

1 **Paleoenvironmental evolution of Picos de Europa (Spain) during Marine Isotopic Stages 5c to 3**
2 **combining glacial reconstruction, cave sedimentology and paleontological findings.**

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25 **ABSTRACT**

26 In glaciated areas, the environmental evolution before MIS 2 is usually poorly constrained mainly due to
27 the later glacial erosion during the global Last Glacial Maximum (LGM). However, in carbonate areas,
28 karst caves can preserve records of pre-LGM paleoenvironment interest. We studied a cave (1350 m
29 altitude) to establish the paleoenvironmental evolution of a glaciated karst area in Picos de Europa (SW

30 Europe). For this objective, a glacial reconstruction, cave sedimentology analyses, macro- and
31 micromammal remains are combined with ten U-Th, OSL and AMS ¹⁴C ages. The paleo-glacial
32 reconstruction indicates glaciers descended down to 810–1040 m of altitude covering an area in 36.18
33 km² of the surroundings of Covadonga Lakes during the glacial local maximum, with the equilibrium line
34 altitude located at 1524 ± 36 m. The geomorphological study of the cave and the U-Th and OSL dates
35 reveal the presence of three allochthonous alluvial sediment sequences at 132-135, 98-60 and ca. 36
36 ka. These last two sequences would come from the erosion of fluvio-glacial sediments including teeth
37 fragments of *Pliomys coronensis* (= *P. lenki*), an unusual species in NW Spain in high areas during the
38 Upper Pleistocene. In addition, found remains of chamois (*Rupicapra pyrenaica*) dated in 37–33 cal ka
39 BP constitutes the oldest evidence of chamois above 800 m asl in the region. All the presented data
40 indicate the development of alpine glacier-free areas covered by fluvio-glacial sediments at ca. 1450 m
41 altitude at 98-60 and 37–33 ka, corresponding to glacial retreat stages.

42

43 **KEYWORDS**

44 Karst, glacial reconstruction, paleoenvironment, *Pliomys coronensis*, *Rupicapra pyrenaica*.

45 **1. INTRODUCTION**

46 Paleoenvironmental records corresponding to Marine Isotope Stages (MIS) 4–3 are relatively scarce in
47 glaciated mountains, mainly due to glacier erosion associated to the Last Glacial Maximum (LGM) of
48 MIS 2. In areas made of limestone or another soluble rock, karst caves often preserve abundant
49 additional paleoenvironmental evidence sheltered from surface weathering (Häuselmann, 2013). Cave
50 evidence can be compared with surface landforms and sedimentary logs in order to reconstruct the past
51 environmental evolution of a territory, improving our understanding on glacial advances and retreats
52 (Myroie and Myroie, 2004; Bočić et al., 2012; Weremeichik and Myroie 2014).

53 In glaciated areas, endokarst sedimentary records are mainly represented by speleothems and fluvial
54 deposits, commonly originated during the Pliocene–Upper Pleistocene (Audra et al., 2006). Among the
55 speleothems, stalagmites frequently grow during interglacial periods, when high CO₂ concentrations
56 related to warm environments favors carbonate dissolution and precipitation in the karst conduits (Isola
57 et al., 2019; Tîrlă et al., in press). However, its growth is not only limited to interglacials, as can be seen
58 in a compilation of stalagmite records from Western Europe (Lechleitner et al., 2018). During glaciations,

59 glacial melting often affects karst aquifers favoring coarse grain sedimentation or erosion processes
60 according to glacial evolution. Pioneering works by Ford (1971, 1979) and Glover (1977) already
61 established that main endokarst detrital aggradation episodes are coeval with glacial retreats and,
62 occasionally, with the onset of glacial advances. Glaciers can inject sediments in cave passages located
63 at more than 1 km depth in glaciated areas (Audra et al., 2002), as well as in shallow caves influenced
64 by glacial outwash and located at distances of over 1000 km from the icefield (Myrloie, 1984). Since
65 these sediments result from the glacial erosion of limestone, they are mostly formed of carbonate-rich
66 silt, the so-called “glacial rock-flour” or “glacial milk” (Bočić et al., 2012; Weremeichik and Myrloie, 2014).
67 In addition, cave detrital aggradation may also include allochthonous cobbles and gravels derived from
68 the erosion of any lithology outcropping in the catchment area (Audra et al., 2002; Ballesteros et al.,
69 2017). In temperate settings, glacial valley incision dominantly occurs during glaciations (Häuselmann
70 et al., 2007). Therefore, the increase of hydraulic gradients in the endokarst favours the development of
71 torrential water flow that broadly erodes and evacuates cave sediments, simultaneously to the general
72 enlargement of previous vadose canyons (Plan et al., 2009; Adamson et al., 2014). However, if glaciers
73 reach the bottom of fluvial valleys, karst springs can be blocked by till, thus triggering inundations in the
74 endokarst (Skoglund et al., 2010). During these floods, glacial carbonate silt decants forming rhythmic
75 slackwater deposits related to sedimentary changes in underground lakes (Weremeichik and Myrloie,
76 2014; Ballesteros et al., 2017).

77 In the NW of Spain, Picos de Europa is an outstanding location worldwide to study glaciokarst processes
78 and more deeply explore the potential of cave archives as records for paleoenvironmental changes,
79 since Picos de Europa combines outstanding glaciokarst landforms (Smart, 1986) with the largest
80 cluster of deep caves worldwide (Ballesteros et al., 2019a). This study focuses on the Covadonga Lakes
81 and their surroundings, located in the NW of Picos de Europa, a reference location for glacial and karst
82 research (e.g. Rodríguez-Rodríguez et al., 2014; Serrano et al., 2017; Telbisz et al., 2019). Gale and
83 Hoare (1997) and Alonso (1998) elaborated glacial reconstruction studies and Jiménez-Sánchez and
84 Farias (2002) concluded that the local Glacial Maximum (local GM) took place ca. 20 ka before the
85 global LGM, proposing a subsequent phase of generalized glacier retreat. Later, Moreno et al. (2010)
86 established the regional paleoenvironmental evolution since 38 ka based on the Enol Lake record and
87 geomorphological evidence, and Jiménez-Sánchez et al. (2013) refined the age of the local GM at ca.
88 45 ka. Likewise, Nieuwendam et al. (2016) studied periglacial processes during late MIS 3 and Ruiz-

89 Fernández et al. (2016) reconstructed the timing of the last deglaciation. Regarding to karst studies,
90 Ballesteros et al. (2015, 2017, 2019b) defined the Quaternary landscape evolution of the area based on
91 cave geomorphology and geochronology.

92 Nevertheless, the environmental evolution of the Covadonga Lakes area before 45 ka remains mostly
93 unknown, especially regarding to ancient fauna that remains virtually unexplored. The present study is
94 focused on the karst cave named Hayéu l'Osu with the aim to establish the paleoenvironmental evolution
95 of the Western Massif of Picos de Europa during MIS 5c–3. To achieve this goal, we carried out a
96 multidisciplinary work combining glacial reconstruction based on field evidence, speleothem U-Th
97 dating, cave detrital sediment analyses and OSL dating, and the identification of micro- and
98 macromammal remains dated by AMS radiocarbon.

99 **2. SETTING**

100 Picos de Europa National Park (NW of Spain) is a high mountainous area up to 2650 m above sea level
101 (asl), located in the northern slope of the Cantabrian Mountains (Figure 1). Picos de Europa is divided
102 in three massifs (Western, Central and Eastern) by deep fluvial gorges. The main rocks that crop out
103 are Carboniferous limestone and, secondly, Ordovician, Carboniferous and Permian–Triassic
104 sandstone and shale (Merino-Tomé et al., 2013). The climate of Picos de Europa is humid and
105 temperate with fresh summers and without a dry season (Dfb and Dfc following the Köppen
106 classification). The annual precipitation ranges from 1000 to 1800 mm and is distributed throughout the
107 year, whilst the average air temperature ranges between -3 and 17°C. Snow is present around 6–9
108 months per year above 1500 m altitude.

109 Picos de Europa is one of the most relevant karst areas worldwide, since it contains 14% of the deepest
110 caves (>1 km deep) in the world (Ballesteros et al., 2019a). The karst evolution was controlled by river
111 incision and past glaciations (Smart, 1986). Fluvial incision created narrow gorges up to 2 km in depth,
112 conditioning the development of at least 3700 caves summing a total documented length of 420 km,
113 which were most likely formed during the Pliocene and Quaternary (Figure 1C; Ballesteros et al., 2015,
114 2019b). Cave detrital infill came from the erosion of the above-mentioned nearby bedrock outcrops
115 (Fernández-Gibert et al., 2000; Smart 1986). During the Upper Pleistocene, glaciers reached their local
116 GM extent, occupying ca. 190 km² and with their fronts descending down to 600–900 m altitude (Figure
117 1C; Serrano et al., 2017). In the study area (Figure 2) glaciers flowed below 1300 m altitude in the
118 surroundings of Covadonga Lakes around 109–95 ka (MIS 5d–c) leading to slackwater sedimentation

119 in caves (Ballesteros et al., 2017). Later, glacial fronts reached at least 900 m altitude (Gale and Hoare,
120 1997; Alonso 1998; Moreno et al., 2010), defining a local maximum at 45 ± 3 ka (Jiménez-Sánchez et
121 al., 2013). Glacier fronts retreated since ca. 45 ka, being already located at ca. 1000 m elevation at 39
122 ka, coeval to the development of the Covadonga Lakes (Moreno et al., 2010; Nieuwendam et al., 2016).
123 According to these authors, this retreat continued during MIS 3, taking place under cold, dry and open
124 conditions until 18 ka, coeval with the occurrence of periglacial processes recorded by the Belbin kame
125 deposit (Figure 2; Ruiz-Fernández et al., 2016). Nevertheless, sporadic forest surrounded Picos de
126 Europe during MIS 3 (Uzquiano et al., 2016). Finally, an advance of the glacier front up to similar
127 altitudes than the local maximum is reported at ca. 23–19 ka, which is ascribed to the global LGM (Ruiz-
128 Fernández et al., 2016; Serrano et al., 2017).

129 **3. METHODOLOGY**

130 The methodology combines geomorphological, paleontological and geochronological analyses,
131 including: (1) paleo-glacier reconstruction; (2) cave geomorphology; (3) paleontological identification of
132 the remains, (4) speleothem U-Th dating, (5) detrital cave sediment OSL dating, and (4) radiocarbon
133 dating of macromammal remains. All the spatial information was managed using the Geographical
134 Information System ArcGIS (ESRI), involving topographic contours, orthophotographies and
135 topographic digital models from the Spanish National Institute of Geography (www.cnig.es; last access
136 on April 2019).

137 **3.1 Paleo-glacier reconstruction**

138 Paleo-glacier topography was reconstructed in the study area (Figure 2) for the local GM stage based
139 on geomorphological evidence compiled in Ballesteros et al. (2015, 2019b) and bed topography
140 information. Terminal moraines, glacial arêtes and cirques were used to infer the location of former
141 glacier margins during the local GM stage. Glacier topography was interpolated from 25 theoretical ice
142 surface profiles reconstructed comprising the routing pathways followed by glacier tongues along the
143 valleys and inferred from geomorphological indicators of glacier flow direction. Theoretical ice surface
144 profiles were adjusted following the methods explained in Benn and Hulton (2010), using the GlaRe
145 toolbox for ArcGIS (Pellitero et al., 2016). Basal shear stress values up to 80–120 KPa were needed to
146 adjust the theoretical ice surface profiles to existing geomorphological evidence, which are consistent
147 with those observed in modern glaciers (50 to 150 KPa; Pellitero et al., 2016). The shape factor of the

148 valley was calculated for 62 cross sections to account for the topographic controls of glacial valley shape
149 on the basal shear stress. Once reconstructed, the digital elevation model of the former glacier
150 topography was used to estimate the Equilibrium Line Altitude (ELA) in steady-state conditions through
151 the Area Altitude Ratio Balance Ratio (AABR) method of Osmaston (2005) using the ELA toolbox
152 (Pellitero et al., 2015). We consider a range of balance ratio values of 1.9 ± 0.8 representative for
153 maritime glacier datasets (Rea, 2009).

154 **3.2 Cave geomorphology**

155 We studied the geomorphology of Hayéu l'Osu Cave in order to establish its development and its
156 sedimentary infill. To achieve this, we carried out the topographic survey in collaboration with
157 speleological groups and the geomorphological mapping of the cavity at 1:100 scale. The cave survey
158 and geomorphological map were developed in ArcGIS following the procedure described in Ballesteros
159 et al. (2015). The cave survey was delineated by means of 569 stations distributed along the cave
160 conduits and 608 measurements of distance, direction and inclination between stations using a DistoX
161 rangefinder, including the vertical and horizontal diameter of the conduit at each station. These
162 measurements were analyzed using the Compass software. Later, the geomorphological map was
163 drawn projecting cave forms and deposits on the cave survey.

164 **3.3 Paleontological analyses**

165 To search for micromammal remains, four samples of detrital sediments (named HAY-07, HAY-08, HAY-
166 09 and HAY-10) summing up to ~90 kg were collected from alluvial sequences of Hayéu l'Osu Cave..
167 Samples were water-screened using two superimposed sieves of 2- and 0.5-mm mesh size. Sieves
168 were not previously used preventing hypothetical contamination from previous samples in the laboratory.
169 Fine sieved samples was examined using a parallel-optics type stereo microscope Nikon SMZ800N
170 under 10x magnification. Photographs were taken with a 5 Mpx resolution digital camera, and image
171 orientation correction was done with Adobe Photoshop CC software. We used teeth samples of current
172 fauna as a comparison material to identify the micromammal remains found in the study cave. The
173 reference material used belongs to *Arvicola monticola*, *Microtus lavernedii*, *Microtus lusitanicus* and
174 *Clethrionomys glareolus*, all of them collected from *Tyto alba* pellets in the Cantabrian Region, as well
175 as MIS 3 fossil material of *Pliomys coronensis* (= *P. lenki*) recovered from the nearby archeological site
176 of La Güelga Cave (Figure 1C).

177 Macromammals were discovered by speleologists from Grupo Espelológico Polifemo (Oviedo) and
178 collaborators. Macro remains were recovered using the archaeological methodology, mapping their
179 occurrence on the geomorphological map (section 3.2). These remains were prepared for taxonomic
180 and taphonomic analyses by removing physically the silt and clay attached to the bones and
181 consolidating the samples with Paraloid B-72. Finally, we calculated the Minimum Number of Individuals
182 (MNI) of each species taking into account each skeletal element. The fossils are stored in the
183 Department of Geology at the University of Oviedo (Spain).

184 **3.4 U-Th dating**

185 Three flowstone samples from the study cave were dated by U decay series. Supplementary Data
186 (Figure S1) includes the geomorphological sections of the sampled flowstones. All samples were
187 collected in-situ with the aid of a hammer and a chisel, and drilled in the laboratory using a hand drill to
188 extract 0.1-0.2 g of carbonate powder, which was treated and analyzed at the Xi'an Jiaotong University
189 (China), following the procedures described in Edwards et al. (1987). Each sample was dissolved with
190 HNO₃ and spiked with a ²²⁹Th – ²³³U – ²³⁶U carrier solution. Once the Fe solution and the ammonium
191 hydroxide is added, the separation of U and Th was carried out using column chromatography with an
192 anion exchange resin. Finally, U and Th fractions were analyzed in a multicollector-inductively coupled
193 plasma mass spectrometer (MC-ICP-MS) ThermoFisher Neptune Plus using U decay constants
194 reported in Cheng et al. (2013). The ages are expressed in years before present (BP) with their
195 2σ uncertainty.

196 **3.5 OSL dating**

197 Optically stimulated luminescence (OSL) dating was applied to date endokarst detrital sediments. We
198 collected five samples from sandy layers recognized in the cave stratigraphic sections detailed in
199 Supplementary Data (Figure S2). Samples were taken driving opaque PVC tubes (550 mm diameter, 4
200 mm wall) in sandy material and then carefully covered with aluminum foil immediately after extraction.
201 Samples were processed in the luminescence laboratory of the Institute of Geology Isidro Parga Pondal,
202 University of A Coruña (Spain). Under red light conditions, sand materials stored within the tubes were
203 dried and sieved. The grain fraction 180–250 μm was dried at 45°C and treated with HCl and H₂O₂ in
204 order to remove carbonates and organic matter, respectively, which constituted 65–90% of the samples.
205 Furthermore, a centrifugation step adding a high-density solution was needed to separate quartz from

206 feldspar and heavy minerals. Later, a HF dilution was used on the quartz-rich fraction to obtain pure
207 quartz. Infrared Stimulated Luminescence (IRSL) was used to verify quartz purity at the end of sample
208 treatment.

209 OSL signals were recorded using an automated RISØ TL/OSL-DA-15 reader equipped with a
210 photomultiplier EMI 9635 QA (PMT) and a $^{90}\text{Sr}/^{90}\text{Y}$ source (dose of $0.120 \pm 0.003 \text{ Gy}\cdot\text{s}^{-1}$). An optical 6
211 mm-thick Hoya U-340 filter was placed between the aliquots and the PMT to measure the UV range
212 emission. The Single Aliquot Regeneration (SAR) protocol (Murray and Wintle, 2000) was applied on
213 multigrain aliquots to estimate the equivalent Dose (D_e), considering the Central Age Model (Galbraith
214 et al., 1999) to date each sample. Frequency histograms of D_e of samples HAY-07, 09, 10 and 11 are
215 included in Supplementary Data (Figure S3). Sample HAY-08 is not included because of its low reliability
216 (only 4 aliquots) but its age is consistent with other OSL datings. Preheat tests were previously
217 performed and dose recovery tests used on bleached aliquots (Murray and Wintle, 2003).

218 The activity concentration of radioisotopes (^{40}K , and ^{238}U , ^{235}U and ^{232}Th decay chains) was estimated
219 using low background gamma-ray spectrometry. Measurements of calcined and grinded sediments
220 were performed in a coaxial Canberra XTRA gamma detector (Ge Intrinsic) model GR6022 within a 10
221 cm-thick lead shield. The alpha dose-rate was neglected due to the HF etching step, and the beta dose-
222 rate corrected (Brennan, 2003). The cosmic dose-rate was estimated following Prescott and Hutton
223 (1994) and using the conversion factors proposed by Guerin et al. (2011). Resultant OSL ages are
224 expressed in years before present (BP) with their corresponding 2σ uncertainty.

225 **3.6 Radiocarbon dating**

226 Two samples from macromammal bones were sampled for radiocarbon dating through accelerator mass
227 spectrometry (AMS). Radiocarbon measurements (reference order 13274/18) were performed at the
228 Poznan Radiocarbon Laboratory, Poland. The obtained ages were calibrated using the software OxCal
229 v.4.3.2 (Bronk Ramsey, 2017) against the INTCAL 13 curve (Reimer et al., 2013), considering the 2σ
230 standard deviation (95.4% probability). The calibrations are included in Supplementary Data (Figure S4)
231 and calibrated dates are expressed in cal ka BP.

232 **4. RESULTS**

233 **4.1 Paleo-glacier reconstruction**

234 Glaciers formed an ice field in the surroundings of Covadonga Lakes during the local GM, occupying a
235 total surface extent of 36.18 km² and covering the entrance of Hayéu l'Osu Cave (Figure 3). Glacier
236 tongues reached total lengths of ca. 2 km along the valleys of Ordiales, Hunhumia, and Pomperi; up to
237 9.5 km along El Brial-Vega de Enol valleys; 5.9 km along Ercina valley; and 6.6 km along the former
238 Belbín glacier. Glacier fronts were placed at ca. 1040 m altitude in the Ordiales, Hunhumia and Ercina
239 valleys; 925–1030 m in the El Brial-Vega de Enol valleys; and 810 m in Belbín (Figure 3). Glacier
240 maximum thickness reached up to 105-220 m along the El Brial-Vega de Enol valleys, 170 m along
241 the Belbín flow line, 170 m along Ercina valley, and between ca. 114 and 168 m along the valleys
242 Ordiales, Hunhumia, and Pomperi. The steady-state ELA was most likely set at 1524 ± 36 m (Figure 3).

243 **4.2 Cave geomorphology**

244 The Hayéu l'Osu Cave is mainly formed by a 1.6 km-long conduit (named Stream Gallery) slightly tilted
245 towards the SE, and by vertical conduits summing up to 135 m in depth (Figure 4A). Vertical conduits
246 connect the Stream Gallery and the topographic surface as shown in the cave longitudinal profile (Figure
247 4B). Geomorphological evidence includes alluvial deposits, breakdown deposits, speleothems and
248 slackwater deposits. Alluvial sediments up to 3 m thick are present along the Stream Gallery
249 (Supplementary Data, Figure S2), involving active channel and terrace deposits. Active channel deposits
250 are located along the cave stream (Figure 4C) and resulted from the erosion of terrace deposits placed
251 at the bottom and walls of the NW of the study cave (Figures 4D and 5A–E). Terrace deposits are
252 perched up to 20 m above the streambed and are occasionally covered by flowstones and stalagmites
253 (Figure 4E). Active channel deposits and most terrace deposits are grain-supported and contain sub-
254 angular to rounded calcareous pebbles and cobbles, containing no matrix or with 5-20% of sandy matrix
255 (70–85% of carbonate and 15–30% of quartz). Both deposits comprise also sub-rounded allochthonous
256 pebbles and cobbles of sandstone, bauxite and diabase. In addition, alluvial sand (70–95% of carbonate
257 and 5–30% of quartz) form also minor terraces or constitute layers interbedded within the pebble and
258 cobble deposits. These sand deposits may eventually contain micromammal remains, which have been
259 identified and described in detail in section 4.3. Breakdown deposits are common along the study cave,
260 including angular calcareous boulders less than 2 m in diameter formed by rock fall processes.
261 Regarding the speleothems, they commonly appear in cave passages perched above the cave stream.
262 Flowstone up to 3 m thick and stalagmites less than 2 m height occasionally precipitated on top of
263 alluvial and breakdown deposits, however, flowstones covered by sandy terrace deposits were also

264 recognized. Finally, slackwater deposits show 0.5–3 m of laminated silt and clay (Figure 4F) deposited
265 essentially in the central part of the study cave (Figure 4A). These deposits would be related to cave
266 floods similar to what has been observed in the nearby Torca La Texa shaft (Figure 2; Ballesteros et al.,
267 2017).

268 **4.3 Paleontology of mammal bones**

269 Seven fragments of arvicoline molars and one fragment of a rodent incisor were found in samples from
270 HAY-7, 8 and 9, collected in the Stream Gallery (Figure 4A). These remains show dentine removal by
271 erosion and four of them show also rounded edges. The best-preserved fragment corresponds to a
272 complete enamel prism found in sample HAY-9. When comparing this fragment with the upper first
273 molars of extinct and living arvicolines from the Cantabrian Region (Figure 5), its size and angle in
274 occlusal view (Figure 5a') matches with the morphology of an upper first or second molar (Figure 5b'–
275 e'). The curvature of the anterior side of the triangle at the tooth's base indicates that it belongs to a
276 rooted molar (Figure 5a''), clearly different respect to ever-growing molars (Figure 5D, E and F). All
277 these mentioned morphological features and the absence of curvature at the basal part of the posterior
278 side of the prism (Figure 5a''), match with the morphology of the buccal salient angle 3 (BSA3) of the
279 first upper molar (M¹). Among the arvicolines from the Upper Pleistocene of the Iberian Peninsula, only
280 two species bear rooted molars. One of them is *P. coronensis* (Figure 5B), a very common vole in rocky
281 environments during MIS 3 and earlier before its extinction during MIS 2 in the Cantabrian Region,
282 territory that constituted the last refuge for this species before its complete disappearance (Cuenca-
283 Bescós et al., 2010). The other rooted-molar species is *C. glareolus* (Figure 5C), which currently inhabits
284 the well-developed forests of the Cantabrian Region and other Eurasian areas, but which is absent in
285 alpine environments. Considering the compared morphology and the chronological context (defined in
286 section 4.4), the enamel fragment of HAY-9 has been ascribed to the species *P. coronensis*. There is
287 another enamel fragment at HAY-7 whose morphological features at its basal part indicate it belongs to
288 a rooted molar, but no further identification can be done due to its poor preservation.

289
290 A total amount of 81 macromammal remains, all of them corresponding to small-sized bovids, were
291 recovered from two sites named Llamaeyu and Stream galleries (Figure 4). In Llamaeyu Gallery, radius,
292 metacarpals, phalanxes, skull fragments, vertebrae, ribs, one molar and other bones were found without
293 anatomic connection on top of a breakdown deposit (Figure 6A) whereas, in the Stream Gallery, a

294 scapula was located on a detrital deposit (Figure 6B). Morphology and morphometry of teeth and
295 skeletal elements are distinctive of chamois (Figure 7), so they are ascribed to *Rupicapra pyrenaica* (a
296 comprehensive discussion about the specific attribution of Upper Pleistocene chamois from the Iberian
297 Peninsula is provided by Álvarez-Lao, 2014). This fossil assemblage corresponds to a minimum of four
298 individuals (MNI): two young and two adults. The lack of anthropic activity signs excludes humans as
299 responsible for the bone accumulation. In general, no carnivore marks are detected, suggesting that the
300 bone accumulation was related to a natural trap. Only one bone shows teeth marks (Figure 7D)
301 produced by a small carnivore, most likely due to scavenging rather than predation. In addition, only one
302 bone (corresponding to one of the young individuals) shows erosion features due to transportation by
303 water (Figure 7C). From an environmental perspective, occurrence of *R. pyrenaica*, a typical alpine
304 ungulate, at Hayéu l'Osu Cave is consistent with the current rocky mountain landscape of the area.
305 Moreover, presence of a herbivore mammal in this cave clearly indicates ice-free conditions in the near
306 surroundings during the time they lived (Álvarez-Lao, 2014).

307 **4.4 Geochronology**

308 Three speleothem samples from the study cave were analyzed using U-Th dating (Table 1). Samples
309 exhibit ^{238}U content lower than 100 ppb and high initial $\delta^{234}\text{U}$ (1000-3000 ppm). Standard procedures to
310 correct the ages assume an initial $^{230}\text{Th}/^{232}\text{Th}$ atomic ratio of $4.4 \pm 2.2 \cdot 10^{-6}$ (Edwards et al., 1987; Cheng
311 et al., 2013) and the obtained ages are considered reliable.. Sample HAY-12 (263 ± 18 ka) corresponds
312 to the base of an overturned set of flowstones and stalagmites, originally precipitated on top of
313 slackwater deposits (Figure 8A). The age provided for HAY-12 represents a minimum age for the
314 slackwater deposits, which would have been decanted by cave flooding before 263 ± 18 ka, during the
315 Middle Pleistocene. Subsequently, the slackwater deposits were eroded causing the collapse of the
316 overlying flowstones and stalagmites. Similarly, samples HAY-06 (132 ± 1 ka) and HAY-13 (135 ± 7 ka)
317 have precipitated fossilizing fluvial deposits (Figure 8B and C), which were eroded later in the case of
318 HAY-06. Both datings indicate the occurrence of a first alluvial sequence older than 135-132 ka,
319 probably during MIS 6.

320 In the study cave, five alluvial deposits described in section 4.2 were dated using OSL from 84 ± 10 to
321 36 ± 3 ka (Table 2, Figure 8C-G). The estimated dose-rates were very low due to the low radioisotope
322 content, being below 1 Gy ka^{-1} for most samples. No disequilibrium is observed in the U and Th decay
323 chains. The OSL signals were dim but fast, and provided poor signal to background ratios, causing the

324 rejection of a high number of aliquots, being the number of accepted aliquots between 4 and 35. The D_e
325 distributions were non-skewed and the over dispersion (Table 2) of the mean of the Central Age Model
326 was low, showing no evidence of incomplete bleaching of the alluvial sand grains before they were
327 introduced into the cave. Thus, the Central Age Model was used for assessing the OSL ages. After
328 bleaching, the quartz was for a short period on the topographical surface before being introduced into
329 the study cave. We consider this time to be short since the study cave is located in a hill that probably
330 acted as a by-pass area to lower zones where widespread glacial and fluvio-glacial sedimentation took
331 place (Figures 2 and 3). However, reworking processes are not totally discarded. The chronological
332 framework provided allows us to define two alluvial sequences occurring after the first alluvial sequence
333 identified by U-Th dates. According to this, a second alluvial sequence corresponds to terrace sediments
334 deposited between 84 ± 10 and 65 ± 16 ka, ranging from MIS 5c to MIS 4 (Figure 8C-F), while a third
335 sequence includes a fluvial terrace formed at 36 ± 3 ka during MIS 3a (Figure 8G).

336 The chronology of the second and third alluvial sequences provides the chronological framework of the
337 arvicolinae remains, while the radiocarbon dates represent the timing of the chamois. A fragment of
338 metatarsal from Llamaeyu Gallery has an AMS ^{14}C age of 36 ± 1 cal ka BP whilst the scapula recovered
339 in Stream Gallery provided an age of 34.5 ± 0.6 cal ka BP (Table 3).

340 **5. DISCUSSION: PALEOENVIRONMENTAL EVOLUTION**

341 Cave geomorphology and U-Th ages provide new data about the origin and evolution of the Hayéu l'Osu
342 Cave during the Middle Pleistocene (Figure 9). Flowstone ages suggest that the cave was formed prior
343 to 263 ka (Figure 9A), like most karst cavities studied in Picos de Europa (Smart, 1986; Ballesteros et
344 al., 2015, 2019). Since its origin, Hayéu l'Osu Cave has undergone inundations that would be related to
345 Middle Pleistocene glaciations, followed by speleothem precipitation at 263 ± 18 ka (MIS 8). Other
346 studies have documented coeval breccia cementation in surficial talus deposits in Puertos de Áliva (Villa
347 et al., 2013), between the Central and Eastern massifs of Picos de Europa (Figure 1C). Later, at the end
348 of MIS 6, flowstone precipitation took place in the cave at 135-132 ka, covering the first alluvial sequence
349 previously deposited. All these speleothems and detrital sediments partially filled the Hayéu l'Osu Cave,
350 as occurred in other nearby caves named Pozu Lluçia and Torca La Texa (Figure 2; Ballesteros et al.,
351 2019).

352 The paleoenvironmental evolution of the surroundings of Covadonga Lakes during MIS 5c-3 is
353 established based on the combination of geomorphological-stratigraphical and paleontological data and

354 kernel density functions (Figure 10) of U-Th, OSL and radiocarbon ages obtained in the cave. This
355 probability analysis considered also previous datings carried out in Enol lacustrine sediments by Moreno
356 et al. (2010) and in Vega de Comeya border polje by Jiménez-Sánchez et al. (2013). Four phases have
357 been distinguished (Table 4 and Figure 11) according to the probabilistic distribution of Figure 10.

358 **5.1 Phase 1 (98-60 ka; MIS 5c–4)**

359 The first phase described for the study area ranges between ca. 98 and 60 ka (Figure 11A). After glacial
360 advances recorded during MIS 5cd, dated in the Central Cantabrian Mountains at 114 ± 7 ka based on
361 *in situ* produced cosmogenic nuclide ^{10}Be (Figure 1B; Rodríguez-Rodríguez et al., 2016), a glacial
362 retreat episode occurred in the study area during MIS 5c-4. In Hayéu l'Osu Cave this episode might
363 correspond to the sedimentation of the second alluvial sequence that includes *P. coronensis*. Alluvial
364 deposits are dominated by carbonate sand and silt (section 4.2), coming from the glacial erosion of
365 Carboniferous limestone, while pebbles and cobbles of sandstone and diabase were eroded from
366 sandstone and igneous dyke outcrops located in higher areas of the Western Massif of Picos de Europa
367 (Ballesteros et al., 2017, 2019b). Thus, the Ercina glacier that flowed from the summit areas elevated
368 more than 2000 m altitude of the Western Massif (Figure 3) eroded the limestone, sandstone and
369 diabase bedrock and transported the resulting sediment load to the glacier fronts located higher than
370 1400 m altitude (Figure 11A). Sediments were probably transported by glacial meltwater to the
371 surroundings of the study cave, in a fluvioglacial environment inhabited by *P. coronensis*. The roundness
372 of sediment particles observed in the alluvial sequence (section 4.2) as well as in the enamel remains
373 discovered in the study cave (section 4.3) are both compatible with this interpretation. Finally, the
374 presence of *P. coronensis* indicates that bedrock was exposed near the cave under relatively cold
375 conditions, and hence, the glacier advance was less extensive than the local GM extent.

376 The sediments of the second alluvial sequence might have formed during MIS 5d glaciation identified
377 directly in the central Cantabrian Mountains (Figure 1B; Rodríguez-Rodríguez et al., 2016) and indirectly
378 in the nearby Torca La Texa shaft (Figure 2; Ballesteros et al., 2017). The decantation of glacial origin
379 rhythmite in this shaft (located at 1350 m elevation) at 109-95 ka suggests that the Ercina glacier front
380 was at around 1350-1400 m at the beginning of phase 1.

381 **5.2 Phase 2 (48–42 ka; MIS 3c)**

382 The second phase (Figure 11B) corresponds to the local GM advance of glaciers in the study area. The
383 Vega de Comeya border polje was occupied by a proglacial lake that was being filled by calcareous
384 alluvial deposits from the south-facing slopes of the Western Massif and siliceous alluvial sediments
385 from the north-facing slopes (Jiménez-Sánchez and Farias, 2002). OSL dating yielded a minimum age
386 of 45 ± 3 ka for the onset of glacio-lacustrine sedimentation in the border polje while organic remains
387 from a sand and gravel unit placed immediately on top yielded a radiocarbon age of 44.1 ± 0.9 cal ka
388 BP, constraining the age of the local GM (Jiménez-Sánchez et al., 2013). Similarly, the nearby Belbín
389 kame terrace deposit (Figure 2) yielded a minimum reference age of 36.5 ± 0.5 cal ka BP for the base
390 of its sequence and, hence, for the Belbín moraine deposition (Ruiz-Fernández et al., 2016). The
391 reconstruction of the local GM extent (section 4.1) suggests that glaciers were less extensive compared
392 to previous reconstructions proposed by Gale and Hoare (1997), but it is in agreement with those
393 developed in Alonso (1998), Serrano et al. (2017), and Ruiz-Fernández et al. (2016). The reconstruction
394 also indicates that glacier fronts descended down to -1040 – 810 m asl, covering the calcareous bedrock
395 where the Hayéu l'Osu Cave develops (Figure 11B), which was located below the estimated ELA (1524
396 ± 36 m). The altitude of the steady-state ELA in our work is consistent with previous regional ELA
397 reconstructions made by Santos-González et al. (2013), but ca. 100 m lower than the mean ELA
398 estimated in Serrano et al. (2017).

399 **5.3 Phase 3 (42-38 ka; MIS 3b)**

400 Phase 3 represents the onset of glacier retreat in the surroundings of Covadonga Lakes (Jiménez-
401 Sánchez and Farias, 2002). Glacier retreat was recorded by proglacial lacustrine sedimentation at Enol
402 Lake at 38 ± 2 cal ka BP, exposing the glacial depression now occupied by Enol Lake but with the glacial
403 front still located close to the lake and supplying ablation water and coarse inorganic sediments (Moreno
404 et al., 2010). During this phase (Figure 11C), the evolution of the Ercina glacier front would have been
405 consistent with that of El Brial-Vega de Enol glacier recording a new episode of detrital sediment infill
406 at 39 ± 3 ka. Hence, the Ercina glacier was likely shorter at ca. 38 ka than previously assumed (Moreno
407 et al., 2010). Glacier retreat prior to 36–39 ka has also been reported in Puertos de Áliva, a site located
408 between the Central and Eastern massifs (Figure 1C; Serrano et al., 2012).

409 **5.4 Phase 4 (37–33 ka; MIS 3a)**

410 Glaciers continued receding during phase 4 (Figure 11D). The Ercina glacier front had already ascended
411 well above 1400 m by 37 ka, while the third alluvial sequence was being deposited within the Hayéu
412 l'Osu Cave. The third detrital sequence is thinner and less extensive than the second detrital sequence,
413 suggesting that the volume of surface sediment was higher during MIS 5d glaciation than during the
414 local GM of MIS 3c. MIS 5d glaciation occurred after the Eemian interglacial substage, when weathering
415 processes would have been more intense than over MIS 4. Besides, the third alluvial sequence
416 deposited at 36 ± 3 ka within the study cave also involved micromammal remains. Consequently, this
417 sequence should come from fluvio-glacial sediments sourcing from the retreating glacier fronts similar
418 to the interpretation for the second alluvial sequence (section 5.1) even if minor reworking processes
419 would take place.

420 Subsequently, at least three chamois accidentally fell inside the cave. The current position of these
421 remains at 50 and 100 m depth (from the topographic surface) and the absence of evidence produced
422 by carnivores, scavengers or humans support the role of the cave as a natural trap. Only one bone
423 shows minor bite marks caused by a small carnivore (e.g. weasel, beech marten). In the Llamaeyu
424 Gallery, bone remains most likely arrived by gravity processes and minor water transport, as the fauna
425 assemblage is not in anatomic connection and is related to a breakdown deposit (section 4.2). In the
426 Stream Gallery, the chamois bone is located in a subhorizontal conduit and have been transported by
427 an underground stream after its accidental fall in the cave. The lack of transport marks recognized in
428 the bone suggests that it may have arrived protected by the soft parts of the animal.

429 The existence of chamois bones points to the presence of an alpine environment with exposure of rocky
430 areas developed under relatively cold climate at 37–33 ka. This time range coincides with a relative cold
431 period according to the NGRIP $\delta^{18}\text{O}$ ice core record (Figure 12; NGRIP, 2004). Nevertheless, at a
432 regional scale, the presence of chamois is coeval with a period of less cold conditions marked by an
433 increase in organic matter and coarse sediments in the paleolake of Puertos de Áliva (1400 m altitude)
434 between 36 and 32 ka (Serrano et al., 2012). In lower areas, the pollen record of El Esquilleu Cave
435 (Figure 1C; 350 m asl) revealed the occurrence of *Pinus* forest with minor deciduous and evergreen
436 oaks, but also heathland shrubs in the SW of Picos de Europa at around 38–34 ka (Uzquiano et al.,
437 2016) that would have been part of the chamois diet.

438 During the late MIS 3, chamois constituted one of the main food sources of the Mousterian–Aurignacian
439 humans who lived in areas below 400 m elevation in the Cantabrian Mountains (Yravedra and Cobo-

440 Sánchez et al., 2015). Around Picos de Europa, archeological excavations discovered abundant
441 remains of hunted chamois in Sopeña (Pinto-Llona et al., 2012), El Esquilleu (Uzquiano et al., 2012;
442 Yravedra et al., 2014), La Güelga (Menéndez et al., 2018) and other cavities suggesting that the hunting
443 zones were located in lower areas (Figure 1C). However, the chamois remains found in Hayéu l'Osu
444 Cave indicate that the populations of this caprine could also have occupied areas of Picos de Europa
445 up to, at least, 1400 m elevation, during 37–33 ka.

446 6. CONCLUSIONS

447 We propose a new paleoenvironmental evolution model during MIS 5c–3 for Picos de Europa based on
448 a multidisciplinary work combining glacial and cave geomorphology, Quaternary paleontology and
449 geochronology on a glaciokarst area. The study of sediment records in Hayéu l'Osu Cave have allowed
450 us to constrain the timing of glacier retreat, and thus complement previous reconstructions on paleo-
451 glacier evolution in Picos de Europa. In addition, mammal remains preserved in caves are exceptional
452 indicators of glacial ice-free areas in the past, pointing out to a paleoenvironment developed over
453 successive pulses of the glacial evolution.

454 Three alluvial stratigraphic sequences have been identified in Hayéu l'Osu Cave. The first sequence
455 was deposited before 135–131 ka (MIS 6), while the second and third sequence, with micromammal
456 remains, were sedimented at 98–60 ka and ca. 36 ka respectively. Additionally, chamois remains (37–
457 33 ka) were found on top of the third sequence. This stratigraphic record suggests the development of
458 alpine ice-free areas at ca. 1400 m altitude during 98–60 ka (MIS 5c–4), when glaciers were probably
459 located at higher altitudes. Later, glaciers with a length of 9.5 km and up to 100–220 m in thickness,
460 descended down to 810–1030 m elevation during the local GM stage, establishing a proglacial lake
461 environment in the Comeya border polje at 48–42 ka (MIS 3c). Over this period, the study cave was
462 located in the glacial ablation zone and covered by glaciers. A general trend of glacier retreat occurred
463 from 42–38 ka, with the glacial fronts located above 1400 m altitude at 37–33 ka. In this setting, chamois
464 inhabited the ice-free rocky steep slopes of Picos de Europa, in agreement with a slight increase in local
465 temperature.

466 In addition, the distribution of species in the Cantabrian Region provides further insights on the
467 paleoenvironmental evolution of the study area. Remains of *P. coronensis* allow us to extend its altitudinal
468 distribution up to ca. 1400 m in the Cantabrian Region during MIS 4, whereas the chamois bone
469 assemblage of Hayéu l'Osu Cave constitutes the oldest evidence of *R. pyrenaica* above 1000 m altitude

470 of the Cantabrian Region. Chamois inhabited the highlands of Picos de Europa at 37-33 ka coevally
471 with human occupation in lower areas, who broadly hunted chamois. However, our outcomes suggest
472 that the studied chamois remains fell accidentally in Hayéu l'Osu Cave, being accumulated in the
473 stratigraphic record by natural processes without any human contribution.

474 **AUTHOR CONTRIBUTION**

475 DB, LRR and MJS conducted the research. MMD and LRR elaborated the paleo-glacier reconstruction.
476 DB performed the cave geomorphology and collected all samples in cooperation with PV, IDF and the
477 speleological team. AAV found and identified rodent remains under the guidance of CL, whilst DAL
478 studied the macromammal assemblages. JS carried out the OSL datings, and CPM obtained the U-Th
479 ages under the direction of HC. DB, LRR, DAL, AAV, IDF, PV and CPM wrote the article and designed
480 the figures. All authors have contributed to the discussion.

481 **ACKNOWLEDGEMENTS**

482 This work was funded by the Geocancosta FC-GRUPIN6IDI/2018/000184 project (FICIY, Gobierno del
483 Principado de Asturias and European Union) and FUO-300-17 project (Consortio Interautonómico del
484 Parque Nacional de los Picos de Europa), receiving the grateful assistance of the National Park staff
485 and the speleologists from Grupo Espeleológico Polifemo (Oviedo), GES Montañeiros Celtas (Vigo),
486 Grupo de Espeleología Diañu Burlón (Corvera de Asturias), and Espéleo Club Aradelas (Vigo). LRR is
487 grant holder of the post-doctoral Clarín-COFUND Program, financed jointly by the 7th WP of the
488 European Union–Marie Curie Actions and Gobierno del Principado de Asturias (Reference ACA-17-19).
489 We appreciate the work of Jo de Waele, Rafael López-Martínez and other reviewers.

490 **REFERENCES**

- 491 Adamson, K.R., Woodward, J.C., Hughes, P.D. 2014. Glaciers and rivers: Pleistocene uncoupling in a
492 Mediterranean mountain karst. *Quaternary Science Reviews*, 94, 28–43.
- 493 Alonso, V. 1998. Covadonga National Park (Western Massif of Picos de Europa, NW Spain): a
494 calcareous deglaciated area. *Trabajos de Geología* 20, 167–181.
- 495 Álvarez-Lao, D.J. 2014. The Jou Puerta Cave (Asturias, NW Spain): a MIS 3 large mammal assemblage
496 with mixture of cold and temperate elements. *Palaeogeography, Palaeoclimatology,*
497 *Palaeoecology* 393, 1–19.
- 498 Audra, P., Quinif, Y., Rochette, P. 2002. The genesis of Tennengerbirge karst and caves (Salzburg,
499 Austria). *Journal of Cave and Karst Studies* 64, 153–164.

500 Audra, P., Bini, A., Gabrovšek, F., Häuselmann, P., Hobléa, F., Jeannin, P.Y., Kunaver, J., Monbaron,
501 M., Šušteršič, F., Tognini, P., Trimmel, H., Wildberger, A. 2006. Cave genesis in the Alps
502 between the Miocene and today: a review. *Zeitschrift für Geomorphologie* 50, 153–176.

503 Ballesteros, D., Jiménez-Sánchez, M., Giralt, S., García-Sanseguno, J., Meléndez-Asensio, M. 2015.
504 A multi-method approach for speleogenetic research on alpine karst caves. Torca La Texa shaft,
505 Picos de Europa (Spain). *Geomorphology* 247, 35–54.

506 Ballesteros, D., Jiménez-Sánchez, M., Giralt, S., DeFelipe, I., García-Sanseguno, J. 2017. Glacial
507 origin for cave rhythmite during MIS 5d–c in a glaciokarst landscape, Picos de Europa (Spain).
508 *Geomorphology* 286, 68–77.

509 Ballesteros, D., Fernández-Martínez, E., Carcavilla, L., Jiménez-Sánchez, M. 2019a. Karst Cave
510 Geoheritage in Protected Areas: Characterisation and Proposals of Management of Deep
511 Caves in the Picos de Europa National Park (Spain). *Geoheritage* 11(4), 1919-1939..

512 Ballesteros, D., Giralt, S., García-Sanseguno, J., Jiménez-Sánchez, M. 2019b. Quaternary regional
513 evolution based on karst cave geomorphology in Picos de Europa (Atlantic Margin of the Iberian
514 Peninsula). *Geomorphology* 336, 133–151.

515 Benn, D.I., Hulton, N.R.J. 2010. An Excel™ spreadsheet program for reconstructing the surface profile
516 of former mountain glaciers and ice caps. *Computers & Geosciences* 36, 605–610.

517 Bočić, N., Faivre, S., Kovačić, M., Horvatinčić, N. 2012. Cave development under the influence of
518 Pleistocene glaciation in the Dinarides – an example from Štirovača Ice Cave (Velebit Mt.,
519 Croatia). *Zeitschrift für Geomorphologie*, 56, 409–433.

520 Bronk Ramsey, C. 2017. Methods for Summarizing Radiocarbon Datasets. *Radiocarbon* 59, 1-25.

521 Brennan, B.J. 2003. Beta doses to spherical grains. *Radiation Measurements* 3, 299–303.

522 Cheng, H., Edwards, L. R., Shen, C.-C., Polyak, V.J., Asmerom, Y., Woodhead, J., Hellstrom, J., Wang,
523 Y., Kong, X., Spötl, C., Wang, X., Alexander, E. C. 2013. Improvements in ^{230}Th dating, ^{230}Th
524 and ^{234}U half-life values, and U-Th isotopic measurements by multi-collector inductively coupled
525 plasma mass spectrometry. *Earth and Planetary Science Letters*, 371-372, 82-91.

526 Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E, Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler,
527 S.W., McCabe, A.M. *Science* 7, 710-714.

528 Colhoun, E.A., Kiernan, K., Barrows, T.T., Goede, A. 2010. Advances in Quaternary studies in
529 Tasmania. *Special Publications*, 346. Geological Society of London. Londres. 165–183.

530 Cuenca-Bescós, G., Straus, L. G., García-Pimienta, J. C., González Morales, M.R., López-García, J.M.
531 2010. Late Quaternary small mammal turnover in the Cantabrian Region: The extinction of
532 *Pliomys lenki* (Rodentia, Mammalia). *Quaternary International* 212, 129–136.

533 Edwards, R.L., Chen, J.H., Wasserburg, G.J. 1987. ^{238}U , ^{234}U , ^{230}Th , ^{232}Th systematics and the precise
534 measurement of time over the past 500,000 years. *Earth and Planetary Science Letters*, 81,
535 175–192.

536 Fernández-Gibert, E., Calaforra, J.M., Rossi, C. 2000. Speleogenesis in the Picos de Europa Massif,
537 Northern Spain, in: Klimchouk, A., Ford, D., Palmer, A., Dreybrodt, W. (Eds.), *Speleogenesis:
538 Evolution of Karst Aquifers*, National Speleological Society, Huntsville, Alabama, pp. 352–357.

539 Ford, D.C. 1971. Characteristics of Limestone Solution in the Southern Rocky Mountains and Sle Kirk
540 Mountains, Alberta and British Columbia. *Canadian Journal of Earth Sciences* 8, 585–609.

541 Ford, D.C. 1979. A review of alpine karst in the southern Rocky Mountains of Canada. *National*
542 *Speleological Society Bulletin* 41, 53–65.

543 Galbraith, R.F., Roberts, R.G., Laslett, G.M., Yoshida, H., Olley, J.M. 1999. Optical dating of single and
544 multiple grains of quartz from Jinmium Rock Shelter, Northern Australia: Part 1, Experimental
545 design and statistical models. *Archaeometry* 41, 339–364.

546 Gale, S.J., Hoare, P.G. 1997. The glacial history of the northwest Picos de Europa of northern Spain.
547 *Zeitschrift für Geomorphologie* 41, 81–96.

548 Glover, R. R. 1977. A conceptual model of cave development in a glaciated region. *Proceedings of 7th*
549 *International Speleological Congress. International Union of Speleology, Sheffield*, pp. 220–221.

550 Guerin, G., Mercier, N., Adamiec, G. 2011. Dose-rate conversion factors: update. *Ancient TL* 29, 5–8.

551 Häuselmann, P. 2013. Large epigenic caves in high-relief areas. In: Shroder, J., Frumkin, A. (Eds.)
552 *Treatise on Geomorphology, Vol 6, Karst Geomorphology. Academic Press, San Diego*, 207–
553 219.

554 Häuselmann, P., Granger, D.E., Jeannin, P.Y., Lauritzen, S.E. 2007. Abrupt glacial valley incision at 0.8
555 Ma dated from cave deposits in Switzerland. *Geology* 35, 143–146.

556 Isola, I., Ribolini, A., Zanchetta, G., Bini, M., Regattieri, E., Drysdale, R. N., Hellstrom, J.C., Bajo, P.,
557 Montagna, P., Pons-Branchu, E. 2019. Speleothem U/Th age constraints for the Last Glacial
558 conditions in the Apuan Alps, northwestern Italy. *Palaeogeography, Palaeoclimatology,*
559 *Palaeoecology* 518, 62–71.

560 Jiménez-Sánchez, M., Farias, P. 2002. New radiometric and geomorphologic evidences of a last glacial
561 maximum older than 18 ka in SW European mountains: the example of Redes Natural Park
562 (Cantabrian Mountains, NW Spain). *Geodinamica Acta* 15, 93–101.

563 Jiménez-Sánchez, M., Rodríguez-Rodríguez, L., García-Ruiz, J.M., Domínguez-Cuesta, M.J., Farias,
564 P., Valero-Garcés, B., Moreno, A., Rico, M., Valcárcel, M. 2013. A review of glacial
565 geomorphology and chronology in northern Spain: Timing and regional variability during the last
566 glacial cycle. *Geomorphology* 196, 50–64.

567 Lechleitner, F.A., Amirnezhad-Mozhdehi, S., Columbu, A., Comas-Bru, L., Labuhn, I., Pérez-Mejías, P.,
568 Rehfeld, K. 2018. The Potential of Speleothems from Western Europe as Recorders of Regional
569 Climate: A Critical Assessment of the SISAL Database. *Quaternary* 1 (3), 30.

570 Menéndez, M., Álvarez-Alonso, D., Andrés-Herrero, M. de, Carral, P., García-Sánchez, E., Jordá-Pardo,
571 J.F., Quesada, J.M., Rojo, J. 2018. The Middle to Upper Paleolithic transition in La Güelga cave
572 (Asturias, Northern Spain). *Quaternary International* 474, 71–84.

573 Merino-Tomé, O., Suárez Rodríguez, A., Alonso, J., González Menéndez, L., Heredia, N., Marcos, A.
574 2013. Mapa Geológico Digital continuo E. 1:50.000, Principado de Asturias (Zonas: 1100–
575 1000–1600) [WWW Document]. GEODE. Mapa Geológico Digital Continuo de España.
576 SIGECO-IGME. URL <http://cuarzo.igme.es/sigeco/default.htm>

577 Moreno, A., Valero-Garcés, B.L., Jiménez-Sánchez, M., Domínguez-Cuesta, M.J., Mata, M., Navas, A.,
578 González-Sampériz, P., Stoll, H., Farias, P., Morello, M., Corella, J., Rico, M. 2010. The last

579 deglaciation in the Picos de Europa National Park (Cantabrian Mountains). *Journal of*
580 *Quaternary Sciences* 25, 1076–1091.

581 Murray, A.S., Wintle, A.G. 2000. Luminescence dating of quartz using an improved single-aliquot
582 regenerative-dose protocol. *Radiation Measurements* 32, 57–73.

583 Murray, A.S., Wintle, A.G. 2003. The single aliquot regenerative dose protocol: Potential for
584 improvements in reliability. *Radiation Measurements* 37, 377–381.

585 Mylroie, J.E. 1984. Pleistocene climatic variation and cave development: *Norsk Geografisk Tidsskrift*
586 38, 151–156.

587 Mylroie, J.E., Mylroie, J.R. 2004. Glaciated karst: how the Helderberg plateau revised the geological
588 perception. *Northeastern Geology and Environmental Sciences* 26, 82–92.

589 Nieuwendam, A., Ruiz-Fernández, J., Oliva, M., Lopez, V., Cruces, A., Freitas, M. da C. 2015.
590 Postglacial landscape changes and cryogenic processes in Picos de Europa (northern Spain)
591 reconstructed from geomorphological mapping and microstructures on quartz grains.
592 *Permafrost and Periglacial Processes* 27, 96–108.

593 NGRIP members 2004. High-resolution record of Northern Hemisphere climate extending into the last
594 interglacial period. *Nature* 431, 147–151.

595 Osmaston H. 2005. Estimates of glacier equilibrium line altitudes by the Area×Altitude, the Area×Altitude
596 Balance Ratio and the Area×Altitude Balance Index methods and their validation. *Quaternary*
597 *International* 138–139, 22–31.

598 Pellitero, R., Rea, B.R., Spagnolo, M., Bakke, J., Ivy-Ochs, S., Lukas, S., Ribolini, A. 2015. A GIS tool
599 for automatic calculation of glacier equilibrium-line altitudes. *Computers & Geosciences* 82, 55–
600 62.

601 Pellitero, R., Rea, B.R., Spagnolo, M., Bakke, J., Ivy-Ochs, S., Frew, C.R., Hughes, P., Ribolini, A.,
602 Lukas, S., Renssen, H. 2016. GlaRe, a GIS tool to reconstruct the 3D surface of palaeoglaciers.
603 *Computers & Geoscience* 94, 77–85.

604 Pinto-Llona, A.C., Clark, G., Karkanias, P., Blackwell, B., Skinner, A.R., Andrews, P., Reed, K., Miller,
605 A., Macías-Rosado, R., Vakiparta, J. 2012. The Sopenña Rockshelter, a New Site in Asturias
606 (Spain) bearing evidence on the Middle and Early Upper Palaeolithic in Northern Iberia. *Munibe*
607 *(Antropología-Arkeología)* 63, 45–79.

608 Plan, L., Filipponi, M., Behm, M., Seebacher, R., Jeutter, P., 2009. Constraints on alpine speleogenesis
609 from cave morphology — A case study from the eastern Totes Gebirge (Northern Calcareous
610 Alps, Austria). *Geomorphology* 106, 118–129.

611 Prescott, J.R., Hutton, J.T. 1994 Cosmic ray contributions to dose rates for luminescence and ESR
612 dating: large depths and long term variations. *Radiation Measurements* 23, 497–500.

613 Railsback, L.B., Gibbard, P.L., Head, M.J., Voarintsoa, N.R.G., Toucanne, S. 2015. An optimized
614 scheme of lettered marine isotope substages for the last 1.0 million years, and the
615 climatostratigraphic nature of isotope stages and substages. *Quaternary Science Reviews* 111,
616 94–106.

617 Rea, B.R. 2009. Defining modern day Area-Altitude Balance Ratios (AABRs) and their use in glacier-
618 climate reconstructions. *Quaternary Science Review* 28, 237–248.

619 Reimer, P., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P., Ramsey, C.B., Buck, C., Cheng, H.,
620 Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hafliðason, H., Hajdas, I., Hatt_e,
621 C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K., Kaiser, K.F., Kromer, B., Manning,
622 S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J., Staff, R.A., Turney,
623 C.S.M., Van der Plicht, J. 2013. Intcal13 and Marine13 radiocarbon age calibration curves 0–
624 50,000 years cal BP. *Radiocarbon* 55, 1869–1887.

625 Rodríguez-Rodríguez, L., Jiménez-Sánchez, M., Domínguez-Cuesta, M.J., Aranburu, A. 2014.
626 Research history on glacial geomorphology and geochronology of the Cantabrian Mountains,
627 north Iberia (43–42°N/7–2°W). *Quaternary International* 364, 6–21.

628 Rodríguez-Rodríguez, L., Jiménez-Sánchez, M., Domínguez-Cuesta, M.J., Rinterknecht, V., Pallàs, R.,
629 Bourlès, D. 2016. Chronology of glaciations in the Cantabrian Mountains (NW Iberia) during the
630 Last Glacial Cycle based on in situ-produced ¹⁰Be. *Quaternary Science Reviews* 138, 31–48.

631 Ruiz-Fernández, J., Oliva, M., Cruces, A., Lopes, V., Freitas, M. da C., Andrade, C., García-Hernández,
632 C., López-Sáez, J.A., Gerales, M. 2016. Environmental evolution in the Picos de Europa
633 (Cantabrian Mountains, SW Europe) since the Last Glaciation. *Quaternary Science Reviews*
634 138, 87–104.

635 Santos-González, J., Redondo-Vega, J.M., González-Gutiérrez, R.B., Gómez-Villar, A. 2013. Applying
636 the AABR method to reconstruct equilibrium-line altitudes from the last glacial maximum in the
637 Cantabrian Mountains (SW Europe). *Palaeogeography, Palaeoclimatology, Palaeoecology* 387,
638 185–199.

639 Serrano, E., González-Trueba, J.J., González-García, M. 2012. Mountain glaciation and paleoclimate
640 reconstruction in the Picos de Europa (Iberian Peninsula, SW Europe). *Quaternary Research*
641 78, 303–314.

642 Serrano, E., González-Trueba, J.J., Pellitero, R., Gomez-Lende, M. 2017. Quaternary glacial history of
643 the Cantabrian Mountains of northern Spain: a new synthesis, in: Hughes, P.D., Woodward,
644 J.C. (Eds.), *Special Publications*, 433: *Quaternary Glaciation in the Mediterranean Mountains*,
645 Geological Society of London, London, pp. 55–85.

646 Skoglund, R.Ø., Lauritzen, S.E., Gabrovšek, F. 2010. The impact of glacier ice-contact and subglacial
647 hydrochemistry on evolution of maze caves: A modelling approach. *Journal of Hydrology* 388,
648 157–172.

649 Smart, P.L. 1986. Origin and development of glacio-karst closed depressions in the Picos de Europa,
650 Spain. *Zeitschrift für Geomorphologie* 30, 423–443.

651 Stuiver, M., Reimer, P.J. 1993. Extended ¹⁴C data base and revised CALIB 3.0 ¹⁴C age calibration
652 program. *Radiocarbon* 35, 215–230.

653 Telbisz, T., Tóth, G., Ruban, D.A., Gutak, J.M. 2019. Notable glaciokarst of the World. In: Veress, M.
654 Telbisz, T., Tóth, G., Lózy, D., Ruban, D.A., Gutak, J.M. (Eds), *Glaciokarst*. Springer, Cham,
655 373–499.

656 Tîrlă, L., Drăgușin, V., Bajo, P., Covaliov, S., Cruceru, N., Ersek, V., Hanganu, D., Hellstrom, J.,
657 Hoffmann, D., Mirea, I., Sava, T., Sava, G., Șandric, I. In press. Quaternary environmental

658 evolution in the South Carpathians reconstructed from glaciokarst geomorphology and
659 sedimentary archives. *Geomorphology*, 354: 107038.

660 Uzquiano, P., Yravedra, J., Ruiz Zapata, B., Gil García, M.J., Sesé, C., Baena, J. 2012. Human
661 behaviour and adaptations to MIS 3 environmental trends (>53–30 ka BP) at Esquilleu cave
662 (Cantabria, northern Spain). *Quaternary International* 252, 82–89.

663 Uzquiano, P., Ruiz-Zapata, M.B., Gil-García, M.J., Fernández, S., Carrion, J.S. 2016. Late Quaternary
664 developments of Mediterranean oaks in the Atlantic domain of the Iberian Peninsula: The case
665 of the Cantabrian region (N Spain). *Quaternary Science Reviews* 153, 63–77.

666 Villa, E., Stoll, H., Farias, P., Adrados, L., Edwards, R.L., Cheng, H. 2013. Age and significance of the
667 Quaternary cemented deposits of the Duje Valley (Picos de Europa, Northern Spain),
668 *Quaternary Research* 79, 1-5.

669 Weremeichik, J., Mylroie, J. 2014. Glacial Lake Schoharie: an investigative study of glaciolacustrine
670 lithofacies in caves, Helderberg Plateau, Central New York. *Journal of Cave and Karst Studies*
671 76, 127–138.

672 Yravedra, J., Gómez-Castanedo, A., Aramendi Picado, J., Baena Preysler, J. 2014. Specialised hunting
673 of Iberian ibex during Neanderthal occupation at El Esquilleu Cave, northern Spain. *Antiquity*
674 88, 1035–1049.

675 Yravedra, J., Cobo-Sánchez, L. 2015. Neanderthal exploitation of ibex and chamois in southwestern
676 Europe. *Journal of Human Evolution* 78, 12–32.

677 **FIGURE CAPTIONS**

678 Figure 1. (A) Map of the SW of Europe with the location of Picos de Europa (northern Spain). (B) DEM
679 of the N of Spain including the local Maximum Ice Extent (local MIE) recorded by former glaciers in the
680 Cantabrian Mountains (Rodríguez-Rodríguez et al., 2014). (C) DEM of the three massifs of Picos de
681 Europa with the position of the study cave (named Hayéu l'Osu) in the surroundings of Covadonga
682 Lakes (Enol and Ercina lakes), within the NW massif. Local glacial maximum (Local GM) extent
683 according to Alonso (1998), Serrano et al. (2012, 2017) and Rodríguez-Rodríguez et al. (2014).
684 Documented cave data is courtesy of the speleological groups reported in Ballesteros et al. (2019a).

685 Figure 2. Main geomorphological features of the study area (which position is shown in Figure 1)
686 projected on the hillshade digital model. Geomorphology is after Ballesteros et al. (2015, 2017, 2019b),
687 who studied the Pozu Lluvia and Torca La Texa shafts.

688 Figure 3. (A) Aerial photo of the Spanish PNOA 2017 Program projected on a digital elevation model of
689 the Western Massif of Picos de Europa (www.cnig.es; last accessed on May 2019); the star marks the
690 location of Hayéu l'Osu Cave. (B) Topographic restitution of glaciers for the local GM stage, showing
691 the location of the Equilibrium Line Altitude (ELA) and the main ice flow pathways: 1- Ordiales, 2-
692 Hunhumia, 3-Pomperi, 4-El Brial (4'-Vega de Enol), 5-Ercina, and 6-Belbín.

693 Figure 4. (A) Geomorphological map of Hayéu l'Osu Cave showing the location of the paleontological
694 sites, the position of dating samples and pictures shown in C, D, E and F. (B) Cave longitudinal profile
695 (P indicates the depth of each shaft in meters, from its top to bottom). (C) Vadose canyon of Stream
696 Gallery showing active channel deposits. (D) Camp Chamber dominated by fluvial terrace deposits. (E)
697 Vadose canyon of Stream Gallery showing fluvial terrace deposits cemented by flowstone and perched
698 above the active channel. (F) Slackwater deposits from the central part of the cavity.

699 Figure 5. Comparison of the enamel fragment from the Stream Gallery of the Hayéu l'Osu Cave (Figure
700 4A) with the upper first molars of some extinct and living arvicolines from the Cantabrian Region.
701 Squares in occlusal view (a'–f') are highlighting the buccal salient angle 3 (BSA3). Squares in buccal
702 view (a''–f'') are highlighting the morphology at the base of the BSA3. (A) Enamel fragment found in
703 HAY–9 sample from the study cave. (B) Rooted molars of *Pliomys coronensis* from La Güelga Cave
704 (Figure 1C). (C) Rooted molar of *Clethrionomys glareolus*. Evergrowing molars of: (D) *Arvicola*
705 *monticola*, (E) *Microtus lavernedii*, and (F) *Microtus lusitanicus*.

706 Figure 6. Chamois (*Rupicapra pyrenaica*) sites from Hayéu l'Osu Cave: (A) Debris deposit with bone
707 remains (Figure 7A and C-K) in the Llamaeyu Gallery (Figure 4). (B) Location of a scapula (Figure 7B)
708 placed on alluvial deposits of the Stream Gallery (Figure 4).

709 Figure 7. Chamois (*Rupicapra pyrenaica*) dental and postcranial remains from Hayéu l'Osu Cave. (A)
710 Left M³ in labial view. (B) Young left scapula in lateral view. (C) Fragment of limb bone diaphysis showing
711 erosion due to transportation by water. (D) Young left radius diaphysis in anterior view showing teeth
712 marks (indicated by white arrows) produced by a small carnivore. (E) Adult right metacarpal in anterior
713 view. (F) Young left metacarpal in anterior view. (G) Adult proximal phalanx in anterior view. (H) Adult
714 middle phalanx in anterior view. (I) Adult distal phalanx in lateral view. (J) Adult right calcaneus in anterior
715 view. (K) Adult right talus in anterior view. Scale bars are in cm.

716 Figure 8. Selected sites of Hayéu l'Osu Cave for U-Th and OSL dating: (A) Toppled stalagmite and
717 flowstone originally located on top of slackwater deposits which were subsequently eroded after 263 ka.
718 (B) Perched flowstone precipitated on a first alluvial sequence. (C, D) Second alluvial sequence
719 deposited on flowstone. (E) Second alluvial sequence covered by speleothems. (F) Zoom of sandy
720 layers dated through OSL. (G) Third alluvial pebble sequence with a sandy layer interbedded and dated
721 by means of OSL. Picture locations are shown in Figures 4A and 8.

722 Figure 9. Cross-section of the surroundings of Covadonga Lakes showing the position of Hayéu l'Osu
723 Cave, Enol and Ercina lakes and Vega de Comeya border polje, which sedimentary infill was previously
724 described and dated in Jiménez-Sánchez and Farias (2002). The position of the cross-section is shown
725 in Figure 2. Bedrock geology is based on Ballesteros et al. (2015). Dates performed in Hayéu l'Osu
726 Cave are detailed in Tables 1, 2 and 3.

727 Figure 10. Kernel density functions of the OSL, U-Th and radiocarbon ages obtained in the Hayéu l'Osu
728 Cave record, including previous ages from the Vega de Comeya and Enol lacustrine sediments (Moreno
729 et al., 2009; Jiménez-Sánchez et al., 2013). Flowstone precipitation ascribable to the end of MIS 6
730 fossilized the first detrital sequence identified inside the study cave. The second important episode of
731 cave sediment infill occurred between ca. 98 and 60 ka (phase 1) as glacio-fluvial sediments from a
732 previous glaciation (most likely MIS 5d glaciation) were washed into the cave. The Vega de Comeya
733 sequence indicates that the local Glacial Maximum (local GM) was attained in this area around 45 ± 3
734 ka (Jiménez-Sánchez et al., 2013), during MIS 3c (phase 2, 48–42 ka). By ~38 ka BP glaciers had
735 already retreated from the Enol Lake depression, allowing proglacial lacustrine sedimentation (Moreno
736 et al., 2010). The retreat of the Ercina glacier front is indirectly recorded in Hayéu l'Osu Cave by the
737 third sedimentary sequence (phase 3, 42–38 ka), suggesting that the Ercina glacier front had also
738 suffered considerable retreat from its previous GM position. The cave entrance and its neighboring areas
739 remained ice-free (phase 4) after ca. 37 ka until, at least, the glacier advance linked to the global LGM
740 of MIS 2 whose extent remains unknown in Picos de Europa (LGM age interval according to Clark et
741 al., 2009).

742 Figure 11. Paleoenvironmental evolution of the Covadonga Lakes surroundings during MIS 5d–3a
743 illustrated using the cross-section shown in Figure 8 (same legend; see Figure 2 for cross-section
744 location). (A) Phase 1: the study cave recorded detrital sediment input at 98–60 ka, evidencing that the
745 cave setting was an ice-free alpine environment and that eventual glacial fronts were located above
746 1400 m altitude. (B) Phase 2: glaciers attained their local GM extent at 45 ± 3 ka, causing proglacial
747 lacustrine sedimentation at Vega de Comeya (Jiménez-Sánchez et al., 2013). The Ercina glacier flowed
748 down to 1040 m asl, and La Picota moraine was formed between Ercina and Enol glaciers (Moreno et
749 al., 2010). (C) Phase 3: onset of a general trend of glacial retreat according to Jiménez-Sánchez and
750 Farias (2002). Glaciers receded from the Enol Lake depression at ca. 38 cal ka BP, while Hayéu l'Osu

751 Cave recorded detrital sedimentation since 36 ± 3 ka (HAY-7). (D) Phase 4: occurrence of ice-free
752 temperate environment inhabited by chamois populations.
753 Figure 12. AMS radiocarbon dates of chamois remains from Llamaeyu and Stream galleries of Hayéu
754 l'Osu Cave, projected over the Greenland $\delta^{18}\text{O}$ ice core record (NGRIP, 2004). MIS 3 substages
755 according to Railsback et al. (2015).