

1 **Divergent in shape and convergent in function: adaptive evolution of the mandible in Sub-Antarctic**
2 **mice**

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19

20 **Abstract**

21 Convergent evolution in similar environments constitutes strong evidence of adaptive evolution.
22 Transported with people around the world, house mice colonized even remote areas, such as Sub-
23 Antarctic islands. There, they returned to a feral way of life, shifting towards a diet enriched in
24 terrestrial macroinvertebrates.

25 Here, we test the hypothesis that this triggered convergent evolution of the mandible, a
26 morphological character involved in food consumption. Mandible shape from four Sub-Antarctic
27 islands was compared to phylogeny, tracing the history of colonization, and climatic conditions.

28 Mandible shape was primarily influenced by phylogenetic history, thus discarding the hypothesis of
29 convergent evolution.

30 The biomechanical properties of the jaw were then investigated. Incisor in-lever and temporalis out-
31 lever suggested an increase in the velocity of incisor biting, in agreement with observations on
32 various carnivorous and insectivorous rodents. The mechanical advantage related to incisor biting
33 also revealed an increased functional performance in Sub-Antarctic populations, and appears to be
34 an adaptation to catch prey more efficiently. The amount of change involved was larger than
35 expected for a plastic response, suggesting microevolutionary processes were evolved.

36 This study thus denotes some degree of adaptive convergent evolution related to changes in habitat-
37 related changes in dietary items in Sub-Antarctic mice, but only regarding simple, functionally
38 relevant aspects of mandible morphology.

39

40 **Keywords**

41 *Mus musculus domesticus*; geometric morphometrics; adaptive convergence; mouse mandible;
42 biomechanics

43

44 **Introduction**

45 Convergent evolution in response to similar environments constitutes one of the most convincing
46 lines of evidence for adaptive evolution (Harmon et al. 2005). It has been shown in traits as diverse as
47 limbs in lizards (Losos et al. 1997), plates, pelvis shape and oral jaws in fishes (Albertson et al. 2003;
48 Shapiro et al. 2006; Marchinko and Schluter 2007), and head morphology in snakes (Aubret and
49 Shine 2009). However, similar functional performance can be achieved by different shapes
50 (Wainwright et al. 2005). Regarding complex traits, convergent adaptation may thus be obscured by
51 the fact that only some aspects will be functionally relevant and hence prone to convergent
52 evolution.

53 The house mouse (*Mus musculus domesticus*) is a highly successful global invader (Lowe et al. 2000).
54 Being commensal, it followed the movement of people around the world and, consequently, is now
55 present on four continents. It colonized even remote and inhospitable environments, such as Sub-
56 Antarctic islands. On these remote islands, the mice face considerable environmental stresses (Berry
57 et al. 1978), with conditions widely departing from their usual commensal habits. These result in
58 strong selective pressures for adapting to the local environments that could trigger convergent
59 evolution. Among the traits that might be under selection, those related to food exploitation would
60 have been important for the survival of the colonizing individuals. Mice shifted their diet from their
61 usual omnivorous-granivorous diet to a larger proportion of terrestrial animal prey, mostly above-
62 ground and litter macroinvertebrates in various Sub-Antarctic islands (Gleeson and Van Rensburg
63 1982; Copson 1986; Rowe-Rowe et al. 1989; Chown and Smith 1993; Le Roux et al. 2002; Smith et al.
64 2002; van Aarde and Jackson 2007). An associated change in mandible shape was documented in
65 mice from the small Guillou Island within the Kerguelen archipelago (Renaud et al. 2013), which
66 provided a functional advantage in biomechanical ratios (Renaud et al. 2015) and was interpreted as
67 an adaptive response to the dietary change of the mice on Guillou Island. It is thus a strong candidate
68 to test convergent morphological evolution in mouse populations that colonized different Sub-
69 Antarctic islands.

70 Here, the mandible shape of the house mice was thus quantified using 2D geometric morphometrics
71 for specimens coming from three remote Sub-Antarctic areas: Falklands, Marion Island, and the
72 Kerguelen archipelago (Fig. 1). As shown by phylogenetic data, colonization of the different islands
73 occurred independently, from different sources populations (Hardouin et al. 2010). Even on the
74 Kerguelen archipelago, two independent colonization events occurred, with two islets having a
75 different phylogenetic signature than the rest of the archipelago (Hardouin et al. 2010). Guillou

76 Island is inhabited by the most common Kerguelen haplogroup, and Cochons Island by the second,
77 more restricted haplogroup. The functional performance of the mandible shape was assessed using
78 out-lever arms describing incisor and molar biting; and out-lever arms approximating the action of
79 the main masticatory muscles. Biomechanical ratios (Anderson et al. 2014) were derived from these
80 in- and out-levers, which were also described as a landmark configuration using geometric
81 morphometrics. A phylogenetic study based on the mitochondrial D-loop and nuclear microsatellites
82 provided a background about the colonization history of each insular population. The objectives of
83 this study were thus: (1) Can convergent morphological evolution be evidenced on the different Sub-
84 Antarctic islands; and (2) Is the convergent evolution more evident in functionally relevant traits than
85 on the overall jaw shape?

86

87 **Material and Methods**

88 ***Material***

89 Four Sub-Antarctic islands were sampled (Fig. 1). Two small islands from the Kerguelen Archipelago
90 (Sub-Antarctic Indian Ocean) were considered, corresponding to different waves of colonization and
91 thus having a distinct genetic signature (Hardouin et al. 2010): Cochons Island and Guillou Island. The
92 Cochons Island sample included 38 mice trapped in 2009 (Program IPEV n°136, J.-L. Chapuis).
93 Temporal variation in mandible shape has been documented in Guillou (Renaud et al. 2013), but
94 does not notably affect the biomechanical parameters of the mandible (Renaud et al. 2015). Two
95 time periods were therefore included in the present analysis, documenting the earliest and latest
96 record available (1993, 18 mice and 2009, 22 mice) (Program IPEV n°136, J.-L. Chapuis). The sample
97 from New Island from the Falklands (south-western Atlantic) included 15 mice captured in 2006 and
98 2010 by the team of Petra Quillfeldt. These Kerguelen and Falklands specimens were prepared and
99 are currently stored at the LBBE, Lyon. The sample from Marion Island, off South Africa, was
100 composed of 12 mice captured in 1997 (collection Institut des Sciences de l'Évolution, Montpellier,
101 France). All of these islands are deprived of permanent human settlement and mice returned to a
102 feral way of life, mainly relying on habitat driven food resources for their maintenance.

103 A large proportion of macroinvertebrate prey has been documented for mice from the Kerguelen (Le
104 Roux et al. 2002) and Marion Island (Smith et al. 2002; van Aarde and Jackson 2007) based on
105 stomach contents. Since a similar shift in diet has also been evidenced in the population from
106 Macquarie Islands (Copson 1986), such foraging behavior was hypothesized for the Falkland

107 population. For comparison, two commensal populations from Western Europe were considered:
108 Gardouch, France and Cologne-Bonn, Germany (68 and 14 mice respectively; Gardouch: collection of
109 the Centre de Biologie et Gestion des Populations, Montpellier, France; Cologne-Bonn: provided by
110 the Max Plank Institute for Evolutionary Biology, Plön, Germany, prepared and currently stored at
111 the LBBE, Lyon) (Renaud et al. 2015). All mice considered were sub-adults and adults, the criteria
112 being the eruption of the third molars that occurs at weaning. Sexual dimorphism was not evidenced
113 in mandible shape in such populations (Renaud et al. 2013). Hence, males and females were pooled
114 for further analyses.

115 Mitochondrial D-loop sequences and 18 microsatellites corresponding to mice from these islands and
116 Western European localities were retrieved from previously published studies (Ihle et al. 2006;
117 Hardouin et al. 2010).

118

119 **Methods**

120 *Phylogenetics*

121 A phylogenetic tree was calculated using Mr. Bayes (Ronquist et al. 2012) and PhyML (Guindon et al.
122 2010) using the substitution model HKY+I+G infer using jmodeltest (Guindon and Gascuel 2003;
123 Darriba et al. 2012). *M. m. musculus* (DQ266060) and *M. m. castaneus* (DQ266061) were used as
124 outgroup. The generation number was set at 5 000 000 with 25% of burn-in. The tree was visualized
125 using FigTree v1.3 (Rambaut 2012). The numbers of haplotypes and haplotype diversity per
126 populations were calculated using DNAsp (Librado and Rozas 2009). Pairwise Fst values using the
127 mitochondrial D-loop were calculated using Arlequin (Excoffier and Licher 2010).

128 The 18 microsatellites were analyzed using the package adegenet (Jombart 2008). The population
129 structure was identified with a Discriminant Analysis of Principal Components (DAPC) (Jombart et al.
130 2010).

131

132 *Mandible size and shape*

133 Mandibles (Fig. 2A) were photographed using a Leica MZ stereomicroscope. The mandible shape was
134 quantified by the 2D outline of the mandibular bone (Fig. 2B), the hemi-mandible being placed flat on
135 its lingual side. The starting point of the outline was positioned at the upper connection between the

136 incisor and the bone, and 64 points were sampled at equal curvilinear distance along the outline
137 using the image analyzing software Optimas 6.5, from which 64 radii (distance from each point to the
138 center of gravity) were calculated. This series was analyzed using a Fourier-based method,
139 decomposing it into a sum of trigonometric functions of decreasing wavelength (harmonic), each
140 weighted by two Fourier coefficients (FCs). The zero harmonic A0 was used as a size estimator and to
141 standardize all other FCs. Seven harmonics (i.e. 14 FCs) were deemed sufficient for describing the
142 mandible shape and filtering measurement error (Renaud and Michaux 2003).

143 By comparing function(s) of a curve, and not the points collected on the outline, Fourier methods
144 allow investigation of shapes deprived of or with few landmarks with clear homology (Bonhomme et
145 al. 2014; Dujardin et al. 2014). Regarding the mandible, most landmarks are located along the
146 outline, and correspond to maxima of curvature (landmarks of type 2). An outline analysis captures
147 this morphological information together with the curvature of the processes and anterior part.
148 Compared to sliding semi-landmarks, outline analyses perform equally well (Sheet et al. 2006), but
149 allow a reduction in the number of variables, by retaining first harmonics only. In the present case, it
150 has the further advantage of quantifying mandible shape without relying on landmarks that were
151 used for biomechanical estimates, thus avoiding any risk of redundancy between the two datasets.

152 Shape differences were described into the morphospace defined by the first axes of a principal
153 component analysis (PCA) on the variance-covariance matrix of the FCs. Univariate differences
154 between groups in mandible size were investigated using a Kruskal-Wallis test and associated
155 pairwise Mann-Whitney tests using Past3 (Hammer et al. 2001).

156 The PCA was run using the package ade4 (Dray and Dufour 2007) in the R environment (R-Core-Team
157 2017). Multivariate differences in mandible shape between groups were tested using a
158 permutational multivariate analysis of variance (Permanova; significance estimated based on 9999
159 permutations) on the 14 FCs using Past3 (Hammer et al. 2001).

160

161 *Biomechanical analysis of the mandible*

162 The mechanical advantage is a measure of the efficiency of mandible geometry to transmit force
163 from the muscles to the bite point. It can be estimated as the ratio of the in-lever (distance from the
164 condyle to the point of muscle attachment) and the out-lever (distance from the condyle to the bite
165 point) (Hiemae 1971). Out-levers (Fig. 2C) were estimated as the distance from the condylar
166 articulation (playing here the role of fulcrum) to the incisor tip, and to the first molar hypocond.

167 Three in-levers were measured (Fig. 2C). The effect of the deep masseter was approximated by the
168 distance from the condyle to the anterior boundary of the angular process, towards the ventral
169 margin of the masseteric fossa, where it attaches. The effect of the superficial masseter was
170 approximated by considering the distance from the condyle to the posterior tip of the angular
171 process. The distance from the condyle to the posterior tip of the coronoid described the action of
172 the temporalis (Anderson et al. 2014; Renaud et al. 2015). The temporalis is mostly used together
173 with incisors for gnawing, whereas the masseter and molars are involved in the action of mastication.
174 The masseter also contributes to bringing the incisors into occlusion. Four mechanical advantages
175 were therefore considered: temporalis/incisor, superficial master/ incisor, superficial
176 masseter/molar, and deep masseter/molar.

177 In- and out-lever distances were calculated from landmark coordinates registered using TPSdig2
178 (Rohlf 2010a). This set of six landmarks was also investigated using geometric morphometrics. The
179 coordinates were aligned, scaled and rotated using a generalized least squares Procrustes
180 superimposition. A principal component analysis was performed on the resulting aligned coordinates
181 using TPSrelw 1.49 (Rohlf 2010b). Visualization of shape changes between group means were
182 obtained using the R package geomorph (Adams and Otárola-Castillo 2013).

183 Finally, the values of the in- and out-levers themselves were considered. To discard any effect of size
184 differences between mandibles, they were computed from the aligned coordinates, hence being
185 standardized by centroid size (e.g. the square root of the sum of squared distance of each landmark
186 to the centroid of the configuration).

187 Univariate differences between groups regarding the in- and out-lever arms and the mechanical
188 advantages were investigated using Kruskal-Wallis tests and associated pairwise Mann-Whitney tests
189 using PAST3 (Hammer et al. 2001). The Kruskal-Wallis test is a non-parametric analogue of an
190 analysis of variance. Being ultimately based on a ranking of the values, it is appropriate even for non-
191 normal variables, such as ratios. Relationships between parameters were assessed using a Pearson's
192 product-moment correlation estimated with R.

193

194 *Measurement error*

195 To assess how much importance of measurement error might impact the results, the mandible
196 outline and the in- and out-lever distances of the 15 specimens from New Islands were measured
197 twice, at an interval of several months. Differences between the two sets of measures were tested

198 using Kruskal-Wallis tests for mandible size, in- and out-levers, and biomechanical ratios. The
199 difference in mandible shape was tested using a permanova (9999 replications) on the 14 FCs and on
200 the aligned coordinates of the biomechanical landmark configuration.

201

202 *Influence of phylogeny and climate on morphology*

203 The relative influences of phylogeny and climate on morphology were investigated using linear
204 models. The variables to be explained were (1) mandible shape, described by the set of PC axes
205 explaining more than 5% of variance, based on the outline analysis; and (2) the biomechanical ratios
206 considered separately.

207 The explanatory sets of variables were constructed as follows:

208 (1) Climatic data were extracted from the WorldClim database with a resolution of 2.5 arc-min
209 using the raster package (Hijmans 2014). The 19 bioclimatic variables available were
210 retrieved: Annual Mean Temperature, Mean Diurnal Range [Mean of monthly (max temp -
211 min temp)], Isothermality, Temperature Seasonality (standard deviation *100), Max
212 Temperature of Warmest Month, Min Temperature of Coldest Month, Temperature Annual
213 Range, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean
214 Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Annual
215 Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month, Precipitation
216 Seasonality (Coefficient of Variation), Precipitation of Wettest Quarter, Precipitation of Driest
217 Quarter, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter. These variables
218 are based on average monthly climate data for minimum, mean, and maximum temperature
219 and for precipitation for the period 1960-1990. They were summarized using a PCA on the
220 correlation matrix. Axes explaining more than 5% of variance were kept in the model. These
221 climatic data were used as a proxy of the local conditions, and hence, indirectly, of the food
222 resources available to mice.

223 (2) Phylogeny was first assessed using mitochondrial D-loop sequences. Fst distances were
224 computed among the six groups (France, Germany, and the four Sub-Antarctic islands). A
225 Principal Coordinate Analysis (PCOA) was performed on this distance matrix using ade4 (Dray
226 and Dufour 2007). The set of axes > 5% were retained in the linear model.

227 (3) Phylogenetic relationships between islands and Western European localities were further
228 assessed using the microsatellites data. The axes of the DAPC > 5% of variance were retained
229 in the linear model. Because of possible redundancy between both phylogenetic data sets,
230 separate models were built with D-loop and microsatellite data.

231 The percentage of variance explained (pve) by each set of explanatory variables and the
232 associated p-value were assessed using the R package *ffmanova* (Langsrud and Mevik 2012). This
233 method is based on type II sum of squares, which has the advantage of being invariant to
234 ordering of the model terms; the *ffmanova* also handles colinear responses. It may inflate the
235 pve but allows an estimation of the relative importance of the explanatory variables.

236

237 **Results**

238 *Phylogeny*

239 Regarding the D-loop data, the continental Western European groups were highly variable (Fig. 3A;
240 Supp. Table 1), each including several of the main haplogroups described in the mouse (Bonhomme
241 et al. 2011; Jones et al. 2013). In contrast, each island displayed a very restricted genetic diversity
242 (Supp. Table 1), evidence of a founder effect, and subsequent resilience to late invaders in these
243 remote environments (Hardouin et al. 2010). Each of the Sub-Antarctic populations considered has
244 its own phylogeographic signature, underlining that each island was colonized independently from a
245 different source population. The only exception is New Island (Falklands) and Guillou Island
246 (Kerguelen), sharing a similar haplotype. These two populations differ, however, when considering
247 their microsatellite signature (Hardouin et al. 2010) (Fig. 3B). Their common haplotypic signature may
248 be the result of common source of colonization, related to the main harbors where whalers came
249 from or made stop on their way to Sub-Antarctic oceans.

250 *Measurement error*

251 The two sets of measurements of the 15 New Island specimens did not differ in mandible size (A0: P
252 = 0.852) nor shape (set of 14 FCs: P = 0.986). They did not differ for any of the scaled in- and out-
253 lever measurements (Incisor: P = 0.548; Molar: P = 0.852; Coronoid: P = 0.548; tip of the angular
254 process: P = 0.373; anterior boundary of the angular process: P = 0.191). As a consequence, none of
255 the mechanical advantage differed between the two replicates (temporalis/incisor: P = 0.633; sup.
256 masseter/ incisor: P = 0.351; sup. masseter/molar: P = 0.494; deep masseter/molar: P = 0.054).

257 Finally, the configuration of biomechanical landmarks did not differ between replicates (permanova
258 on the aligned coordinates: $P = 0.661$).

259

260 *Mandible size and shape*

261 Mandible size was variable among mainland and insular populations ($P < 0.0001$; pairwise tests:
262 Table 1). Mandibles were the largest on Marion Island. The smallest were documented on New Island
263 (Falklands) and for the mice trapped on Guillou Island (Kerguelen) in the earliest record, 1993 (Fig.
264 4A). Western European populations were variable and overall intermediate between the insular
265 ones.

266 Regarding mandible shape, three axes of the PCA on the Fourier coefficients explained more than 5%
267 of the total variance (PC1: 49.8%, PC2 = 25.3; PC3: 11.8%, PC4 = 4.7%). On the first principal plane,
268 populations from Western Europe were grouped on one side of the morphospace (Fig. 4B). All insular
269 populations were different from this reference shape (permanova $P < 0.0001$ for all pairwise tests).
270 Mandibles from the two Kerguelen islands, Cochons and Guillou, were shifted along the first axis
271 (49.8% of total variance). Mandibles from Guillou caught in 1993 were the most divergent along this
272 axis. Mandibles from New Island (Falklands) were divergent mostly along the second axis (25.3%).
273 Marion Island was slightly divergent from Western Europe along the second axis but mostly along the
274 third axis (11.8%) together with Cochons Island (Kerguelen) (data not shown).

275 These differences, although statistically highly significant, were subtle in terms of shape (Fig. 4C).
276 Mandibles from Guillou, Cochons and New Island tended to display a reduced angular process.
277 Guillou mandibles also had a ventrally narrower molar zone than continental mice. Marion mandibles
278 displayed a pronounced angular process, originating from a smooth ventral edge of a ventrally
279 narrow molar zone.

280 *Biomechanics*

281 First, the geometric morphometric analysis of the six biomechanically relevant landmarks (Fig. 5)
282 provided an image of the differentiation between populations close to the one delivered by the
283 outline analysis. Continental mandibles cluster together, and Sub-Antarctic populations differ in
284 different directions around this cluster. Similar to the outline analysis, Marion and Guillou mandibles
285 are the most differentiated, New Island mandibles being rather intermediate. Based on the six
286 landmarks, Cochons mandibles fall close to New Island ones. These two populations share a

287 backward shift of the tip of the angular process together with an anterior shift of its anterior edge.
288 Marion mandibles share a posteriorly shifted tip of the angular process, but associated with a
289 forward shift of the coronoid tip. Guillou mandibles display an anterior shift of the angular anterior
290 edge, but associated with a backward shift of the coronoid tip.

291 These geometric differences translated into differences in the scaled in- and out-lever arms (Fig. 6;
292 Table 2). The most consistent patterns shared by all Sub-Antarctic populations and differentiating
293 them from continental ones were: (1) an increased incisor out-lever. A longer out-lever arm favors
294 speed to the detriment of force at the point of occlusion. (2) An increased temporalis in-lever arm.
295 (3) A decreased in-lever arm characterizing the tip of the angular process, approximating the action
296 of the superficial masseter.

297 These differences in out- and in-lever arms had consequences on the mechanical advantages (MA)
298 characterizing the main systems for biting (Fig. 7; Table 3). The most consistent pattern is displayed
299 by the superficial masseter/incisor MA, for which all islands were highly significantly below
300 continental values, but did not differ between them (Table 3). All islands also strongly differed from
301 the continental values for the superficial masseter/molar MA, islands displaying lower values than
302 the continent, but differences existed between islands. The temporal/incisor MA tended to be higher
303 in Sub-Antarctic mice than on the continent, but this difference was less pronounced for Marion
304 island. Finally, the deep masseter/molar MA was the less consistent among islands, with Cochons
305 and New Island displaying values similar to the continent.

306 Overall, this resulted in a negative relationship between the temporal/incisor and superficial
307 masseter/molar MA (Fig. 7E) ($R = -0.584$, $P < 0.001$). This relationship may reflect a trade-off existing
308 even within populations, since a similar relationship was evidenced within the well-sampled
309 population from Gardouch ($R = -0.318$, $P = 0.008$).

310

311 *Relationship between morphology, phylogeny and climate*

312 Models considering mandible geometry and biomechanical properties in relation to phylogeny and
313 climate were investigated. Sets of variables to be explained were defined as follow. (1) Mandible
314 shape was described by the first three axes of the PCA on the 14 FCs, these axes explaining more
315 than 5% of variance (see above). (2) Several biomechanical advantages were further considered
316 separately in relation to phylogeny and climate. Regarding explanatory variables, the sets of variables
317 were designed as follow. (1) Environmental conditions were summarized by the first three axes of a

318 PCA on the 19 bioclimatic variables of WorldClim. These three axes explained more than 5% of
319 variance (63.0%, 25.9%, 8.5%). The climate clearly opposes the continental localities to all Sub-
320 Antarctic islands, Marion displaying the most extreme conditions. This set of variables will thus tend
321 to characterize the Sub-Antarctic environment vs. continental conditions. (2) The phylogeny based on
322 D-loop sequences was summarized by the first three axes of a PCOA on the Fst matrix (Supp. Table
323 2), all explaining more than 5% of variance (48.7%, 32.2%, 18.9%). (3) The phylogenetic relationships
324 based on the microsatellites were summarized by the first three axes of the DAPC on the 18
325 microsatellites (68.2%, 21.0%, 6.4% of variance, respectively).

326 Considering first phylogeny estimated by the D-loop, the model for mandible shape indicated a
327 primary influence of phylogeny (12.6%) and a lesser influence of climate (9.4%), both factors being
328 significant.

329 Regarding the mechanical advantages, all were primarily correlated with climate and only secondarily
330 with phylogeny (temporalis/incisor: climate = 18.1%, phylogeny = 9.6%; deep masseter/molar:
331 climate = 22.3%, phylogeny = 14.0%; superficial masseter/molar: climate = 37.5%, phylogeny =
332 10.4%; superficial masseter/incisor: climate = 17.9%, phylogeny = 3.1%).

333 These results were corroborated when considering the phylogenetic relationships based on
334 microsatellites. Phylogeny explained 12.6% of mandible shape, whereas climate explained only 6.1%.
335 Mechanical advantages were all better explained by climate (temporal/incisor: climate = 18.1%,
336 microsatellites = 9.6%; deep masseter/molar: climate = 17.4%, microsatellites = 14.0%; superficial
337 masseter/molar: climate = 28.5%, microsatellites = 10.4%; superficial masseter/incisor: climate =
338 13.1%, phylogeny = 3.1%).

339

340 **Discussion**

341 *Divergence in mandible shape primarily influenced by phylogeny*

342 This study demonstrates a divergence of mouse jaws in these four Sub-Antarctic islands when
343 compared to the Western European continental morphology. This matches previous results showing
344 a divergence of insular jaw morphologies in settings as diverse as Faroe in the North Atlantic (Davis
345 1983), and Corsica and Sardinia in the Mediterranean Sea (Renaud and Auffray 2010). The
346 phylogenetic source of the founding population appeared of primary importance in the
347 diversification. These results echo recent findings on mouse tooth shape (Ledevin et al. 2016),

348 suggesting that constraints related to the set of founder individuals constrain the subsequent
349 diversification. As a consequence, despite a significant role of environmental conditions driving
350 divergence, mandible shape from the different Sub-Antarctic populations did not diverge from the
351 continental Western Europe towards a common morphology. Each population displayed its own
352 idiosyncratic morphological signature.

353 Surprisingly, mandible size did not display a coherent increase in insular populations. Some
354 populations (New Island from [Falklands], Guillou [Kerguelen]) even displayed smaller mandible size
355 than continental populations. Covariation between mandible and body size has been repeatedly
356 evidenced, between and within populations, in rodents (Cardini and Tongiorgi 2003; Renaud 2005)
357 including house mice (Renaud et al. 2017). If mandible size is considered as a rough estimate for body
358 size, it might have been expected to increase due to the combined effect of two well-known rules.
359 First, the Bergman's rule predicts increased body size in mammals towards high latitude (Meiri and
360 Dayan 2003). Second, the insular rule predicts that small mammals should become larger on islands
361 (Lomolino 1985, 2005). However, the results suggest no consistent trends in size despite the
362 supposed combination of the Bergman's and island rules regarding our insular samples. Possibly, the
363 mice are close to their physiological limits in Sub-Antarctic environments (Berry et al. 1978), and low
364 availability in resources of quality may limit growth in body and even investment in skeletal traits
365 such as the mandible (Renaud et al. 2015). Such limitation may vary from island to island, explaining
366 the range of variation from the small Guillou and the large Marion mandibles.

367

368 *Functional adaptation to an increased role of prey catching*

369 To focus on potential adaptive traits, the mandible geometry was also described by a simple set of
370 landmarks describing functionally relevant in- and out-levers. The geometry of this landmark
371 configuration shows, as the outline analysis, continental mice from Western Europe sharing a similar
372 zone of the morphospace, and Sub-Antarctic populations diverging from them in different directions.
373 Guillou and Marion mandibles appear, once again, the most different among Sub-Antarctic ones.

374 However, when considering in- and out-lever arms based on this geometry, some consistent patterns
375 emerged. Sub-Antarctic mice share an increase in the incisor out-lever. Such increased out-lever arm
376 is unfavorable to bite force, but favors velocity. Such trait facilitates the capture of prey and
377 accordingly, an elongated rostrum has been evidenced in insectivorous rodents (Samuels 2009). Sub-
378 Antarctic mice further share an increase in the temporalis in-lever arm. The temporalis plays a role in

379 moving incisors into occlusion (Baverstock et al. 2013), another important aspect for catching prey.
380 An increase in the in-lever arm is favorable to increased bite force, and may compensate the
381 elongation of the out-lever. Sub-Antarctic mandibles also tend to share a decrease in the superficial
382 masseter in-lever, although this decrease is less pronounced for Marion mandibles. The molar out-
383 lever and the deep masseter in-lever do not show consistent trends among Sub-Antarctic mice,
384 evidencing their mosaic divergence from the continental stock.

385 As a consequence of these differences in the in- and out-lever values, consistent differences
386 characterizing Sub-Antarctic mice also emerged when considering their ratios, i.e. mechanical
387 advantages, characterizing the biomechanical efficiency of the mandible tool. Three consistent
388 trends were evidenced. First, despite the increase of the incisor out-lever, the temporalis/incisor MA
389 is increased in Sub-Antarctic mice. In contrast, the superficial masseter/incisor MA is decreased.
390 Increased action of the temporalis and decreased contribution of the masseter have been described
391 in carnivorous murine rodents (Fabre et al. 2017). They may contribute, together with the increased
392 incisor out-lever arm, to an action favoring speed instead of force at incisor biting. This constitutes an
393 adaptation to the food resources of Sub-Antarctic mice, which largely prey on macro-invertebrates
394 (Copson 1986; Le Roux et al. 2002; Smith et al. 2002; van Aarde and Jackson 2007). Sub-Antarctic
395 mice also share a decrease in the superficial masseter/molar MA, which seems detrimental to exert
396 force at molar biting. Possibly, this aspect related to chewing resistant food became less important
397 than in continental mice, which being commensal, mostly rely on seeds and other items of vegetal
398 origin in an agricultural context.

399 The different Sub-Antarctic populations do not share exactly the same resources, being context
400 dependent on the availability of local fauna and flora, plus is influenced by climate, for instance
401 preventing access to subterranean invertebrates such as earthworms (Le Roux et al. 2002). Some
402 Sub-Antarctic populations even include vertebrate prey, such as chicks of sea birds, in their diet
403 (Cuthbert and Hilton 2004). These differences may contribute to explain why the different
404 populations did not achieve exactly the same biomechanical signature. Adaptation to local food
405 resources may further include the muscle architecture (Satoh and Iwaku 2006), or even the digestive
406 system (Samuels 2009), but the role of these aspects in adaptation at the intra-specific level remain
407 to be documented.

408

409 *Adaptive mechanical convergence despite morphological differentiation*

410 The mandibles of the different Sub-Antarctic islands thus display a similar adaptive shift in functional
411 aspects that does not echo any similar evolution in shape (Alfaro et al. 2004; Wainwright 2007). Shall
412 this evolutionary pattern be termed convergence, or parallelism? Considering that continental mice
413 share a similar morphology, the repeated evolution from this common ancestor morphology of
414 'insectivorous-like' biomechanical properties may be termed parallelism. However, continental
415 populations also displayed some differences, and the phylogenetic data clearly show that the
416 ancestral stocks invading each island were indeed different. We therefore favor the term of
417 convergent evolution, although in the present case, parallelism and convergence may be very close.

418 Tools can achieve the same function even when having differences in shape, leading to a many-to-
419 one mapping of form to function (Wainwright et al. 2005; Wainwright 2007; Losos 2011). The mouse
420 mandible may display here such a complex relationship between shape and function, exemplifying
421 results of modelling suggesting that convergence can be demonstrated only when considering a
422 simplified genotype-phenotype map (Salazar-Ciudad and Marín-Riera 2013). Morphological details,
423 such as those captured by the morphometric analysis, may trace phylogenetic idiosyncrasy that are
424 not of functional relevance and thus not prone to adaptive evolution, corresponding to 'neutral
425 morphological evolution' (Wainwright 2007). They may also correspond to different ways to achieve
426 the same functional change, and/or correspond to different fine tuning to local resources. In
427 contrast, considering simple ratios, such as the mechanical advantage, may place the focus on
428 functionally relevant features prone to the detection of adaptive convergence.

429 Indeed, many documented instances of convergent evolution rely on simple morphological
430 estimates, such as jaw length in snakes (Aubret et al. 2004), in- and out-levers in cichlid fishes' jaws
431 (Albertson et al. 2003), number of plates in sticklebacks (Marchinko and Schluter 2007) or limb
432 length in lizards (Losos et al. 1997; Calsbeek and Irschick 2007). When complex traits are considered,
433 multidimensional aspects of the niche partitioning may be involved (Harmon et al. 2005), further
434 complicating the identification of convergent evolution.

435

436 *Decrease of performance of other functions of the mandible*

437 While our results indicate an adaptive improvement in the functioning of biting at the incisors, we
438 observed at the same time a decrease in the mechanical advantage associated with chewing at the
439 molars (Baverstock et al. 2013). This masseter/molar complex is used primarily in the consumption of
440 hard or resistant food items. This type of functioning should be important for commensal mice

441 feeding mostly on grains in agricultural buildings, but should become less relevant for Sub-Antarctic
442 mice relying on other food resources. The decrease in the masseter / molar mechanical advantage is
443 thus probably related to a relaxation of the pressure on this function. Previously observed on Guillou
444 Island (Kerguelen) (Renaud et al. 2015), this decrease in performance of the masseter / molar
445 complex appears as a general feature of the Sub-Antarctic mice. Beyond the relaxation of the
446 pressure related to mastication, this decrease in performance may correspond to a trade-off
447 between incisor and molar biting. Since the negative relationship between the temporalis/incisor and
448 masseter/molar mechanical advantages is also displayed at the intra-population level, it supports the
449 idea that optimizing one of the functions is detrimental to the other. The mandible of omnivorous
450 murine rodents is known as a paradigm example of a versatile generalist tool adapted to all feeding
451 modes (Cox et al. 2012). Yet, species specializing towards carnivory or insectivory display specific
452 adaptations that modulate this generalist morphology (Samuels 2009; Fabre et al. 2017). The case of
453 the Sub-Antarctic mice suggests that such fine-tuning may occur even at the intra-specific level.

454

455 *Plasticity and/or heritable changes?*

456 The question arises of the mechanisms involved in this convergent biomechanical response. Only
457 experiments could definitely answer this issue, but these are difficult for animals from such remote
458 places. A comparison with a former experiment on laboratory mice may however shed some light on
459 this aspect. Inbred laboratory mice were bred from weaning up to six months on food of different
460 consistency: one group was fed the regular rodent pellets (considered as hard food), another group
461 the same food served as jelly (soft food). This difference in food consistency triggered a change in
462 mandible shape (Renaud and Auffray 2010). This shape change was shown to have mechanical
463 consequences: the temporalis/incisor and masseter/molar mechanical advantages both decreased in
464 the mice served food as jelly (Anderson et al. 2014). For both mechanical advantages, the decrease
465 was by 3-6% (Anderson et al. 2014). This was interpreted as a difference in bone remodeling that
466 occurs in response to stimulations by muscle activity. Mandibles subjected to less activity resulted in
467 less efficient morphologies.

468 The decrease in performance observed for the masseter/molar complex in Sub-Antarctic mice (-3.2%
469 for Marion Island up to -5.7% for Guillou Island [Kerguelen] in 2009) falls within the range of values
470 compatible with the plastic response observed in laboratory mice. In contrast, the increase in
471 performance for the temporalis/incisor complex (+7.2% for Marion Island up to +20.1% for New

472 Island [Falklands]) by far exceeds the plastic change in laboratory mice, which was however related
473 to a substantial change in food consistency (Anderson et al. 2014).

474 This adaptive increase in performance of the temporalis/incisor complex may not be only due to
475 plasticity. The occurrence of the convergent response in several independent cases indicates that
476 directional selection related to a similar diet shift likely drove this morphological change. Even if
477 plastic response allows the first step of response following invasion, genetic assimilation will likely
478 take over and lead to selection for gene coding for the new morphology (Aubret and Shine 2009).
479 Sub-Antarctic islands have been colonized by explorers and whalers in the course of the 19th century
480 [e.g. (Frenot et al. 2001)], and evidence of mice on these islands date back to the middle of the 19th
481 century (Kidder 1876). Thus, mice had more than hundred years to evolve, and thus probably more
482 than 500 generations (considering a generation time of three or four generations per year). This time
483 lapse is short compared to usual evolutionary scale, but large compared to recent findings of
484 contemporary evolution (Reznick and Ghalambor 2001; Collyer et al. 2007; Kinnison and Hairston
485 2007).

486 In contrast, the masseter/molar mechanical advantage decreased by about what would be expected
487 for a plastic response, based on the laboratory experiment (Anderson et al. 2014). Since no
488 directional selection was exerted on it, and instead there was a release of selection, the
489 morphological signal may simply correspond to a plastic response, due to less muscular stress
490 exerted on the mandible in relation with a decrease of the consumption of hard / resistant food.

491

492 **Conclusions**

493 The results indicate a convergent adaptive evolution of the biomechanical function of the jaw of Sub-
494 Antarctic mice, related to their shift towards a diet enriched with invertebrate prey. Yet, the adaptive
495 component of this morphological change was only evidenced when considering simple but
496 mechanically relevant in- and out-levers, and their ratios. When considering shape in all its
497 complexity, the dominant signal was the idiosyncrasy of each insular population, related to its history
498 of colonization and possibly, fine-tuned response to local resources. The amount of adaptive
499 morphological change appears larger than expected for a plastic response due to bone remodeling
500 under the action of the masticatory muscles. This suggests that even if plasticity contributed in the
501 first step of the mouse establishment on a new island, genetic assimilation likely took place over the
502 century or more of insular evolution. This complex relationship between shape evolution and the

503 adaptive response may render the identification of underlying genetic changes more complex than
 504 for more simple traits. Possibly, each island reached adaptive morphology by the selection of
 505 different genes and by tinkering the gene pool inherited from the founder population.

506

507 **Acknowledgements**

508 Jean-Pierre Quéré (CBGP Montpellier) is thanked for access to his collection and Louise Souquet and
 509 Lionel Hautier for numerous discussions. Professor Robert Britton contributed to improve the writing
 510 of the manuscript. We thank two anonymous reviewers and J.X. Samuel, as well as the editor Alistair
 511 Evans, for their constructive and challenging remarks that greatly improved this study. This study was
 512 supported by the French Polar Institute (IPEV programme 136), and by the CNRS (zone atelier de
 513 Recherches sur l'Environnement Antarctique et Subantarctique), and by the ANR Bigtooth (ANR-AA-
 514 BSV7-008). Emilie A. Hardouin benefited from an invited lecturer scholarship of the University Lyon 1
 515 that eased the redaction of the manuscript.

516

517 **Data Archiving**

518 Title: Data from: Divergent in shape and convergent in function: adaptive evolution of the mandible
 519 in Sub-Antarctic mice
 520 DOI: doi:10.5061/dryad.1c3k32r
 521

522

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679

680

681 **Tables**

	Mean A0	σ (A0)	Continent	Guillou 1993	Guillou 2009	Cochons	New Island	Marion
Continent	27.5	3.5	-					
Guillou 1993	28.8	1.6	< 0.001	-				
Guillou 2009	29.4	2.0	0.056	<i>0.017</i>	-			
Cochons	28.5	2.2	<i>0.016</i>	< 0.001	0.002	-		
New Island	30.1	2.0	0.072	0.086	0.938	0.002		
Marion	32.4	2.0	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	-

682

683 **Table 1.** Size differences between mandibles of the different populations. Size is estimated by A0
684 provided by the Fourier analysis. Group mean and standard deviation (σ) are provided in the first two
685 columns. Probabilities of two-by-two Mann-Whitney tests are provided (in bold $P \leq 0.01$; in italics $P \leq$
686 0.05).

687

	Mean	σ	Continent	Guillou 1993	Guillou 2009	Cochons	New Island
Out-Inc	Continent	1.072	0.011	-			
	Guillou 1993	1.097	0.008	< 0.001	-		
	Guillou 2009	1.088	0.007	< 0.001	0.001	-	
	Cochons	1.104	0.009	< 0.001	<i>0.021</i>	< 0.001	-
	New Island	1.101	0.008	< 0.001	0.277	< 0.001	0.435
	Marion	1.098	0.010	< 0.001	0.871	0.007	0.086
Out-Mol	Continent	0.549	0.017				
	Guillou 1993	0.551	0.010	0.950			
	Guillou 2009	0.544	0.007	0.063	<i>0.024</i>		
	Cochons	0.567	0.009	< 0.001	< 0.001	< 0.001	
	New Island	0.568	0.009	< 0.001	< 0.001	< 0.001	0.775
	Marion	0.562	0.016	<i>0.034</i>	<i>0.027</i>	< 0.001	0.199
In-Temp	Continent	0.198	0.018				
	Guillou 1993	0.223	0.024	< 0.001			
	Guillou 2009	0.223	0.014	< 0.001	0.802		
	Cochons	0.239	0.015	< 0.001	<i>0.020</i>	0.001	
	New Island	0.246	0.018	< 0.001	0.008	< 0.001	0.273
	Marion	0.217	0.024	0.004	0.444	0.439	0.005
In-SMass	Continent	0.357	0.014				
	Guillou 1993	0.337	0.011	< 0.001			
	Guillou 2009	0.331	0.009	< 0.001	0.114		
	Cochons	0.337	0.010	< 0.001	0.643	0.007	
	New Island	0.333	0.011	< 0.001	0.514	0.259	0.158
	Marion	0.343	0.017	0.009	0.186	<i>0.012</i>	0.137
In-DMass	Continent	0.486	0.013				
	Guillou 1993	0.474	0.012	0.002			
	Guillou 2009	0.460	0.009	< 0.001	0.001		
	Cochons	0.500	0.010	< 0.001	< 0.001	< 0.001	
	New Island	0.495	0.012	<i>0.038</i>	< 0.001	< 0.001	0.158
	Marion	0.502	0.018	< 0.001	0.001	< 0.001	0.207

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689 **Table 2.** Scaled in- and out-lever values, calculated on the aligned coordinates after Procrustes
690 superimposition, of the mandibles of the different populations, and differences between groups. Inc
691 = incisor; Mol = molar; Temp = temporalis; SMass = superficial masseter; DMass = deep masseter. P-
692 values of two-by-two Mann-Whitney tests are provided (in bold $P \leq 0.01$; in italics $P \leq 0.05$). Group
693 mean and standard deviation (σ) are provided in the first two columns.

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		Mean MA	σ (MA)	Continent	Guillou 1993	Guillou 2009	Cochons	New Island
MA Temp/Inc	Continent	0.185	0.016	-				
	Guillou 1993	0.203	0.020	0.001	-			
	Guillou 2009	0.205	0.012	< 0.001	0.918	-		
	Cochons	0.216	0.013	< 0.001	<i>0.027</i>	<i>0.005</i>	-	
	New Island	0.223	0.015	< 0.001	0.005	< 0.001	0.164	-
	Marion	0.198	0.021	<i>0.014</i>	0.444	0.340	0.008	0.001
MA SMass/Inc	Continent	0.333	0.015	-				
	Guillou 1993	0.307	0.009	< 0.001	-			
	Guillou 2009	0.304	0.009	< 0.001	0.308	-		
	Cochons	0.305	0.010	< 0.001	0.563	0.524	-	
	New Island	0.303	0.011	< 0.001	0.149	0.676	0.309	-
	Marion	0.312	0.018	< 0.001	0.275	0.069	0.120	0.102
MA SMass/Mol	Continent	0.651	0.037	-				
	Guillou 1993	0.612	0.019	< 0.001	-			
	Guillou 2009	0.609	0.019	< 0.001	0.545	-		
	Cochons	0.595	0.019	< 0.001	0.004	0.008	-	
	New Island	0.587	0.022	< 0.001	0.004	0.006	0.203	-
	Marion	0.610	0.035	0.001	0.659	0.928	0.184	0.092
MA DMass/Mol	Continent	0.885	0.027	-				
	Guillou 1993	0.861	0.021	0.001	-			
	Guillou 2009	0.846	0.015	< 0.001	<i>0.028</i>	-		
	Cochons	0.883	0.016	0.486	0.001	< 0.001	-	
	New Island	0.871	0.016	<i>0.037</i>	0.138	< 0.001	0.062	-
	Marion	0.893	0.028	0.269	0.005	< 0.001	0.143	<i>0.016</i>

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698 **Table 3.** Biomechanical ratios characterizing the mandibles of the different populations, and
699 differences between groups. MA Temp/Inc = Mechanical advantage Temporalis / Incisor; MA
700 SMass/Inc = Mechanical advantage Superficial Masseter / Incisor; MA DMass/Mol = Mechanical
701 advantage Deep Masseter / Molar. P-values of two-by-two Mann-Whitney tests are provided (in bold
702 $P \leq 0.01$; in italics $P \leq 0.05$). Group mean and standard deviation (σ) are provided in the first two
703 columns.

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711 **Figure captions**712 **Figure 1.** Map of the localities considered in this study.

713 **Figure 2.** (A) Examples of mandibles of the house mouse (*Mus musculus domesticus*) in Western
 714 Europe and the different Sub-Antarctic islands. B. Outline of the mandible, used for the Fourier
 715 analysis providing the shape variables. The dot represents the starting point. C. Biomechanical
 716 variables used to quantify the functional performance of the mandible. The condyle being the
 717 fulcrum, in-lever corresponded to the distance from this fulcrum to the zone of muscle insertions;
 718 out-lever corresponded to the distance from the fulcrum to the bite point.

719 **Figure 3.** (A) Bayesian phylogenetic tree based on D-loop sequences. The posterior probabilities as
 720 well as bootstrap values are displayed on the branches. The sequences included roughly correspond
 721 to the morphometric sampling areas. (B) Representation of the microsatellite variation on the first
 722 three axes of a DAPC.

723 **Figure 4.** Morphological variation of the mandible in the Sub-Antarctic islands and two commensal
 724 populations. (A) Mandible size. Each dot corresponds to a specimen. (B) Mandible shape
 725 differentiation in the morphospace based on the outline analysis of the mandible. Ellipses
 726 correspond to the 95% confidence interval around the centroid. Populations: Western Europe (CB:
 727 Cologne-Bonn; GAR: Gardouch); Sub-Antarctic islands: New Island, Falklands (NI); Cochons (COCH)
 728 and Guillou (G93: 1993 and G09: 2009) in the Kerguelen archipelago; Marion Island (MAR).

729 **Figure 5.** Geometric variations of the biomechanical landmark configuration between the Sub-
 730 Antarctic islands and two commensal populations. Middle panel, geometric differentiation in the
 731 morphospace based on the six biomechanically relevant landmarks. Ellipses correspond to the 95%
 732 confidence interval around the centroid. Populations: Western Europe (CB: Cologne-Bonn; GAR:
 733 Gardouch); Sub-Antarctic islands: New Island, Falklands (NI); Cochons (COCH) and Guillou (G93: 1993
 734 and G09: 2009) in the Kerguelen archipelago; Marion Island (MAR). The other panels represent the
 735 deformation from the continental consensus configuration to the consensus geometry of each island
 736 (deformation magnified x2).

737 **Figure 6.** In- and out-lever arms describing the main biomechanical properties of the mandible
 738 geometry. Out-levers were estimated as the distance from the condylar articulation to (1) the incisor
 739 tip, and to (2) the first molar main cusp (hypoconid). In-levers were the distances from the condyle
 740 to: (1) the tip of the coronoid (describing the action of the temporalis); (2) the tip of the angular
 741 process (approximating the action of the superficial masseter); (3) the anterior boundary of the
 742 angular process (approximating the deep masseter action).

743 **Figure 7.** Biomechanical variation of the mandible in Sub-Antarctic and two commensal continental
 744 populations. Mechanical advantages (= In/Out lever arms) are: (A) temporalis/incisor; (B) superficial
 745 masseter / molar; (C) superficial masseter / molar; (D) superficial masseter / incisor. (E) Relationship
 746 between two mechanical advantages: superficial masseter/molar vs. temporalis/incisor.

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