anterior edge of a coxal, a large elongated bone (Fig. 3H). In lateral view, on the ilium the preacetabular spine and dorsal crest are absent. The acetabulum is rounded.

Only the proximal end of the femur is preserved. It shows a well-developed, ventrally expanded femoral condyle. The internal trochanter is small and is not well defined. Both structures are separated by a large and deep intertrochanteric fossa in ventral view.

REMARKS

The traits described on the material (unfused premaxilla, morphology of the teeth, straight ventral end of the dentaries, open Meckelian groove, presence of a thicker area in the palatine process of the pterygoid, vertebrae with the end of the neural spine overtaking the posterior of the postzygapophysis, and absence of the preacetabular spine and dorsal crest in the coxal) are consistent with the genus *Chalcides* (Barbadillo 1989; Bailon 1991; Caputo *et al.* 1995; Blain 2009; Villa & Delfino 2019a; Čerňanský *et al.* 2020). At present, there are three species of that genus in the Iberian Peninsula, the autochthonous *Chalcides striatus* (Cuvier, 1829) and *Chalcides bedriagai*, and the introduced *Chalcides ocellatus* Forsskal, 1775 (Bisbal-Chinesta *et al.* 2020). In the latter species, teeth are robust with enlarged crowns (Kosma 2004; Villa & Delfino 2019a). This morphology differs strongly from other members of the genus *Chalcides* (Kosma 2004). As we describe above, the COLT fossils do not show these traits on the teeth. Their morphology and width/high proportion do not differ from those of the modern species *Chalcides bedriagai*, which is characterized by 15 to 18 dental positions and a width/height ratio of 0.3 (Barbadillo 1989; Caputo 2004); in contrast to *C. striatus*, which is characterized by 18 to 21 dental positions (Caputo 2004) and a tooth width/height ratio of 0.22 (López-Ruiz *et al.* 2002).

The fossil record of the genus *Chalcides* in the Mediterranean islands is scarce. In this sense, cf. *Chalcides* has been reported from the late Miocene/early Pliocene of Menorca (Bover *et al.* 2014) and indeterminate species of the genus had been reported from the Pleistocene of Menorca (Estes 1983), and Mallorca (Holman 1998). Skinks are highly capable of transmarine migration, as shown by the diversification of the genus *Chalcides* in the Canary Islands. However, in the case of the Balearic Islands sites, it has been proposed that *Chalcides* colonized the archipelago during the Messinian Salinity Crisis (MSC), when these islands were connected to the mainland (Carranza *et al.* 2008). A similar scenario was proposed for the origin of the endemic herpetofauna of the Balearic Islands (Pinya & Carretero 2011), and the spread of *Chalcides bedriagai* in the Iberian Peninsula (Carranza *et al.* 2008). The MSC event had a strong influence in the Mediterranean herpetofauna (e.g. Georgialis *et al.* 2019a). Currently, *C. bedriagai* inhabits numerous islands close to both the Atlantic and Mediterranean coasts of the Iberian Peninsula (Pollo 2015; and references in Ruiz-Sánchez *et al.* 2019).

ECOLOGY

Chalcides bedriagai is an Iberian endemic species localized throughout the Iberian Peninsula, except its northermost area. The distribution range of this taxon is included into the Mediterranean bioclimatic region, except for some localities of northwestern Iberia; although *C. bedriagai* always occupies thermal areas or Mediterranean-like environments. *Chalcides bedriagai* frequents a wide variety of habitats, which are mainly characterized by sandy or earthy substrate with an abundance of shelters (rocks, roots, leaves and shrubs) and high sun exposure, which constitutes a limiting factor of their presence (Pollo 2015).

Family LACERTIDAE Oppel, 1811

Genus *Podarcis* Wagler, 1830

Lacerta (Podarcis) Wagler, 1830: 155.

Podarcis – Arnold 1973: 343.

TYPE SPECIES. — *Seps muralis* Laurenti, 1768, subsequent designation by Fitzinger (1843).

NOTES

Böhme (1997) regarded the gender of *Podarcis* to be masculine; Arnold (2000) proposed to retain the gender of the genus as femenine; and Böhme & Köhler (2005, current taxonomy) established it as masculine gender.

cf. *Podarcis* sp.
(Fig. 3I-M)

MATERIAL EXAMINED. — 4 premaxillae (COLT-15, 16 and 43); 4 left maxillae (COLT-18, 19 and 39); 2 right maxillae (COLT-17); 2 left pterygoids (COLT-21 and 22); 1 dorsal vertebra (COLT-40); 1 possible sacral vertebra (COLT-53); 2 caudal vertebrae (COLT-41); 1 centrum of caudal vertebra (COLT-48); 1 right coxal (COLT-42); 2 left humeri (COLT-45 and 57); 1 right humerus (COLT-46).

DESCRIPTION

The premaxillae of this species are represented in the Columbretes Islands by four small-sized remains, with an average with of the premaxillary shelf of 1.23 mm ($n = 3$; $\sigma = 0.13$). The posterodorsal process is thin and has parallel lateral margins (Fig. 3I). The most complete specimen (COLT-43) has seven dental positions, but only three teeth are present. These are pleurodont, isodont, cylindrical, and monocuspid with a blunt apex. COLT-16 shows the distal end of the posterodorsal process slightly expanded (Fig. 3J). The nasal foramina are present at the base of the posterodorsal process. In posterior view, this process has a well-defined medial crest.

The maxilla bears pleurodont, isodont, cylindrical, mono or bicuspid teeth with a blunt apex. In dorsal view, the remains have a wide palatal shelf with a large superior dental foramen. The anterior margin of the maxilla has short anteromedial and anterolateral processes. The two processes are similar in size; however, the anterolateral process seems to be slightly larger than the anteromedial one. The notch formed on the anterior concavity between both processes is shallow. A wide vomeronasal foramen is located in the basis of the anterior margin of the dorsal process. In lingual view, the anteromedial process does not show any lappet. However, in COLT-39 the anteromedial process, although broken, seems to be elevated and, probably, formed a lappet. It is impossible to evaluate the degree of development of the eroded prefrontal process. The posterior process is short and with a step on its dorsal margin (Fig. 3K). In labial view, the surface of the maxilla is smooth and shows three labial foramina.

The dentaries are fragmentary (Fig. 3L). The recovered remains bear pleurodont, isodont, cylindrical, bi- and monocuspid teeth, with a more or less pointed principal cuspid. In lingual view, the Meckelian groove is open and the subdental shelf is arched.

The vertebrae are procoelous and longer than wide. In dorsal view, they show a marked interzygapophyseal constriction. In the foremost part, the remains show a rudimentary zygosphene-zygantrum articulation, *sensu* Hoffstetter (1969) and Hoffstetter & Gasc (1969). The neural spine runs along the entire length of the neural arch, except its first quarter. The neural arch terminates in a point, which does not overtake the postzygapophysis. In lateral view, the neural spine is low. The vertebra has an oval-shaped synapophysis, which is slightly anteroposteriorly projected. The ventral margin of the centrum is convex. In ventral view, the centrum is subtriangular in shape with its anterior part wider than the posterior one. The haemal keel is absent. A pair of small not well-defined subcentral foramina is present. In anterior and posterior view, the condyle and the cotyle are small and have a subcircular shape. COLT-48 consists in a centrum of a procoelous caudal vertebra, slightly wider than longer with well-developed and dorsoventrally flattened transverse processes.

The coxal is a large elongated triradiate compound bone (Fig. 3M). It is formed by the complete fusion of the ilium, ischium, and pubis, without any trace of suture line. In the posterior region of the ilium, a hooked preacetabular spine is dorsally projected. The coxal does not show any dorsal crest. The acetabulum is oval and large. The pubis is broken. Although the ischium is broken, it seems to be large and wide. It forms a posterior angle of about 90° with the ilium.

The recovered humeri have only the distal end preserved. The epiphysis is wider than the diaphysis. In ventral view, it shows a deep radioulnar fossa. The radial condyle is oval in shape and transversely compressed, whereas the ulnar condyle is slightly larger and rounded. The ectepicondyle is not well differentiated. The entepicondyle is reduced. The entepicondylar foramen is large.

Remarks

The fossils described here show typical traits of Lacertidae: fused premaxilla with a slender posterodorsal process; pleurodont, isodont and mono or bicuspids teeth; ventral edge of the dentary concave in lingual view; Meckelian groove of the dentary open along its whole length in lingual view; procoelous vertebra with the centrum transversally convex and the neural spine not exceeding the posterior limit of the postzygapophysis; coxal with preacetabular spine but no dorsal crest, humerus with a laterally flattened radial condyle, rounded ulnar condyle, and the presence of an ectepicondylar foramen (Bailon 1991; Barahona 1996; Russell & Bauer 2008). Although the osteology of the lacertids is poorly studied, some taxonomic ascription can be tried. Thus, the presence of a step in the posterior process of the maxilla is a characteristic reported by Barahona & Barbadillo (1997) and Villa & Delfino (2019a) for the lacertid genera *Iberolacerta* Arribas, 1997, *Lacerta* Linnaeus, 1758, and *Podarcis*. Regarding the premaxilla, the parallel position of lateral margins of the posterodorsal process and the number of dental positions exclude some lacertid species, reducing the options to *Podarcis*, *Iberolacerta*, *Psammodromus* Fitzinger, 1826 and *Acanthodactylus* Wiegmann, 1834 (Barahona & Barbadillo 1997). The last two can be discarded due to the absence of a step in the posterior process of the maxilla (Barahona & Barbadillo 1997; Villa & Delfino 2019a). The mean size of the premaxilla shelf is included in the range of the *Podarcis* species provided by Barahona (1996), except for *Podarcis bocagei* (Seoane, 1884), considered as *Podarcis bocagei bocagei* in the refereed work, and *Iberolacerta bonnali* (Lantz, 1927), in which sizes are larger than those recorded for the COLT lacertid premaxilla. On the other hand, the number of premaxillary teeth (7) restrains the options to *Podarcis muralis* (Laurenti, 1768), *P. bocagei*, *Podarcis hispanica* sensu lato (Steindachner, 1870) and *Iberolacerta bonnali* (Lantz, 1927) (Barahona & Barbadillo 1997). Following biogeographic criteria, the presence of a species of *Iberolacerta* seems unlikely because these lacertids are almost entirely confined to small widely separated mountain areas (e.g. *I. bonnali* only inhabited the Central Pyrenees) and they tend to be taxa adapted to cold environments (Ortega *et al.* 2016). Thus, all these characteristics permit an attribution of the COLT fossils to cf. *Podarcis* sp.

The fossil record of lacertids is known in the larger Mediterranean islands (Bailon 2004). The insular record of the genus *Podarcis* is limited to Crete, Sicily, Sardinia, Corsica, Mallorca, Ibiza, and Menorca (Bailon 2004; Villa & Delfino 2019b). Several works (Bover *et al.* 2014; Rodríguez *et al.* 2017; Spilani *et al.* 2019) proposed that the ancestors of the current *Podarcis* species that inhabit these islands reached them via land bridges. However, the populations of *Podarcis siculus* (Rafinesque-Schmaltz, 1810), present in Menorca, Sardinia and Corsica, have been introduced by humans in historical times (Silva-Rocha *et al.* 2018).

Current ecology

Podarcis is a circummediterranean genus that is widespread in Southern Europe, the Anatolian Peninsula and Northern Africa (Spreybroeck *et al.* 2016). At least, 12 species are endemic of the Mediterranean islands, especially in the Aegean Sea (Spreybroeck *et al.* 2020). At present, the Columbretes archipelago is inhabited by *Podarcis liolepis atratus* (Boscá, 1916), until recently considered as an endemic insular subspecies

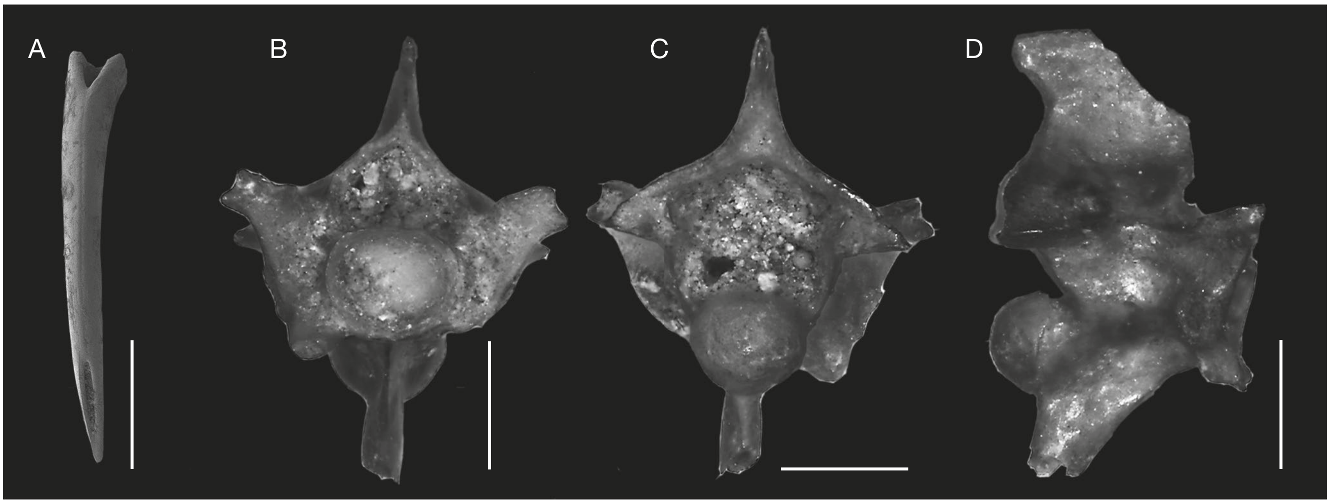

FIG. 4. — *Vipera* cf. *latastei* Boscá, 1878 from COLT (Illa Grossa, Columbretes Island, Eastern Spain): **A**, solenoglyph fang (COLT-2); **B**-**D**, precaudal vertebra (COLT-5) in anterior (**B**), posterior (**C**) and right lateral (**D**) views. Scale bars: 1 mm.

(Ruiz-Sánchez *et al.* 2019 and references therein). This lizard is present in all islands and islets of the Columbretes, except in the Ferrera group (Castilla *et al.* 1998a). The absence of the species in Ferrera is not understood, since this island include potential habitats for this lizard. The presence of fossils of a Wall Lizard (*Podarcis* sp.), or related taxa, in a palaeontological context confirms the ancient occupation of the Columbretes Islands by this taxon. The open taxonomical attribution proposed for the lacertid fossils does not allow further inferences about the palaeoecological context during the formation of the site.

Sub-order SERPENTES Linnaeus, 1758
Clade CAENOPHIDIA Hoffstetter, 1939
Family VIPERIDAE Oppel, 1811
Genus *Vipera* Laurenti, 1768

Vipera cf. ***latastei*** Boscá, 1878
(Fig. 4)

Vipera latastei Boscá, 1878: 121 (original description of the species). — Boscá 1879: 30.

Vipera berus aspis var. *latastei* – Camerano 1889: 231.

Vipera latastii [sic] – Boulenger 1896: 484.

Rhinaspis (Latastea) latastei Reuss, 1930: 69.

Vipera ammodytes latastei – Saint-Girons 1977: 605 (the author pointed out that *V. latasti* was a *lapsus calami*, thus he proposed that the correct name is *V. latastei*; designation of a lectotype). — ICZN 2017: opinion 2381 (case 3629), confirmation that *V. latastei* is the correct specific name for the taxon.

MATERIAL EXAMINED. — 15 venom fangs (COLT-2 and 10); 1 left dentary (COLT-49); 8 precaudal vertebrae (COLT-5, 6, 50 and 52); 8 centra of precaudal vertebrae (COLT-51); 1 caudal vertebra (COLT-53).

DESCRIPTION

The fangs are strongly curved (Fig. 4A). Their anterior surface shows an elongated, slender venom discharge distal orifice, which is long and narrow. The pulp cavity and a canal, with a circular cross-section, can be observed in the teeth. The canal is completely closed, without any groove or suture in the external surface of the teeth.

COLT-49 is a fragment of dentary bone with three dental positions, but only two teeth preserved. The teeth, which are inserted on small alveoli, are conical and curved posteriorly.

The precaudal vertebrae are small-sized (CL_{med} = 2.76 mm; n = 5; σ = 0.43; CL_{min} = 2.10 mm; CL_{max} = 3.21), procoelus and longer than wide. In anterior view, the zygosphene is straight (Fig. 4B). The cotyle is rounded and large. A pair of large and well-defined paracotylar foramina are present. The articular facets of the prezygapophyseal process is dorsolaterally inclined. In posterior view, the neural arch is dorsoventrally flattened (Fig. 4C). The condyle is rounded and large. Its diameter is smaller than the neural arch one. In dorsal view, the vertebrae show a trilobated zygosphene, where the central and the lateral ones are of similar size. The neural spine runs along the whole extension of the neural arch. The prezygapophyses are anterolaterally projected, whereas the postzygapophyses are posterolaterally projected. The prezygapophyseal process is short and pointed. In ventral view, the centrum is triangular in shape, wider anteriorly than posteriorly and with not well-defined lateral margins. The subcentral foramina are situated in the anterior part of the centrum and are large and well defined. In lateral view, the neural spine is high (Fig. 4D). The lateral margins of the neural arch are not well defined. The prezygapophyses are anterolaterally projected, whereas the postzygapophyses are posterolaterally projected. The parapophyseal process is well defined and antero-ventrally projected. The inferior margin is well defined. The centrum is transversally convex. The hypapophysis is broken, but seems to be long and straight. In ventral view, the centrum is triangular in shape. It is wider anteriorly than posteriorly.

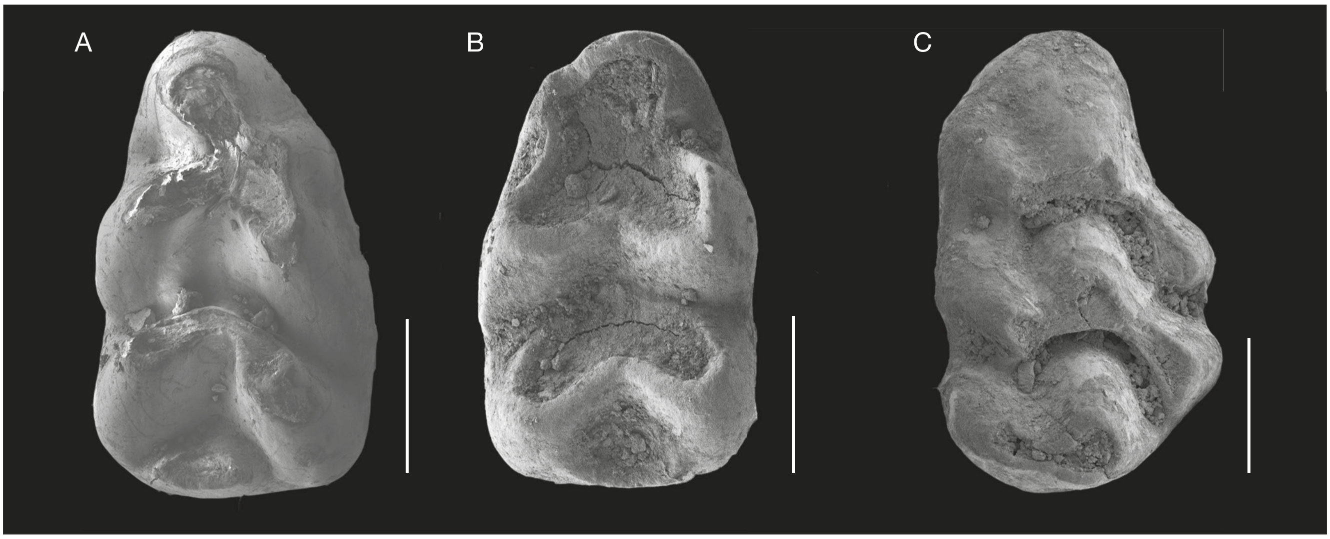

Fig. 5. — *Mus* cf. *musculus* Linnaeus, 1758 from COLT (Illa Grossa, Columbretes Island, Eastern Spain): **A**, right m1 (COLT-31); **B**, left m1 (COLT-37); **C**, right M1 (COLT-38). Both pictures are in occlusal view. Scale bars: 0.5 mm.

The lateral margins of the centrum are not well defined. The subcentral foramina are situated in the anterior part of the centrum and are large and well defined. The condyle and the cotyle are large and rounded. In posterior view, the diameter of the condyle is smaller than the diameter of the neural arch. The presence of a pair of haemapophysis indicates that COLT-53 belongs to a caudal vertebra.

REMARKS

The recovered fossils are attributable to *Vipera* by: the presence of a venom fang of solenoglyph type without any groove or suture in the external surface of the tooth; the presence of a closed venom canal which originated from the dentine floding throughout ontogeny; dorsal vertebrae with hypapophysis, neural arch dorsoventrally depressed, vertebral centrum longer than wide, ventrally convex centrum with diffuse lateral margins, well developed condyle and cotyle, parapophyseal processes present, and the articular surface of the pre and postzygapophyses dorsally inclined (Szyndlar 1984; Bailon 1991; Bailon *et al.* 2002; Georgalis *et al.* 2019a). According to the size of the examined vertebrae (CL: 2.76 mm), the material from Illa Grossa belongs to a “European Viper” (CL < 5mm). Within the latest group, there are two complexes that differ in their vertebral morphology: the “*Vipera berus* complex” and the “*V. aspis* complex” (Szyndlar & Rage 1999, 2002). Their isolated trunk vertebrae may be distinguished by their shape and size. The vertebrae of the “*V. berus* complex” are small, elongated, and provided with low neural spine and hypapophyses, whereas the vertebrae of the “*V. aspis* complex” bear more developed hypapophyses and neural spine (Szyndlar & Rage 1999). In the material from COLT, the hypapophyses are broken but they appear to be straight and well-developed; this trait, together with the presence of a high posterior edge of the neural spine (higher than the centrum in lateral view), allow us to attribute the remains to the “*V. aspis* complex”. Unfortunately, the hypapophyses from the COLT fossils are broken, and the posterior edge of the neural spine is preserved only in COLT-5, where it is high (higher than the centrum in lateral view) as in the “*V. aspis* complex” members. For morphological, palaeobiogeographical, and biostratigraphical reasons, the species present at the Illa Grossa Island most probably was *Vipera latastei*. Therefore we propose here an open attribution to this taxon until new fossils can definitively settle this problem. This attribution is more extensively discussed in the section on the identity of the Columbretes snakes below.

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Family MURIDAE Illiger, 1811
Genus *Mus* Linnaeus, 1758

***Mus* cf. *musculus* Linnaeus, 1758**
(Fig. 5)

Mus musculus Linnaeus, 1758: 62 (original description of the species).

Mus domesticus Rutty, 1772: 281.

Mus abbotti Watherhouse, 1837: 77.

Mus nordmanni – Keyserling & Blasius 1840: 330 (*nomen nudum*).

Mus molossinus Temminck, 1845: 51.

Mus varius – Fitzinger 1867: 70 (*nomen nudum*).

Mus musculus yonakuni Kuroda, 1924: 8. — Kaneko & Maeda 2002: 12.

Mus albula Kishida, 1924: 143. — Kaneko & Maeda 2002: 12.

Mus bactrianus tantillus Allen, 1927: 9. — Schwarz & Schwarz 1943: 62 (reviewed along with the rest of the genus). — Ellerman & Morrizon-Scott 1951: 607.

MATERIAL EXAMINED. — 3 I (COLT-33 to COLT-35); 1 M1 (COLT-30); 1 M2 (COLT-29); 2 m1 (COLT-28, COLT-31); 1 m2 (COLT-32).

DESCRIPTION

Upper incisors are rounded and curved.

The recovered first upper molars are brachyodont and bunodont, and do not present the t7. The t1 is placed towards the posterior part of the tooth.

The first lower molars are brachyodont and bunodont and there is no anterocentral tubercle. On the anterior region, the tE is not well individualized, and it develops a trilobed morphology in one specimen (COLT-31). COLT-28 has its tE broken, while COLT-37 is quite worn. No external cingular margin with a well-developed secondary cusp (c1), is present in any of the three specimens.

The second molars are also brachyodont and bunodont, with no trace of the antero-labial tubercle. The labial cingulum is not developed, and the posterior tubercle is big, round or oval.

REMARKS

The absence of the t7 tubercle in the upper first molars is characteristic of the genus *Mus*, contrary to what it is seen in the genus *Apodemus* Kaup, 1829, in which the t7 is always present (Chaline 1974). Moreover, the first lower molars recovered from in Columbretes lack the anterocentral tubercle, as it is the case in *Mus* (Pasquier 1974; Gosàlbez 1987). The trilobed morphology observed in the anterior part of the first lower molars is characteristic of *Mus musculus* (Darviche & Orsini 1982). In addition, the clear absence of an external cingular margin with a well-developed secondary cusp in the first lower molars also points to *M. musculus*, whereas it is quite common in *Mus spretus* Lataste, 1833 (Darviche & Orsini 1982; Darviche *et al.* 2006). Regarding the metrics of the first lower molars, the mean length and width values fall between *Mus spretus* lowest mean values (Fig. 6A), although if we take into account specimens values, those are placed in an overlapping area between both species values (Fig. 6B) (Darviche & Orsini 1982; Domínguez García *et al.* 2019).

Species within the genus *Mus* can be distinguished based on morphotypes percentages. Unfortunately, the very low population size does not allow us to extract percentages. However, all morphologic characters are typical of *Mus musculus*. On the other hand, metric values are compatible with some big individuals from a *Mus musculus* population as shown in the record (Darviche & Orsini 1982). Due to the aforementioned reasons, we ascribe the studied mammal material to *Mus* cf. *musculus*.

Class AVES Linnaeus, 1758

Aves indet. spp.

Aves Linnaeus, 1758: 12, 78-80.

MATERIAL EXAMINED. — 58 undetermined remains (COLT-58 to 92).

DESCRIPTION

Among the recovered vertebrate remains, a total of 35 bone fragments could be attributed to birds, all small-sized, and 30 of them belonging to small passerines. Unfortunately, these bone remains lack diagnostic features allowing a more precise taxonomic ascription. Among the recovered bones is a proximal part of humerus, but its poor preservation state prevents its identification. The remaining five bones belonged to seabirds. Three fragments of pedal phalanges belonged to shearwaters (Procellariidae), and a wing phalanx and a cranial part of scapula to very small species of other families within the procellariiforms group. All the recovered bones correspond to adult individuals.

REMARKS

The recovered avian fossils comprise at least six undetermined species of birds (two of seabirds and four passerines). Currently, many of the birds that make their migratory trips along the eastern coast of the Iberian Peninsula arrive to the Columbretes due to adverse weather conditions, particularly, with westerly winds. For this reason and despite their small surface, these islands are home to a varied ornithocenosis, made up of dozens of passerine species. They constitute also a safe place for breeding colonies of several marine species of birds (Díaz *et al.* 1996). It can be assumed that the avian ranges did not undergo major changes in the region during the late Holocene.

DISCUSSION

CHRONOLOGY

The two radiocarbon (^{14}C) dated samples of the site yielded similar chronologies: 2780-2724 cal BP for COLT-SNAILS and 2600-2492 cal BP COLT-BONES. In general, terrestrial snails provide older ^{14}C shell dates (Evin *et al.* 1980), which is attributed to the fact that many taxa incorporate ^{14}C-deficient carbon from limestone and other carbonate rocks when building their shells, the so-called "Limestone Problem" (Goodfriend & Stipp 1983). However, this phenomenon seems to be related with large specimens (Brennan & Quade 1997) and is strongly dependant of the species (Pigati *et al.* 2010). Moreover, small land snails recovered from fossil deposits in arid environments, as it is the case of the Columbretes Islands (Castilla & Bauwens 1991), may yield reliable ^{14}C ages (Pigati *et al.* 2010). The sample of terrestrial gastropods used in the present study was composed of a mixture of shell fragments of small and large species.

FOSSIL ASSEMBLAGE

The COLT site has provided a rich fossil assemblage of terrestrial gastropods and vertebrates (fishes, reptiles, birds and mammals). The only vertebrates previously described here are dermal denticles of *Raja clavata* Linnaeus, 1758 or a very close taxon (Ferrón *et al.* 2015). The gastropod remains recovered from the COLT site are currently under study. A preliminary examination reports the occurrence of several families of terrestrial snails: Ferussaciidae Bourguignat, 1883; Geomitridae

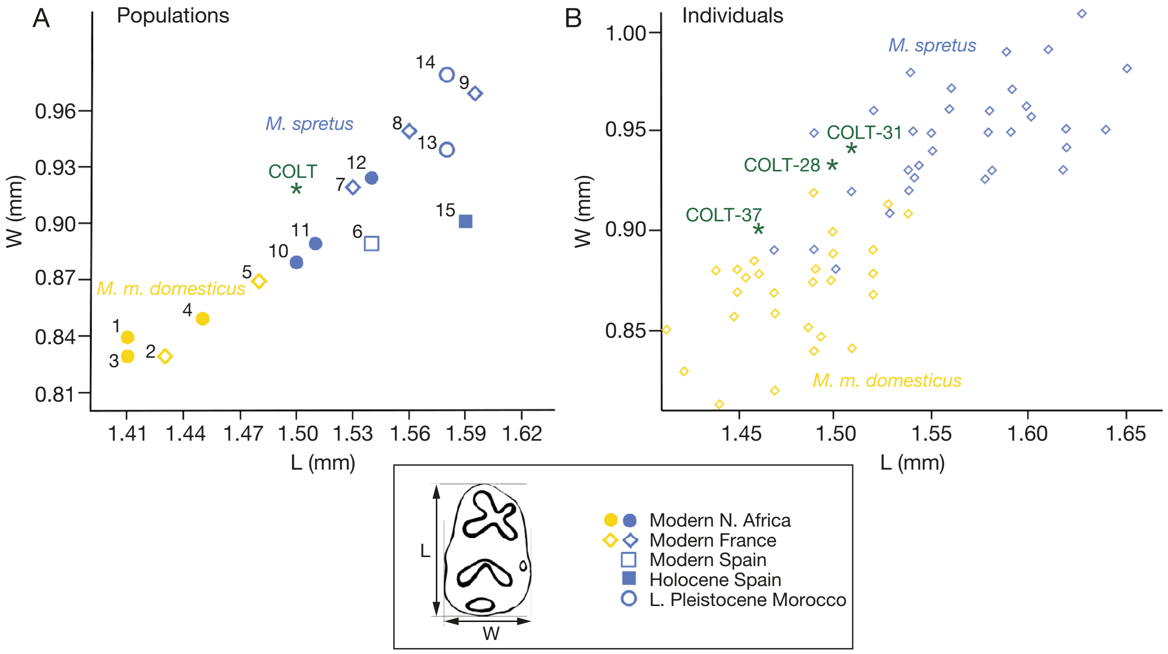

Fig. 6. — Scatterplot comparing mean length (**L**) and mean width (**W**) of first lower molar from *Mus m. domesticus* Linnaeus, 1758 (**yellow**) and *Mus spretus* Lataste, 1883 (**blue**) in several localities from the Late Pleistocene until recent time in the western mediterranean area: **A**, mean values for populations (modified from Domínguez-García *et al.* 2019); **B**, values for individuals (modified from Darviche & Orsini 1982). Numbers: **1**, Azemour (Morocco) (n = 14); **2**, Toulouse (n = 16); **3**, Algeria (n = 14); **4**, Tunisia (n = 19); **5**, Southern France (n = 29); **6**, Granada (n = 20); **7**, Montpellier (n = 22); **8**, Southern France (n = 33); **9**, Southern France (n = 7); **10**, Tunisia (n = 25); **11**, Morocco (n = 40); **12**, Morocco (n = 41); **13**, Doukkala (n = 17); **14**, El Harhoura II (n = 263); **15**, Cerro de la Encantada (n = 14). Abbreviation: **CB**, Castillejo del Bonete (n = 164). Sources: 1-4, 7, 10, 11, 13, Darviche *et al.* 2006; 5, 8, Darviche & Orsini 1982; 6, Morales Muñiz 1986; 9, Gerasimov *et al.* 1990; 12, 14, Stoetzel 2009; Stoetzel *et al.* 2010. Credits: modified from Domínguez-García *et al.* 2019.

Boettger, 1909; Helicidae Rafinesque, 1815; Lauriidae Steenberg, 1925; Pomatiidae Newton, 1891; Punctidae Morse, 1864; and Vertiginidae Fitzinger, 1833. Fossils of marine gastropods (Littorinidae Children, 1834) are also present.

A total of 239 remains of reptiles, mammals, and birds have been studied in this paper. The fossil assemblage determined in the present work is composed by two lizards (*Chalcides bedriagai* and cf. *Podarcis* sp.), a snake (*Vipera* cf. *latastei*), a rodent (*Mus* cf. *musculus*) and, at least, six species of birds belonging to seabirds (two) and passerines (four).

The COLT association clearly differs from the present terrestrial fauna of Illa Grossa, which is limited to a single non-flying vertebrate species: the Columbretes' Wall Lizard, *Podarcis liolepis atratus* (Jiménez *et al.* 2002; Mestre *et al.* 2010). Castilla & Bauwens (2000) noted that the divergence within the Columbretes' lizard population took place at most one million years ago. The oldest reference about Wall Lizards in the Columbretes Islands is provided by Salvator (1895), whereas the occurrence of snakes was already reported by the Ancient Greeks (Bernis 1968; Silva-Rocha *et al.* 2018). In this sense, the remains described here are the oldest specimens of Wall Lizards in the Columbretes Islands.

One of the most remarkable discoveries in the COLT association is the presence of *Chalcides bedriagai*, since no historical reports the presence of skinks in the Columbretes Islands. This lack of reports in the Illa Grossa Island might be related to the cryptic behaviour of this species, which remains hidden most of the time (López-Jurado *et al.* 1978). Alternatively, some specimens could have been misidentified as snakes by non-expert observers due to of their elongated body. Their extirpation on the island most probably took place before the start of the scientific study of the islands (last third of the 19th century) (Ruiz-Sánchez *et al.* 2019) and, in general, could be related with the profound human-induced changes that affected the terrestrial ecosystems.

The description of the vegetation of the Illa Grossa Island in some classical texts (Smyth 1831; Salvator 1895; Bru 1913) pointed out the presence of *Opuntia ficus-indica* Miller, 1754, an invasive species in Mediterranean and semiarid areas (Sanz-Elorza *et al.* 2004), which is still present in the Columbretes Islands (Mestre *et al.* 2010). The colonization of the archipelago by this species could be early, since *O. ficus-indica* was already present in the coastal areas of eastern Spain in the 18th century (Sanz-Elorza *et al.* 2004). However, the negative impacts of the modifications in the terrestrial biological communities (fires and introduction of exotic species) that were produced in the Illa Grossa during the construction of the lighthouse in the 19th century cannot be ruled out. In this sense, some populations of *C. bedriagai* have undergone strong recessions or have disappeared due to the human-induced habitat alteration in different areas of the Iberian Peninsula (Jiménez *et al.* 2002; Pollo 2015).

About the identity of the snakes from the Columbretes archipelago

Although the historical abundant presence of snakes in the Columbretes archipelago is a widely known fact, their identity remains unclear and is a matter of debate since the middle of the 20th century (Mertens 1957; Klemmer 1961; Bernis 1968; Ruiz-Sánchez *et al.* 2019). Herpetologists have worked with two hypotheses:

Colubrid hypothesis: in the middle of the last century, Mertens (1957) and Klemmer (1961) proposed that the snakes from the Columbretes Islands were actually colubrids. These researchers based its proposal on: 1) absence of bite reports. With such a high density of alleged vipers, it is difficult to explain why none of the lighthouse construction workers were ever bitten. However, according to Salvator (1895), the herpetologist Eduard Boscà claimed that, in fact, these incidents did occur; 2) the high densities reported in the historical texts could only be supported by a wide availability of terrestrial prey, but theoretically this does not seem to be the case at the Illa Grossa Island. Therefore, the colubroid species must have exploited other resources of marine origin (fishes and crustaceans); and 3) there are no cases of insular populations of vipers in islands similar to Illa Grossa. At present, there are several island populations of vipers in the Mediterranean Basin (Speybroeck *et al.* 2016). Thus, in the Aegean Sea, *Vipera ammodytes* (Linnaeus, 1758) is present on numerous Cycladic islands, *Macrovipera schweizeri* (Werner, 1935) inhabits the eastern Cyclades, *Macrovipera lebetinus* (Linnaeus, 1758) is present in Cyprus, but its autochthony is still under debate (Torres-Roig *et al.* 2020), and, finally, *Montivipera xanthina* (Gray, 1849) is present on numerous Greek islands off the Turkish coast. All seem to have an origin related to natural dispersal from the Anatolian mainland to the islands after the formation of the mid-Aegean Trench (Poulakakis *et al.* 2015). In contrast, the origin of viper populations from the western Mediterranean islands is much less clear. While it has been demonstrated that the population of *Vipera aspis* (Linnaeus, 1758) on the island of Montecristo was introduced by humans around the 5th century, it is not clear whether the origin of the populations on the island of Elba is due to natural dispersal during episodes of marine transgression or to human-induced dispersal (Masseti & Zuffi 2011). As for the colonization of Sicily by *V. aspis*, it seems to be result from the low-stand sea level during the Pleistocene (Barbanera *et al.* 2009). In this sense, the anthropogenic introduction of snakes in western Mediterranean islands seems to be a recurrent event in the historical times (i.e., Insacco *et al.* 2015; Silva-Rocha *et al.* 2018). However, natural colonization has also been documented on Western Mediterranean islands. This is the case of the today extinct *Vipera latastei ebusitana* Torres-Roig, Alcover & Bailon, 2020, from the Late Pleistocene-Holocene of Es Pouàs (Ibiza, Balearic Islands, Spain) (Torres-Roig *et al.* 2020). These authors proposed that the arrival of the ancestor of this taxon occurred through oversea rafting between 1.31 Ma and *c.* 30 000 BP.

Thus, basing on the three reasons described above, Mertens (1957) and Klemmer (1961) ascribed the snakes from the Columbretes Archipelago to a natricine colubroid; specifically Klemmer (1961) suggested that it probably was *Natrix maura* Linnaeus, 1758, one of the most common snake species in the Iberian Peninsula. In this sense, *N. maura* displays a viper-like defensive behaviour mimicry (Aubret & Mangin 2014), resulting in an easy confusion between both species. Moreover, there are islands populations close to the mainland in the Atlantic and Mediterranean coast of Europe and North Africa (Mateo 1990, 1997; Mateo *et al.* 2009) with the presence of this species. On the other hand, the *N. maura* populations from larger islands, such as Mallorca or Menorca, were probably introduced by humans (Corti *et al.* 1999). Additionally, it is known that *N. maura* is capable to exploit marine resources in many areas of its distribution range (Fuentes & Escoriza 2015). A few years ago, a snake vertebra was recovered from the sediment form the around of the cistern area in the Columbretes Islands. Altough preliminarily attributed to the genus *Coronella* Laurenti, 1768 (Jiménez *et al.* 2002), this remain is currently lost and, to the best of our knowledge, no photograph or description that can support or refute this determination (I. Lacomba, comm. pers.).

Viperid hypothesis: The classical reports identified the species as a viper (Vicent 1885; Bru 1913; Bernis 1968), some of them with doubts (Salvator 1895; Español 1958). In this sense, no direct rest is available to confirm or discard this identification. The MNCN-CSIC houses a supposedly preserved specimen (reference number 468 in the herpetological collection), but the history of its origin is controversial. The original identification label of the specimen is currently lost, and the copy presents some typographic errors. In fact, the collector's name ("Sr. Mojaelos") is erroneous because nobody with that name is present in any workers' list during the construction of the lighthouse in the Illa Grossa Island. As Bernis (1968) points out, it is possible that, actually, this name was an erroneous transcription of Mojades, the surname of one of the engineers who were in charge of the works between 1856 and 1857. Bernis (1968) did not found any differences between the conserved specimen and Lataste's viper individuals from south-eastern Spain. The only direct description of living individuals, which is compatible with vipers, was written by Smyth (1831).

As it has been described above, the morphology of the recovered material in the COLT site belongs to a viperid of the genus *Vipera*. During the Pleistocene, the fossil record of vipers in the southern half of the Iberian Peninsula is limited to the *Vipera aspis* complex, while the remains of the *Vipera berus* group is located in the northern Iberian region (Szyndlar & Rage 2002; Böhme & Ilg 2003). The same pattern is observable in the current distribution of the three Iberian vipers (Pleguezuelos *et al.* 2002). In this sense, the only viper that inhabits southern Iberia is *Vipera latastei*, and it is the only species reported from palaeontological and archaeological sites during the Pleistocene. Although there are some reports of *Vipera aspis* in some localities of north-eastern (North of the province of Barcelona, Catalonia) and north-central Spain (North of the province of Burgos, Castilla y León) (Bailon 1991; Blain & Bailon 2006; Blain 2009; Bisbal-Chinesta & Blain 2018), none of these reports are located below 40°N latitude. Thus, basing on those criteria, together with the historical reports and the specimen stored in the MNCN-CSIC, it is highly probable that the vipers that inhabited the Illa Grossa Island until the 19th century belonged to *V. latastei*.

Table 1. — Fossil record of Viperidae in Mediterranean islands. In **bold**, taxa included in the *Vipera aspis* group.

Taxon	Locality	Chronology	Island	Reference
Vipera sp. (_Vipera aspis_ group)	**Oschiri**	**Early Miocene**	**Sardinia**	**Venczel & Sanchíz 2006**
Viperidae indet.	Aliveri	Early Miocene (MN4)	Euboea	Georgalis *et al.* 2019b
Viperidae indet.	Punta Nati 2	Middle Miocene	Menorca	Bailon *et al.* 2002
Viperidae indet. (Oriental viper)	Gargano palaeoisland	Late Miocene-Early Pliocene	–	Delfino 2002
Vipera sp.	Punta Nati 3 and 12	?Pliocene	Menorca	Bailon *et al.* 2002
Vipera natiensis	**Punta Nati 12**	**Pliocene**	**Menorca**	**Bailon _et al._ 2002**
Viperidae indet. (Oriental viper)	Caló den Rafelino	Pliocene	Mallorca	Bailon *et al.* 2010
cf. _Vipera natiensis_	**Caló den Rafelino**	**Pliocene**	**Mallorca**	**Bover _et al._ 2014**
Viperidae indet. (Oriental viper)	Na Burguesa-1	Zanclean (Early Pliocene)	Mallorca	Torres *et al.* 2014
Vipera sp.	**Capo Mannu D1 LF**	**Late Pliocene**	**Sardinia**	**Delfino _et al._ 2011**
Vipera sp.	Monte Tuttavista	Late Pliocene-Early Pleistocene	Sardinia	Abbazzi *et al.* 2004
Vipera sp. (*Vipera berus* group)	Laghada B	Pleistocene	Kos	Szyndlar 1991
cf. _Vipera_ sp.	**Cova de ca na Reina**	**Calabrian (Early Pleistocene)**	**Ibiza**	**Torres-Roig _et al._ 2020**
Viperidae indet. (Oriental viper)	Latomi	Middle Pleistocene	Chios	Szyndlar 1991
Vipera sp. (_Vipera aspis_ group)	**Contrada da Pianetti**	**Late Pleistocene**	**Sicily**	**Delfino 2002**
Vipera sp. (_Vipera aspis_ group)	**K22 (San Vito Lo Capo)**	**Late Pleistocene/Holocene**	**Sicily**	**Delfino 2002**
Vipera latastei ebusitana	**Es Pouàs**	**Late Pleistocene to Holocene**	**Ibiza**	**Torres-Roig _et al._ 2020**
Viperidae indet. (Oriental viper)	Khirotikia	Holocene	Cyprus	Watson *et al.* 1977
Macrovipera lebetina	Akrotiri-Aetokremnos	Holocene (Mesolithic)	Cyprus	Bailon 1999
Macrovipera lebetina	Kisonerga-Myloudia	Holocene (Neolithic)	Cyprus	Croft *et al.* 2017
Vipera ammodytes	**Sanctuary of Poseidon at Kalaureia**	**Holocene (Archaic-Hellenistic)**	**Poros**	**Lymberakis & Iliopoulos 2019**
Vipera sp. (_Vipera aspis_ group)	**Vallone Inferno**	**Holocene (Early Bronze-Late Roman)**	**Sicily**	**Forgia _et al._ 2013**
Vipera cf. _latastei_	**Columbretes**	**Holocene (Iron Age)**	**Illa Grossa**	**This work**

As mentioned above, we propose an open specific attribution until more remains are recovered and studied. The fossils here studied differ from the recently established *Vipera latastei ebusitana*, from the Late Pleistocene–Holocene of Es Pouàs (Ibiza, Balearic Islands, Spain) (Torres-Roig *et al.* 2020) in the following traits: presence of a trilobate zygosphene with the central lobe of similar size to the lateral ones in dorsal view; well-defined parapophyses, and, well-defined subcentral ridge. All these features are similar to those described for *Vipera latastei latastei* Boscà, 1878 (Torres-Roig *et al.* 2020). However, the COLT fossils may belong to small specimens (with CL slightly longer than 3 mm), with biometric indexes in the size range of *V. l. ebusitana* and not of *V. l. latastei* (see Appendix).

The palaeontological record of vipers from the Mediterranean islands is scarce, only 23 palaeontological sites are known on eleven islands (Table 1; a complete review of the Mediterranean Islands fossil record of snakes is presented in Georgialis *et al.* 2019b). Fossils with a morphology attributable to the *Vipera aspis* group are restricted to Western Mediterranean islands, except for the remains of *Vipera ammodytes* recovered from the Sanctuary of Poseidon at Kalaureia (Poros island, Greece) (Lymberakis & Iliopoulos 2019). The oldest report corresponds to the *Vipera* sp. fossils from the early Miocene of Oschiri (Sardinia) (Venczel & Sanchíz 2006). Also, Bover *et al.* (2014) reported cf. *Vipera natiensis* from Na Burguesa-1 (Mallorca, Balearic Islands; late Miocene/early Pliocene). From the Pliocene localities, the *V. aspis* group is cited as *Vipera* sp. in Capo Mannu D1 site in Sicily (Italy), MN15 (early Pliocene; Delfino *et al.* 2011) and as *Vipera natiensis*, an endemic taxon in Punta Nati 12 site (Menorca, Balearic Islands, Spain, early Pliocene) (Bailon *et al.* 2002). In Quaternary deposits, the *Vipera aspis* group has been reported in the Late Pleistocene of Contrada da Pianetti; the Late Pleistocene/Holocene from K22 (San Vito Lo Capo), and in the Early Bronze and Late Roman levels (3.1 and 3.4, respectively) of Vallone Inferno (Forgia *et al.* 2013), all these sites from Sicily (Delfino 2002), and, finally, the above mentioned *Vipera latastei ebusitana* of Es Pouàs (Ibiza) and cf. *Vipera* sp. from the Cova de ca na Reina (Ibiza) (Torres-Roig *et al.* 2020).

Taphonomical approach

The low number of mammal remains recorded at Illa Grossa exhibit digestion traits in some of the molars (absent, light and moderate categories) that allow us to establish a predation origin for those remains but prevent us from any further conclusion about the taxonomic identity of the predator agent that produced the fossil association. The preliminary results of the taphonomical analysis shows that in the studied material the digestion marks are mainly absent, with only a few specimens having light and moderate damage. The presence of intact bones is rare. Discerning how this breakage has occurred is complicated, therefore, and to avoid over-representing the fragmentation degree in the analysis we do not study in detail the fragmentation of reptile's bones.

The vertebrate assemblage of the COLT site is clearly dominated by reptiles (81% of the remains), followed by birds (35%). Mammals only represent 11% of the studied material. Moreover, the diversity of species is low compared to mainland. This reduced biodiversity is typical of island in contrast to continental areas (Grant 1988). On islands, reptiles are often abundant and reach sometimes elevated densities (Pérez-Mellado *et al.* 2008), whereas terrestrial mammals are infrequent (Lawlor 1986).

Following Andrews (1990) and Pinto Llona & Andrews (1999), the digestion degree of the assemblage could correspond with a predator category 1. Within this category have been included *Tyto alba* (Scopoli, 1769) and *Asio flammeus* (Pontoppidan, 1763) (Andrews 1990). No breeding population of nocturnal bird of prey is present currently in the Columbretes Islands. However, the existence of reproductive colonies of owls is possible during historical times. The Short-eared Owls (*Asio flammeus*) is a common wintering species in Spain, with the eastern peninsula as one of its main Iberian wintering areas (Onrubia *et al.* 2003). Until the 1990s, breeding of *A. flammeus* in Iberia was occasional, but the expansion of *Microtus arvalis* (Pallas, 1778) in the Northern Plateau, and its periodic population explosions, have allowed the settlement of a variable number of nesting Short-eared Owls (Onrubia *et al.* 2003). As for the barn owl (*T. alba*) it is a widespread species, with breeding populations both on the mainland and on numerous islands in the Mediterranean and Macaronesia (Janžekovič & Klenovšek 2020). Although reptiles are not an important part of the diet of this species (Roulin & Dubey 2012), their consumption are higher on islands, especially on the smaller ones, than on the continental areas (Janžekovič & Klenovšek 2020). In this sense, Delgado (1993) pointed out that reptiles (mainly the single species: *Tarentola angustimentalis* Steindachner, 1891) are the main trophic resource of the eastern canarian endemic subspecies *Tyto alba gracilirostris* (Hartert, 1905) in the Alegranza Islets (Canary Islands); particularly in summer time, when *T. angustimentalis* represents 69.7% of the consumed preys. A similar situation has been described for the *T. alba* populations of the Branco and Raso islets (Cabo Verde Islands) (Naurois 1982). Worth considering are several preliminary results in Macaronesia pointing to a shift in the trophic spectrum of *T. alba*, from reptiles to small mammals, coinciding with the human colonisation of the islands, which reflects the trophic flexibility of the species (Siverio *et al.* 2007, 2008). Another strategy reported from insular populations of *T. alba* is breeding on small islets (s'Espalmador, Balearic Islands) and foraging (mainly small mammals, but also birds and reptiles) on larger islands (Ibiza and Formentera) and other islets surrounding s'Espalmador (Guerra *et al.* 2014). These owls fly at least 11 km on each occasion (s'Espalmador to Ibiza) (Guerra *et al.* 2014). Nevertheless, the sea stretch that separates Illa Grossa from the continent is significantly wider (around 50 km).

Other potential biologic taphonomic agents are seagulls. Breeding colonies of two taxa: *Larus michahellis* Naumann, 1840, and *Larus audouinii* Payradeau, 1826 are located in the archipelago (Mestre *et al.* 2010). Experimental data based on the use of plasticine models of lizards demonstrated that the Yellow-legged Gull (*Larus michahellis*) is the main predator of *Podarcis liolepis atratus* in Illa Grossa (Castilla & Labra 1998). In the literature, there are some reports of *L. michahellis* preying on lizards, especially in insular contexts (Martín & López 1990; Carretero *et al.* 1993; Vervust *et al.* 2007; Piorno *et al.* 2016). However, lizards do not seem to be a common prey in *L. michahellis* diet, at least in the Colom Island (Balearic Islands), and the attacks recorded to lizard models can rather be attributed to the exploratory behaviour of the Yellow-legged Gull (Pérez-Mellado *et al.* 2014). On the other hand, all the small mammal species present on the Colom Island were preyed by *L. michahellis* (Pérez-Mellado *et al.* 2014). As generalist feeders, seagulls prey on snakes too; however, there are few reports in this sense in the scientific literature (i.e., Martín & López 1990). To our knowledge, no study has been carried out yet on the degree of taphonomic alteration of prey bones caused by gulls.

Origin of the historical faunal community

The origin of the vertebrate terrestrial fauna of Columbretes has been explained by three hypotheses: 1) isolated populations on the islands due to the sea-level rising (Castilla 2000; Ruiz-Sánchez *et al.* 2019); 2) colonization through marine dispersion on floating rafts (Harris & Sá-Sousa 2002); or 3) human introduction (Bernis 1968). The latter probably explains the origin of the terrestrial mammals, as it is reflected in the historical references. Salvator (1895) was the first author who reported the presence of mammals, pointing out that they has recently appeared on the island, around 1888, and went extirpated in an indeterminate moment of the 20th century (Jiménez 1991). Thus, the mammal fossils described here belong to an older colonization phase, previous to the historical reports. The Columbretes Islands, due to their geographical position between Ibiza and the mouth of the Ebro river, are present in the Western Mediterranean commercial routes since the Antiquity. The seabed around the Columbretes archipelago has preserved numerous shipwrecks since the early Roman Period. The oldest archaeological remains have been dated around the 3-4th centuries BC (Fernández Izquierdo 2013), i.e., within an age range similar to the COLT radiocarbon datings. This material, a B3-type Iberian amphora, was probably manufacturated by the Laietani (Fernández Izquierdo 2013), an ancient Iberian population who occupied the coast of the present Barcelona province between the Llobregat and Tordera rivers (Balsera Moraño 1997). It is interesting to note that the closest Iberian people to the Columbretes Islands were not the Laietans but the Ilercavones, located in the area occupied by the current provinces of Castellón and Tarragona (Crespo *et al.* 2017).

Since *Mus musculus* is a strongly human-dependant taxa (Palomo *et al.* 2007), its ocurrence could be treated as an indicator of some kind of human presence or/and activity in the area, as for example voyaging (Vigne 2015). In 1976, *Mus musculus* and *Mus spretus* were recognized by genetic criteria as different species (Britton *et al.* 1976; Britton & Thaler 1978). According to Domínguez García *et al.* (2019), the genus *Mus* could have arrived to the southwestern European coasts around 6000 BP or even before, but evidence is not completely solid. In the case of *Mus spretus*, an Iberomagrebian species, a colonization of Europe linked to anthropogenic translocation from North Africa to the Iberian Peninsula through the Strait of Gibraltar, probably during the Chalcolithic, has been proposed (Domínguez García *et al.* 2019; Olalde *et al.* 2019). On the other hand, *Mus musculus* would

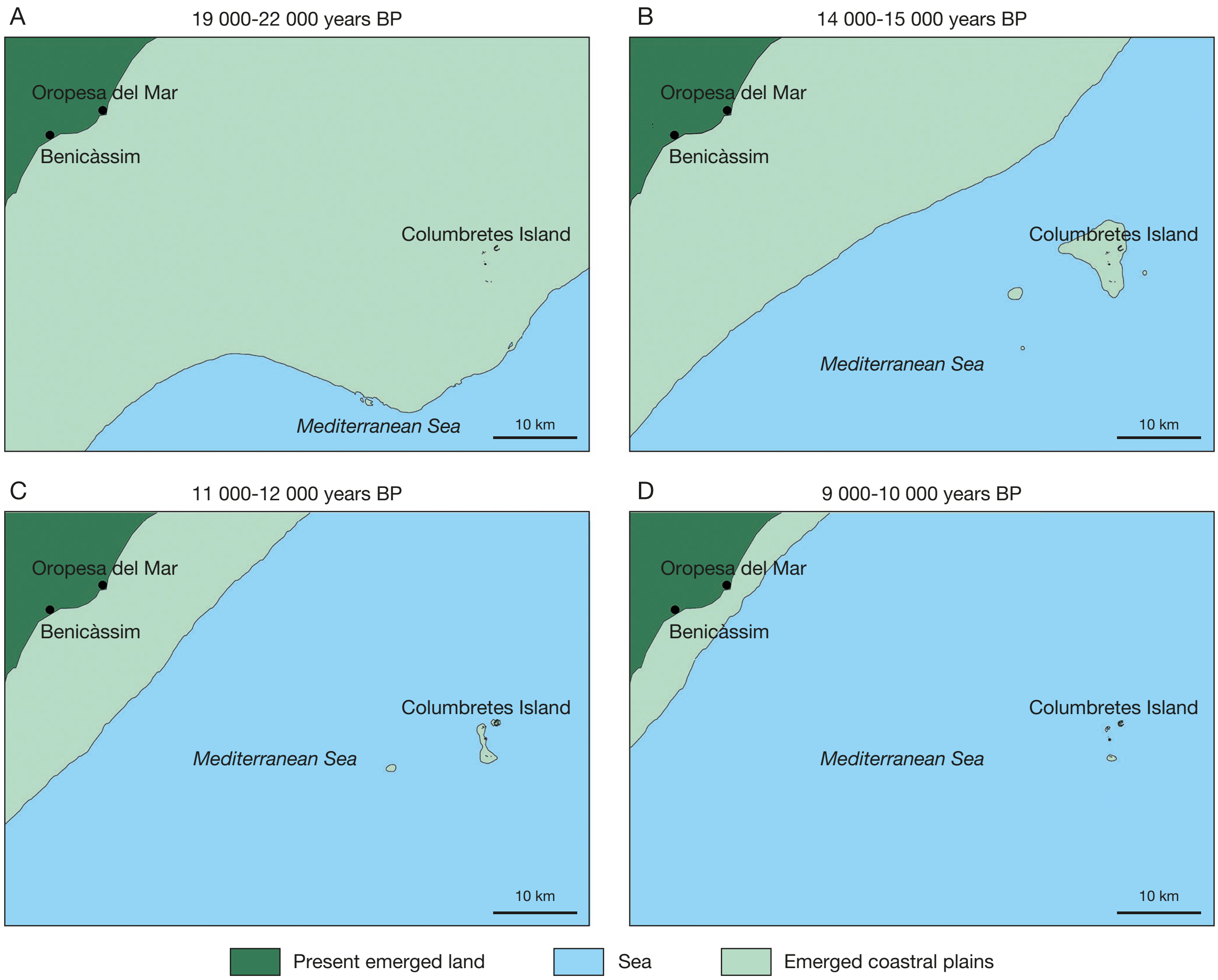

FIG. 7. — Palaeogeographical scenario of Columbretes Islands at: **A**, 19 000-22 000 years BP; **B**, 14 000-15 000 years BP; **C**, 11 000-12 000 years BP; **D**, 9 000-11 000 years BP. The reconstruction is based in the model proposed by Lambeck & Bard (2000).

have arrived with human migrations from South-East Asia, following the "Mediterranean Route" sometime after 3 000 BP (Auffray *et al.* 1990; Bonhomme & Searle 2012). According to this chronology, the most plausible hypothesis would be that mice would have been introduced on the islands by the Phoenicians, who established an intense commercial activity since the 6th century BC in the nearby coast of the current Castellón Province (Elias Ramos & Fernández 2012). In agreement with this, Bisbal-Chinesta *et al.* (2020) have pointed out that a recently discovered population of *Chalcides ocellatus* in Serra del Molar (SE Spain), was probably introduced by Phoenicians.

Vipera latastei is a species capable of transmarine dispersal, as recently demonstrated by Torres-Roig *et al.* (2020). These authors, based on a phylogenetic analysis of an almost complete mitochondrial genome obtained from fossil material of *Vipera latastei ebusitana* (Late Pleistocene-Holocene, Es Pouàs, Ibiza, Balearic Islands, Spain), proposed that this taxon colonized the island of Ibiza crossing the seaway from the Peninsula less than 1.5 Myr ago. Given that the last connection between the Balearic Islands and the European mainland occurred during the Messinian Salinity Crisis (5.97-5.32 Mya) (Bover *et al.* 2014), the arrival of the species to Ibiza must have taken place through floating rafts, probably from the northeastern Iberian region (Torres-Roig *et al.* 2020). Regarding the Columbretes vipers, Bernis (1968) suggested a possible anthropic introduction or a very recent colonization of Illa Grossa. In fact, this authors did not identify any difference in the external morphology between the specimen presumably found on the island and the vipers of the eastern Iberian Peninsula. The only characteristic noted by Bernis (1968) is the remarkable length of the examined specimen (72-73 cm), which makes it the largest specimen of *Vipera latastei* known to date (Brito 2017). It is however dubious whether this is a case of island gigantism due to the scarcity of material (only one specimen). In addition snakes exhibit indeterminate growth throughout their life (Andrews 1982), so this specimen could also be just an old individual. However, as Boback (2003) pointed out, viperids show a body size decrease trend in island populations. This author based its conclusions mainly in pitvipers of the genus *Crotalus*, and only three of the 11 analyzed species belonged to the genus *Vipera*. Recently, this insular dwarfism has been reported for the *Vipera aspis* population from the Montecristo Island (Luiselli *et al.* 2015) and for the Middle/Late Pleistocene-Holocene fossil remains of *V. latastei ebusitana* from Ibiza (Balearic Islands) (Torres-Roig *et al.* 2020). The fossil viper specimens recovered from the COLT site are also small-sized; however, their small number together with the large size of the specimen stored at the MNCN-CSIC prevent us from inferring the existence of an insular dwarfism in the Illa Grossa population.

About the possible anthropic origin for the *V. latastei* population of Illa Grossa, Bernis (1968) hypothesised that some specimens were released by a local chief to avoid the use of the island by pirates. The use of snakes as war weapons during the Antiquity is far knowledge (Mayor 2003). In this sense, the habit of launching earthenware jars filled with snakes against rival ships to spread chaos among the enemies was the proposed origin for the Montecristo Island *Vipera aspis* population (Bruno 1985). However, there are no registered naval battles in the vicinity of this island (as in the case of the Columbretes Islands). Genetic studies in the Montecristo Island demonstrated a more plausible origin for the snakes population around the middle of the first millennium AD, when the island was inhabited by anchorites, either due to involuntary introduction or for medical purposes (Masseti & Zuffi 2011).

Due to the relatively low latitude range of the Iberian Peninsula (36-43° N), far from the European glacial zones, and the tempering effect of the proximity of the sea, the eastern and south-eastern coast of Spain only manifested subtle changes in temperature, during the Late Pleistocene-Holocene boundary except in those area located at high altitude. Major changes seem to be related with eustatic oscillations as well as humidity variations (Aura *et al.* 1998). Sea level oscillations have been associated mainly with exchanges between the ocean and the ice sheets during hot and cold periods (Lambeck & Bard 2000). A sea-level decrease of approximately 120 m has been documented during the Last Glacial Maximum (LGM) (22 000-19 000 years before present) (Shackleton *et al.* 1984). Furthermore, according to Shackleton *et al.* (1984), the sediment layer produced during the Holocene must be thin, given the presence of few large rivers and the negligible effect of vertical tectonic movements throughout the Mediterranean Sea basin. At present, the Columbretes Islands are located between the 75 and 100 m isobates (Ancochea & Huertas 2021). Considering its bathymetric context, it is likely that the Columbretes archipelago was part of the continent during the LGM (Fig. 7A). At that moment, Illa Grossa was located within the mainland area, 9.47 km from the contemporaneous coastline (the current mainland shoreline is situated at 61.69 km from the Illa Grossa, Fig. 7A). According to this hypothesis, *Chalcides bedriagai*, *Vipera* cf. *latastei* and cf. *Podarcis* sp. reached Illa Grossa in an undetermined moment when it was part of the continent. Later, with the gradual Holocene transgression, the locality was once again isolated from the mainland, thus originating the insular populations of these species. According to the model proposed by Lambeck & Bard (2000) for the sea-level change along the French Mediterranean coast for the Late Pleistocene and Holocene, between approximately 14 000 and 15 000 years ago, the Columbretes Islands were already separated from the mainland, at which time the coastline was 70-75 m below the current sea level. At that time, the current different islands and islets could be included in a single island (Fig. 7B). Around 11 000-12 000 years BP, the Illa Grossa group was isolated from the rest of groups (Ferrera, Foradada and El Carallot), which were connected (Fig. 7C). Muñoz *et al.* (2005) reported the existence of submarine volcanic structures without evidence of erosion, which could be originated at depths low enough to be eroded by waves, or even, as was proposed by Ancochea & Huertas (2021), originated in subaerial context. The age of these structures has been proposed as 13 000 BP based on different considerations regarding the speed of sea level rise (Muñoz *et al.* 2005). At 9 000-10 000 years ago the different island groups were already isolated from each other (Fig. 7D). Finally, the present sea level was reached approximately at 6 000 years ago (Lambeck & Bard 2000).

The taxa identified in the fossil record of the COLT site have been recorded in localities from the central and northern Mediterranean Spanish coasts from the Piacenzian (MN17, late Pliocene) up to the present time (Blain 2009). Therefore, the composition and origin of those taxa can be tested.

Regarding wall lizards, Harris & Sá-Sousa (2002) proposed a possible colonization of the islands by rafting following the southerly sea currents. In this sense, the genus *Podarcis* contains species with markedly different dispersion capability across the sea. Thus, *Podarcis peloponnesiacus* (Bibron & Bory, 1833), *Podarcis filfolensis* (Bedriaga, 1876), *Podarcis cretensis* (Wettstein, 1952) and *Podarcis levendis* Lymberakis, Poulalakis, Kaliontzopoulou, Valakos & Mylones, 2008 show limited over-sea dispersal capacity (Salvi *et al.* 2014; Spilani *et al.* 2019). On the other hand, species such as *Podarcis vaucheri*, seem to have spread from Morocco-West Algeria to the south of the Iberian Peninsula by crossing the Gibraltar Strait around 2.81 Mya (Pinho *et al.* 2006). Other species that could have dispersed over sea is *Podarcis gaigeae* (Werner, 1930), in which a gene flow has been reported between the subspecies *Podarcis gaigeae weigandi* (Gruber & Schultze-Westrum, 1971), from the Piperi Island and *Podarcis gaigeae gaigeae* (Gruber, 1986), which inhabits the Skyros Island (40 km north from Piperi) and satellite islets (Runemark *et al.* 2012). The capacity of transmarine dispersal in *Podarcis liolepis* in general and *P. l. atratus* in particular, is unknown. The absence of this species in the Ferrera group (Castilla *et al.* 1991, 1998a) might be due either to its weak oversea migration capacity or to its later extirpation at an undetermined moment. The hypothesis of colonization of the Illa Grossa Island via rafting is supported by the close presence of a large river (Ebro), and the dominant southerly sea current in this area (Font 1990); however, the small size of the island implies small colonization rates. Since this process is totally random, small islands receive fewer dispersion events than the bigger ones (MacArthur & Wilson 1967). On the other hand, human introduction (voluntary or not) cannot be discarded, at least for the wall lizards. In fact, human-introduced populations of *Podarcis* species have been detected in 222 Mediterranean islands in recent years (Silva-Rocha *et al.* 2019). Moreover, the high leves of genetic divergence in the *Podarcis liolepis* populations from the different islands of the Columbretes archipelago (Castilla *et al.* 1998b), suggest several phases of colonisation of the different islands by various genetic lines of mainland *P. liolepis* or even by other Iberian *Podarcis* species (Harris & Sá-Sousa 2002). If this is confirmed, it is not inconceivable that at least, some of these colonisation waves were human-induced. Castilla *et al.* (1998b) pointed out that the wall lizard population of the Foradada Group Islands (Foradada and Lobo Islands) possibly derived from an early colonization wave. The same authors proposed that the divergence between the wall lizards of these islands and those from the Illa Grossa Island took place 80 000 years ago. However, these results should be taken with caution since they are based on a small sample of continental individuals from the central Spanish Mediterranean region (only eight individuals from Valencia, Burjassot and Grau de Castelló).

In summary, the origin of the fossil assemblage is unclear. It is even probable that the different taxa recovered from the COLT site colonised Illa Grossa through different ways, i.e., during the probable connection of the archipelago with the mainland, by means of marine dispersal or via human-facilitated introduction. In this sense, the arrival of *Mus* cf. *musculus* to the island was probably mediated by human activity. Future genetic studies based on mainland and insular populations of *Podarcis liolepis* could shed light about this issue. The same could be carried out for the vipers, provided that the genetic material of the stored specimen of *Vipera latastei* at the MNCN-CSIC is not degraded. The case of *Chalcides bedriagai* is more problematic since the recovering of ancient DNA from the fossils is unlikely due to the high temperatures recorded on the island.

Palaeoecology

According to the palynological study of Expósito & Burjachs (2007) the palaeoflora of Illa Grossa consisted of a shrubland dominated by herbaceous plants and low bushes, not different from the current vegetation. The sample "Mostra 3" of Expósito & Burjachs (2007), and recovered from the same COLT deposit, is dominated by herbaceous species, mainly Poaceae Barnhart (45.5%) and Apiaceae Lindl. (27.3%); other reported taxa are *Artemisia* L. (4.5%) and other ligulliflora (4.5%). On the other hand, arboreal pollen is constituted by *Pinus* sp. (9.1%) and *Quercus ilex-coccifera* (9.1%). Thus, the described landscape based on pollen analyses correspond to an open Mediterranean maquia (Expósito & Burjachs 2007), which is in agreement with the vertebrate species identified in the present work.

The present herpetological community on Columbretes is composed by a single taxon, *Podarcis liolepis atratus*. Several works showed the varied trophic resources that this species exploited on the archipelago, which comprise plants, arthropods (including marine isopods in the intermareal zone), carcasses and congeneric specimens (Castilla & Bauwens 1991; Castilla *et al.* 1991, 2008, 2009; Castilla & van Damme 1996). Moreover, "cross predation" between the Wall lizard and the scorpion *Buthus occitanus* (Amoreux, 1789) has been reported; both species are abundant in the Illa Grossa Island (Castilla *et al.* 2009). In the recent past, when the vertebrate community was more diverse, as shown by the study of the COLT fossils, the interactions between the different species might have been more complex. In reptile communities, several constraints, such as evolutionary history, habitat use and intrinsic morphology, determine the relationship between the different species (Capula & Luiselli 1994, Carretero *et al.* 2010). Thus, it is expected that at least one of those constraints was a conditioning factor in the palaeoherpetological community of the Columbretes islands. For example, the lizard microcommunity inhabiting the Lampione islet (2.1 ha; Pelagian islands, South Italy) is composed by the skink *Chalcides ocellatus* (Forskål, 1775) and the lacertid *Podarcis filfolensis* (Bedriaga, 1886) (Carretero *et al.* 2010; Lo Cascio & Pasta 2012). Both species show a moderate trophic overlap, and while *C. ocellatus* consumes hard medium to large prey, *P. filfolensis* prefers more diverse and smaller sized preys than the former (Carretero *et al.* 2010). Plant consumption and cannibalism have been reported in both species (Carretero *et al.* 2010). The exploitation of both trophic resources increases in insular lizards due to the scarcity of other supplies and high population densities (Pérez-Mellado & Corti 1993; Carretero 2004). However, there is a clear size difference between *C. ocellatus* (TL: 30 cm) and *P. filfolensis* (TL: 25 cm) (Carretero *et al.* 2010; Speybroeck *et al.* 2016). In this case, the reported cases of predation of *P. filfolensis* by *C. ocellatus* (Carretero *et al.* 2010) could be explained by the higher size of the latter (Cohen *et al.* 1993). However, *Chalcides bedriagai* is smaller than the European *Podarcis* taxa, except for the *Podarcis hispanicus* species complex, which is similar in size (Speybroeck *et al.* 2016). Thus, the trophic relationships in Illa Grossa were presumably different than those described for the Lampione islet between *Chalcides* and *Podarcis*. *Chalcides bedriagai* is considered an opportunistic and euryphagous predator (Seva & Escarré 1976; López-Jurado *et al.* 1978). In an insular context, *C. bedriagai* preys on a wider spectrum of arthropods than in mainland localities (López-Jurado *et al.* 1978). Most of the preys consumed by *C. bedriagai* are typically ground-dwelling taxa or live in the lower parts of the vegetation (Seva & Escarré 1976). The adaptation to plant consumption requires some evolutionary time (Carretero 2004) and this may explain why it has not been reported in the islands of Nova Tabarca (Seva & Escarré 1976; López-Jurado *et al.* 1978); where this species has been isolated for only a short time interval. On the other hand, the Mediterranean small lacertid *Podarcis* is considered as a food generalist and an active forager (Arnold 1987). In particular, as mentioned above, *Podarcis liolepis atratus* shows a wide range of food sources (Castilla & Bauwens 1991; Castilla *et al.* 1991, 2008, 2009; Castilla & van Damme 1996).

Although, both species seem to feed on the same preys, they select different microhabitats. Thus, whereas *C. bedriagai* forages under rocks and other elements on the ground (Hailey *et al.* 1987), members of the *Podarcis hispanicus* species complex, in which *P. l. atratus* is included, are active foragers on a wide spectrum of substrates (rocks, tree trunks, human structures, etc.) (Desfilis *et al.* 1993). It is possible that the extirpation of *C. bedriagai* on Illa Grossa made it possible for *P. l. atratus* to exploit new trophic resources previously unavailable to the species.

Vipera latastei (*Vipera* cf. *latastei* in the fossil record of the COLT site) may have been the terrestrial top predator in Illa Grossa. In fact, skinks and wall lizards are part of the prey spectrum of the species (Santos *et al.* 2007a). However, the frequency of predation varies according to the age classes of vipers and local faunal community. Predation over skinks seems to be anecdotal, whereas wall lizards are the most consumed reptiles (Santos *et al.* 2007a). There are variations in the diet according to the age of the specimen; in juveniles the consumption of reptiles and arthropods is higher than in adults, which prey mainly on rodents and birds (Bea & Braña 1988; Santos *et al.* 2007a). In islands with low density or absence of small mammals, viperids seem to be specialized in feeding mainly on birds (Nilson *et al.* 1999; Shine *et al.* 2002; Luiselli *et al.* 2015). As in the mainland, an ontogenetic shift in the selected prey has been recorded on islands. For example, only lizards have been reported in the stomach content of road-killed young individuals of *Macrovipera schweizeri*, an insular species from the western Cyclades Islands, whereas in adults specimens only bird feathers were detected (Nilson *et al.* 1999). *Bothrops alcatraz*, an insular viper species from the Alcatrazes Islands (35 km off the coast of southeastern Brazil), is considered a paedomorphic taxon based in, among other traits, its diet composed of centipedes and lizards (Marques *et al.* 2002). As Bernis (1968) proposed the Illa Grossa vipers fed on invertebrates during their juvenile stage, whereas as adults they fed on lizards and, during the migration epoch, on passerine birds. According to Castilla (2000), the observed difference in scalation, color-pattern and body dimensions between the *P. l. atratus* of Illa Grossa those of the rest of the islands could be partly due to the intense selective pressures exerted by vipers. Moreover, laboratory experiments have shown that individuals of *P. l. atratus* responded to the chemical signal of *V. latastei*, even though this snake became extirpated more than 100 years ago (van Damme & Castilla 1996).

Implications for the conservation

In the last decades, the application of palaeontological data to conservation biology has greatly increased (Lyman 2012). This new field, known as Conservation Palaeobiology, has numerous applications (Barnosky *et al.* 2017). Palaeontology provides valuable information about which species were present in the past in a determined region, especially in disturbed habitats (Faith 2012). The knowledge of a baseline biological community is strongly interesting for the land-management perspective (Barnosky *et al.* 2017), primarily in protected areas. Moreover, the palaeontological record is essential for the theoretical body of any translocation or reintroduction project (Faith 2012).

Our results demonstrate the presence of vipers in Illa Grossa, providing a solid empirical basis for a hypothetical reintroduction project of the species on the Columbretes archipelago. The main cause of the extirpation of *Vipera latastei* on the island is clear: active human hunting. This factor has resulted in the extirpation on numerous populations of vipers from different areas of Europe (see Brito *et al.* 2001). This persecution is derived from the consideration of snakes as disgusting, harmful and feared animals (Brito *et al.* 2001). Given the absence of a permanent human population, with the exception of the technical staff of the Nature Reserve, this problem is currently totally absent in the Columbretes Islands. Therefore, it could be interesting to carry out a study on the possibility of reintroducing the species in Illa Grossa, assessing any potential impacts on the current community of vertebrates, especially on the endemic *Podarcis liolepis atratus*. After the evaluation of potential risks and benefits for the ecological system of the island, as indicated by the IUCN/SSC (2013) guidelines, a further point would be to discern which population is genetically the closest to the one that was present in the archipelago. For this purpose, samples from the specimen deposited in the MNCN-CSIC might be used; given that, in principle, the contrasting temperatures recorded in dry areas, as Illa Grossa, provoked a high degradation of the ancient DNA potentially present in the recovered fossils remains from COLT (Bollongino & Vigne 2008). The fact that it is the only known insular population of *V. latastei* in historical times together with the high number of localities where this species has disappeared (Santos *et al.* 2007b) further supports its reintroduction. However, previous to this, an in-depth study of the fossil record of the species on this island and others in the archipelago together with the search and study of new potential sites are necessary. In this respect, Hernández-Pacheco & Asensio Amor (1966) report the existence of loess deposits in other sites on Illa Grossa, and Boira & Carretero (1991) cite the existence of a poorly developed formation at Ferrera. The same question, a possible reintroduction of the taxon in Illa Grossa, arise for *Chalcides bedriagai*, although the causes of its extinction are unclear.

CONCLUSIONS

The study of the fossil assemblage from the COLT site yielded an unexpected diverse community of vertebrates composed by two lizards (*Chalcides bedriagai* and cf. *Podarcis* sp.), one snake (*Vipera* cf. *latastei*), one rodent (*Mus* cf. *musculus*) and, at least, six undetermined species of birds (two seabirds and four passerines). The historical presence of vipers in the Illa Grossa Island is confirmed, thus settling the controversy about the identity of the snakes of the Columbretes archipelago. For the first time, the historical presence of *Chalcides bedriagai* is reported in the archipelago.

Two different samples: COLT-SNAILS (fragments of terrestrial gastropods) and COLT-BONES (fragments of undetermined bones) were AMS radiocarbon-dated. Both yielded strongly similar chronologies: COLT-SNAILS has been dated at 2780-2724 cal BP and COLT-BONES at 2600-2492 cal BP.

The origin of the fossil assemblage from the COLT locality is probably linked to the palaeogeography of the western Mediterranean area, conditioned by the sea level rise after the Last Glacial Maximum, and more recently, to the expansion of Phoenician trade shipping routes in the western Mediterranean. We proposed three possible ways of colonization of the archipelago: isolation of the vertebrate fauna during the the sea-level rise in the last 10 000 years, rafting, and human introduction. Although the latter was case of the colonisation of Illa Grossa by *Mus* cf. *musculus*, it remains unclear how the rest of the taxa reached the island.

Due to the strong human-dependence, the record of *Mus* cf. *musculus* could be linked to some kind of anthropic exploitation of Illa Grossa. If confirmed, this might be the earliest evidence of human presence in the archipelago.

The results obtained in the present work could provide a theoretical basis for the development of future programmes focused on the eventual reintroduction of *Vipera latastei* in the Columbretes Islands, since it constitutes the only known insular population of the species in historical times.

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APPENDIX

Appendix 1. — Measurements (in mm) and biometric indices of the trunk vertebrae of *Vipera* cf. *latastei* Boscá, 1878 (COLT), mainland *Vipera latastei* (IMEDEA 106925 and MNHN-ZA-AC-2020-1), and *Vipera latastei ebusitana* Torres-Roig, Alcover & Bailon, 2020. Data of mainland *V. latastei* and *V. l. ebusitana* obtained from Torres-Roig *et al.* (2020). Abbreviations: **σ**, standard deviation; **CL**, vertebral centrum length, measured ventrally and including the condyle; **CL/NAW**, ratio between the length and the width of the neural arch; **CTH**, cotyle height; **CTW**, cotyle width; **CTW/CTH**, ratio between width and height of the cotyle; **CTW/NAW**, ratio between cotyle width and the width of neural arch; **Max**, maximum value; **Min**, minimum value; **N**, number of specimens; **NAW**, width of the neural arch, measured at the maximum interzygapophyseal constriction; **PO-PO**, width of the external borders of the articular surfaces of the postzygapophysis; **PO-PO/NAW**, ratio between the width of the external borders of the articular surfaces of the postzygapophysis and the width of the neural arch; **PR-PR**, width of the external borders of the articular surfaces of the prezygapophysis; **PR-PR/NAW**, ratio between the width of the external borders of the articular surfaces of the prezygapophysis and the width of the neural arch; **ZW**, zygosphene width; **ZW/NAW**, ratio between the width of the zygosphene and the width of the neural arch.

		COLT	**IMEDEA 106925**	**MNHN-ZA-AC-2020-1**	***Vipera latastei ebusitana***
CL	Mean	2.76	3.74	4.31	2.74
	N	5.00	–	–	18
	σ	0.43	–	–	0.27
	Min	2.10	–	–	2.29
	Max	3.21	–	–	3.19
NAW	Media	1.81	2.53	2.87	1.96
	N	4.00	–	–	18
	desv	0.29	–	–	0.24
	Min	1.41	–	–	1.63
	Max	2.08	–	–	2.4
CTW	Media	1.00	1.84	2.22	1.22
	N	4.00	–	–	18
	desv	0.55	–	–	0.08
	Min	0.19	–	–	1.07
	Max	1.35	–	–	1.33
CTH	Media	1.17	1.41	1.56	1
	N	4.00	–	–	18
	desv	0.09	–	–	0.09
	Min	1.11	–	–	0.85
	Max	1.30	–	–	1.13
PR-PR	Media	3.22	5.45	5.82	3.62
	N	3.00	–	–	18
	desv	0.50	–	–	0.46
	Min	2.70	–	–	2.97
	Max	3.70	–	–	4.39
PO-PO	Media	3.11	5.27	5.57	3.5
	N	2.00	–	–	15
	desv	0.73	–	–	0.45
	Min	2.59	–	–	2.97
	Max	3.62	–	–	4.3
ZW	Media	1.16	2.18	2.80	1.74
	N	1.00	–	–	16.00
	desv	–	–	–	0.15
	Min	–	–	–	1.48
	Max	–	–	–	1.98
CTW/CTH	Media	0.84	1.30	1.42	1.23
	N	4.00	–	–	18
	desv	0.45	–	–	0.06
	Min	0.17	–	–	1.14
	Max	1.16	–	–	1.35
PO-PO/NAW	Media	1.85	2.08	1.94	1.8
	N	2.00	–	–	15
	desv	0.02	–	–	0.07
	Min	1.84	–	–	1.65
	Max	1.87	–	–	1.9
ZW/NAW	Media	0.82	0.86	0.98	0.9
	N	1.00	–	–	16
	desv	–	–	–	0.05
	Min	–	–	–	0.8
	Max	–	–	–	0.98
CTW/NAW	Media	0.47	0.73	0.77	0.63
	N	3.00	–	–	18
	desv	0.33	–	–	0.05
	Min	0.09	–	–	0.54
	Max	0.68	–	–	0.73

Appendix 1. — Continuation.

		COLT	**IMEDEA 106925**	**MNHN-ZA-AC-2020-1**	***Vipera latastei ebusitana***
CL/ZW	Media	1.81	1.72	1.54	1.56
	N	1.00	–	–	16
	desv	–	–	–	0.08
	Min	–	–	–	1.44
	Max	–	–	–	1.69
PR-PR/NAW	Media	1.88	2.15	2.03	1.84
	N	3.00	–	–	18
	desv	0.05	–	–	0.06
	Min	1.83	–	–	1.67
	Max	1.91	–	–	1.94
CL/NAW	Media	1.47	1.48	1.50	1.4
	N	4.00	–	–	18
	desv	0.02	–	–	0.08
	Min	1.45	–	–	1.24
	Max	1.49	–	–	1.55