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1 The missing *Myopus*: plugging the gaps in Late Pleistocene small
2 mammal identification in western Europe with geometric
3 morphometrics

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20 **Abstract**

21 *Lemmus* and *Myopus* are two lemming species with distinct habitat requirements but which
22 show very similar dental morphologies. They are thus extremely difficult to distinguish from
23 one another in the fossil record on the basis of their dental remains, leading to poor
24 understanding of the palaeobiogeographical evolution of *Myopus* as well as inaccurate
25 paleoenvironmental reconstructions. Currently, the presence of *Myopus* in the fossil register
26 from the Pleistocene is still debated and no firm occurrence of this lemming in western Europe
27 has yet been confirmed during the Late Pleistocene. In this paper, we used geometric
28 morphometrics on modern material to establish morphological differences between *Lemmus*
29 and *Myopus* teeth (first lower and third upper molars). Morphological data was then used to
30 build a robust linear discriminant model able to confidently classify isolated teeth of these two
31 genera, and finally, linear discriminant models were used on fossil remains of *Lemmus/Myopus*
32 from two Late Pleistocene archaeological/palaeontological sites (Grotte des Gorges and Gully
33 Cave). This study demonstrates, for the first time, the presence of *Myopus schisticolor* in west
34 European Late Pleistocene sites between the end of MIS 3 and the beginning of Holocene,
35 during climatic events that favoured the development of taiga forest of birch and pine in these
36 regions.

37 **Keywords**

38 Geometric morphometrics, Lemming, Late Glacial, Paleobiogeography, Molar shape, Boreal
39 environment, Taxonomy

40 **1. Introduction**

41 Rodents are characterized by a significant taxonomic diversity associated with various
42 ecological and biological traits, thereby ensuring their widespread occurrence throughout all
43 modern biotopes. They have been intensively studied with respect to the fields of evolution,

44 biochronology and palaeoenvironmental change (e.g. Chaline and Mein, 1979; Cox and
45 Hautier, 2015; Fejfar and Heinrich, 1990; Hernandez Fernandez, 2006; van Kolfschoten, 1995;
46 Kowalski, 1995; Montuire et al., 1997; Rekovets and Kovalchuk, 2017). Their remains, well
47 preserved in many archaeological and palaeontological contexts, have therefore contributed to
48 the reconstruction of patterns of Quaternary palaeoclimatic change, still a major challenge in
49 our understanding of continental chronostratigraphies today. Among the methods applied for
50 paleoclimate reconstructions, many are based on species associations, such as the
51 presence/absence or relative abundance of species, hence the need to have accurate taxonomic
52 identifications (e.g. Gobalet 2001; Lyman, 2002, 2019; Royer et al., 2020; Stahl, 1996).

53 Numerous obstacles hinder the identification of small-bodied animals, even when their skeletal
54 remains are recovered (Stahl, 1996). One problem is that while modern zoologists have many
55 criteria by which to identify animals (e.g. fur, size, skull and post-cranial anatomy, geographical
56 range), most of these criteria cannot be applied to fossils. A second problem is that identification
57 of small mammals is based on limited types of remains, generally the teeth, which are most
58 resistant to mechanical taphonomical processes. Despite dental remains being the most
59 diagnostic elements at the genus or species levels, teeth may exhibit very similar morphologies,
60 which could potentially prevent confident identifications. The last problem also reflects the
61 differential state of diagnostic information for relevant taxa (Lyman, 2019; Stahl, 1996). Many
62 criteria have been proposed to identify these smallest-size species, but most of them rely on the
63 “holotypic” morphology (i.e. the typical form as defined by characteristic specimens of this
64 species), without taking into account geographical or inter-population variability, except to
65 point out very unusual cases. The ensuing large number of criteria proposed for species
66 identification often leads either to disagreement or to differential use of these criteria among
67 taxonomists. As said by Stahl (1996), it must always be remembered that higher level
68 taxonomic categories are necessarily dynamic and constantly open to revision.

69 Among the rodents, voles and lemmings, which show substantial tooth variability throughout
70 species, time and space, are key taxa for tracking Quaternary environmental and climatic
71 changes (e.g. Kowalski, 2001; Montuire et al., 2019; Nadachowski 1982; Royer, 2013).
72 Lemmings are reliable biomarkers of specific and typical high latitude environments (Chaline,
73 1972; Kowalski, 1995). In Eurasia, four lemming genera are found in fossil contexts: 1)
74 *Dicrostonyx* and *Lagurus*, which are regularly present during the coldest or driest phases of the
75 Late Pleistocene extending as far as the south of France (Chaline, 1972; Marquet, 1993; Royer
76 et al., 2016); 2) *Lemmus*, which is also frequently found throughout Eurasia in open and cold
77 environments, but still in modest abundance (Kowalski, 1995, 2001), and 3) *Myopus*, which
78 has so far only been attested in Russia at this time, associated with more temperate species (e.g.
79 Markova et al., 2019; Ponomarev et al., 2013a, 2013b, 2013c).

80 As *Lemmus* (Link, 1795) and *Myopus* (Miller, 1910) have two strong but divergent ecological
81 signals, their taxonomic discrimination in the fossil assemblages is essential in order to
82 investigate past faunal associations and understand their significance in paleoclimatic
83 reconstructions. The True Lemming genus (*Lemmus*) is a complex of several species which
84 have a northern distribution restricted to Arctic tundra environments associated with high
85 seasonality and little vegetation. These taxa use the thick snow covering as a shelter, giving
86 them access to the vegetation persisting under this natural shield during winter (Domine et al.,
87 2018; Reid et al., 2011; Stenseth and Ims, 1993), as well as using bogs and wetlands during
88 summer and eschewing forest as much as possible (Le Vaillant et al., 2018; Wilson et al., 2017).
89 The wood lemming (*Myopus schisticolor* [Lilljeborg, 1844]) is the only representative of its
90 genus and inhabits exclusively coniferous forest with a thick moss cover, which constitutes its
91 main food source (Bobretsov and Lukyanova, 2017; Calandra et al., 2015; Eskelinen, 2002).
92 Contrary to *Lemmus*, this taxon avoids bogs and marshes and is present throughout the taiga
93 forests from Scandinavia to the eastern coast of the Sea of Okhotsk.

94 Although *Myopus* and *Lemmus* are separated by a large phylogenetic distance (Abramson and
95 Petrova, 2018) and are easily distinguishable in their external appearance (Gromov and
96 Polyakov, 1992; Wilson et al., 2017), they express a great deal of similarity in terms of their
97 dental morphology (Borodin, 2009; Chaline et al., 1988; Koenigswald and Martin, 1984;
98 Kowalski, 1995), resulting in their fossil remains often being impossible to separate or being
99 lumped together as “*Lemmus-Myopus*” (Kowalski, 2001). This problem of differentiation has
100 therefore greatly reduced the palaeoecological utility of these taxa, which is particularly
101 problematic considering their occurrence in many Quaternary deposits. Several authors have
102 accordingly attempted to separate these two genera through morphometrical analysis of the first
103 lower molar (m1) and the third upper molar (M3) but with varying degrees of accuracy (Chaline
104 et al., 1988; Markova et al., 2018; Ponomarev et al., 2013b; Smirnov et al., 1997).

105 The present paper aims to resolve this problem by providing a robust means of differentiating
106 between the teeth of these two genera, *Lemmus* and *Myopus*. This study uses geometric
107 morphometrics, which has never been applied on these two genera, despite its efficiency in
108 identifying similar species in modern and fossil record (e.g. McGuire, 2011; Cucchi et al., 2014;
109 Hulme-Beaman et al., 2018; Stoetzel et al., 2017; Navarro et al., 2018; Kolendrianou et al.,
110 2020). Several modern populations were considered, both to establish differences in their dental
111 morphologies and to evaluate the reliability of traditional criteria previously used to separate
112 the two genera. The geometric morphometric approach is then coupled with a discriminant
113 function analysis in order to separate these two genera before being applied to European fossil
114 specimens from two Late Pleistocene sites. The outcomes of this paper consequently propose
115 not only a novel and replicable means of identifying and separating the two genera, but also
116 allow a new view of the past environments and biogeographical evolution of lemming
117 populations.

118 2. Taxonomy and Morphology

119 *Lemmus* and *Myopus* genera belong to the tribe Lemmini (Gray, 1825), which is part of the
120 Arvicolinae subfamily (Gray, 1821). The genus *Lemmus* is currently divided into four distinct
121 species (Abramson and Petrova, 2018; Wilson et al., 2017): the Nearctic North American brown
122 lemming *Lemmus trimucronatus* (Richardson, 1825) and the Palearctic Norway lemming
123 *Lemmus lemmus* (Linnaeus, 1758), Siberian lemming *Lemmus sibiricus* (Kerr, 1792) and the
124 Amur lemming *Lemmus amurensis* (Vinogradov, 1924). Originally, *Myopus* was recognized as
125 a member of the genus *Lemmus* and named as *Lemmus schisticolor* (Lilljeborg, 1844) due to
126 osteological similarities, such as the general shape of the skull (Ognev, 1948), the convergence
127 of the maxillary tooth rows and the inclination of the mandibular tooth rows (Abramson, 1993).
128 Miller (1910, 1912) separated *Myopus* from *Lemmus*, leading to the recognition of *Myopus*
129 *schisticolor*, a species characterized by a combination of *Lemmus* characters (skull and teeth)
130 and vole characters (general body-form and foot structure). Recent DNA studies clearly attest
131 to the separation of these two genera (Abramson and Petrova, 2018; Buzan et al., 2008; Cook
132 et al., 2004; Robovský et al., 2008).

133 Molars of *Lemmus* and *Myopus* are hypsodont with a flat grinding surface and have a prismatic
134 structure composed of alternate triangles and deep re-entrant angles filled with cement (fig. 1).
135 The first lower molar (m1) is constituted by a posterior loop (PL), three closed alternating
136 triangles (T1-T3), two confluent triangles (T4 and T5) and an anterior loop (AL). The third
137 upper molar (M3) shows a similar structure (fig. 1), with an anterior loop, five triangles and a
138 posterior loop (PL). For these two molars, some authors note a high variation in the outer loops
139 (anterior loop for m1, posterior loop for M3), which exhibit different stages of complexity, with
140 the development of supplementary re-entrant angles on both labial and buccal sides (e.g.
141 Markova et al., 2018; Ponomarev et al., 2013b). In general, *Lemmus* shows a higher tendency
142 to complexity (i.e. development of supplementary re-entrant angles) and *Myopus* has a simpler

143 morphology. However, due to a large overlap, these trends cannot be used to definitively
144 attribute individuals to one or the other of these genera. Based on biometrical approaches, linear
145 measurements are the most commonly used features to distinguish these two genera on isolated
146 teeth (*e.g.* Borodin, 2009; Ponomarev et al., 2013b; Roberts and Parfitt, 1999; Tiunov and
147 Panasenکو, 2011), with the following features identified as being of potential significance: 1)
148 differences in the length/width ratio of M3 (Smirnov et al., 1997), with the M3 shape in *Myopus*
149 tending to be more compact and that in *Lemmus* tending to be more elongated; 2) ratios obtained
150 from several linear measurements to characterize the global shape of the different molars
151 (Chaline et al., 1988); and 3) the size of the teeth, with a greater tooth length in *Lemmus* (Chaline
152 et al., 1988; Smirnov et al., 1997). Finally, a supplementary criterion based on cementum was
153 recently proposed by Ponomarev et al. (2013b). This last work shows that the frequency of
154 cementum deposits in the last re-entrant angles of the outer loops of both M3 and m1 (LRA3
155 and BRA4 of m1) differs between the two genera. The cementum deposits are absent in *Myopus*
156 teeth, whereas they are present in 40 to 70% of *Lemmus* individuals (Cheprakov, 2016; Markova
157 et al., 2018; Ponomarev et al., 2013).

158 **3. Materials and methods**

159 3.1. Modern specimens

160 Since the focus of this paper is the application of the geometric morphometrics method to
161 western European fossil sites, modern *Lemmus* and *Myopus* individuals were targeted from
162 Scandinavia and Russia. The modern samples are composed of research laboratory collections
163 and Snowy Owl (*Bubo scandiacus*) pellets and are housed in the research laboratory collections
164 in Biogéosciences at the University of Burgundy and in the Arctic Research Station of
165 Labytnangi in Russia. In total, 30 *Myopus* and 96 *Lemmus* m1 specimens, and 31 *Myopus* and
166 91 *Lemmus* M3 specimens were analysed (see table 1 for details). Since the *Myopus* genus is
167 monospecific, our sample was only composed of individuals of *Myopus schisticolor*. To

168 describe most of the current morphological variability of the *Lemmus* genus, our sample
169 included specimens from the three different species. Most of our sample belong to two
170 palearctic species, with 50 Norway Lemming (*L. lemmus*) and 34 western Siberian Lemming
171 (*L. sibiricus*). The two species are closely related in their phylogeny but were already separated
172 during the Late Pleistocene (Abramson and Petrova, 2018). Few individuals of eastern *L.*
173 *sibiricus* from Chukotka district were included to capture the range of potential variability of
174 the genus. Additionally, 12 m1 and 8 M3 of North American Brown Lemming (*L.*
175 *trimucronatus*) were included to clarify the distinction amongst the different representatives of
176 *Lemmus*. Numbers and origins of the specimens are detailed in table 1 and figure 2. Only well-
177 preserved and complete molars were used in the analyses; all broken and digested teeth were
178 discarded.

179 3.2. Fossil samples

180 Fossil specimens come from two archaeological/palaeontological sites from Late Pleistocene,
181 la Grotte des Gorges (France) and Gully Cave (England) (fig. 2). As for the modern material,
182 broken and digested teeth were not included in this study. All dates of la Grotte des Gorges
183 have been calibrated using IntCal13 (Reimer et al., 2013).

184 **La Grotte des Gorges** is located close to Amange village (Jura, France) and was excavated
185 between 2008 and 2017. Two layers (1a and 1b) yielded archaeological material (David et al.,
186 2014, 2017), from the end of MIS 3 with AMS dates ranging from $33,030 \pm 750$ to $29,390 \pm$
187 170 uncal. BP. The site yields a diverse association of mammalian species demonstrating a
188 transition from arctic toward steppe environment. *Lemmus/Myopus* remains come from the
189 upper part of the sequence (layer 1a), dominated by typical taxa of cold-climate phases such as
190 reindeer (*Rangifer tarandus*), mammoth (*Mammuthus primigenius*), rhinoceros
191 (Rhinocerotidae) and collared lemmings (*Dicrostonyx torquatus*) The second phase of the
192 sequence (layer 1b) is dominated by bison (*Bison priscus*), which is typical taxa of steppe

193 environment. A total of 11 first lower and 3 third upper molars attributed to *Lemmus/Myopus*
194 has been analysed (table 1 and figure 2).

195 **Gully Cave** is located in Ebbor Gorge (Somerset, UK) and has been the subject of ongoing
196 excavation since 2006. The upper stratigraphic units (of relevance here) consist of matrix-rich
197 limestone breccias of Lateglacial Interstadial and Holocene age respectively, separated by a
198 coarse, open-framework limestone breccia deposited during the Younger Dryas, the
199 stratigraphy underpinned by radiocarbon dates on mammalian faunal remains from throughout
200 the sequence. The cave was completely filled by around 10,000 cal years BP and the sequence
201 was capped by a discontinuous flowstone. A total of 35 m1 teeth were analyzed, 12 from the
202 Younger Dryas levels (date range 12409-12037 cal. BP to 11950-11259 cal. BP) and the other
203 23 from the boundary level between the Allerød interstadial and the Younger Dryas (date range
204 12379-12637 cal. BP to 13214-13444 cal. BP), and 43 M3s, with 17 from the Younger Dryas
205 and 26 from the Allerød interstadial-Younger Dryas transition. The mammalian assemblage
206 from the Younger Dryas levels sampled here includes *Lepus timidus*, *Myodes* sp., *Dicrostonyx*
207 *torquatus*, *Lemmus/Myopus*, *Microtus agrestis* or *arvalis*, *Lasiopodomys gregalis*,
208 *Alexandromys oeconomicus*, *Vulpes* sp. and *Rangifer tarandus*. The sample from the Allerød
209 interstadial-Younger Dryas transition has yielded *L. timidus*, *Ochotona pusilla*, *Arvicola*
210 *amphibius*, *Clethrionomys glareolus*, *D. torquatus*, *Lemmus/Myopus*, *M. agrestis* or *arvalis*, *L.*
211 *gregalis*, *Al. oeconomicus*, *V. lagopus*, *R. tarandus* and *Cervus elaphus*.

212 3.3. Landmark schemes and data acquisition

213 All teeth were photographed using a macro objective (Canon EOS6D mark II, macroscopic
214 objective MP-E 65mm f/2.8) and saved in .jpg format with a 72-dpi resolution. To avoid
215 between-picture deformation, all specimens were photographed one by one with the same
216 distance from the objective and with the same focus. Outlines were then extracted from pictures
217 using ImageJ v.1.52a. The m1 outline was then orientated with a manual marking of two

218 landmarks (Lm 3 and 7, fig. 1), which define the tooth's vertical axis, in order to correctly
219 position the tooth following the protocol of Navarro et al. (2018). No satisfactory orientation
220 could be obtained with this protocol on the M3, so the procedure was adapted as follows. The
221 outline pixels were rotated along the first principal component axis of the outline pixel
222 coordinate matrix. These standardized orientations then enabled landmarks located at the
223 extreme tips of the salient and reentrant triangles to be automatically detected, as well as those
224 at the extreme tips of the posterior and anterior loops. All landmarked teeth were further
225 inspected for gross error, and the entire procedure was performed by a single operator, thereby
226 avoiding inter-operator biases.

227 In total, seven landmark schemes and two biometric measurements were defined to describe
228 the morphological variability of the m1 and M3 (table 2 and fig.1). The global shape of each
229 tooth was analysed with a fixed landmark scheme (**FL**), using 14 landmarks for the m1 (**m1-**
230 **FL**) and 11 landmarks for the M3 (**M3-FL**). A total of 20 semi-landmarks for m1 and 50 semi-
231 landmarks for M3 were used to characterize the outer loops (anterior loop dataset **m1-AL** and
232 posterior loop dataset **M3-PL**). The **SL** schemes, **m1-SL** and **M3-SL** correspond to FL datasets
233 combined with semi-landmarks of outer loops (**m1-AL** or **M3-PL**). Another semi-landmark
234 scheme describes the alternation between T2 and T3 of M3 (**M3-TR**) by using a total of 4 fixed
235 landmarks and 30 semi-landmarks. In all semi-landmark configurations, few fixed landmarks
236 were removed to treat whole loops only using semi-landmarks (landmark removed for each
237 dataset: **m1-SL/AL**: Lm8, 9, 10; **M3-SL/PL**: Lm 9, **M3-TR**: Lm3).

238 In addition, the tooth length (**TL**) of the two teeth was estimated based on the Euclidean distance
239 between the most anterior and posterior landmarks (Lm1 and 9 for m1; Lm1 and 7 for M3).

240 3.4. Geometric morphometrics

241 All configurations of each landmark dataset (**m1-FL**, **m1-SL**, **m1-AL**, **M3-FL**, **M3-SL**, **M3-**
242 **PL**, **M3-TR**) were superimposed using partial Generalized Procrustes Analysis (GPA),

243 performed independently for each dataset. This procedure aims to separate the shape component
244 from the position, size and orientation components contained within the coordinates of
245 landmark configurations. GPA proceeds by 1) translating each individual configuration so that
246 their centroids coincide, 2) scaling each landmark configuration to unit centroid size, and 3)
247 rotating each configuration onto the dataset mean shape by minimizing Procrustes distances
248 between each configuration and this mean shape (Dryden and Mardia, 1998; Rohlf and Slice,
249 1990; Zelditch et al., 2012). For **m1-SL**, **m1-AL**, **M3-SL**, **M3-PL** and **M3-TR**, semi-landmarks
250 are allowed to slide to minimize the bending energy between the specimen configurations and
251 the meanshape of the dataset under consideration (Bookstein, 1997).

252 The obtained coordinates (Procrustes coordinates) were then projected onto the Euclidean
253 tangent space (the tangent point being the mean shape of the dataset). These tangent space
254 coordinates are finally rotated by a Principal Component Analysis (PCA) to keep only principal
255 components with non-null eigenvalues (the rank deficient nature of tangent space data resulting
256 from loss of degree of freedom during GPA, and, in our case, to some datasets with fewer
257 individuals than shape variables). For each dataset, a few outliers were identified as those
258 individuals with high Procrustes distances compared to their mean shape (i.e. lying beyond the
259 third quartile increased by 1.5 times the interquartile range) and were sequentially removed
260 after a new GPA (table 2).

261 In order to avoid any influence of fossil specimens on the molar shape variation depicted by the
262 tangent space, which was then used to build the discriminant model among both genera, we
263 treated fossil specimens as supplementary specimens in our analyses (see Navarro et al. 2018).
264 Fossil specimens were so aligned on the modern mean shape so that, for a given dataset, they
265 lay on the same shape and tangent spaces as the modern individuals. Then, the rotation
266 computed on the tangent space for the modern individuals was used to rotate the projection of
267 fossil specimens in the same way.

268 All geometric morphometrics analyses were performed with the geomorph package version
269 3.2.0 on R v3.6.2 (R Core team, 2019).

270 3.5. Statistical classification

271 The predictive model was built using linear discriminant analysis (LDA) quantifying the shape
272 differences between the two genera (*Myopus* vs *Lemmus*), and the quality of the obtained model
273 was assessed by Leave-One-Out Cross-Validation (LOOCV). This procedure removes one
274 specimen from the sample at a time and predicts its classification between groups using LDA
275 functions calculated on the remaining specimens. Then, the removed specimen is classified by
276 a new function, computed using data that do not take the specimen into consideration, thereby
277 reducing potential inflation of the prediction error and avoiding issues of circular reasoning and
278 over-fitting problems (Kovarovich et al., 2011).

279 LDA can be extremely sensitive to the relation between the number of groups, the number of
280 predictor variables and the total sample size. As rule-of-thumb, the total number of predictor
281 variables needs to be smaller than the sample size of the smallest predicted group (Kovarovich
282 et al., 2011). Special attention has been paid to this rule due to our small sample size and the
283 high number of predictor variables. Firstly, we reduced the number of predictors used to build
284 the discriminant functions by applying the method of Baylac and Friess (2005). This method
285 substitutes primary data (Procrustes coordinates) by PCs scores to build the model. This was
286 done by building each model and its LOOCV based on the first k PCs, with k varying from 1 to
287 p (p being the sample size of the smallest group under consideration). The optimal number of
288 PCs for the most efficient model was determined by the lowest prediction error rate (i.e. the
289 maximum number of correctly assigned specimens).

290 Secondly, the method of Evin et al. (2013) was used to evaluate possible biases due to our
291 unbalanced dataset. For a given unbalanced dataset, 100 balanced samples were built by
292 randomly picking a subset of individuals from the largest group, and for each such sample,

293 LDA was computed. The observed classification score for each unbalanced dataset was then
294 compared with these 100 balanced samples. Models were also compared with the null
295 hypothesis of no shape difference between genera (hence the classification would be only due
296 to chance, resulting in a 50% error rate). 100 such null models were generated for balanced
297 samples of the two species by randomly reassigning specimens to genera. Finally, the quality
298 of the models was evaluated by checking at posterior probabilities of correctly assigned genus
299 for each dataset.

300 All codes including automatic landmark placement and data treatment are available on request.

301 **4. Results**

302 4.1. Morphospaces and morphological variation

303 4.1.1. The first lower molar

304 In the tooth shape analyses (**m1-FL**, **m1-SL** and **m1-AL**), the two first PCs account,
305 respectively, for 32.6%, 56.6% and 69.6% of the explained variance (table 3, fig. 3). The
306 number of PCs explaining at least 90% of the initial shape variation is 13, 12 and 6, respectively.
307 For the **m1-FL** configuration, shape changes mainly concern the buccal triangles (T2-T4)
308 shifting labially and the Lm1 and 9 shifting laterally. For the **m1-SL**, the main behaviour is
309 focused on the anterior loop, which tends to roundness enhancing the confluence of T4/T5 (fig.
310 3B). The shape variation on **m1-AL** exhibits a more pronounced development of the re-entrant
311 angles (fig. 3C). The most important part of the variation is expressed by PC1 and tends to
312 separate the two genera for all datasets, with the least overlap for the **m1-SL** analysis and the
313 largest one for the **m1-FL** (fig. 3A). On the two first PCs from these three landmark schemes,
314 one can note no specific distinction between *Lemmus* species (fig. 3). The tooth lengths of
315 *Lemmus* and *Myopus* range from 1.6 to 2.4 mm and from 1.4 to 1.7 mm, respectively (fig. 3H).
316 A large overlap in the tooth length range is observed between the two genera, with 86% of the

317 *Myopus* specimens being included within *Lemmus*'s tooth length range. Within the *Lemmus*
318 genus, *L. sibiricus* is the species which has the longest tooth length compared to the two others.

319 4.1.2. The third upper molar

320 The same pattern as m1 is observed on the M3 with the first two PCs explaining 46.1%, 70.0%,
321 75.7% and 57.7% of variation respectively **M3-FL**, **M3-SL**, **M3-PL** and **M3-TR** (table 3, fig.
322 3). The number of PCs explaining at least 90% of the initial shape variation is 10, 8, 5 and 6,
323 respectively. The shape variation illustrated by PC1 for **M3-FL** concerns the width and length
324 of the teeth, with a tendency to be more "compact" (i.e. thinner and smaller) (fig. 3D). For **M3-**
325 **SL**, the main changes occur on the lingual triangles and anterior loop, with an enlargement on
326 the lingual side (fig. 3E). Similar changes on the posterior loop are also observed on **M3-PL**.
327 The first PC of **M3-TR** describes the T3/T4 alternation, with a T3 tending to close. As for m1,
328 the PC1 tends to separate the two genera, with least overlap for the **M3-SL** analysis and the
329 largest overlap for the **M3-TR** for which no separation is observed between the two genera (fig.
330 3G). Again, the two first PCs do not show any clear difference between *Lemmus* species across
331 all landmark schemes. The M3 tooth lengths follow the same pattern as for m1 with a large
332 overlap between the two genera. *Lemmus* range from 1.2 to 1.8 mm and *Myopus* from 1.0 to
333 1.4 mm, with 90% of *M. schisticolor* being included in the *Lemmus* tooth length interval (fig.
334 3I).

335 4.2. Statistical classification of modern specimens and shape differences

336 Although there was only a relatively small number of individuals from *Myopus* (the smallest
337 sample), the unbalanced prediction error curves of the landmark schemes do not show particular
338 bias compared to the balanced ones (fig. 4a). Nonetheless, a bias was noted between the
339 dimensionality of the predictor (the number of PCs included to build the LDA) and the
340 prediction error, with an increase when a high number of predictors is used (fig. 4a). This pattern
341 could be due to the small size of the model samples in relation to the large dimensionality of

342 the shape space, as encountered by Evin et al. (2013). It is likely that with a larger dataset, such
343 as that presented by Navarro et al. (2018), this pattern would not be observed. The optimal
344 number of predictors (PCs), *i.e* the one giving the lowest prediction error rate, was selected to
345 build the discriminant functions of the models and are detailed in table 3. Six models (**m1-FL**,
346 **m1-SL**, **m1-AL**, **M3-FL**, **M3-SL** and **M3-PL**) have low prediction errors inferior to 5% for
347 unbalanced samples (the real samples). Models of the m1 tend to have a lower prediction error
348 compared to those from the M3 (fig. 4b; table 3). Landmark schemes of the m1 taking in account
349 the anterior loop (**m1-SL** and **m1-AL**) give the best classifications, up to 0.96 and 0.93. The
350 same pattern is visible on the M3 and the posterior loop, with **M3-SL** having 0.95 optimal
351 classification score, with **M3-FL** and **M3-PL** having comparable scores of 0.89 and 0.88. In
352 contrast, the tooth length (**m1-TL** and **M3-TL**) has very low classification scores, with 0.41
353 and 0.42 respectively, which is comparable to a classification only due to chance.

354 Figure 5 illustrates the shape differences between *Lemmus* and *Myopus* for modern individuals
355 along the first discriminant axis from the LDA regarding the different landmark schemes. In
356 terms of the m1 shape, *Myopus* tends to differ from *Lemmus* with: 1) a different orientation of
357 the lingual triangles, tending to sweep upwards; 2) a simpler anterior loop with a less marked
358 labial peak; and 3) a LRA3 that extends less deeply over the BRA2 without generating a new
359 re-entrant angle on the buccal side of the anterior loop. For the M3, *Myopus* tends to differ from
360 *Lemmus* as follows: 1) an overall stockier tooth; 2) a simpler posterior loop, almost flat; and 3)
361 a shorter distance between Lm2 and Lm8. For m1 and M3, tooth lengths show a large overlap
362 with almost all *Myopus* plotting with the smaller *Lemmus* specimens.

363 4.3. Fossil identifications

364 The best performing model (**m1-SL**) obtained with modern specimens allows the identification
365 of at least one *Myopus* individual in Grotte des Gorges and one in Gully Cave from the Allerød
366 interstadial-Younger-Dryas transition level, with posterior probabilities at 0.998 and 0.935,

367 respectively (table 4, figure 6a). For these two individuals, similar attributions to *Myopus* were
368 obtained with other models (**m1-FL**, **m1-AL**) (see supplementary table A). The **m1-TL** model
369 (table 4, figure 6b) cannot attribute any individuals as a *Myopus* with significant posterior
370 probabilities and only 9 individuals are confidently identified as *Lemmus*. Most of the
371 specimens are undetermined.

372 For the M3 (table 4, figure 6c), one tooth has been attributed to *Myopus* at Gully Cave for the
373 same level, with the best model (**M3-SL**) giving 0.994 of posterior probability. This attribution
374 was equally obtained with **M3-FL** and **M3-PL** models. No model suggests the presence of
375 *Myopus* in the M3 sample from Grotte des Gorges, but only three teeth were analysed. As for
376 **m1-TL**, the **M3-TL** model cannot attribute any individual to *Myopus* with high posterior
377 probabilities (figure 6d), and the model is unable to confidently identify a large majority of the
378 specimens (table 4, figure 6).

379 **5. Discussion**

380 *Myopus schisticolor* and *Lemmus sp.* are two lemmings that are currently widespread
381 throughout north Eurasia. They have two distinct habitat preferences, the first inhabits
382 exclusively taiga forest, whereas the second prefers an open tundra environment (e.g. Mitchell-
383 Jones et al., 1999; Niethammer and Krapp, 1982). They both consume mosses, but with variable
384 seasonal proportions: the diet of *Myopus schisticolor* is restricted only to this vegetation type,
385 whereas *Lemmus sp.* diversifies its diet during spring and summer with dicots, grasses and
386 sedges being consumed (e.g Batzli and Pitelka, 1983; Calandra et al., 2015; Eskelinen, 2002;
387 Rodger and Lewis, 1986). If distinguishing between these two species is relatively easy at the
388 present day, due to their distinctive external morphology, they are extremely difficult to identify
389 with fossil material, on account of their similar tooth morphologies.

390 5.1. Molar shape differentiation

391 Despite the similarity in tooth morphology of these two lemming genera, the geometric
392 morphometric approach used in this paper has been able to describe and quantify intergeneric
393 shape differentiation of the first lower molar (m1) and the third upper molar (M3) of modern
394 specimens. Describing the whole shape of the molars with a set of landmarks associated with
395 semi-landmarks on the anterior loop of m1 or posterior loop of M3 (**m1-SL** and **M3-SL**)
396 appears to be the best landmark scheme among those tested here for the modern reference
397 framework. These two landmark schemes have allowed us to separate the two genera with high
398 statistical probabilities, around 0.95 confidence (table 3).

399 These landmark schemes suggest that the main differences between these two genera relate to
400 the tooth complexity with the outer loops more developed in *Lemmus* than in *Myopus*. The
401 anterior loop on the m1 or the posterior loop on the M3 tend to exhibit a supplementary angle,
402 which is not observed in *Myopus*. For *Myopus*, teeth tend to be stockier and simpler in shape.
403 This increased complexity of the anterior m1 loop in *Lemmus*, always absent in *Myopus*, and
404 the organisation of the buccal triangles shifting anteriorly on *Lemmus*, are congruent with the
405 taxonomic literature (Chaline et al., 1988; Markova et al., 2018; Smirnov et al., 1997;
406 Ponomarev et al., 2013b). Some of these authors also noted that on the M3, the T3/T4
407 alternation and asymmetry could be used to distinguish both genera. The morphometrical
408 approach developed in this paper thus offered the opportunity to evaluate these criteria (M3-
409 TR). Despite the relevance of these criteria, we demonstrate here that they cannot be used to
410 clearly differentiate the two genera because of a large overlap in their morphology (figure 3;
411 table 3).

412 Among the external morphological criteria allowing differentiation between these two genera,
413 their differences in sizes have been regularly mentioned, with *Myopus* being smaller (Borodin,
414 2009). This criterion was often applied to fossil material through measurement of the length of
415 the teeth or dental row (e.g. Borodin, 2009; Kowalski, 1977; Rhodes et al., 2018). Nonetheless,

416 as illustrated in figure 3, there is a high overlap between the two genera in terms of tooth length.
417 This overlap is mainly observed between *M. schisticolor* and *L. lemmus*, whereas *L. sibiricus*
418 teeth are taller, with a clear separation from other lemmings (figure 3H, I). Applying the
419 criterion of size to Western European fossil assemblages with lemmings is therefore likely to
420 conflate *L. lemmus* and *M. schisticolor*, affirming presence of the former but obscuring the
421 presence of the latter. In any case, size always has to be used very cautiously on fossil species
422 because it can be highly variable according to the time period, the climate or even the latitude
423 and altitude (e.g. Delpech, 1999; Klein, 1986, Klein and Scott, 1989).

424 By its ability to capture the whole geometry of an object, geometrics morphometrics has
425 therefore become increasingly popular in archaeological and palaeontological studies (e.g.
426 Cucchi et al., 2014; Escudé et al., 2008; Evin et al., 2013; Killick., 2012; Marr, 2016; McGuire,
427 2011; Miele et al., 2020; Navarro et al., 2018). Associated with classification analysis, such as
428 a LDA, it is a powerful approach that allows differentiation of morphologically close species,
429 thereby assisting in the robust identification of fossil remains and in our understanding of
430 changing faunal communities.

431 5.2. *Myopus* fossil identifications: palaeobiogeographical implications

432 During Late Pleistocene glaciations, cold environmental conditions were favourable to
433 lemmings and facilitated their dispersal throughout a large part of Europe (Markova et al., 2019;
434 Royer, 2013), from the Urals (Ponomarev et. al., 2013) to Ireland (Monaghan, 2017; Sutcliffe
435 and Kowalski, 1976; Woodman et al., 1996), including for example France (Marquet, 1993;
436 Royer et al., 2016), Denmark (Bennike et al., 1994; Larsen and Mangerud, 1990) or
437 Czechoslovakia (Horacek and Sanchez-Marco, 1984). Until the present paper, the presence of
438 *Myopus* in Western Europe was either not envisaged at all or, at best, still questioned. Our
439 results attest its presence in two sites from two distinct periods of Late Pleistocene: la Grotte
440 des Gorges, located in East of France, which is from the end of MIS 3, around 30 ka cal BP,

441 and Gully Cave, situated in the Somerset (England), from the Allerød interstadial - Younger
442 Dryas transition level.

443 Occurrences of *M. schisticolor* have already been suggested for European Early and Middle
444 Pleistocene site at Boxgrove (England, Roberts and Parfitt, 1999) and Vergranne (France,
445 Chaline et al., 1989) and suspicions of its presence (records of *Myopus/Lemmus*) have raised in
446 Chlum-4 (Czech Republic, Kowalski, 2001), Nyaravai-2 (Lithuania, Kowalski, 2001), and
447 Sudmer-Berg 2 (Germany, von Koenigswald, 1972). In general, these suspicions are based on
448 both the morphology of the teeth and on the faunal associations, which are characteristic of a
449 forest environment. However, these tentative suggestions were not uniformly accepted (van
450 Kolfschoten, 1995; 1996; Kowalski, 1995, 2001); for example at Vergranne, Kowalski (1995)
451 stated that the *Myopus* identification cannot be accepted as definitive. His opinion was that it is
452 not possible to separate *Lemmus* and *Myopus* in the fossil record, and that *Myopus* did not reach
453 Europe during Pleistocene (Kowalski, 2001). Approaches as geometric morphometrics or
454 ancient DNA, which provide reliable identification, imply reconsidering certain determinations
455 based on presuppositions of past studies (geographical area, morphological features, faunal
456 assemblages). The same issues were recently underlined for other species as for example *Sorex*,
457 with the identification of the boreal *Sorex tundrensis* in Germany during the end of MIS3
458 (Freund, 1998; Prost et al., 2013), a species that was not supposed to reach Europe.

459 Lemming specimens from older Early and Middle Pleistocene sites are generally assigned to
460 ancestral forms of *Lemmus*, possibly *Lemmus kowalskii*. This extinct species is then assumed
461 to have lived under temperate conditions in a more wooded environment, as suggested by the
462 forest taxa with which it was associated (van Kolfschoten, 1995; 1996; Kowalski, 1995; 2001).
463 However, identification of *Lemmus kowalskii* is highly controversial, since it is
464 morphologically similar to *Myopus*, but much closer in size to *Lemmus* (Harrison et al., 1989).

465 For the Late Pleistocene, several studies attest the presence of *Myopus* in the Ural (Ponomarev
466 et al., 2013a, b, c) by using the ratios of Smirnov *et al.* (1997) or morphotype differentiation
467 associated with non-metric multidimensional scaling (Ponomarev et al., 2013a, c). In Europe,
468 *Lemmus* / *Myopus* remains from this period are always identified as *Lemmus* (*Lemmus lemmus*
469 in the western part of Europe and *Lemmus sibiricus* in the eastern part). To our knowledge, only
470 one previous occurrence of *Myopus schisticolor* has been suggested for this period in western
471 part of Europe, in Level 4 of King Arthur's Cave (Wye Valley, England) (Price, 2003), which
472 has been attributed to the Bølling-Allerød interstadial (Bronk Ramsey, 2002). Nevertheless,
473 these determinations (obtained on 12 teeth from a total sample of 17) were only based on tooth
474 length (Price, 2003) and were not corroborated by another approach, although the presence of
475 boreal species in the same level, such as *Clethrionomys rufocanus*, tends to strengthen this
476 hypothesis (Price, 2003). The identification of *Myopus* in the Allerød - interstadial layer of
477 Gully Cave corroborates Price's suppositions, suggesting the presence of this species during
478 milder climatic phases in the southern part of England. This presence throughout the
479 septentrional region of Western Europe (i.e. latitude > 45°N) during the Late Pleistocene, raises
480 the question of whether its occurrence was (semi)continuous, or sporadic related to specific
481 climatic events favouring its expansion from eastern regions.

482 5.3. Palaeoenvironmental implications of *Myopus* occurrence in Late Pleistocene

483 Since *Myopus* is today closely linked to the taiga, its identification has strong implications for
484 palaeoenvironmental reconstructions, suggesting past local environments with boreal forest
485 cover mainly composed of *Pinus*, *Betula* and *Picea*, which is favourable to the development of
486 the thick moss cover that constitutes nearly all of its diet (Bobretsov and Lukyanova, 2017;
487 Eskelinen, 2002). Our results from both sites (Grotte des Gorges and Gully Cave) suggest the
488 association of individuals from both genera *Lemmus* and *Myopus*. While this might appear
489 contradictory due to their distinct environmental preferences, they were found within a

490 diversified faunal association, including for instance *Dicrostonyx torquatus*, *Alexandromys*
491 *oeconomus* or *Lasiopodomys gregalis*. Although these fossil faunal communities are
492 'disharmonious' by comparison to present-day small mammal associations and might therefore
493 reflect a palimpsest of distinct phases, the stratigraphical integrity of our study samples is clear.
494 It is therefore more likely that these diverse assemblages reflect the mosaic environment of
495 boreal forest and steppes that are increasingly recognised as typical of the Late Pleistocene of
496 northern Europe.

497 Multi-proxy investigations on sediment archives have demonstrated continental vegetation to
498 be highly sensitive to Dansgaard-Oeschger events (Fletcher et al., 2010), consequently
499 impacting small mammal communities. Pollen from the Bergsee lacustrine record in Germany
500 demonstrates a high frequency succession of steppe and boreal forest phases, consistent with
501 stadial-interstadial oscillations, and underpinned by increases in *Juniperus* and *Pinus* pollen
502 during Greenland Interstadials 8 and 7 (Becker et al., 2006; Duprat-Oualid et al., 2017). The
503 presence of *Myopus* in la Grotte des Gorges could therefore be related to one of these Greenland
504 Interstadial events.

505 For Gully Cave, two levels have been investigated, one attributed to the Allerød interstadial -
506 Younger Dryas transition, and one from the Younger Dryas. Among individuals from the older
507 level, at least two teeth suggest the presence of *M. schisticolor* according to the most efficient
508 models (**m1-SL**: 1, **M3-SL**: 1), but for the cold-climate level of Younger Dryas, no specimens
509 have been attributed to *M. schisticolor*. Vegetation in Britain was highly sensitive through Late
510 Glacial stadials and interstadials, with regional variation depending of the latitude (e.g. Birks
511 and Birks, 2014; Huntley and Birks, 1983; Jones and Keen, 2012; Pennington, 1977; Walker et
512 al., 2003). In southern England, the Allerød interstadial was a temperate-climate phase
513 characterized by an increase in forest taxa (Hill et al., 2007; Walker et al., 2003), in particular
514 the spread of *Betula* (Birks and Birks, 2014). The development of this semi-open boreal

515 environment in southwestern England (Hills et al., 2007) is echoed by the apparent
516 disappearance of *Equus ferus* at this time (Kaagan, 2000), and favoured the coexistence of both
517 arctic and boreal species, such as *Cervus elaphus* and *Rangifer tarandus* in Cheddar Gorge
518 (Currant and Jacobi, 2011). King Arthur's Cave, which is located 80 km north of Gully Cave,
519 has equally yielded both forested and cold-adapted taxa (e.g. *Dicrostonyx torquatus*,
520 *Alexandromys oeconomicus*, *Lasiopodomys gregalis*, *Clethrionomys rufocanus*, *Microtus*
521 *agrestis*, *Lemmus lemmus*; Price, 2003), suggesting a mosaic environment. This environment
522 was able to support both *Lemmus* and *Myopus* populations during the Allerød interstadial, with
523 the presence of both open and forested areas. The abruptness of the succeeding Younger Dryas
524 cooling event led to drastic vegetation changes, with a decline in forested environments, a
525 decrease in *Betula*, and a rise of *Artemisia* in southern England (Birks and Birks, 2014).
526 European *Betula* macrofossils from this period only belong to *Betula nana* (Birks and Birks,
527 2014), reflecting the reduction of forest and inhibiting the development of the moss cover
528 needed by *Myopus*.

529 **6. Conclusion**

530 Our results highlight that: i) the presence of *Myopus schisticolor* is confirmed for the first time
531 in the Late Pleistocene fossil record of western Europe, although it remains to be established
532 whether its occurrence was (semi)continuous or sporadic, only related to specific climatic
533 events favouring its expansion from eastern regions; ii) its presence has important consequences
534 for palaeoenvironmental interpretations, implying the existence of boreal open/semi open
535 environments.

536 **Author contributions**

537 Conceptualization, L.A., S.M. and A.R.; Methodology and Software, L.A. and R.L.; Formal
538 analysis, Investigations and Data Curation, L.A.; Validation: R.L.; Resources, S.M., D.S. and

539 S.D.; Writing original draft preparation and Visualisation, L.A., S.M. and A.R.; Writing,
540 Review and Editing, L.A., S.M., A.R., D.S., R.L. and S.D.

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546 and Natalia Sokolova of the Ural branch of Russian Science Academy for their loan of Siberian
547 lemming's specimens. Danielle Schreve acknowledges the support of the National Trust and
548 Natural England in the excavation of Gully Cave.

549 Figure captions

550 Figure 1: Landmark schemes (in grey squares) defined for Lemmini first lower molar (m1) and
551 third upper molar (M3). Hand-placed landmarks are in white, automatically detected landmarks
552 are in black, and semi-landmarks are in blue (for **m1-SL**, **m1-AL**, **M3-SL** and **M3-AL**) and in
553 yellow (for **M3-TR**). Abbreviations: T = triangles, LRA = lingual re-entrant angles, BRA =
554 buccal re-entrant angles, AL = anterior loop, PL = posterior loop. Modified after van der Meulen
555 (1973).

556

557 Figure 2: A) Global climate evolution and chronology of the last part of the last glacial
558 following the NGRIP-ice record (Andersen et al., 2004) with the position of the two fossil sites.
559 Abbreviations: MIS: marine isotope stage, HE: Heinrich events, LGM: last glacial maximum,
560 BA: Bølling - Allerød interstadial, YD: Younger-Dryas. B) Geographical range of *Lemmus*
561 *lemmus* (blue), *Lemmus sibiricus* (red) and *Myopus schisticolor* (yellow) with the overlap area
562 (orange). Circles indicate the location of the modern samples and squares (brown) the
563 localisation of the fossil samples. Site number: 1. Karigasniemi, 2. Kilpisjärvi, 3. Pällasjarvi-
564 Muonio, 4. Rovaniemi, 5. Sabetta, 6. Erkuta, 7. Bely Island, 10. Sotkamo area, 11. Posio, 12.

565 Grotte des Gorges, 13. Gully Cave. Localities from North America and Eastern Siberia are not
566 shown (see text for detail).

567

568 Figure 3: Morphospaces (PC1 – PC2 planes) of modern specimens with associated shape
569 variation for all landmark schemes (A: m1-FL; B: m1-SL; C: m1-AL; D: M3-FL; E: M3-SL;
570 F: M3-PL) and violin plots for tooth length (H: m1-TL; I: M3-TL). For PCA, displayed shape
571 variation corresponds to morphological changes along the 1st PC axis, depicted by lollipop
572 graphs (grey outline and black dots for the mean shape, black segments for the shape deviation
573 from the mean shape to the most distant individual score on the considered PC). Percentage of
574 shape variation explained by each PC are reported. *Myopus* are in yellow, *Lemmus lemmus* in
575 blue, *Lemmus sibiricus* in red and *Lemmus trimucronatus* in cyan.

576

577 Figure 4: A) Variation of the LDA's prediction error according to the number of PCs included
578 to build the model for each landmark scheme, with m1 on the left and M3 on the right. For each
579 plot, continuous coloured lines show the prediction error for the original samples, dotted
580 coloured lines show the prediction error for the set of 100 balanced samples, and the grey line
581 show the prediction error for the set of 100 randomly reassigned samples with the associated
582 error bars standing for the 95% confidence intervals (null hypothesis). B) Model prediction
583 error with the optimal number of PCs for each landmark scheme. Coloured points correspond
584 to the observed prediction error on the real datasets, black points correspond to the prediction
585 error for the set of 100 balanced samples with the associated 95% confidence interval, grey
586 points show the prediction error for the set of 100 randomly reassigned samples with the
587 associated error bars standing for the 95% confidence interval (null hypothesis).

588 Figure 5: Distribution histograms of the modern samples along the linear discriminant axis with
589 associated shape changes. *Lemmus* are in blue, *Myopus* are in yellow. The displayed shapes
590 correspond to the extreme individual scores on the discriminant axis for each landmark scheme.

591 Figure 6: Distribution histograms of the fossil samples along the discriminant axis from the
592 model based on modern samples for m1-SL, m1-TL, M3-SL and M3-TL datasets. Fossil
593 samples are reported by archaeological/palaeontological levels (scatter plot). *Lemmus* are in
594 blue, *Myopus* are in yellow.

595 Table captions

596 Table 1: List of the analysed specimens with their origin and counts (neighbour localities are
597 merged). See figure 1 for localities.

598 Table 2: Datasets used in the present study. FL = Fixed landmarks, SL= Semi landmarks
599 (including FL and AL for m1 and FL and PL for M3), PL = Posterior loop, AL = Anterior loop,
600 TL = ToothLength.

601 Table 3: Abbreviations: Tot. PCs= Total Number of PCs, Opt. PCs = Optimal Number of PCs
602 used in the model, PC1+PC2 = cumulative proportion of variance explained by PC1 + PC2, %
603 Opt. class. actual = percentage of prediction error of modern specimens with the optimal
604 number of PCs.

605 Table 4: Fossil identification for m1 and M3. The number of specimens identified with
606 associated posterior probabilities > 0.9 are in brackets

607 Supplementary data captions

608 Supplementary table 1: classification of fossil specimens for each dataset with associated
609 posterior probabilities for m1 and M3.

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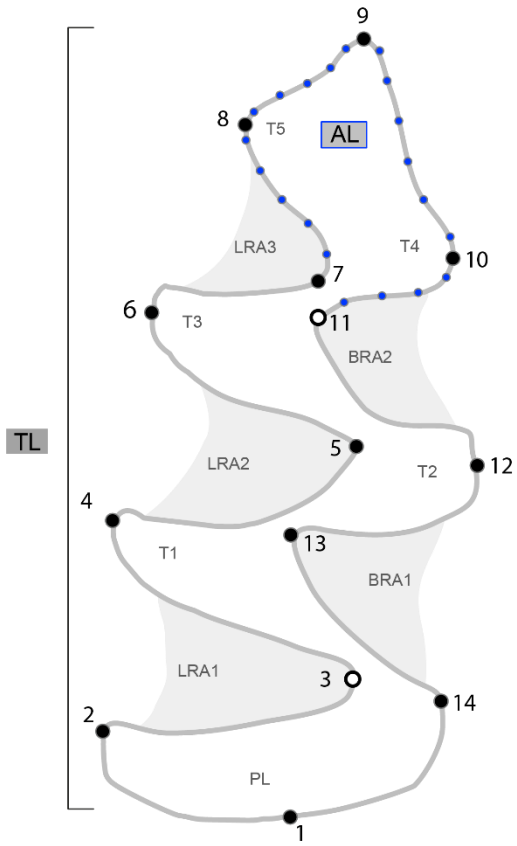
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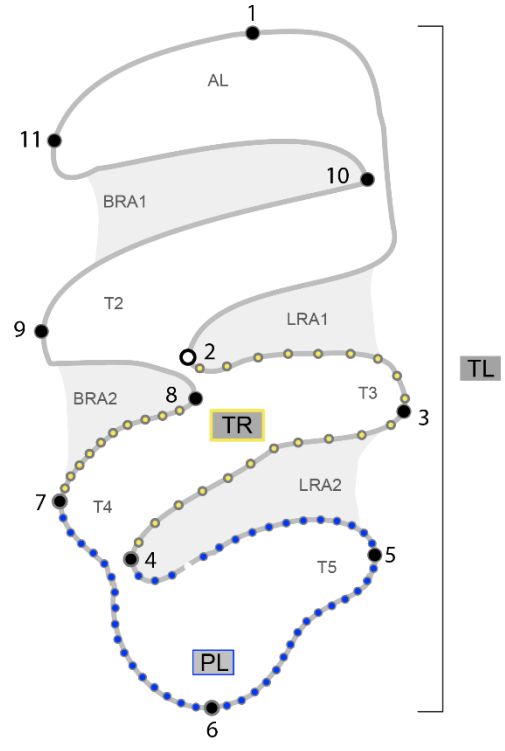
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SL [FL [○ Landmarks operated manually
 ● Automatic landmarks
 AL [● Semi landmarks



First lower molar (right)

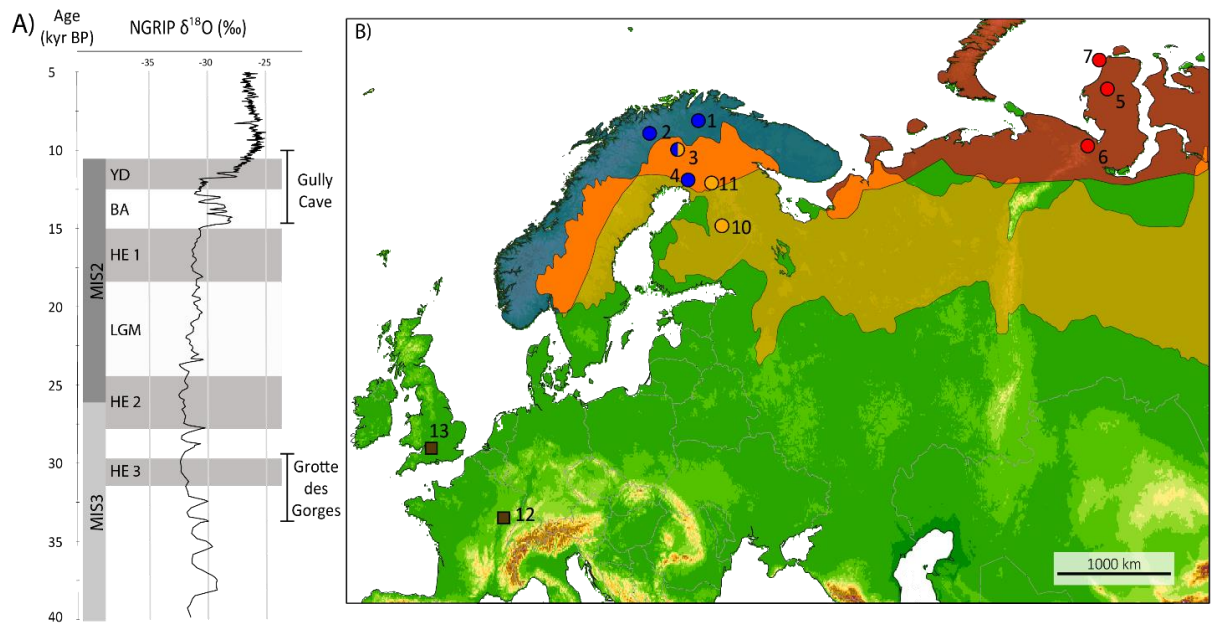
SL [FL [○ Landmarks operated manually
 ● Automatic landmarks
 PL [● Semi landmarks
 TR [● Semi landmarks



Third upper molar (right)

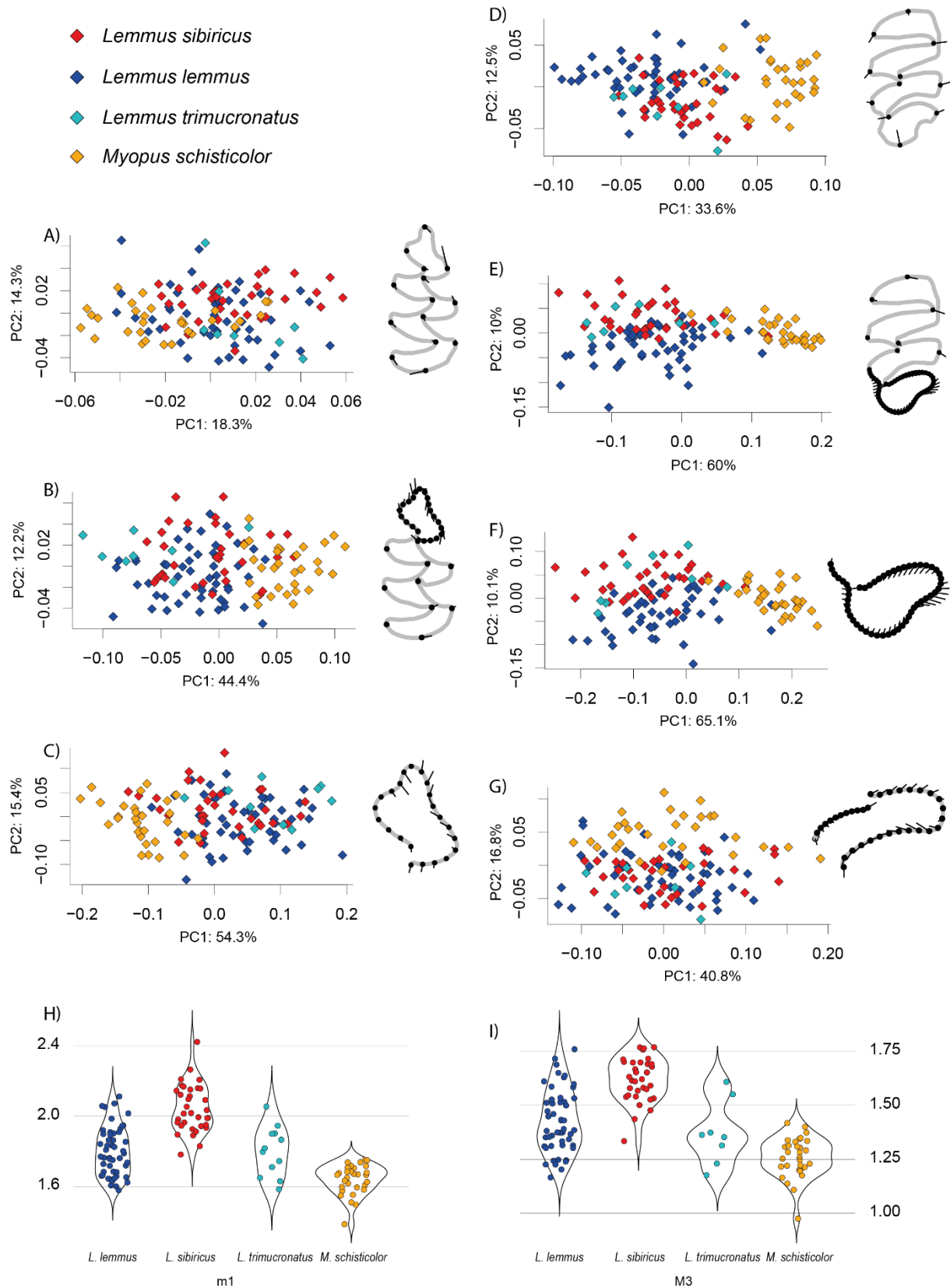
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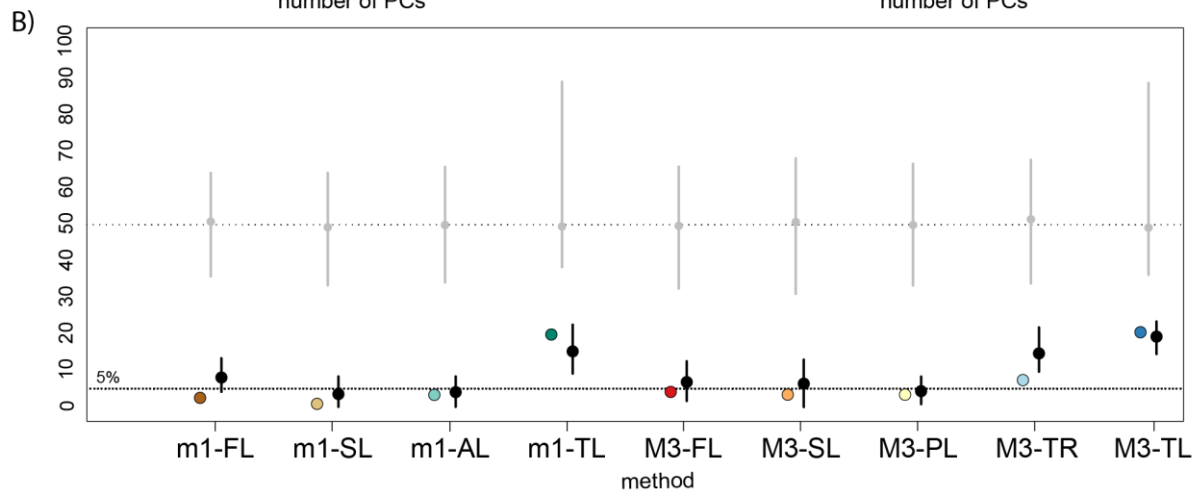
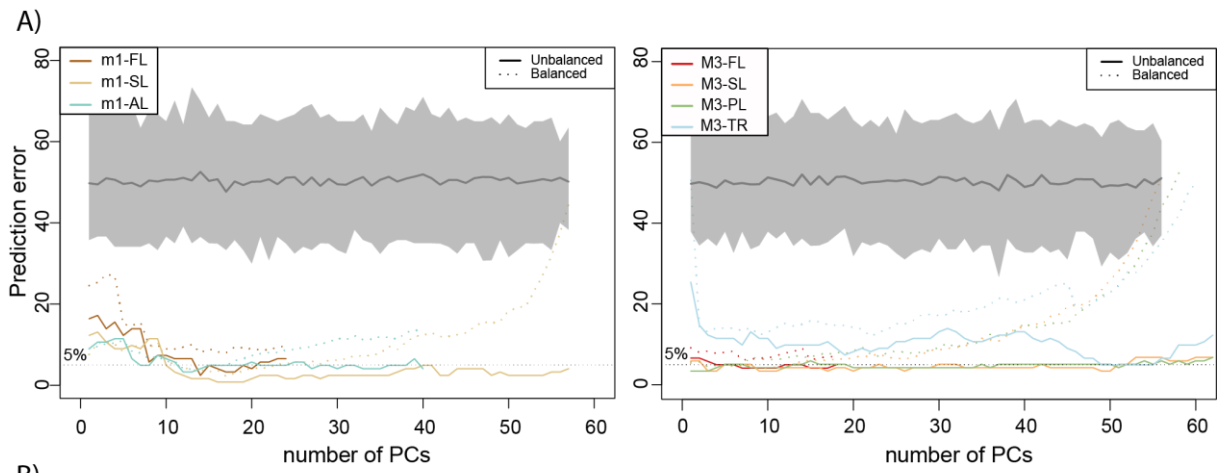
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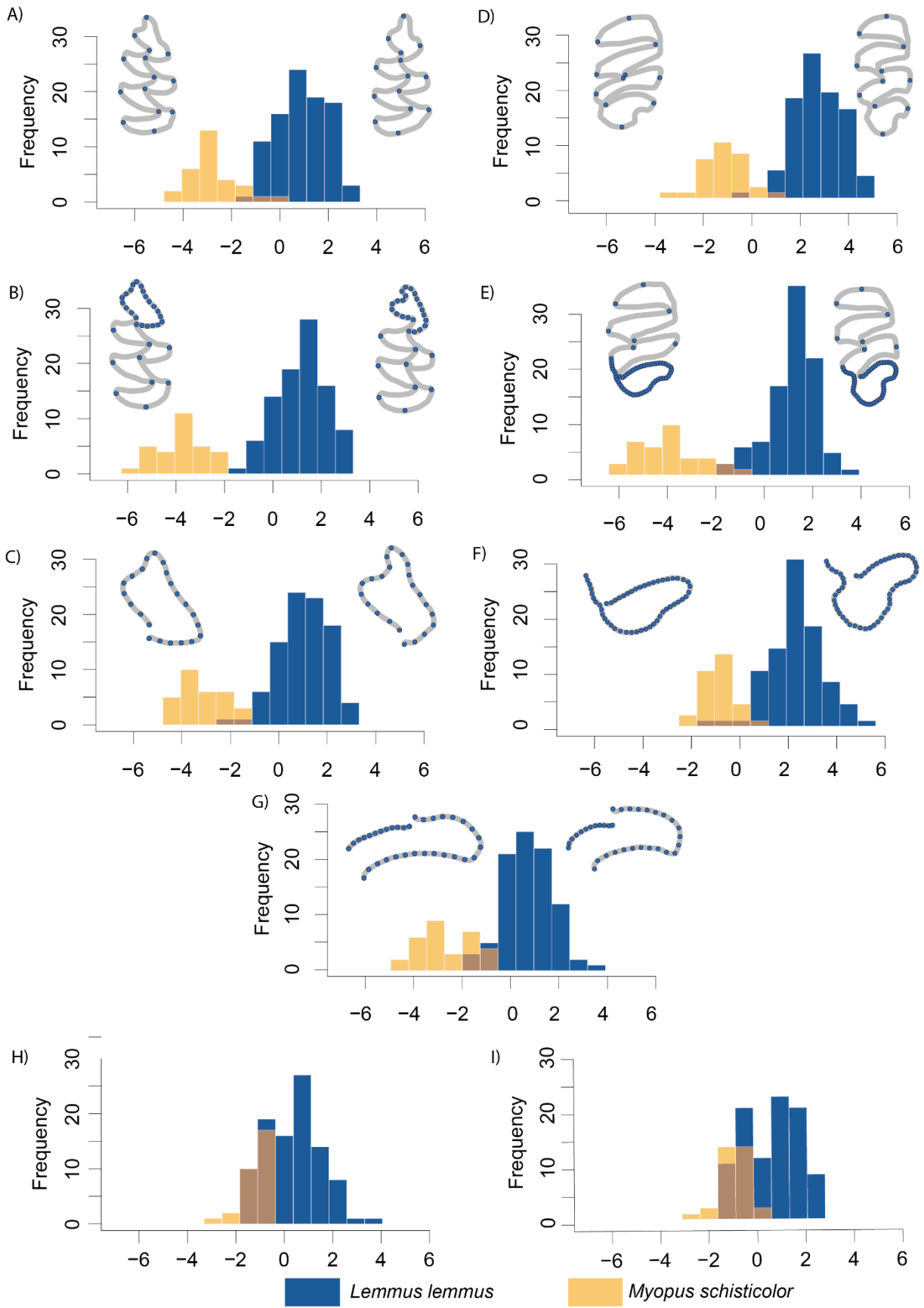
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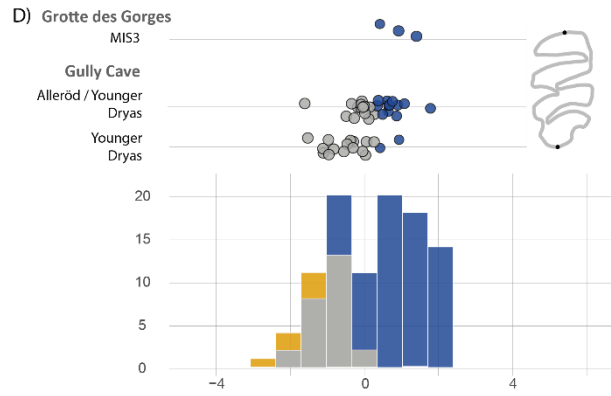
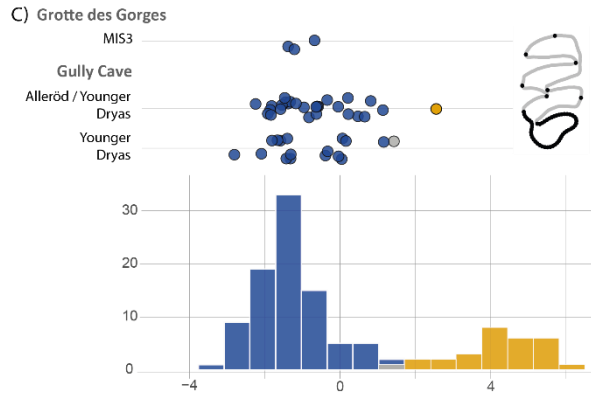
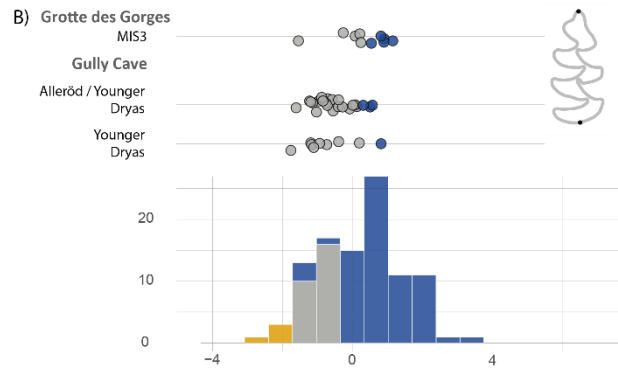
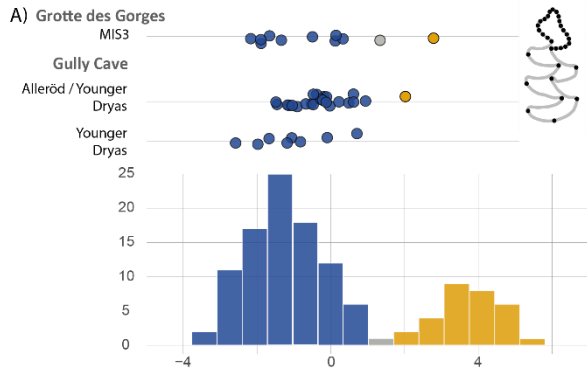
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● *Lemmus* sp. ● Undetermined (posterior probabilités > 0,9)

● *Myopus* sp.

948 Table 1: List of the analysed specimens with their origin and counts (neighbouring localities are merged). See figure 1 for localities.

	Species	Location	Lower m1	Upper M3
Modern specimens	<i>Lemmus lemmus</i> (50)	1- Karigasniemi	3	3
		2- Kilpisjärvi	15	14
		3- Pallasjärvi, Muonio	11	10
		4- Rovaniemi	21	18
	<i>Lemmus sibiricus</i> (34)	5- Sabetta	9	11
		6- Erkuta	10	10
		7- Bely Island	11	11
		(8)- Wrangel Island	4	1
	<i>Lemmus trimucronatus</i> (12)	(9)-Victoria Island	12	8
	<i>Myopus schisticolor</i> (31)	10-Sotkamo, Valtimo, Kuhmo, Lieka,	20	21

		11-Posio	1	1
		(3)-Pallasjarvi, Muonio	8	8
Fossil specimens	Amange	MIS3	11	3
	Gully Cave (M3: 43 ; m1: 35)	Boundary Allerød / Younger Dryas	23	26
		Younger Dryas	8	17
		Younger Dryas?	4	0

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951 Table 2: Datasets used in the present study. FL = Fixed landmarks, SL= Semi landmarks (including FL and AL for m1 and FL and PL for M3),
 952 PL = Posterior loop, AL = Anterior loop, TL = ToothLength.

	Landmark scheme	Number of		Evaluated criteria	Reference
		Landmarks	Semi-landmarks		
M3	FL	11	-	Width of the teeth	Chaline, 1988
	PL	2	50	Complexity of the posterior loop	Ponomarev et al., 2013, Markova et al., 2017
	SL	9	50	Complete shape	-
	TR	4	10 + 20	Depth of A1	Chaline, 1988
				Confluence of FL2	Ponomarev et al., 2013
				Asymmetry of FL2	Markova et al., 2017
TL	2	-	Tooth length	Chaline, 1988	
M1	FL	14	-	Organisation of the buccal triangles	Chaline, 1988
	AL	2	20	Complexity of the anterior loop	Ponomarev et al., 2013, Markova et al., 2017
	SL	11	20	Complete shape	-
	TL	2	-	Tooth length	Chaline, 1988

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957 Table 3: Abbreviations: Tot. PCs= Total Number of PCs, Opt. PCs = Optimal Number of PCs used in the model, PC1+PC2 = cumulative
 958 proportion of variance explained by PC1 + PC2, % Opt. class. actual = percentage of prediction error of modern specimens with the optimal number
 959 of PCs (see text for details).

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	Dataset	Tot. PCs	Opt. PCs	PC1 + PC2	% Pred. Error	% Opt. class. actual	% Opt. class. fossil	Fossil identification	
								<i>Lemmus</i>	<i>Myopus</i>
M1	FL	28	14	32.6	2.5	85.5	80.4	38	8
	SL	62	19	56.6	0.8	95.9	97.8	44	2
	AL	44	12	69.6	3.3	93.4	71.7	27	19
	TL	-	-	-	19.8	41.3	19.6	39	7
M3	FL	18	17	46.1	4.1	89.3	80.4	36	1
	SL	99	26	70	3.4	94.9	100	42	1
	PL	92	3	75.7	3.4	88.1	65.2	22	1
	TR	62	19	57.7	7.3	83.6	76.1	27	5
	TL	-	-	-	20.5	41.8	34.8	13	5

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966 Table 4: Fossil identification for m1 and M3. The number of specimens identified with associated posterior probabilities > 0.9 are in brackets

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		m1				M3				
Sites	Genera	m1FL	m1SL	m1AL	m1TL	M3FL	M3SL	M3PL	M3TR	M3TL
Gully Cave (Younger Dryas)	<i>Myopus</i>	0 (0)	0 (0)	3 (3)	3 (0)	2 (0)	0 (0)	2 (0)	1 (1)	3 (0)
	<i>Lemmus</i>	12 (12)	12 (12)	9 (2)	9 (0)	15 (15)	17 (16)	15 (10)	16 (1)	14 (2)
Gully Cave (Allerød-Younger Dryas)	<i>Myopus</i>	6 (4)	1 (1)	13 (9)	3 (0)	2 (1)	1 (1)	10 (6)	3 (1)	1 (0)
	<i>Lemmus</i>	17 (10)	22 (22)	10 (9)	20 (3)	24 (19)	25 (25)	16 (9)	23 (19)	25 (12)
Grotte des Gorges	<i>Myopus</i>	2 (2)	1 (1)	3 (3)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	<i>Lemmus</i>	9 (9)	10 (9)	8 (7)	10 (6)	3 (2)	3 (3)	3 (3)	3 (3)	3 (3)

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