

Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave (Peñamellera Alta, Asturias, Spain)

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave (Peñamellera Alta, Asturias, Spain)

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Submitted on 8 October 2019 | Accepted on 24 June 2020 | Published on 2 August 2021

urn:lsid:zoobank.org:pub:87A2AA95-839F-4334-9558-BA7DF695C569

Núñez-Lahuerta C., Sauqué V., Sanchis A., Duarte E. & Rasilla M. de la 2021. — Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave (Peñamellera Alta, Asturias, Spain). *Comptes Rendus Palevol* 20 (30): 627-640. <https://doi.org/10.5852/cr-palevol2021v20a30>

ABSTRACT

Birds are abundant in fossil assemblages of Quaternary sites; they can be used in landscape reconstruction as they are well adapted to the environment. Here we present the analysis of the avian assemblage from the Middle Paleolithic levels of the Llonin Cave, where 558 bird remains have been recovered from levels G-VI and CP-VIII, belonging to at least ten different taxa: Aves indet., Galliformes indet., *Lagopus lagopus* Linnaeus, 1758, *Tetrastes bonasia* Linnaeus, 1758, *Columba livia/oenas* Gmelin, 1789/Linnaeus, 1758, Passeriformes indet., Alaudidae indet., *Motacilla* sp., *Turdus* sp., Corvidae indet., *Garrulus glandarius* Linnaeus, 1758, *Pyrrhocorax* sp., *Pyrrhocorax pyrrhocorax* Linnaeus, 1758, *Pyrrhocorax graculus* Linnaeus, 1766 and *Corvus corax* Linnaeus, 1758. This assemblage is similar to other assemblages from the Upper Pleistocene of the north of the Iberian Peninsula, and it reflects a mixed landscape, with open areas and woodland. The taphonomic analysis points to a mixed origin of the accumulation, mainly formed by medium-sized corvids dying in the cave, and also raptors accumulating their prey.

KEY WORDS

Avifauna,
karstic system,
Middle Paleolithic,
Iberian Peninsula,
Lagopus,
Tetrastes.

RÉSUMÉ

Restes d'oiseaux des niveaux du Paléolithique moyen (MIS3) de la grotte de Llonin (Peñamellera Alta, Asturias, Espagne).

Les oiseaux sont abondants dans les assemblages de fossiles de sites quaternaires ; ils peuvent être utilisés dans la reconstruction du paysage car ils sont bien adaptés à l'environnement. Nous présentons ici l'analyse de l'assemblage aviaire des niveaux du Paléolithique moyen de la grotte de Llonin, où 558 restes d'oiseaux ont été trouvés dans les niveaux G-VI et CP-VIII, appartenant à au moins dix taxons différents : Aves indet., Galliformes indet., *Lagopus lagopus* Linnaeus, 1758, *Tetrastes bonasia* Linnaeus, 1758, *Columba livia/oenas* Gmelin, 1789/Linnaeus, 1758, Passeriformes indet., Alaudidae indet., *Motacilla* sp., *Turdus* sp., Corvidae indet., *Garrulus glandarius* Linnaeus, 1758, *Pyrrhocorax* sp., *Pyrrhocorax pyrrhocorax* Linnaeus, 1758, *Pyrrhocorax graculus* Linnaeus, 1766 et *Corvus corax* Linnaeus, 1758. Cet assemblage est similaire aux autres assemblages du Pléistocène supérieur du Nord de la péninsule Ibérique et reflète un paysage mixte, avec des zones boisées et des clairières. L'analyse taphonomique indique une origine mixte de l'accumulation, principalement formée par des corvidés de taille moyenne, morts dans la grotte et des proies accumulées par des rapaces.

MOTS CLÉS

Avifaune,
système karstique,
Paléolithique moyen,
péninsule Ibérique,
Lagopus,
Tetrastes.

INTRODUCTION

The Marine Isotopic Stage 3 (between 60 and 27 ka ago) is a period within the Upper Pleistocene with strong climatic fluctuations, showing both warming (Dansgaard *et al.* 1993) and cooling events (Heinrich 1988). In this context, fossil birds play a key role in the palaeoecological and paleoenvironmental reconstruction, as they appear as direct remains in paleontological and archaeological sites, but also could have participated as main actors in the accumulation of small vertebrates (Andrews 1990). Also, birds have interacted with the Paleolithic human populations, having been used as a nutritional source and also for ornamental/symbolic purposes (e.g. Laroulandie *et al.* 2016; Blasco *et al.* 2019; Rodríguez-Hidalgo *et al.* 2019). For these reasons, the analysis of the MIS3 fossil avifauna is a main step towards the understanding of the past environment and ecology, and also human subsistence and behavior.

The Upper Pleistocene avifaunas from the northernmost part of the Iberian Peninsula have been thoroughly analyzed in recent years (Elorza 1990, 2000; Sánchez-Marco 2005; Margalida & Marín-Arroyo 2013; Eastham 2017; Moreno-García 2017; Núñez-Lahuerta *et al.* 2018b; Demarchi *et al.* 2019; Suárez-Bilbao *et al.* 2020, among others). The paleontological record of birds during that period is abundant, but relatively scarcer than the record of other vertebrates. In the case of the middle part of MIS3 in this area, the present data is diverse regarding the accumulating agents and the human exploitation thereof (Gómez-Olivencia *et al.* 2018; Marín-Arroyo *et al.* 2018). In this context, the Llonin Cave contains an archaeofaunal assemblage where Neandertals and carnivores also show interaction, so it is interesting to go further in depth into their interrelations with other faunal species such as birds, which are quite numerous in the assemblage. This study focusses on the two excavated sectors of the cave (Galería and Cono Posterior) where the Middle Palaeolithic is documented, both containing Mousterian lithic remains (Rasilla & Santamaría 2011-2012; Sanchis *et al.* 2019; Rasilla *et al.* 2020).

The main objectives of this work are the identification of the taxa present in the avian association, the palaeoecological analysis of the avifauna remains, and the characterization of the origin of the accumulation, in order to ascertain the characteristics of the environment during this part of the MIS3 (as also including the interaction of the birds with the rest of the faunal specimens, and any possible exploitation by Neandertals).

LLONIN CAVE

The Llonin Cave is located in Peñamellera Alta, Asturias, in the north of Spain (Fig. 1A). The karstic system opens at 112 m above sea level, in the Cares-Deva rivers basin, surrounded by mountainous relief (Fig. 1B), with the Cuera Range at the north, the Picos de Europa central massif at the south, and the Peñamellera peak at the center. The archaeological research carried out reveals an important cultural sequence, including rock and portable art (Forza *et al.* 1992, 1995, 1999, 2007; Forza 2001; González-Pumariega 2007; Ríos *et al.* 2007; Rasilla & Santamaría 2011-2012; Rasilla 2014; Rasilla *et al.* 2014, 2016, 2020). The archaeological sequence contains: Middle Palaeolithic (Mousterian dated around 43.000 uncalBP), Upper Palaeolithic/Mesolithic (Gravettian, Upper Solutrean, Badegoulian, Middle and Upper Magdalenian, Azilian dated between c. 28.000-10.000 uncalBP), and Bronze Age remains (c. 1.800-700 BC).

The cave consists of a small vestibule which bifurcates into a narrow dead-end gallery at the right, and a big chamber with a vast dejection cone at the left. The excavation works have been carried out at several sectors of the cave (Fig. 1C): Galería (G), Vestíbulo (V), Cono Anterior (CA) and Cono Posterior (CP), each of which presents a different stratigraphical setup. However, only Middle Palaeolithic levels were recovered in Galería (G-VI) and Cono Posterior (CP-VIII), and they constitute the occupational base of the cave. G is located in the highest part of the cave and near the vestibule area (the actual entrance), while CP is in the lower part of the cave but its entrance is different and nowadays collapsed (Fig. 1D, E). Here we analyzed the bird fossil remains recovered in G-VI and CP-VIII.

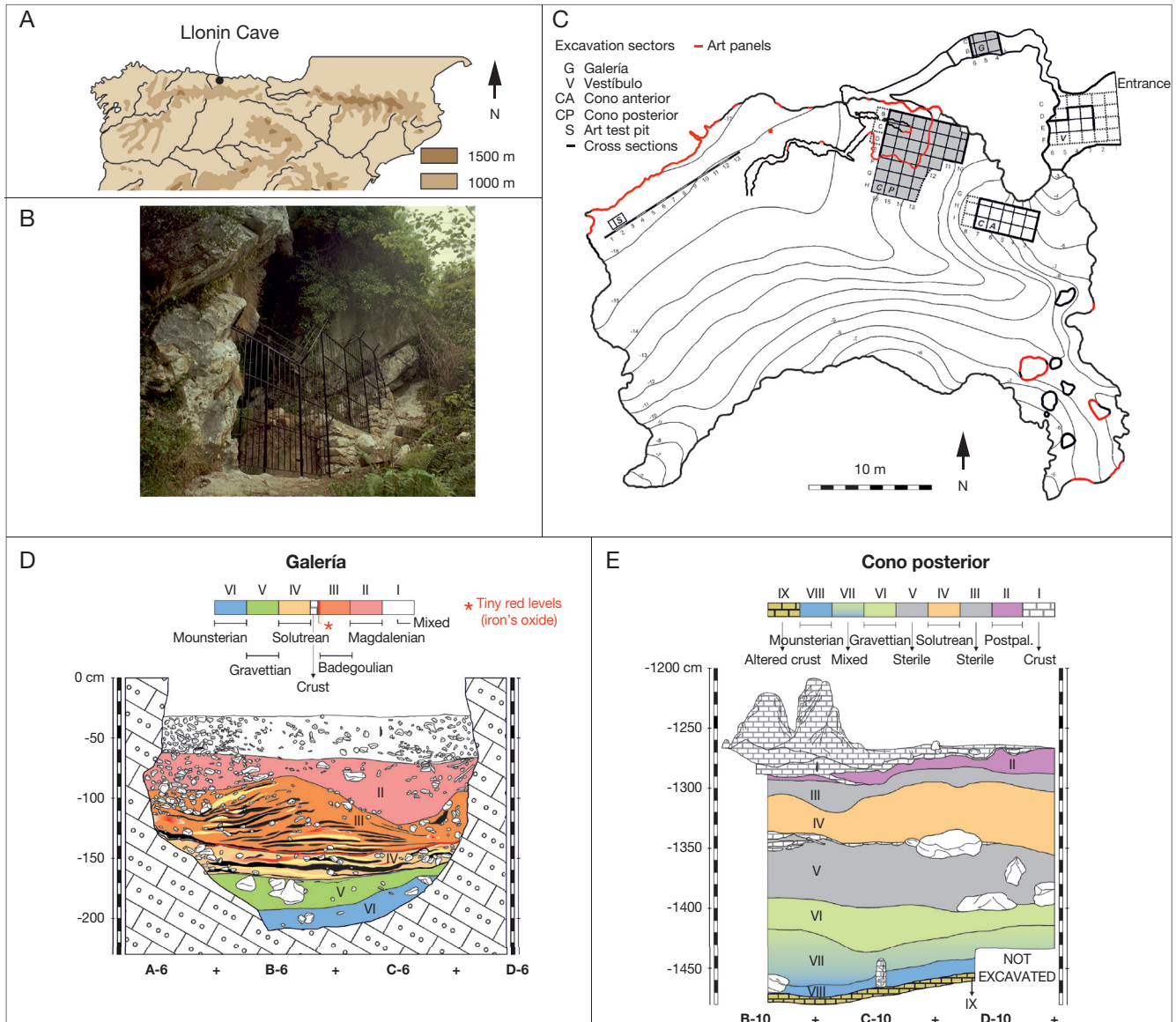


FIG. 1. — Llonin Cave geographical and stratigraphic context: **A**, geographical location of the site; **B**, view from the entrance (photo: J. Fortea); **C**, cave plan and location of the different sectors (study areas shown in **grey**); **D**, stratigraphic cross-section of Galeria; **E**, stratigraphic cross-section from Cono Posterior. From Sanchis *et al.* 2019.

THE ARCHEOLOGICAL ASSEMBLAGE OF THE MIDDLE PALEOLITHIC LEVELS (G-VI AND CP-VIII)

The macromammalian faunal remains recovered in the analyzed levels reveal a diverse association with six different ungulate species (highlighting *Rupicapra pyrenaica*, *Capra pyrenaica* and *Cervus elaphus*) and seven carnivore species (highlighting *Ursus spelaeus*, *Crocuta spelaea*, *Canis/Cuon* and *Panthera pardus*), all of them present in both levels (except *Crocuta spelaea*, which only appears in CP-VIII). The taphonomic analyses of these levels reveal a predominant use of the cave as a den by hyenas and leopards. Human presence in the cave is sporadic, given their limited interaction with deer, and the scarce lithic toolkit ($N = 159$). The leopards accumulated the caprines, and the hyenas introduced the bears and scavenged over the remains left by the Neandertals.

The micromammals (*Microtus agrestis-arvalis* group, *Sorex araneus-coronatus*, *Microtus lusitanicus*, *Pliomys lenki*, *Arvicola sapidus*, *Arvicola terrestris*, *Talpa europaea*, *Apodemus flavicollis*) show an habitat of open forests, with abundant shrubby and open areas, humid environments, and with Atlantic or Central European climates. The flora analysis points in that direction as well, representing open forests and an Atlantic mild or Central European climate. The anthracological analysis shows a predominance of species whose current optimum environment includes montane and subalpine environments; thus, it suggests that the conditions at the moment of the accumulation would have been cooler and arid. A deer ulna with cutmarks recovered in CP-VIII has been radiocarbon dated using ultrafiltration pretreatment (43.539 ± 2419 BP) (Rasilla & Santamaría 2011-2012; Sanchis *et al.* 2019; Rasilla *et al.* 2020).

TABLE 1. — Avifaunal spectrum expressed as number of identified specimens (NISP) and minimum number of individuals (MNI) for levels G-VI and CP-VIII dated from MIS3.

	G-VI		CP-VIII		TOTAL
	NISP	MNI	NISP	MNI	NISP
Aves indet.	13	–	168	–	181
Galliformes indet.	–	–	6	–	6
<i>Lagopus lagopus</i>	–	–	2	2	2
<i>Tetrastes bonasia</i>	–	–	1	1	1
<i>Columba livia/oenas</i>	–	–	2	1	2
Passeriformes indet.	5	–	31	–	36
Alaudidae indet.	–	–	1	1	1
<i>Motacilla</i> sp.	–	–	1	1	1
<i>Turdus</i> sp.	–	–	10	3	10
Corvidae indet.	11	–	114	–	125
<i>Garrulus glandarius</i>	–	–	1	1	1
<i>Pyrrhocorax</i> sp.	4	–	33	–	37
<i>P. pyrrhocorax</i>	8	2	115	13	123
<i>P. graculus</i>	3	1	26	3	29
<i>Corvus corax</i>	–	–	3	1	3
TOTAL	44	–	514	–	558

METHODOLOGY

The fossil remains were recovered by using two sieves with a mesh size of 2.38 and 1.41 mm, respectively. The analyzed bird remains were measured with a digital caliper (Mitutoyo Digilmatic Caliper CD-8^CX, Japan, with a theoretical precision of 0.01 mm) and photographed. The general nomenclature used is that of Baumel & Witmer (1993). For the systematic study, the identification keys are those from Erbersdobler (1968), Kraft (1972), Fick (1974), Jánossy (1983), Gilbert *et al.* (1985), Tomek & Bochenski (2000, 2009), Wójcik (2002), Bochenski & Tomek (2009) and Kessler (2015). The reference collection was the Gabinete de Fauna Cuaternaria Innocenci Sarrión, located in the Museu de Prehistòria de València. For the analysis of the fossil record of the taxa the works of Elorza (1990), Hernández-Carrasquilla (1993) and Tyrberg (2007) have been used. For the paleoenvironmental reconstruction, the current distribution of each identified taxa has been analyzed, and the results have been compared with the other groups present in the assemblages.

For the taphonomic analysis, the state of the remains has been studied in order to infer the origin of the accumulation of bird bones (Andrews 1990; Laroulandie 2000). For this purpose, the presence of modifications related to human action, mainly cutmarks, and modifications related to the action of other predators (digestion, pits, punctures, beak or claw marks, etc.) has been taken into account. Also, the percentage of complete bones has been calculated (Bochenski 2005), with the wing versus leg elements (Ericson 1987) and proximal versus distal elements (Bochenski & Nekrasov 2001) parameters calculated additionally.

RESULTS

A total of 558 avian remains recovered from the G-VI and CP-VIII levels have been analyzed. The remains belong to at least

ten taxa, albeit some of them were not identified beyond the Aves Class (Table 1). The number of remains recovered in each level strongly differs, with 44 remains in G-VI and 514 in CP-VIII. The remains identified as Aves indet. represent a similar proportion in both levels, with 29.5% in G-VI and 32.6% in CP-VIII.

Concerning the groups identified within each level, only the family Corvidae is present in the G-VI level. The diversity in level CP-VIII is slightly more varied, with the family Corvidae also being the most common in the assemblage (representing the 56.8% of the NISP), but with other groups also having been identified, such as the order Galliformes (representing 1.8%), the Columbiformes (0.4%), and the non Corvidae Passeriformes (8.5%). The differences in the number of remains recovered in G-VI and CP-VIII could be due to the structure of the cave, as a similar scenario can also be found in the macromammal remains, where a larger amount of remains were recovered in level CP-VIII, and with a lesser presence of anthropic modifications and more evidence of carnivores in level G-VI (Sanchis *et al.* 2019). The Cono Posterior area had a different entrance at a lower level, which is inaccessible nowadays, and could have been less exposed than the Galería sector, which is accessible from the current main entrance of the cave. Evidence of human occupation was found in the outer part of the main entrance, although it has to be taken into account that the human occupation of the cave was sporadic (Sanchis *et al.* 2019; Rasilla *et al.* 2020), and that humans and birds would not have frequented the cave at exactly the same time.

SYSTEMATICS

Order GALLIFORMES Temmink, 1820

Galliformes indet.

MATERIAL. — Six remains have been recovered: CP-VIII: left diaphysis fragment of a carpometacarpus, two sternum fragments, proximal femur, a left proximal ulna and a distal tibiotarsus.

Family PHASIANIDAE Horsfield, 1821

Genus *Lagopus* Brisson, 1760

Lagopus lagopus Linnaeus, 1758

MATERIAL. — CP-VIII: complete left tarsometatarsus and right distal tarsometatarsus (Fig. 2A).

DESCRIPTION

The two tarsometatarsus are the same size. The total length of the tarsometatarsus (38.6 mm) fits several representatives of the order Galliformes but allows to rule out the larger-sized taxa (Erbersdobler 1968). The proximal (7.5 mm) and distal length (8.2 mm for both remains) fits both *Lagopus lagopus* and *Perdix perdix* Linnaeus, 1758 (Kraft 1972). Morphologically,



FIG. 2. — Bird bone remains recovered from levels G-VI and CP-VIII: **A**, *Lagopus lagopus* Linnaeus, 1758, left tarsometatarsus, dorsal view; **B**, *Tetrastes bonasia* Linnaeus, 1758, right coracoid, ventral view; **C**, *Columba livia/oenas* Gmelin, 1789/Linnaeus, 1758, right ulna, ventral view. *Pyrrhocorax pyrrhocorax* Linnaeus, 1758 remains: **D**, left coracoid, ventral view; **E**, left humerus, posterior view; **F**, left ulna, ventral view; **G**, right carpometacarpus, posterior view; **H**, left femur, posterior view; **I**, right tarsometatarsus, plantar view. *Pyrrhocorax graculus* Linnaeus, 1766 remains: **J**, right humerus, posterior view; **K**, left carpometacarpus, posterior view; **L**, left tarsometatarsus, plantar view. Scale bar: 1 cm.

the tarsometatarsus recovered shows round epicondyles in trochlea metatarsi II; also, the trochleae are spread. That, along with the proportions of the smallest width of the shaft (3.6 mm) and the total length (Fig. 3), allows us to assign these remains to *Lagopus lagopus* (Kraft 1972).

REMARKS

The current European distribution of the willow grouse is limited to Scandinavia and Scotland (Juana *et al.* 2019); nevertheless, during the Pleistocene it expanded its habitat southwards, outranging its current distribution (Sánchez-Marco 2004; Holm & Svenning 2014). The contraction of their refuges during the Holocene explains the current distribution of the species (Lagerholm *et al.* 2017). Nowadays the distribution of the willow grouse is related to tundra areas and openings of boreal forests (Juana *et al.* 2019). In the Iberian Upper Pleistocene, the willow ptarmigan appears in Aitzbitarte IV (Elorza 1990), Ermitia (Elorza 1993), Urratxa III (Elorza 1997), Laminak II (Hernández-

Carrasquilla 1993), Abauntz (Altuna *et al.* 2002), Praileaitz 1 (Moreno-García 2017) and Santa Catalina (Elorza 2014; Laroulandie 2014).

Genus *Tetrastes* Linnaeus, 1758

Tetrastes bonasia Linnaeus, 1758

MATERIAL. — CP-VIII: complete right coracoid (Fig. 2B).

DESCRIPTION

The coracoid shows the morphology of Galliformes, the medial length of the coracoid (33.7 mm) fits the size of *Tetrastes bonasia*, *Perdix perdix* and *Alectoris graeca* Meisner 1804. The acrocoracoid shows a tuberculum craniale more laterodistally positioned than the tuberculum caudale. The foramen pneumaticum, is well developed, unlike in *Alectoris* Kaup, 1829 (which presents a hump in that position) and is

located further from the articulation with the sternum than in *Perdix* Brisson 1760. Those characters allow the assignation of the bone to *Tetrastes bonasia* (Kraft 1972).

REMARKS

The hazel grouse breeds in mixed coniferous woodland with understory (Juana & Kirwan 2019). It currently inhabits forests and mountain systems in the northern areas of Europe (Bergman & Klaus 1994). In the Iberian Peninsula its presence is limited to sporadic observations (Catusse *et al.* 1992). In the north of the Iberian Peninsula the hazel grouse has been identified in the Holocene of the B-8 cave (Núñez-Lahuerta *et al.* 2018b).

Order COLUMBIFORMES Latham, 1790
Family COLUMBIDAE Leach, 1820
Genus *Columba* Linnaeus, 1758

Columba livia Gmelin, 1789/*Columba oenas* Linnaeus, 1758

MATERIAL. — CP-VIII: complete right ulna (Fig. 2C); complete left distal ulna.

DESCRIPTION

Both ulnae present a similar size and the morphology of Columbiformes, with a prominent straight crista pectoralis in the proximal end, and a scar located more proximally than the proximal end of the condylus dorsalis in the distal end. The total length of the bone (51.4 mm) fits both *Columba livia* and *Columba oenas* (Fick 1974).

REMARKS

Both the rock and the stock doves can be found nowadays in the Iberian Peninsula. The rock dove breeds in caves and cliffs while the stock dove breeds mainly in open country and punctually in open woodland (Baptista *et al.* 2019a, b). In the Upper Pleistocene of the northern Iberian Peninsula the remains attributed to *Columba livia/oenas* are very common. They are registered among others in the Abric Romani, Avenc del Gegant (Sánchez-Marco 2004), Brechas de la Cantera de l'Altissent, Cueto de la Mina, Valdegoba, Cueva del Toll (Sánchez-Marco 2005), and Praileaitz 1 (Moreno-García 2017).

Order PASSERIFORMES Linnaeus, 1758

Passeriformes indet.

MATERIAL. — 36 remains have been recovered: five from G-VI and 31 from CP-VIII.

Family ALAUDIDAE Vigors, 1825

Alaudidae indet.

MATERIAL. — CP-VIII: right humerus.

Family MOTACILLIDAE Horsfield, 1821
Genus *Motacilla* Linnaeus, 1758

Motacilla sp.

MATERIAL. — CP-VIII: a right humerus.

DESCRIPTION

Humerus with two confluent fossae, nearly not separated by the cruss dorsale fossae, with a narrow habitus and a reduced wall of cruss dorsale fossae and a prominent epicondylus ventralis in ventral view (Jánossy 1983).

Family TURDIDAE Rafinesque, 1815
Genus *Turdus* Linnaeus, 1758

Turdus sp.

MATERIAL. — CP-VIII: three complete femora, three complete humeri, two complete coracoids, a tibiotarsus fragment and a tarsometatarsus.

DESCRIPTION

The size and morphology of these bones fits a medium-sized Passeriform. The coracoids show a distinct spine-shaped facies articularis clavicularis, with a short and pointed processus acrocoracoideus (Gilbert *et al.* 1985; Kessler 2015). The humeri show the two fossae confluent, and a reduced medial bar (Jánossy 1983; Wójcik 2002). The femora show a well-developed condylus fibularis and a rounded muscle attachment proximal to it (Gilbert *et al.* 1985), and the epicondylus medialis is not arching (Kessler 2015). The comparison with the comparative anatomy collection specimen of *Turdus philomelos* (TUPH-001) allowed the assignation of the remains to *Turdus* sp.

Family CORVIDAE Leach, 1820

DESCRIPTION

The family Corvidae is the best represented in Llonin MIS3 MP levels. 319 corvid remains have been analyzed, 26 from G-VI, and 292 from CP-VIII (Table 2), representing 59% and 56.8% of the assemblages respectively.

Corvidae indet.

MATERIAL. — 125 remains were analyzed: 11 from the G-VI, and 114 from CP-VIII (Table 2).

DESCRIPTION

The remains identified as Corvidae indet. are mostly long bones. The state of conservation, along with the similarities in the anatomy of corvids hampered the assignation of these remains to discrete taxa. It is of note that juvenile remains are also present (Fig. 5B).

TABLE 2. — Anatomic representation of the Corvidae remains recovered in the MIS3 levels of Llonin, expressed in number of remains. Abbreviations: **CAR**, carpal-ular; **CMC**, carpometacarpus; **COR**, coracoid; **CRA**, cranium; **FEM**, femur; **FUR**, furcula; **HUM**, humerus; **MAN**, mandible; **PDA**, alular phalange; **PEL**, pelvis; **PHA**, phalange; **RAD**, radius; **RIB**, ribs; **SCA**, scapula; **STE**, sternum; **TBT**, tibiotarsus; **TMT**, tarsometatarsus; **ULN**, ulna; **VER**, vertebra.

	CRANIAL				AXIAL				WING				LEG							
	TOTAL	CRA	MAN	VER	FUR	STE	RIB	COR	SCA	HUM	RAD	ULN	CMC	CAR	PDA	PEL	FEM	TBT	TMT	PHA
G-VI	26	–	–	–	–	–	–	5	–	2	1	6	–	–	5	–	3	2	1	1
Corvidae indet.	11	–	–	–	–	–	–	5	–	–	1	–	–	–	3	–	1	–	1	–
<i>G. glandarius</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrrhocorax</i> sp.	4	–	–	–	–	–	–	–	–	–	–	3	–	–	1	–	–	–	–	–
<i>P. pyrrhocorax</i>	8	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	2	–	–	1
<i>P. graculus</i>	3	–	–	–	–	–	–	–	–	2	–	–	–	–	1	–	–	–	–	–
<i>C. corax</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CP-VIII	292	1	5	–	–	5	–	17	7	37	7	45	22	–	3	–	27	35	22	1
Corvidae indet.	114	1	4	2	1	6	–	7	12	20	4	10	4	–	1	1	10	23	6	2
<i>G. glandarius</i>	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
<i>Pyrrhocorax</i> sp.	33	–	1	–	–	–	–	1	–	1	1	7	5	–	2	–	3	–	12	–
<i>P. pyrrhocorax</i>	115	–	–	–	–	–	–	11	1	14	5	25	11	–	3	–	19	13	13	–
<i>P. graculus</i>	26	–	2	–	–	–	–	4	–	6	–	2	5	–	–	–	–	4	3	–
<i>C. corax</i>	3	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1	–

Genus *Garrulus* Brisson, 1760

Garrulus glandarius Linnaeus, 1758

MATERIAL. — CP-VIII: right carpometacarpus.

DESCRIPTION

A complete carpometacarpus with a cranial length of 22.6 mm with Corvidae morphology. The size, along with the slender shape of the processus extensorius and the straight ventral edge of the trochlea carpalis allows the assignation of the bone to *G. glandarius* (Tomek & Bochenski 2000).

REMARKS

The Eurasian jay is currently present in the Iberian Peninsula; it inhabits woodlands and forests (Madge *et al.* 2019). It is common in the Upper Pleistocene sites of the Iberian Peninsula, as in El Castillo (Sánchez-Marco 2018), L'Arbreda, Reclau Viver (García i Petit 2002), La Riera (Sánchez-Marco 2005) and El Esquilieu (Baena *et al.* 2005).

Genus *Pyrrhocorax* Tunstall, 1771

Pyrrhocorax sp.

MATERIAL. — 37 remains were analyzed: four from G-VI and 33 from CP-VIII (Table 2).

DESCRIPTION

Most of the remains belong to the genus *Pyrrhocorax*, very common in the Upper Pleistocene avian assemblages. The size of the *Pyrrhocorax* species is very similar; in order to distinguish them, measurements have been taken following the methodology of Tomek & Bochenski (2000) (Fig. 4) and compared with bibliographic data.

Pyrrhocorax pyrrhocorax Linnaeus, 1758

MATERIAL. — 123 remains were analyzed: eight from G-VI and 115 from CP-VIII (Figs 2D-I; 4; Table 2).

DESCRIPTION

All the remains have the morphology of a medium sized Corvidae, with osteological features that fit with several species, as *Pyrrhocorax* spp. and *Corvus monedula*. Several characters allow the assignation of the remains to the genus *Pyrrhocorax*, such as the lack of a depression at the base of the acrocoraoid, and the shape of the bony crest in the coracoid, or the presence of two openings in the plantar surface of the tarsometatarsus. The size of the bones also allowed the assignation of the remains to the genus *Pyrrhocorax*, specifically to *P. pyrrhocorax*, which is in general slightly bigger than the sister species *P. graculus* Linnaeus, 1766 (Tomek & Bochenski 2000) (Fig. 4).

REMARKS

The red billed chough appears in the south of Europe, and it breeds in cliffs and high mountain pastures with rocky areas (Madge 2019a). It is one of the most common species in the Upper Pleistocene of Europe (Tyrberg 2007), and *P. pyrrhocorax* underwent expansions in both cold and warm pulses during the last part of the Pleistocene (Holm & Svenning 2014). It has been found among others in Aitzbitarte, Ermitia, Urriaga (Elorza 1990), Abauntz (Altuna *et al.* 2002) Praileaitz 1 (Moreno-García 2017), B-8 cave (Núñez-Lahuerta *et al.* 2018b), Artazu VII (Suárez-Bilbao *et al.* 2020) and Axlora (Gómez-Olivencia *et al.* 2018).

Pyrrhocorax graculus Linnaeus, 1766

MATERIAL. — 27 remains were analyzed, three from G-VI and 24 from CP-VIII (Table 2; Figs 2J-L; 4).

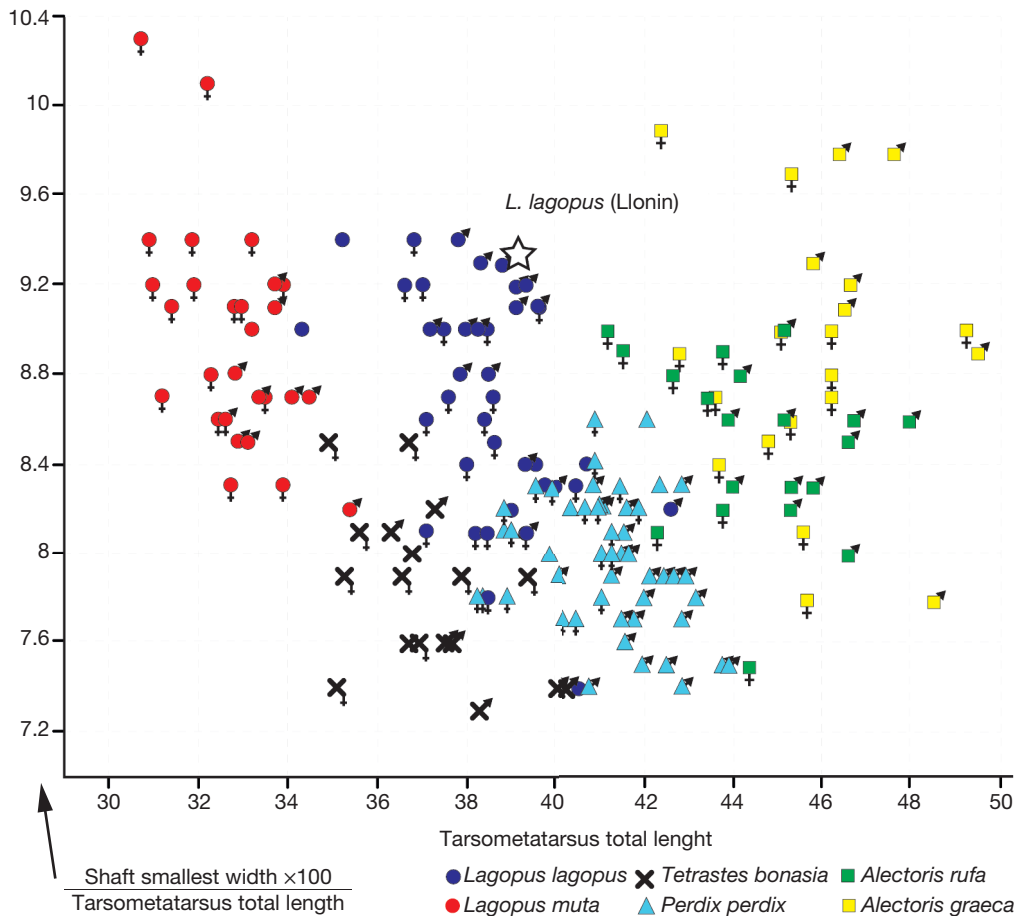


FIG. 3. — Dispersion graphic of the measurements of the tarsometatarsus of several Galliformes taxa, expressed in millimeters. Modified from Kraft 1972.

DESCRIPTION

The remains have the morphology of a medium sized Corvidae. As with the remains assigned to *P. pyrrhocrorax*, the various bones show features that allow their assignation to the genus *Pyrrhocrorax*. The size of the remains allows their assignation to *P. graculus*, which are generally smaller than those of *P. pyrrhocrorax* (Tomek & Bochenski 2000) (Fig. 4).

REMARKS

The yellow billed chough appears nowadays in the south of Europe, as does its sister species *P. pyrrhocrorax*, but it is confined to high mountain areas with rocky crags (Madge 2019b). For this reason, it has been used as a cold climate indicator; nevertheless, as it happens with the red billed chough, *P. graculus* is practically a cosmopolitan species, and its use as climate indicator must be done taking into account the other taxa present in the associations (Núñez-Lahuerta *et al.* 2018a). It has been recorded among others in Olha, Aitzbitarte (Elorza 1990), Praileaitz 1 (Moreno-García 2017), B-8 cave, D-2 cave, Los Batanes (Núñez-Lahuerta *et al.* 2018b) and Artazu VII (Suárez-Bilbao *et al.* 2020).

Corvus corax Linnaeus, 1758

MATERIAL. — Three remains were analyzed from CP-VIII (Table 2).

DESCRIPTION

The remains show the features of a large-sized Corvidae. The species *Corvus corax* is the largest species of the genus *Corvus* in the Palearctic, and the size of the two ulnae and the tarsometatarsus fits this species (Tomek & Bochenski 2000).

REMARKS

the raven is the biggest passerine bird. It appears thorough all the Iberian Peninsula, and is a generalist bird. It can appear in a wide range of habitats, generally in more open habitats (Marzluff 2019). It appears among other sites in the Iberian Upper Pleistocene sites of Urtiaga, Aitzbitarte, Santimamiñe (Elorza 1990), Amalda (Eastham 1989) El Castillo (Sánchez-Marco 2018), Praileaitz 1 (Moreno-García 2017) and Axlor (Gómez-Olivencia *et al.* 2018).

TAPHONOMICAL REMARKS

Most of the anatomical elements have been recovered in the Llonin MIS3 levels. As remarked above, the family Corvidae is the most represented in the two analyzed levels, followed by the Galliformes (Fig. 5C; Table 1). As discussed previously, the number of remains for each level is clearly different (44 remains in G-VI and 514 in CP-VIII), and those

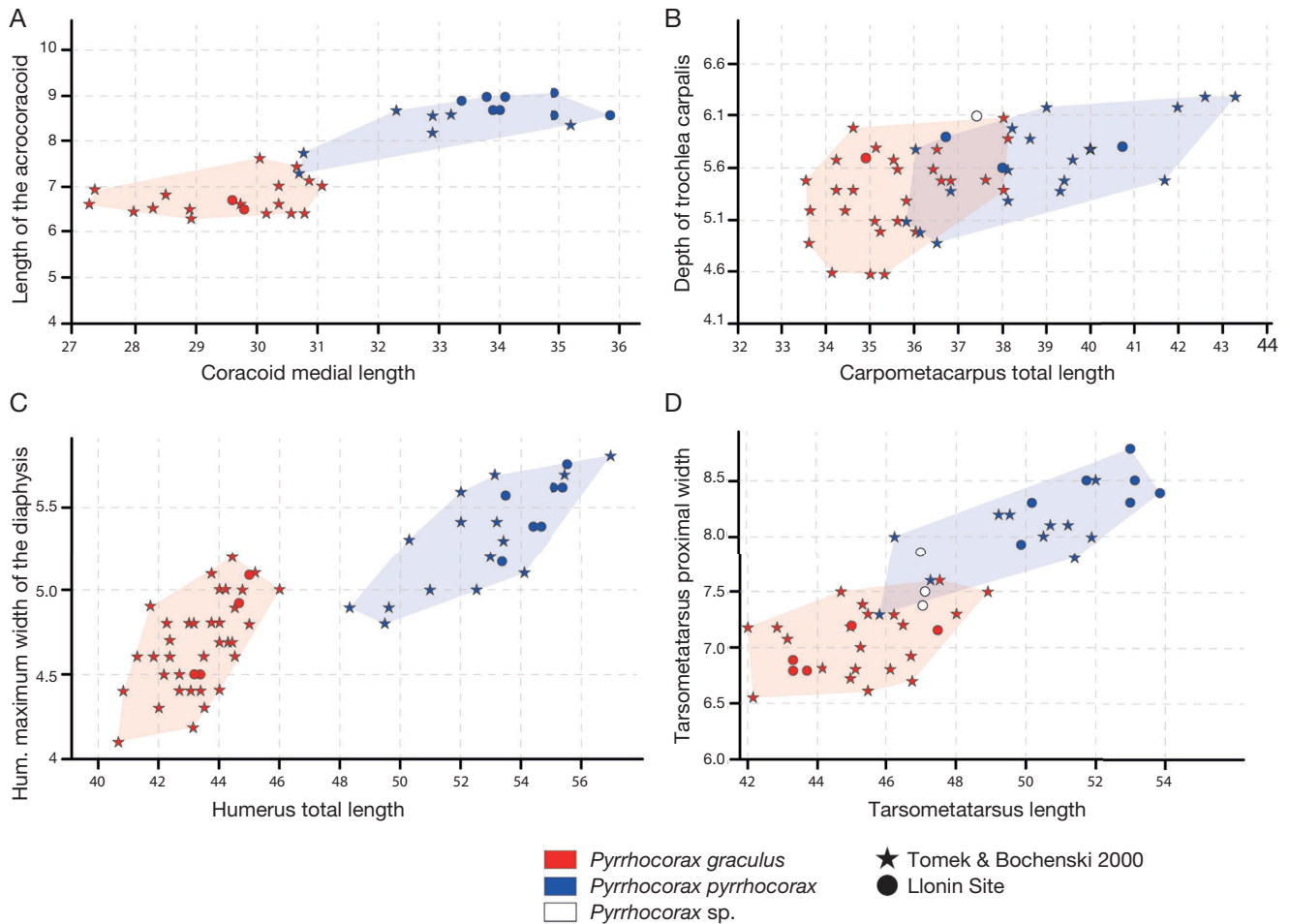


FIG. 4. — Dispersion graphics of the measurements of the chough (*Pyrrhocorax* Tunstall, 1771) remains from Llonin (circles) in comparison with the data from Tomek & Bochenski (2000) (stars): **A**, coracoid measurements comparison, total length vs length of the acrocoracoid; **B**, carpometacarpus measurements comparison, total length vs depth of the trochlea carpalis; **C**, humerus measurements comparison, total length vs maximum width of the diaphysis; **D**, tarsometatarsus measurements comparison, total length vs proximal width. Data expressed in millimeters.

differences could be due to the structure of the cave, with its different entrances and dynamics (Sanchis *et al.* 2019; Rasilla *et al.* 2020).

No cutmarks have been detected on the remains. The digestion is scarce in the sample. In G-VI, five elements (11% of the G-VI Aves sample) show light or medium digestion (an undetermined fragment and a coracoid and three femora assigned to corvids); and in CP-VIII five remains (1% of the CP-VIII Aves sample) present light or medium digestion (ulna, proximal femur and a tibiotarsus assigned to undetermined Aves, and two femora assigned to Corvidae). Some of the bones present punctures that could be due to the action of birds of prey (Bochenski *et al.* 2018). In the level CP-VIII four long bones show punctures (one undetermined, three corvid long bones, representing the 0.7% of the remains). The presence of carbonate crusts in the remains could hide some modifications, but only a low percentage of remains present crusts (6% of the CP-VIII birds sample and 9% of the G-VI birds sample), thus, the effect of the crusts in the taphonomic interpretation is not very relevant. Most of the modification appears in undetermined Aves or corvids, which are the most abundant remains in the assemblages.

The percentage of complete bones varies in each level, and is apparently higher in level CP-VIII, nevertheless the differences are not statistically representative (31.6% in CP-VIII, with a Confidence interval of 95%, between 27%-36.6%; and 21.4% in G-VI, CI 95%: 9%-41.4%) (Fig. 5D). The low number of remains recovered in G-VI prevents the calculation of proportions and therefore to perform deeper taphonomic analyses. For this reason, the wing versus leg and proximal versus distal were calculated only for the CP-VIII level assemblage. In this level, the data from Corvidae and the rest of the Aves taxa have been analyzed separately. The small amount of remains of non-corvid groups hampers the possibility of analyzing each group separately.

The wing versus leg results of CP-VIII shows approximately a 50% ratio for both corvids and non-corvids, and the wing elements are more abundant in both groups (Fig. 5E), but this abundance is not significant ($p = 0.8$). These results are similar to those given for uneaten remains from diurnal birds of prey and pellets from nocturnal birds of prey. The predominance of wing elements and the absence of cutmarks allow for discarding the human processing of the bird remains (Ericson 1987). The results of the proximal

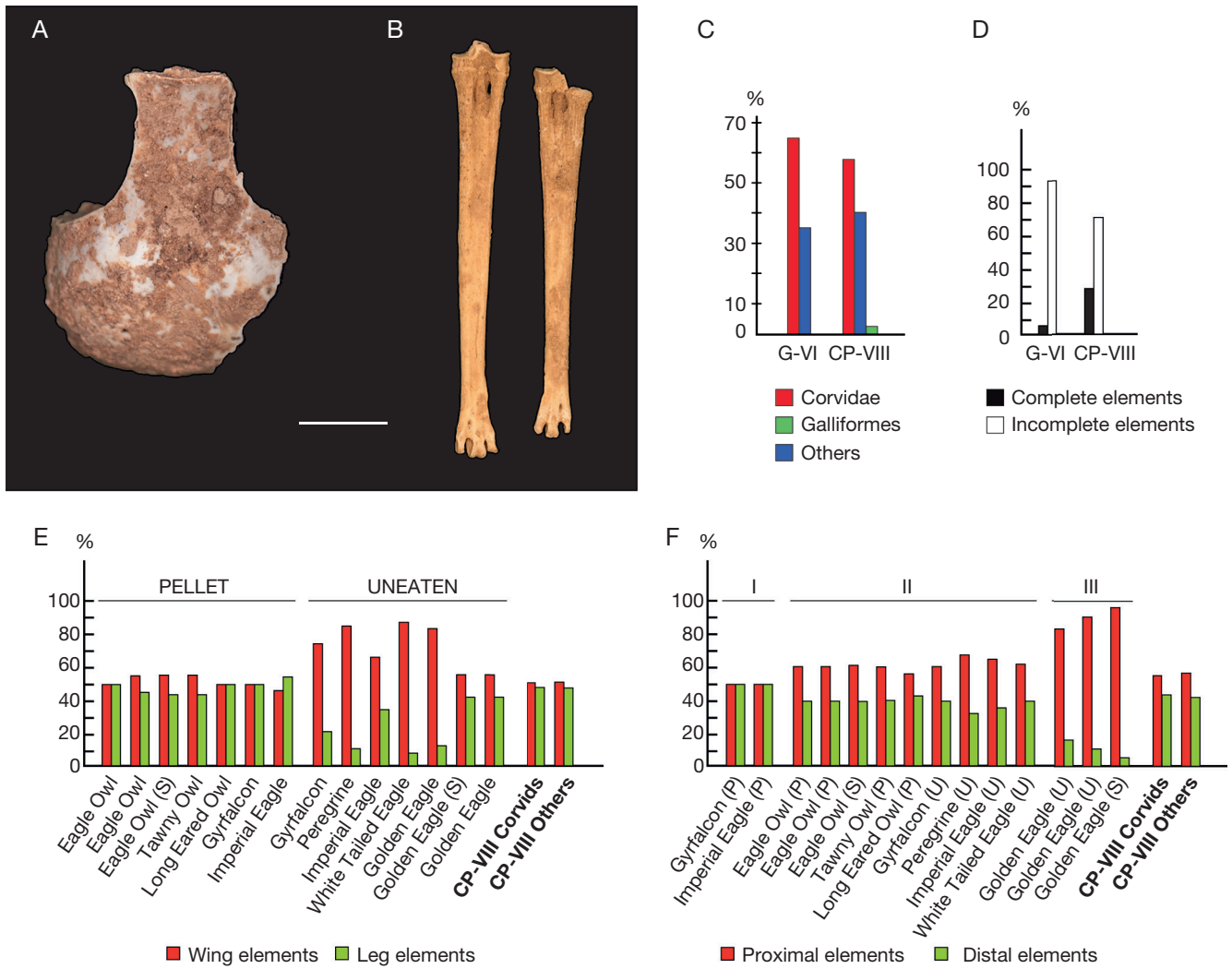


Fig. 5. — Taphonomic remarks from the Llonin MIS3 bird assemblages: **A**, cranial remains from CP-VIII level; **B**, juvenile tarsometatarsus from CP-VIII level; **C**, proportions between the main groups present in the assemblages, according to the NISP; **D**, percentage of whole bones in the assemblages; **E**, wing vs leg elements proportions; **F**, proximal vs distal elements proportions. **E**, **F**, modified from Bochenski 2005. Data from Bochenski *et al.* 1993, 1997, 1998, 1999; Bochenski & Tomek 1994; Bochenski & Nekrasov 2001; Bochenski & Tornberg 2003; Bramwell *et al.* 1987; Laroulandie 2000, 2002; Mlikovsky 1996.

versus distal analysis shows a 56-44% ratio between them for the corvids and 57-44% for the rest of the bird remains (Fig. 5F), and these proportions correspond to a group II predator, also including pellets from nocturnal birds of prey and uneaten remains from diurnal birds of prey (Bochenski & Nekrasov 2001). The results need to be interpreted carefully, as these ratios have been criticized (Livingston 1989; Laroulandie 2010), and also, some authors proposed that the predominance of wing elements in Neanderthal sites reflects the use of the feathers by the humans (Finlayson *et al.* 2012).

DISCUSSION

ORIGIN OF THE ACCUMULATION

Both groups (corvids and non-corvids) yielded similar results in the analyzed parameters. The high proportion of broken

bones in the assemblage could be due to postdepositional processes, such as trampling produced by the animals and humans occupying the cave (Sanchis *et al.* 2019).

The clear domination of cave dwelling corvids in the assemblage (Fig. 5C), the presence of fragile remains such as skulls or sternums (Fig. 5A), together with the presence of juvenile remains of this group (1%) (Fig. 5B) and the scarce amount of modifications on the assemblages, points to a natural accumulation of the corvids inhabiting the cave. Nevertheless, it has been shown that the processing of corvids by Neanderthals does not necessarily leave anthropic marks, due to the small size of the birds, and because the exploitation of corvids by humans is an extended activity (Finlayson *et al.* 2012), and the sporadic presence of humans in the Llonin Cave is clear (Sanchis *et al.* 2019; Rasilla *et al.* 2020). Also, corvids are well-known scavengers that could have visited the cave following the carcasses which had been left by the different predators that acted in the cave.

The evidence points to a mixed origin of the accumulation of birds: with some individuals of medium-sized corvids (*P. pyrrhonorax* and *P. graculus*) mostly dying naturally in the cave, representing the majority of the assemblage, and other groups of birds being sporadically accumulated by birds of prey. But a Neanderthal role in this accumulation cannot be ruled out with the available data.

PALEOENVIRONMENTAL RECONSTRUCTION

Several species that have been considered interesting due to their climate-related behavior (Sánchez-Marco 2004; Holm & Svenning 2014) appear in the assemblage: the willow ptarmigan (*Lagopus lagopus*), the hazel grouse (*Tetrastes bonasia*) and the choughs (*Pyrrhonorax pyrrhonorax* and *Pyrrhonorax graculus*). The current distribution of the willow ptarmigan (*L. lagopus*) does not include the Iberian Peninsula (Juana *et al.* 2019). Nevertheless, it expanded its habitat southwards during the Pleistocene, and then contracted its geographical range back during the Holocene, remaining at some punctual areas outside its current range as a relict (Sánchez-Marco 2004; Holm & Svenning 2014). This contraction of its refuge during the Holocene explains the current distribution of the species, which is nowadays related to tundra areas and openings of boreal forests (Lagerholm *et al.* 2017). The hazel grouse (*B. bonasia*) inhabits mixed coniferous woodland with understory in the north of Europe (Juana & Kirwan 2019), and its occurrence in the Iberian Peninsula is limited to sporadic observations (Catusse *et al.* 1992). During the Late Pleistocene these three species show a strong relation with forested areas (Núñez-Lahuerta *et al.* 2018a).

Both chough species (*Pyrrhonorax pyrrhonorax* and *Pyrrhonorax graculus*) inhabit similar areas in Europe, although the yellow billed chough (*P. graculus*) appears at higher altitudes than the red-billed chough (*P. pyrrhonorax*). It has been proposed that this difference is due to a higher tolerance to low temperatures by the yellow billed chough (Tyrberg 1991). Due to its current distribution, the presence of *P. graculus* has been interpreted as an indicator of a colder climate; nevertheless, the yellow billed chough was present in all of Europe during both cold and warm periods of the Late Pleistocene (Tyrberg 2007). In summary, the avian association points to a mixed landscape, composed of open areas and woodlands, with understory.

Concerning the other faunal elements identified in the analyzed levels, the small vertebrate assemblage also points to a landscape mainly composed of open areas, such as meadows, grasslands, and rushes, with low density forests. This presence of open forest has been also confirmed by the anthracological analysis. Additionally, the small mammal assemblage points to a humid environment, and the presence of permanently wet areas, which is reflected by the presence of semiaquatic taxa such as the Pyrenean desman (*Galemys pyrenaicus* Geoffroy, 1811) and the southwestern water vole (*Arvicola sapidus* Miller, 1908) (Sanchis *et al.* 2019). The presence of water bodies in the surroundings of the cave is not so strongly reflected by the avian association,

but nevertheless, one remain assigned to a genus generally related to water bodies has been identified: *Motacilla* sp.

Both the small mammal association and the anthracological analysis point to a colder climate in the Llonin Cave area. Although most of the avian taxa identified in the levels are present nowadays. The existence of some taxa (today absent in the Iberian Peninsula and only inhabiting the northern part of Europe) can be justified due to this past colder climate, which is reflected by the mammals and anthracological analysis, although it has to be taken into account that birds tend to reflect more middle temperatures rather than other proxies, and their distribution also strongly depends on the landscape (Lorenc 2007).

CONCLUSIONS

The analyzed remains (N = 558) have revealed at least ten different taxa: Aves indet., Galliformes indet., *Lagopus lagopus*, *Tetrastes bonasia*, *Columba livia/oenas*, Passeriformes indet., Alaudidae indet., *Motacilla* sp., *Turdus* sp., Corvidae indet., *Garrulus glandarius*, *Pyrrhonorax* sp., *Pyrrhonorax pyrrhonorax*, *Pyrrhonorax graculus* and *Corvus corax*. The assemblage is similar to others of the Upper Pleistocene of the north of the Iberian Peninsula. The scarcity of modifications (digestion, punctures), and the absence of cutmarks, together with the presence of juvenile remains, point to a mixed origin of the accumulation, with small corvids naturally dying in the cave, and raptors accumulating their preys.

Despite the presence of species considered typical of colder areas (*Lagopus lagopus* and *Tetrastes bonasia*), the whole avian association present in the levels under study points to an environment similar to that of today. A mixed landscape with open and woodland areas occurred near the cave during the accumulation of the Middle Paleolithic levels, with this landscape interpretation correlated by the small mammal association and the anthracological data present.

Acknowledgements

CN-L was awarded a grant by the Regional Government of Aragón, co-funded by the European Social Fund, and with a position in the Universidade NOVA de Lisboa within the project TDC/CTA-PAL/31656/2017, financed by Fundação para a Ciência e Tecnologia (FCT). This work has been funded under Project MINECO2015-HAR2014-59183-P “Paleoambiente, Economía y Sociedad durante el MIS 3 en el Occidente Cantábrico” (Palaeoenvironment, Economy and Society during MIS 3 in the western Cantabrian region). We are grateful for the financial support to GeoBioTec (UIDB/04035/2020). We would like to thank I.G.I for the revision of the text in French, and A.F. for the revision of the text in English. The authors also thank Hanneke Meijer and the anonymous reviewer for their useful comments and suggestions that greatly improved the manuscript.

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Submitted on 8 October 2019;
accepted on 24 June 2020;
published on 2 August 2021.