The Early Pleistocene herpetofauna of Rivoli Veronese (Northern Italy) as evidence for humid and forested glacial phases in the Gelasian of Southern Alps

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1   **The Early Pleistocene herpetofauna of Rivoli Veronese (Northern Italy) as evidence for humid**

2   **and forested glacial phases in the Gelasian of Southern Alps**

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14   **Abstract**

15   Among the Early Pleistocene Italian fossil herpetofaunas, Rivoli Veronese is remarkable in having

16   yielded the youngest known allocaudates, represented by *Albanerpeton pannonicum*, together with

17   remains of other amphibians and reptiles. The assemblage includes at least 15 other taxa, including

18   two caudates (*Speleomantes* sp., *Ichthyosaura alpestris*), four anurans (*Bombina* sp., *Bufo bufo*,

19   *Hyla* gr. *H. arborea*, *Rana* sp.), five lizards (*Lacerta* gr. *L. viridis*, cf. *Zootoca vivipara*, a third,

20   small-sized lacertid, *Anguis* gr. *A. fragilis*, cf. *Pseudopus* sp.) and four snakes (*Coronella* sp.,

21   *Zamenis longissimus*, *Natrix* sp., *Vipera* gr. *V. aspis*). The finding of *Speleomantes* is particularly

22   interesting as it is one of only a handful of fossil occurrences of this genus, being only the second

23   one outside of its extant range. Excluding the extinct *Albanerpeton* and *Speleomantes*, which has a

24   very narrow environmental range, the remainder of the assemblage suggests a Mean Annual

25   Temperature rather similar or slightly colder than the present one in Rivoli Veronese (11.6 °C

26   versus 12.4 °C), with much higher Mean Annual Precipitation (1322 mm versus 834 mm). The

27   palaeoenvironment would have included either permanent or temporary water bodies, located in a

28   forested area. More open landscapes might have also been present in the local vicinity. The

29   palaeoherpetofauna of Rivoli Veronese supports the hypothesis of *Albanerpeton* favouring a moist

30   environment, and confirms the presence of a humid forested landscape on the northern side of the

31   Po Plain during the cold phases of the Gelasian, as already suggested by the pollen record for its

32   southern margin.

35   **1. Introduction**

36   During the Early Pleistocene glacial phases, northern Italy is considered to have had peculiar

37   climatic conditions, different from those characterizing other parts of the Appennine Peninsula

38   (Fauquette and Bertini, 2003; Bertini, 2010). According to pollen data, northern Italy, and the Po

39   Plain in particular, lacked a trend leading towards drier conditions with a more open vegetation

40   during the glacial phases opposed to humid and forested periods during the interglacial ones

41   (Fauquette and Bertini, 2003; Bertini, 2010). Instead, humidity remained a main feature of the

42   climate during both glacial and interglacial phases, where the main difference is found in the

43   composition of the forested landscape. This was composed of coniferous forests in the former and

44   by subtropical/warm temperate forests in the latter. This is particularly evident in Gelasian

45   sediments from localities such as the Stirone River (Fauquette and Bertini, 2003), the Marecchia

46   Valley (Rio et al., 1997) and Monte Falcone-Rio Crevalese (Monegatti et al., 2002), all located in

47   the southern part of the Po Basin. Similar conditions persisted into the Calabrian also, although

48   brief periods characterized by a drier climate and open landscapes seem to have been present (e.g.,

49   in the Leffe Basin; Ravazzi and Rossignol Strick, 1995).

50   The Italian fossil-bearing site of Rivoli Veronese, located in the Verona province, has

51   yielded a number of fossil remains dating back to the Gelasian, among which the youngest

52   representatives of the extinct lissamphibian clade Allocaudata that are known worldwide (Delfino

53   and Sala, 2007). European Neogene members of the genus *Albanerpeton*, the only allocaudate so

54   far known from the Cenozoic (Sweetman and Gardner, 2013), were considered dry adapted by

55   Böhme (2003), but later, a more probable preference for moist and forested karstic environments

56   was also suggested (Gardner and Böhme, 2008). In this context, the last occurrence of this taxon in

57   an area possibly characterized by a peculiar climate is intriguing, suggesting the possibility to better

58   understand the causes of its definitive extinction.

59   We here describe and identify the whole herpetofauna from Rivoli Veronese, and use this

60   assemblage to reconstruct both palaeoclimate and palaeoenvironment around the site during the

61   time of deposition of the fossil remains. Amphibians and reptiles are particularly useful in this sense

62   because they have strong relationships with climatic and environmental factors of the areas where

63   they live (among others, Antúnez et al., 1988; Currie, 1991; Rage and Roček, 2003; Blain et al.,

64   2008; Vitt and Caldwell, 2009). Moreover, given that the pollen-based palaeoclimatic

65   reconstruction of the Po Plain during the Gelasian are mainly dependent on sites located in the

66   Appennine side of the plain (see references above), this analysis is a good chance to obtain some

67   data on the Alpine side too.

68   **2. Geological and chronological setting of the Rivoli Veronese fissure filling**

69   The fossiliferous locality of Rivoli Veronese is located in the Verona province, near the

70   village of the same name next to the Adige River and northwest of the city of Verona (Fig. 1). It is

71   represented by a fissure, which originated from karstic processes in limestone, and then was later

72   filled with limestone clasts and fluvial sediments (Sala et al., 1994). A rather diverse fauna has been

73   recovered from the fissure, including fish, birds, mammals and the herein-studied amphibians and

74   reptiles. Micromammals are particularly diverse, with at least 28 taxa of insectivores and rodents so

75 far reported in the literature (among which *Pliopetaurista*, *Mimomys pliocaenicus*, *Mimomys*

76 *pitymyoides*, *Mimomys tigliensis*, *Ungaromys dehmi* and *Dinaromys allegranzii*; Sala et al., 1994;

77 Sala, 1996; Fanfani and Masini, 1997; Sala and Masini, 2007). Following Kotsakis et al. (2003) and

78 Sala and Masini (2007), the rodent assemblage from Rivoli Veronese can be assigned to the *M.*

79 *pliocaenicus* zone, which is correlated with the late Villanyan and the MN 17. Moreover, the

80 mammalian fauna is included in the Coste S. Giacomo Faunal Unit (Gliozzi et al., 1997; Kotsakis et

81 al., 2003; Sala and Masini, 2007), which represents the first half of the c2r.1r subchron (roughly

82 between 2.13 and 2.0 Ma) according to Bellucci et al. (2014).

83 **3. Material and methods**

84 The study presented in this paper is based on the fossil remains of amphibians and reptiles

85 found at Rivoli Veronese and currently stored at the Dipartimento di Biologia ed Evoluzione,

86 Università di Ferrara, Italy (acronym: RV-H = Rivoli Veronese, herpetological fossil material).

87 Remains of *Albanerpeton pannonicum* previously published by Delfino and Sala (2007) are not re-

88 described here. Pictures of the most significant specimens have been taken at the University of

89 Torino using a Leica M205 microscope equipped with the Leica application suite V 4.10.

90 The Mutual Ecogeographic Range (MER; Blain et al., 2009, 2016c) has been applied to the

91 recovered herpetofauna, in order to reconstruct the palaeoclimate. Extant distributions are based on

92 the atlas of amphibians and reptiles from Europe (Sillero et al., 2014), with 50 × 50 km resolution

93 maps in the Universal transverse Mercator (UTM) georeferenced system. Estimated climatic

94 parameters for each 50 × 50 km UTM square are calculated based on climatic database from

95 Climate-Data.org (years 1982-2002).

96 **4. Results**

97 **4.1. The palaeoherpetofauna of Rivoli Veronese**

98   Representatives of all major clades of lissamphibians besides caecilians have been found in

99   the fissure filling of Rivoli Veronese. In addition to the remains reported by Delfino and Sala

100   (2007), two small and fragmentary dentaries are tentatively attributed to *Albanerpeton* (Fig. 2), even

101   if their poor preservational status does not allow a more confident attribution to *A. pannonicum*.

102   Caudate remains are represented almost completely by presacral vertebrae. Most of these can be

103   assigned to the plethodontid genus *Speleomantes* (Fig. 3A-C), but the size and morphology of a

104   single specimen is fully comparable with the salamandrid *Ichthyosaura alpestris* (Fig. 3D-F). A

105   single caudal vertebra (Fig. 3G-H) displays a peculiar morphology, which is more similar to

106   *Speleomantes* than to *Ichthyosaura*, but, since it differs from the available comparative material, it

107   is attributed only to undetermined caudates. Among anurans, three humeri display the diagnostic

108   morphology of *Bombina* (Fig. 4A-B). The presence of *Bufo bufo* is testified by a number of large

109   and robust bones (Fig. 4C-E), whereas a single trunk vertebra belongs to a hylid of the *Hyla*

110   *arborea* species complex (Fig. 4F-G). The most frequently represented anurans are ranids, and in

111   particular, brown frogs of the genus *Rana* (whose presence is testified by scapulae and humeri

112   showing the morphology of this genus according to Bailon, 1999; Fig 4H-I). The presence of

113   juvenile representatives of *Pelophylax* cannot be confidently excluded, due to the presence of small

114   ilia that resemble those of young green frogs (Fig. 4J). Pending a more detailed analysis of the ranid

115   remains from Rivoli Veronese, we here assign all ranid ilia to Ranidae indet., even if at least one

116   specimen (Fig. 4K-L) might represents *Rana temporaria*, following the diagnostic criteria of Bailon

117   (1999).

118   The material includes remains of both lizards and snakes. Several large-sized lizard

119   specimens, including an almost complete frontal (Fig. 5A-B), are assigned to the *Lacerta viridis*

120   species complex. A single pair of small-sized fused frontals is tentatively attributed to *Zootoca*

121   *vivipara* (Fig. 5C-D). Lacertids are also represented by numerous remains that can be identified

122   only at the family level. Nevertheless, at least a small fragment of parietal (Fig. 5E-F) and a

123   premaxilla (Fig. 5G-H) might belong to a second small-sized taxon different from *Z. vivipara*, given

124   that their morphology is not congruent with the viviparous lizard. *Anguis* gr. *A. fragilis* is largely

125   represented in the fossil material, with both cranial and postcranial remains (Fig. 5I-L). However,

126   the attribution to *Anguis* of a small-sized dentary that showed the general morphology of the slow

127   worm (Fig. 5M-N) is questionable because of the presence of a fused posterior end of the

128   intramandibular septum, an unusual feature for this genus (Klembara et al., 2014). Few remains are

129   tentatively assigned to the large-sized anguid of the genus *Pseudopus* (Fig. 5O-R). At least four

130   different snakes have been identified based on the morphology of the trunk vertebrae: *Coronella* sp.

131   (Fig. 6A-D), *Zamenis longissimus* (Fig. 6E-H), *Natrix* sp. (Fig. 6I-L) and *Vipera* gr. *V. aspis* (Fig.

132   6M-P). Nevertheless, a series of trunk vertebrae, whose morphology differs from those of both

133   *Coronella* and *Zamenis*, suggest the presence of other, unrecognised "colubrines" (operational

134   taxon sensu Szyndlar, 1991) snakes.

135   A complete list of the amphibians and reptiles found in Rivoli Veronese is given in Tab. 1,

136   with complete descriptions and identifications of the remains being reported in the supplementary

137   material.

138   **4.2. Palaeoclimatic reconstruction**

139   The MER is a robust methodology for reconstructing Pleistocene climatic conditions as it

140   permits the estimation of quantitative data for temperature and precipitation (e.g., Blain et al., 2009,

141   2014, 2016c). However, sometimes a whole fossil assemblage has no modern analogue because its

142   extant taxa do not co-occur. This is the case with the very diverse assemblage of Rivoli Veronese.

143   Nevertheless, overlap of the ranges of most of the taxa is possible, although excluding

144   *Speleomantes* from the analysis due to its very restricted modern range. Such an overlap gives a

145   unique 50 x 50 km UTM square, located at the boundary between Slovenia and Croatia, mainly

146   centered on the southwestern Slovenian city of Ilirska Bistrica (red square in Fig. 7A). Such an area

147   (comprised between 400 and 600 meters above sea level) corresponds to a mean annual temperature

148 (MAT) that varies between 12.4 and 9.8ºC and very high mean annual precipitation (MAP)

149 comprised between 1320 and 1340 mm.

150   If we closely compare Ilirska Bistrica and Rivoli Veronese modern values (1982-2002; Tab.

151 2), the Early Pleistocene climate deduced for Rivoli Veronese would have been characterized as

152 cold and with a very high atmospheric temperature range, temperate summer and cold winter

153 (Figure 7B; Tab. 3). Rainfall was very abundant, with a regular distribution over the year and with

154 the highest amount occurring during winter and to a lesser extent, spring. No dry month is

155 evidenced, thus characterizing the climate as mountainous humid to very humid, according to the

156 Aridity Indexes (Tab. 3). In comparison with the current climatic data from Rivoli Veronese area,

157 the MER-estimated MAT would have been somewhat colder (-0.8ºC) than at present (Tab. 2). Such

158 colder climatic conditions during the Early Pleistocene are linked with a decrease in temperature

159 during the spring and summer months (between -1.1ºC and -1.9ºC), but not during the winter, which

160 is warmer (+0.2ºC and +2.0ºC). The total amount of rainfall would have been much higher (+488

161 mm) than at present in the Rivoli Veronese area. The frequency of precipitation would also have

162 been much higher than the modern-day climate, especially during the fall and winter months (from

163 September to January). Such higher humidity is confirmed by the De Martonne Index (Tab. 3).

164   To confirm these results, a second overlap is undertaken, excluding from the analysis the

165 genus *Pseudopus*, a large anguid lizard currently absent from Italy, as it was the taxon that strongly

166 constrained the previous one-UTM square overlap. According to the MER method, when a taxon is

167 removed from the analysis, the resulting overlap is supposed to be still valid even if less precise.

168 When removing *Pseudopus* from the assemblage, the obtained overlap is much larger, comprising a

169 total of 90 UTM squares (black and red squares on Fig. 7A). These UTM 50 x 50 km squares

170 mainly correspond to mountainous areas and are distributed from the western borders of Romania

171 and Bulgaria, the eastern border of Hungary in the East, and up to the western-central part of France

172 in the West. It also encompasses the south of Austria and Switzerland, northernmost Italy and a

173 large area of central-eastern France. Such an overlap corresponds to a mean annual temperature of

174 10.6 ± 1.7ºC and a mean annual precipitation of 839 ± 233 mm. This further verifies a cold (-1.8ºC

175 compared to present conditions in Rivoli Veronese) and humid (similar to present values in that

176 case) pattern for the palaeoclimatic reconstruction of the Early Pleistocene site.

177 **5. Discussion**

178 **5.1. Rivoli Veronese: a humid and forested refugium for the last allocaudates?**

179 Within the biochronological range given by the rodent assemblage from Rivoli Veronese

180 (Kotsakis et al., 2003; Sala and Masini, 2007) that suggest a late Villanyan (MN17) age, which has

181 also been constrained by palaeomagnetism studies (Bellucci et al., 2014) that is between 2.13 and

182 2.0 Ma, our palaeoherpetofaunal based climate reconstruction suggests that fossil remains found at

183 Rivoli Veronese may have been deposited during a cold phase (i.e. MIS 78, 76 or 74) of the late

184 Gelasian. Similar to the conditions evidenced by the pollen record in the Appennine side of the Po

185 Plain (Bertini, 2010; Fauquette and Bertini, 2003), the climate in Rivoli Veronese during this cold

186 phase was characterized by a rather strong degree of humidity (Tab. 3). This confirms the climatic

187 peculiarity of Northern Italy during the Gelasian when compared with the drier glacial phases of the

188 rest of the peninsula. The presence of either temporary or permanent water bodies is further

189 evidenced by the high number of water-linked taxa recognised in the herpetofauna, particularly

190 *Natrix* and all other amphibians. Given the absence of both palynological and palaeobotanical data

191 from the locality, an estimate of the probable vegetation must be indirectly inferred from the usual

192 environmental preferences of the identified taxa. On the whole, the amphibians and reptiles

193 assemblage includes taxa that are indicative of a forested environment (see Speybroeck et al., 2016,

194 for a brief summary of their ecological requirements). Extant *I. alpestris* and plethodontids of the

195 genus *Speleomantes*, for example, frequent water bodies and intersticies, crevices and caves that are

196 surrounded by forests respectively. *Zamenis longissimus* is also considered a forest-dweller (even

197 though alternating with more open basking areas). *Hyla* gr. *H. arborea*, cf. *Zootoca vivipara* and

198   *Coronella* might support the presence of open environments near the edge of the forest (Speybroeck

199   et al., 2016), but the few remains confidently attributed to these taxa might suggest that open areas

200   were not the dominant environment in the vicinity of the karst fissures of Rivoli Veronese. In any

201   case, these open meadows might have been also used by *Lacerta* gr. *L. viridis* for basking.

202   Generalist taxa such as *B. bufo* and *Rana* were also present, neither confirming nor contradicting the

203   palaeoenvironmental indications as given by the rest of the herpetofauna. A humid and forested

204   environment is also consistent with the mammal remains, due to the finding of hygrophilous

205   insectivores and flying squirrels (Sala et al., 1994; Fanfani and Masini, 1997).

206   As noted by Delfino and Sala (2007), such a humid environment contrasts with the past

207   common view of Neogene and Quaternary allocaudates being dry-adapted taxa, and is more

208   consistent with Gardner and Böhme's (2008) hypothesis of a group with wider habitat tolerances,

209   but with a preference for moist and forested karstic areas. Given these ecological preferences,

210   questions might be raised as to why they went extinct after the Early Pleistocene. Such humid and

211   forested conditions were still present in the Southern Alps during the Calabrian, despite some

212   possible and brief drier period with more open vegetation (Ravazzi and Rossignol Strick, 1995). It

213   can be argued that whilst these periods may have had a negative impact on the survival of

214   allocaudates in Northern Italy, an even stronger change in environmental conditions from a forested

215   to a grassland/steppe environment had had virtually no effects on *A. pannonicum* in its type locality,

216   Csarnóta 2 (Venczel and Gardner, 2005). The burrowing lifestyle of allocaudates has been

217   suggested as the likely reason behind the low impact of the environmental changes at Csarnóta 2,

218   and so this hypothesis might also hold true for those living in Northern Italy. Yet these organisms

219   still went extinct. It is interesting to note that another interstitial amphibian found in Rivoli

220   Veronese, *Speleomantes*, also disappeared from the area after the Gelasian. Therefore it seems

221   likely that the cause of their disappearance could still overcome the resilience provided by their

222   interstitial habits.

223   It is commonly thought that glacial phases during the first part of the Early Pleistocene were

224   of a rather low amplitude, with the first major glaciation occurring during the Marine Isotope Stage

225   (MIS) 22 (0.87 Ma; Muttoni et al., 2003, 2007). According to Muttoni and colleagues (2007), the

226   magnitude of this glacial event was comparable to that of the Last Glacial Maximum, and it is

227   possible that during this period, the ice cap covering the Alps were also similarly expanded towards

228   the southern margin of the mountain range. Reconstructions of the Last Glacial Maximum place the

229   ice cap margin very close to, if not covering, the area of Rivoli Veronese (see fig. 1 in Muttoni et

230   al., 2003, and fig. 1a in Muttoni et al., 2007). It is therefore possible that the proximity of the ice

231   cap might have made the karstic fissures unsuitable for both *Albanerpeton* and *Speleomantes*, which

232   were not able to either migrate further south or recolonize the area during the following interglacial.

233   Following the reconstructions reported in Muttoni et al. (2003, 2007), Rivoli Veronese was

234   encircled by two different extensions of the ice cap during the Last Glacial Maximum, both from

235   the Lake Garda and the Adige River sides. If a similar pattern is also valid for the MIS 22

236   glaciation, the Rivoli Veronese amphibians and reptiles may have found themselves trapped, with

237   low possibilities of moving away from the glacier margin. In any case, if this part of Northern Italy

238   acted as an Early Pleistocene refugium for allocaudates (as it seems suggested by the absence of

239   other coeval or younger findings), it appears that the loss of suitable conditions resulted in, or at the

240   very least pushed them towards, their extinction..

241   Herpetofaunal extinction or extirpation events during the Pleistocene are also well known in

242   the two other European peninsulae facing the Mediterranean (namely, the Iberian and the Balkan

243   Peninsulae). In both cases, the disappearance of taxa followed a southward trend, with their

244   distributional ranges showing a contraction towards the southern portions of the two peninsulae

245   over time (see e.g., varanids in Greece, Georgalis et al., 2017, and agamids in Spain, Delfino et al.,

246   2008b; Blain et al., 2016a). It is interesting to note how the disappearance of "exotic" amphibians

247   and reptiles in Iberia seems to be geographically linked with particular moments in time (Blain et

248   al., 2016a): i.e., the Olduvai palaeomagnetic event in the northern part of the country and the

249 Jaramillo event in the southern part. However, it must be stressed that these extirpations concern

250 mainly thermophilous reptiles (with the only exception of the green toad, *Bufotes viridis* s.l.), whose

251 disappearance is usually linked with the cooling associated with glaciation events (even if

252 competitive exclusion caused by other taxa could have also played a role). Given that, it is most

253 likely that their local disappearance, and that of the cold-tolerant *Albanerpeton* and *Speleomantes* in

254 the northern side of the Po Plain, might not be linked to the same causes.

255 **5.2. Amphibians and reptiles from Rivoli Veronese and the Pleistocene herpetological**

256 **assemblages of Italy**

257   *Albanerpeton* is not the only peculiar taxon present in the rather diverse herpetological

258 assemblage of Rivoli Veronese. The occurrence of *Speleomantes* is rather interesting too. Currently,

259 this cave-dwelling plethodontid has a rather restricted distribution, limited to Sardinia, Liguria and

260 the Appennines in Italy and to the southeastern corner of France (Lanza et al., 1995, 2006).

261 Introduced populations are reported from Southern France and the eastern border of Northern Italy

262 (*Speleomantes strinatii*; Sillero et al., 2014), as well as from Lower Saxony in Germany (probably

263 *Speleomantes italicus*; Alexander Kupfer, pers.comm. to AV). Given this, the presence of an

264 undetermined species of *Speleomantes* in Rivoli Veronese is identified as one of the very few fossil

265 occurrences of this genus outside the current distributional range. Indeed, the very poor fossil record

266 of *Speleomantes* is largely limited to the Pliocene to Holocene discoveries coming from localities

267 inside areas inhabited by its extant representatives (for a summary, see Böhme and Ilg, 2003,

268 Delfino, 2004, and Delfino et al., 2005). A single occurrence, other than Rivoli Veronese, is located

269 far outside from this range: the middle Miocene trunk vertebra from Devínska Nová Ves, in

270 Slovakia, attributed to a possible new species of *Hydromantes* (*Speleomantes*) by Venczel and

271 Sanchiz (2005). The Rivoli Veronese finding testifies for a wider distribution of the genus during

272 the Pleistocene. Nevertheless, it cannot shed clear lights on its evolutionary dynamics in Europe, due

273 to the presence of older occurrences that are already established in the current range and the absence

274 of late Miocene- or Pliocene-aged extralimital fossils that might give clues on possible colonization

275 routes.

276   All others amphibians found in Rivoli Veronese, except *I. alpestris*, have a rich fossil record

277 (Böhme and Ilg, 2003). *Ichthyosaura alpestris* or morphologically-related forms, on the other hand,

278 have been found in a few sites. These are: one locality from the Oligocene/Miocene boundary of

279 Germany (Böhme and Ilg, 2003), one locality from the early Pliocene of Slovakia (Hodrová, 1984;

280 Ivanov, 2007), one locality from the Early Pleistocene of Italy (Delfino and Bailon, 2000), four

281 localities from the Middle Pleistocene of England (Gleed-Owen, 1998), France (Hanquet et al.,

282 2010), Germany (Böhme, 1997; Holman, 1998) and Russia (Böhme and Ilg, 2003) and one locality

283 from the Late Pleistocene of Spain (Holman, 1998). Including the single vertebra found in Rivoli

284 Veronese, these remains represent only a handful of fossil occurrences of a species that was present

285 in Europe since the beginning of the Neogene. It is interesting to note that the Middle Pleistocene

286 was a period of large diffusion of this caudate into the continent, with a range that was far more

287 extended than the current one (see Sillero et al., 2014) spreading from England and Southeastern

288 France in the West to European Russia in the East. Rivoli Veronese represents only the second

289 fossil occurrence of this species in mainland Italy, and the first one inside its current Italian range.

290 The other remains, identified only tentatively as *Ichthyosaura* cf. *I. alpestris*, come from the slightly

291 younger (Calabrian) fissure fillings of Cava dell'Erba, in the Pirro Nord karst network in Apulia

292 (Delfino and Bailon, 2000). More remains are required from Central and Southern Italy to

293 understand whether this species once had a stable and continuous distribution in the Appennine

294 Peninsula, or the Pirro Nord fossils and the extant isolated populations in Calabria (Sindaco et al.,

295 2006; Lanza et al., 2007; Sillero et al., 2014) are just the results of sporadic dispersal events.

296   A high number of taxa (at least five) composes the lizard assemblage from the Early

297 Pleistocene of Rivoli Veronese. If not taking into account the third, small and undetermined

298 lacertid, all these taxa but *Pseudopus*, are still present in the Verona province today. The current

299 range of the genus *Pseudopus* has its western limit near the border between Slovenia and Italy

300 (Sillero et al., 2014), where it is represented by the sole extant species, *Pseudopus apodus*.

301 Nevertheless, the genus is also reported at sites in the Appennine Peninsula, occurring in deposits

302 since the late Miocene (Böhme and Ilg, 2003), and has its youngest Italian occurrences right in the

303 Verona province (Delfino, 2002; Delfino et al., 2008a). The *Pseudopus* osteoderm reported from

304 the Calabrian site of Pirro Nord by Delfino and Bailon (2000) is now considered as an intrusion of

305 an older (Neogene) fossil in the Early Pleistocene sample (Delfino and Atzori, 2013). Apart from

306 Rivoli Veronese, *Pseudopus* remains in the Verona area have been found in the Early Pleistocene of

307 Monte La Mesa, the Middle Pleistocene of Cengelle, Viatelle and Zoppega 2 and the Late

308 Pleistocene of Grotta della Volpe (Delfino, 2002; Delfino et al., 2008a). These remains were at first

309 attributed to the extinct *Pseudopus pannonicus* (Delfino, 2002), but later reallocated to an

310 undetermined *Pseudopus* species (Delfino et al., 2008a). Given that, it is not possible to clearly state

311 whether they represent a residual occurrence of *P. pannonicus* in Italy (and then also one of the

312 oldest occurrences of the species in Europe; Böhme and Ilg, 2003) or rather a western expansion of

313 *P. apodus* during the Pleistocene. Nevertheless, it appears clear that *Pseudopus* inhabited the area

314 during the whole Pleistocene, eventually disappearing before the beginning of the Holocene.

315 Among others lizards identified in Rivoli Veronese, cf. *Zootoca vivipara* is the first report in Italy

316 of a fossil form morphologically similar to the viviparous lizard, whose fossil record is known only

317 from countries in the northern part of Europe (Gleed-Owen, 1998; Holman, 1998; Böhme and Ilg,

318 2003). Moreover, this is one of the oldest occurrences of this lizard, together with findings reported

319 from the Early Pleistocene of Bad Deutsch-Altenburg, in Austria (Rauscher, 1992). Both *Lacerta*

320 gr. *L. viridis* and *Anguis* gr. *A. fragilis*, on the other hand, were already reported from Italian sites,

321 and they also have a more widespread fossil record in Europe (Holman, 1998; Böhme and Ilg,

322 2003). Still, those from Rivoli Veronese are the oldest remains of the slow worm currently known

323 in Italy (Delfino, 2002; Böhme and Ilg, 2003; Delfino et al., 2008a).

324   Snakes are represented in Rivoli Veronese by taxa that are known from a number of other

325   Italian Pleistocene localities, often as part of the same assemblages (Delfino, 2002; Böhme and Ilg,

326   2003; Delfino et al., 2008a). All of these are also currently present in the area (Sillero et al., 2014).

327   As far as *Coronella* and *Z. longissimus* are concerned, they represent the oldest occurrences of the

328   respective taxa known thus far in Italy. It is worth to note the apparent absence of *Hierophis*

329   *viridiflavus*, which otherwise, is rather common at other Quaternary sites located in the Veneto

330   region (Delfino et al., 2008a). Given the high adaptability of this snake, it is likely that this absence

331   is not environmentally controlled. In any case, it is not possible to exclude that unrecognised *H.*

332   *viridiflavus* vertebrae may have been included in the high number of trunk vertebrae identified only

333   as undetermined "colubrines", whose morphological differences suggest the possible presence of

334   unrecognised colubrine taxa other than *Coronella* and *Zamenis*.

335   The Gelasian herpetofauna of Rivoli Veronese appears to have been rather diverse then,

336   including at least 16 different taxa (probably more, taking into account the possible presence of

337   other, unrecognised colubrines). Except for a few occurrences (namely, *Albanerpeton*,

338   *Speleomantes* and *Pseudopus*), all the identified taxa are still present in the area, indicating that the

339   extant amphibians and reptiles association was already setting up during the Early Pleistocene. If

340   compared with the other well-known Early Pleistocene Italian site of the karst network at Pirro

341   Nord, which is considered to be slightly younger (Calabrian) in age (Arzarello et al., 2007, 2009;

342   López-García et al., 2015), the assemblage of Rivoli Veronese is slightly less diverse (18 taxa found

343   in the fissure fillings of Pirro Nord versus 16 in the herein studied locality; Delfino and Bailon,

344   2000; Delfino and Atzori, 2013; Blain et al., 2016b). Apart from a certain similarity in the snake

345   component, the rest of the herpetofauna from Pirro Nord is distinctly different from that of Rivoli

346   Veronese, including an amphisbaenian and a rather diverse chelonian fauna (three different co-

347   occurring taxa; Delfino and Bailon, 2000), notably missing from the Northern-Italian site. This

348   difference might be linked to a dryer and warmer, Mediterranean climate in Southern Italy during

349   the Calabrian, but also to the trans-Adriatic influence of Balkan faunistic elements colonizing the

350 area by the beginning of the Pleistocene (e.g., *Pelobates syriacus*; Blain et al., 2016b). Moreover,

351 the involvement of some kind of taphonomic bias in the lack of larger taxa such as turtles from the

352 palaeoherpetofauna of the Northern-Italian site must be also taken into account, given that the

353 Rivoli Veronese fissure is filled with fine-grained sediments and large faunal elements (e.g., large

354 mammals) are lacking as a whole.

355 **6. Conclusions**

356 The analysis of fossil remains of amphibians and reptiles coming from Rivoli Veronese has

357 resulted in the identification of a highly diverse herpetofauna that shares numerous taxa with the

358 extant herpetological population of the same area. Moreover, the Early Pleistocene assemblage

359 includes important findings, such as one of the very few extralimital occurrences of *Speleomantes*,

360 the first record of the viviparous lizard from Italy (even though only tentatively recognised), as well

361 as the oldest occurrence of the slow worm, the smooth snake and the Aesculapian snake in the

362 country. These add to the fact that the sites hosted the youngest remains of allocaudates that are

363 globally known.

364 The palaeoclimatic and palaeoenvironmental reconstruction indicates a cold and humid

365 climate and a forested environment, possibly with less represented, more open areas in the

366 surroundings. The Po Basin is considered peculiar in the frame of the Gelasian climate of Italy

367 because of the presence of forested glacial phases, but until recently, evidence showing this came

368 mainly from the southern margin of the basin. Our analysis confirms that the northern side of the Po

369 Plain was characterized by environmental conditions similar to those present in the south (that is, a

370 forested, cold and humid environment), as well as new evidence supporting the hypothesized

371 preference for humid environmental condition by *Albanerpeton*.

372 **Acknowledgments**

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Figure captions

536 **Figure 1.** Map of Northern Italy, showing the position of Rivoli Veronese. [planned for single
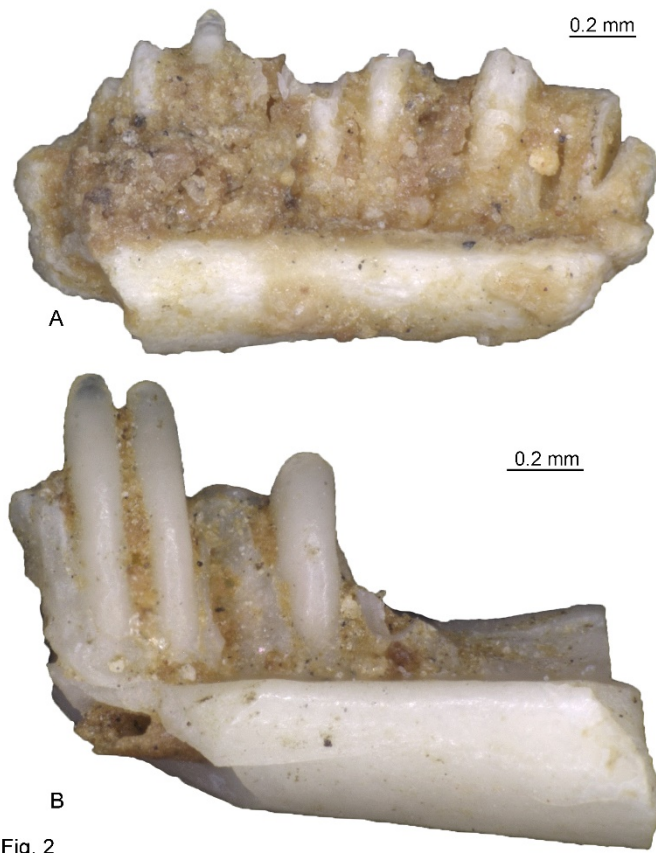
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540 **Figure 2.** cf. *Albanerpeton* sp. from Rivoli Veronese. A: left dentary (RV-H-027) in medial view.

541 B: right dentary (RV-H-234) in medial view. Scale bar = 1 mm. [planned for single column width]


542 Fig. 2

543

544 **Figure 3.** Caudates from Rivoli Veronese. A-C: *Speleomantes* sp., presacral vertebra (RV-H-003)

545 in dorsal (A), ventral (B) and left lateral (C) views. D-F: *Ichthyosaura alpestris*, presacral vertebra

546 (RV-H-004) in dorsal (D), ventral (E) and right lateral (F) views. G-H: Caudata indet., caudal

547 vertebra (RV-H-257) in right lateral (G) and dorsal (F) views. Scale bars equals 1 mm (A-F) and 0.5

548 mm (G-H). [planned for single column width]
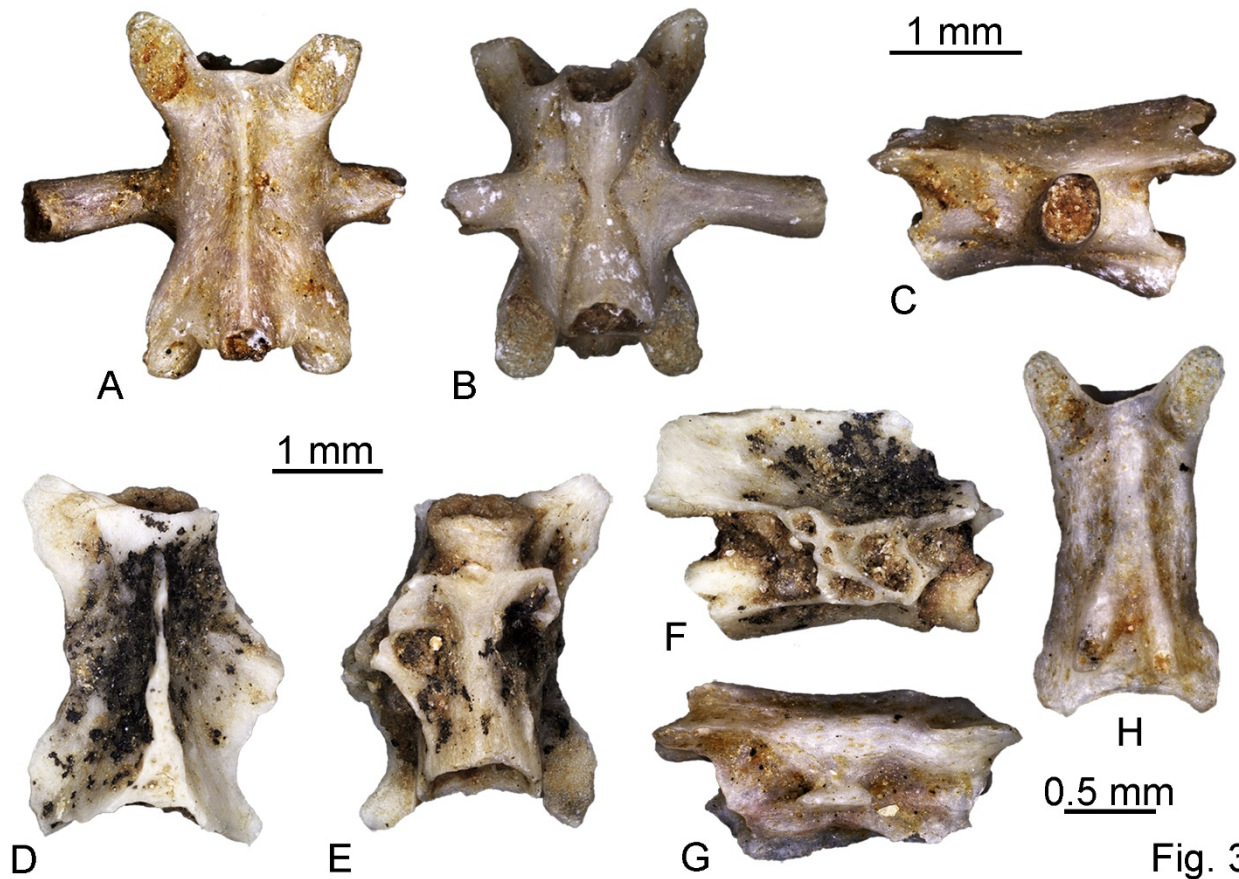
Figure 4. Anurans from Rivoli Veronese. A-B: *Bombina* sp., left humerus (RV-H-010) in ventral

552 (A) and lateral (B) views. C-D: *Bufo bufo*, right scapula (RV-H-001) in ventral (C) and dorsal (D)

553 views. E: *Bufo bufo*, left ilium (RV-H-107) in lateral view. F-G: *Hyla* gr. *H. arborea*, trunk vertebra

554 (RV-H-135) in dorsal (F) and anterior (G) views. H-I: *Rana* sp., left humerus (RV-H-006) in ventral

555 (H) and medial (I) views. J: Ranidae indet., right ilium (RV-H-005) in lateral view. K-L: Ranidae

556 indet., left ilium (RV-H-042) in lateral (K) and dorsal (L) views. Scale bars equals 1 mm (A-E, H-J)

557 and 0.5 mm (F-G, K-L). [planned for double column width]

558

559

560 **Figure 5.** Lizards from Rivoli Veronese. A-B: *Lacerta* gr. *L. viridis*, right frontal (RV-H-143) in

561 dorsal (A) and ventral (B) views. C-D: cf. *Zootoca vivipara*, fused frontals (RV-H-144) in dorsal

562 (C) and ventral (D) views. E-F: Lacertidae indet., parietal (RV-H-165) in dorsal (E) and ventral (F)

563 views. G-H: Lacertidae indet., premaxilla (RV-H-156) in anterior (G) and posterior (H) views. I:

564 *Anguis* gr. *A. fragilis*, left dentary (RV-H-034) in medial view. J-L: *Anguis* gr. *A. fragilis*, trunk

565 vertebra (RV-H-036) in dorsal (J), ventral (K) and left lateral (L) views. M-N: ?*Anguis* sp., left

566 dentary (RV-H-235) in medial (M) and ventromedial (N) views; the arrow marks the fused

567 intramandibular septum. O: cf. *Pseudopus* sp., fragment of dentary (RV-H-033) in medial view. P-

568 R: cf. *Pseudopus* sp., caudal vertebra (RV-H-030) in right lateral (P), dorsal (Q) and ventral (R)

569 views. Scale bars equals 1 mm (A-D, I-N, P-R) and 0.5 mm (E-H, O). [planned for double column
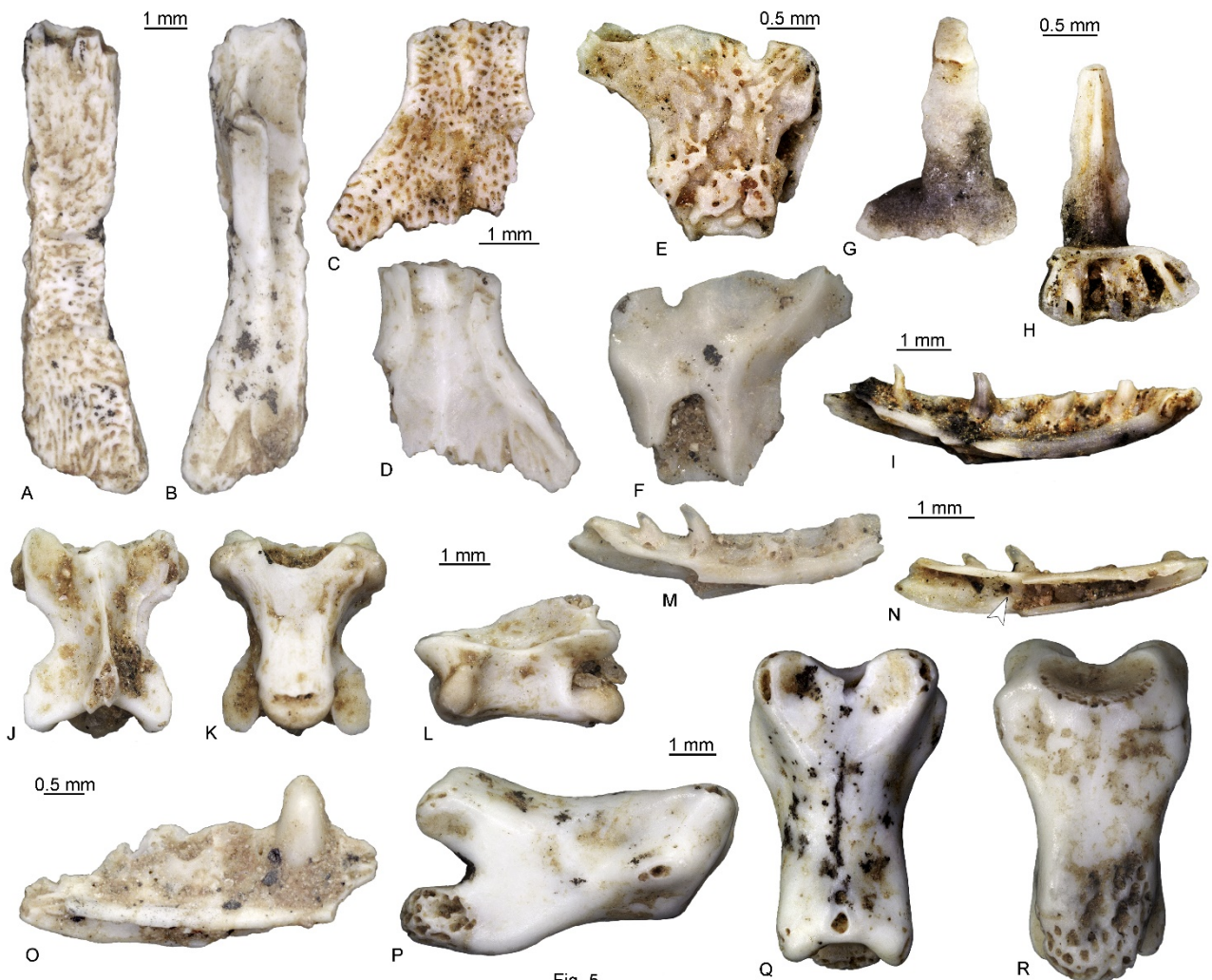
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Fig. 5

571

Figure 6. Snakes from Rivoli Veronese. A-D: *Coronella* sp., trunk vertebra (RV-H-011) in dorsal

573   (A), anterior (B), left lateral (C) and ventral (D) views. E-H: *Zamenis longissimus*, trunk vertebra

574   (RV-H-255) in dorsal (E), anterior (F), left lateral (G) and ventral (H) views. I-L: *Natrix* sp., trunk

575   vertebra (RV-H-076) in dorsal (I), anterior (J), left lateral (K) and ventral (L) views. M-P: *Vipera*

576   gr. *V. aspis*, trunk vertebra (RV-H-009) in dorsal (M), anterior (N), left lateral (O) and ventral (P)

577   views. Scale bars equals 1 mm (E-P) and 0.5 mm (A-D). [planned for double column width]

578

579

580 **Figure 7.** Monthly palaeoclimatic reconstructions for Rivoli Veronese based on its fossil

581 herpetofaunal assemblage. A: overlaps of the current distribution done in 50 × 50 km UTM squares

582 without *Speleomantes* (red square) and without *Speleomantes* and *Pseudopus* (black and red

583 squares). B: climatograms from Ilirska Bistrica (southwestern Slovakia; red square) that would

584 represent the Early Pleistocene paleoclimate occurring at Rivoli Veronese according to the MER

585 method compared with current data of Rivoli Veronese. (Colour online) [planned for double column
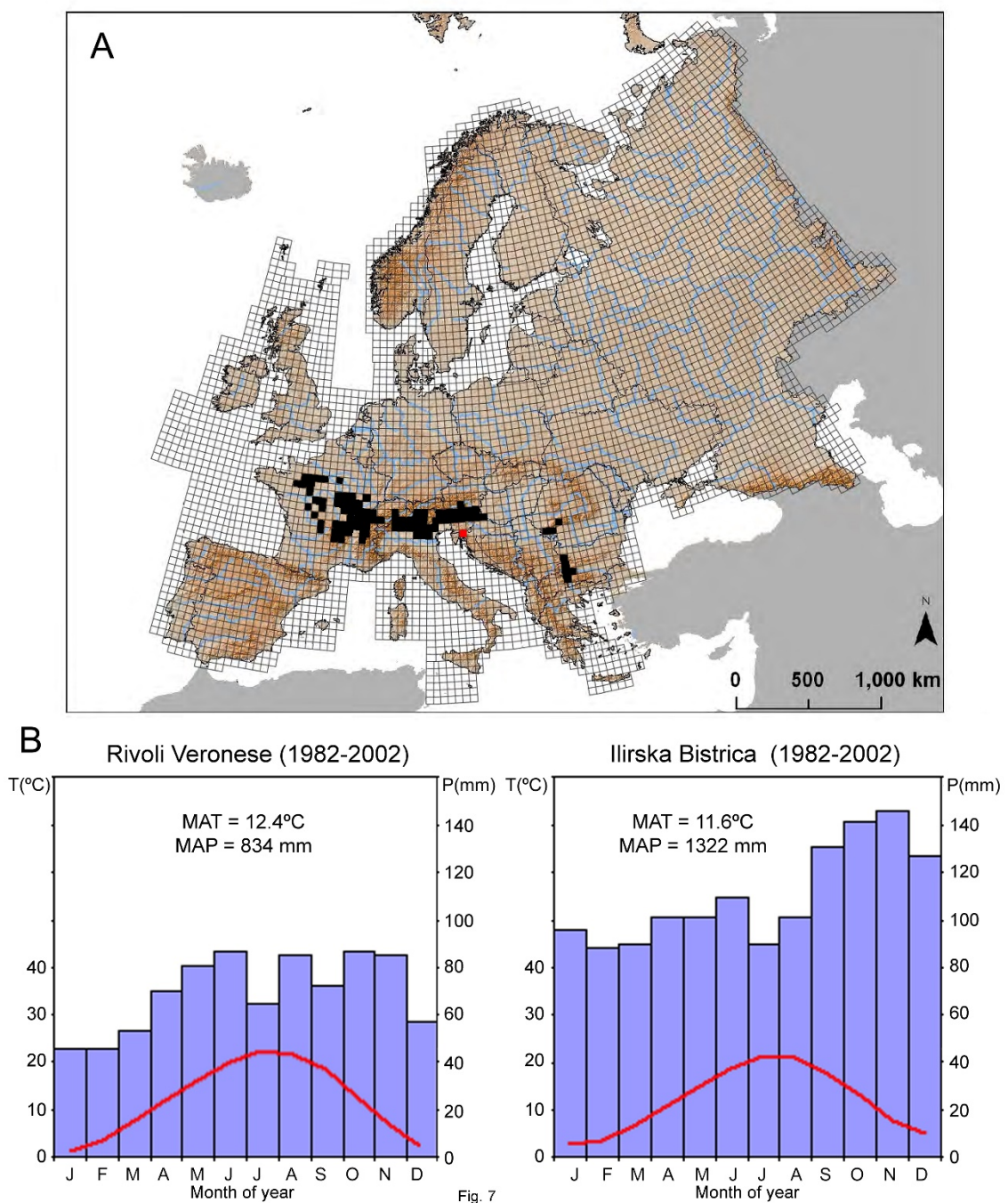
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587

588   **Table 1.** List of the amphibians and reptiles identified in Rivoli Veronese.

Allocaudata	cf. *Albanerpeton* sp.
Caudata	*Speleomantes* sp.
	Ichthyosaura alpestris
	Caudata indet.
Anura	*Bombina* sp.
	Bufo bufo
	Hyla gr. *H. arborea*
	Rana sp.
	Ranidae indet.
	Anura indet.
"Lacertilia"	*Lacerta* gr. *L. viridis*
	cf. *Zootoca vivipara*
	Lacertidae indet.
	Scincomorpha indet.
	Anguis gr. *A. fragilis*
	?*Anguis* sp.
	cf. *Pseudopus* sp.
	"Lacertilia" indet.
Serpentes	*Coronella* sp.
	Zamenis longissimus
	"Colubrines" indet.
	Natrix sp.
	Vipera gr. *V. aspis*
	Serpentes indet.

589

590

591   **Table 2.** Comparison between modern climatic parameters of Ilirska Bistrica and Rivoli Veronese.

					Temperature (in ºC)							
	MAT	J	F	M	A	M	J	J	A	S	O	N	D
Ilirska Bistrica	11.6	2.8	3.3	6.3	10.3	14.7	18.3	21.1	20.7	17.3	12.6	7.5	4.7
Rivoli Veronese	12.4	1.4	3.9	8.0	12.2	16.5	20.2	22.6	21.8	18.6	13.0	7.3	2.7
Difference	-0.8	+1.4	-0.6	-1.7	-1.9	-1.8	-1.9	-1.5	-1.1	-1.3	-0.4	+0.2	+2.0
					Precipitation (in mm)							
	MAP	J	F	M	A	M	J	J	A	S	O	N	D
Ilirska Bistrica	1322	96	88	90	101	101	110	90	101	131	141	146	127
Rivoli Veronese	834	46	46	53	70	81	87	65	85	72	87	85	57
Difference	+488	+50	+42	+37	+31	+20	+23	+25	+16	+59	+54	+61	+70

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594 **Table 3.** Climatic interpretation of Rivoli Veronese and Ilirska Bistrica.

		Rivoli Veronese (1982-2002)		Ilirska Bistrica (1982-2002)	
Temperature	Mean annual temperature	12.4°C	cold-temperate	11.6°C	cold
	Atmospheric temperature range	21.2°C	very high	18.3°C	very high
	Summer temperature	0 months>22°C	temperate	0 months>22°C	temperate
	Winter temperature	MTC[i] = 1.4°C	cold	MTC = 2.8°C	cold
Rainfall	Mean annual precipitation	834 mm	abundant	1322 mm	very abundant
	Distribution of rainfall	no month<30 mm	regular	no month<30 mm	regular
	Type of precipitation	rain		rain	
Aridity	Gaussen Index	0	Mountain	0	Mountain
	Lautensach-Mayer Index	0	humid	0	humid
	Dantin-Revenga Index	1.5	humid	0.9	humid
	De Martonne Index	37.2	humid	61.2	very humid

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[i] MTC: mean temperature of the coldest month