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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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Abstract

Among the Early Pleistocene Italian fossil herpetofaunas, Rivoli Veronese is remarkable in having yielded the youngest known allocaudates, represented by *Albanerpeton pannonicum*, together with remains of other amphibians and reptiles. The assemblage includes at least 15 other taxa, including two caudates (*Speleomantes* sp., *Ichthyosaura alpestris*), four anurans (*Bombina* sp., *Bufo bufo*, *Hyla* gr. *H. arborea*, *Rana* sp.), five lizards (*Lacerta* gr. *L. viridis*, cf. *Zootoca vivipara*, a third, small-sized lacertid, *Anguis* gr. *A. fragilis*, cf. *Pseudopus* sp.) and four snakes (*Coronella* sp., *Zamenis longissimus*, *Natrix* sp., *Vipera* gr. *V. aspis*). The finding of *Speleomantes* is particularly interesting as it is one of only a handful of fossil occurrences of this genus, being only the second one outside of its extant range. Excluding the extinct *Albanerpeton* and *Speleomantes*, which has a very narrow environmental range, the remainder of the assemblage suggests a Mean Annual

Temperature rather similar or slightly colder than the present one in Rivoli Veronese (11.6 °C versus 12.4 °C), with much higher Mean Annual Precipitation (1322 mm versus 834 mm). The palaeoenvironment would have included either permanent or temporary water bodies, located in a forested area. More open landscapes might have also been present in the local vicinity. The palaeoherpetofauna of Rivoli Veronese supports the hypothesis of *Albanerpeton* favouring a moist environment, and confirms the presence of a humid forested landscape on the northern side of the Po Plain during the cold phases of the Gelasian, as already suggested by the pollen record for its southern margin.

Keywords

Albanerpeton pannonicum; *Speleomantes*; amphibians; reptiles; palaeoclimatology; Quaternary

1. Introduction

During the Early Pleistocene glacial phases, northern Italy is considered to have had peculiar climatic conditions, different from those characterizing other parts of the Appennine Peninsula (Fauquette and Bertini, 2003; Bertini, 2010). According to pollen data, northern Italy, and the Po Plain in particular, lacked a trend leading towards drier conditions with a more open vegetation during the glacial phases opposed to humid and forested periods during the interglacial ones (Fauquette and Bertini, 2003; Bertini, 2010). Instead, humidity remained a main feature of the climate during both glacial and interglacial phases, where the main difference is found in the composition of the forested landscape. This was composed of coniferous forests in the former and by subtropical/warm temperate forests in the latter. This is particularly evident in Gelasian sediments from localities such as the Stirone River (Fauquette and Bertini, 2003), the Marecchia Valley (Rio et al., 1997) and Monte Falcone-Rio Crevalese (Monegatti et al., 2002), all located in the southern part of the Po Basin. Similar conditions persisted into the Calabrian also, although brief periods characterized by a drier climate and open landscapes seem to have been present (e.g., in the Leffe Basin; Ravazzi and Rossignol Strick, 1995).

The Italian fossil-bearing site of Rivoli Veronese, located in the Verona province, has yielded a number of fossil remains dating back to the Gelasian, among which the youngest representatives of the extinct lissamphibian clade Allocaudata that are known worldwide (Delfino and Sala, 2007). European Neogene members of the genus *Albanerpeton*, the only allocaudate so far known from the Cenozoic (Sweetman and Gardner, 2013), were considered dry adapted by Böhme (2003), but later, a more probable preference for moist and forested karstic environments was also suggested (Gardner and Böhme, 2008). In this context, the last occurrence of this taxon in an area possibly characterized by a peculiar climate is intriguing, suggesting the possibility to better understand the causes of its definitive extinction.

We here describe and identify the whole herpetofauna from Rivoli Veronese, and use this assemblage to reconstruct both palaeoclimate and palaeoenvironment around the site during the time of deposition of the fossil remains. Amphibians and reptiles are particularly useful in this sense because they have strong relationships with climatic and environmental factors of the areas where they live (among others, Antúnez et al., 1988; Currie, 1991; Rage and Roček, 2003; Blain et al., 2008; Vitt and Caldwell, 2009). Moreover, given that the pollen-based palaeoclimatic reconstruction of the Po Plain during the Gelasian are mainly dependent on sites located in the Appennine side of the plain (see references above), this analysis is a good chance to obtain some data on the Alpine side too.

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

The fossiliferous locality of Rivoli Veronese is located in the Verona province, near the village of the same name next to the Adige River and northwest of the city of Verona (Fig. 1). It is represented by a fissure, which originated from karstic processes in limestone, and then was later filled with limestone clasts and fluvial sediments (Sala et al., 1994). A rather diverse fauna has been recovered from the fissure, including fish, birds, mammals and the herein-studied amphibians and reptiles. Micromammals are particularly diverse, with at least 28 taxa of insectivores and rodents so far reported in the literature (among which *Pliopetaurista*, *Mimomys pliocaenicus*, *Mimomys pitymyoides*, *Mimomys tigliensis*, *Ungaromys dehmi* and *Dinaromys allegranzii*; Sala et al., 1994; Sala, 1996; Fanfani and Masini, 1997; Sala and Masini, 2007). Following Kotsakis et al. (2003) and Sala and Masini (2007), the rodent assemblage from Rivoli Veronese can be assigned to the *M. pliocaenicus* zone, which is correlated with the late Villanyan and the MN 17. Moreover, the mammalian fauna is included in the Coste S. Giacomo Faunal Unit (Gliozzi et al., 1997; Kotsakis et al., 2003; Sala and Masini, 2007), which represents the first half of the c2r.1r subchron (roughly between 2.13 and 2.0 Ma) according to Bellucci et al. (2014).

3. Material and methods

The study presented in this paper is based on the fossil remains of amphibians and reptiles found at Rivoli Veronese and currently stored at the Dipartimento di Biologia ed Evoluzione, Università di Ferrara, Italy (acronym: RV-H = Rivoli Veronese, herpetological fossil material). Remains of *Albanerpeton pannonicum* previously published by Delfino and Sala (2007) are not re-described here. Pictures of the most significant specimens have been taken at the University of Torino using a Leica M205 microscope equipped with the Leica application suite V 4.10.

The Mutual Ecogeographic Range (MER; Blain et al., 2009, 2016c) has been applied to the recovered herpetofauna, in order to reconstruct the palaeoclimate. Extant distributions are based on the atlas of amphibians and reptiles from Europe (Sillero et al., 2014), with 50 × 50 km resolution maps in the Universal transverse Mercator (UTM) georeferenced system. Estimated climatic parameters for each 50 × 50 km UTM square are calculated based on climatic database from Climate-Data.org (years 1982-2002).

4. Results

4.1. The palaeoherpetofauna of Rivoli Veronese

Representatives of all major clades of lissamphibians besides caecilians have been found in the fissure filling of Rivoli Veronese. In addition to the remains reported by Delfino and Sala (2007), two small and fragmentary dentaries are tentatively attributed to *Albanerpeton* (Fig. 2), even if their poor preservational status does not allow a more confident attribution to *A. pannonicum*. Caudate remains are represented almost completely by presacral vertebrae. Most of these can be assigned to the plethodontid genus *Speleomantes* (Fig. 3A-C), but the size and morphology of a single specimen is fully comparable with the salamandrid *Ichthyosaura alpestris* (Fig. 3D-F). A single caudal vertebra (Fig. 3G-H) displays a peculiar morphology, which is more similar to *Speleomantes* than to *Ichthyosaura*, but, since it differs from the available comparative material, it is attributed only to undetermined caudates. Among anurans, three humeri display the diagnostic morphology of *Bombina* (Fig. 4A-B). The presence of *Bufo bufo* is testified by a number of large and robust bones (Fig. 4C-E), whereas a single trunk vertebra belongs to a hylid of the *Hyla arborea* species complex (Fig. 4F-G). The most frequently represented anurans are ranids, and in particular, brown frogs of the genus *Rana* (whose presence is testified by scapulae and humeri showing the morphology of this genus according to Bailon, 1999; Fig 4H-I). The presence of juvenile representatives of *Pelophylax* cannot be confidently excluded, due to the presence of small ilia that resemble those of young green frogs (Fig. 4J). Pending a more detailed analysis of the ranid remains from Rivoli Veronese, we here assign all ranid ilia to Ranidae indet., even if at least one specimen (Fig. 4K-L) might represents *Rana temporaria*, following the diagnostic criteria of Bailon (1999).

The material includes remains of both lizards and snakes. Several large-sized lizard specimens, including an almost complete frontal (Fig. 5A-B), are assigned to the *Lacerta viridis* species complex. A single pair of small-sized fused frontals is tentatively attributed to *Zootoca vivipara* (Fig. 5C-D). Lacertids are also represented by numerous remains that can be identified only at the family level. Nevertheless, at least a small fragment of parietal (Fig. 5E-F) and a premaxilla (Fig. 5G-H) might belong to a second small-sized taxon different from *Z. vivipara*, given that their morphology is not congruent with the viviparous lizard. *Anguis* gr. *A. fragilis* is largely represented in the fossil material, with both cranial and postcranial remains (Fig. 5I-L). However, the attribution to *Anguis* of a small-sized dentary that showed the general morphology of the slow worm (Fig. 5M-N) is questionable because of the presence of a fused posterior end of the intramandibular septum, an unusual feature for this genus (Klembara et al., 2014). Few remains are tentatively assigned to the large-sized anguid of the genus *Pseudopus* (Fig. 5O-R). At least four different snakes have been identified based on the morphology of the trunk vertebrae: *Coronella* sp. (Fig. 6A-D), *Zamenis longissimus* (Fig. 6E-H), *Natrix* sp. (Fig. 6I-L) and *Vipera* gr. *V. aspis* (Fig. 6M-P). Nevertheless, a series of trunk vertebrae, whose morphology differs from those of both *Coronella* and *Zamenis*, suggest the presence of other, unrecognised “colubrines” (operational taxon sensu Szyndlar, 1991) snakes.

A complete list of the amphibians and reptiles found in Rivoli Veronese is given in Tab. 1, with complete descriptions and identifications of the remains being reported in the supplementary material.

4.2. Palaeoclimatic reconstruction

The MER is a robust methodology for reconstructing Pleistocene climatic conditions as it permits the estimation of quantitative data for temperature and precipitation (e.g., Blain et al., 2009, 2014, 2016c). However, sometimes a whole fossil assemblage has no modern analogue because its extant taxa do not co-occur. This is the case with the very diverse assemblage of Rivoli Veronese. Nevertheless, overlap of the ranges of most of the taxa is possible, although excluding *Speleomantes* from the analysis due to its very restricted modern range. Such an overlap gives a unique 50 x 50 km UTM square, located at the boundary between Slovenia and Croatia, mainly centered on the southwestern Slovenian city of Ilirska Bistrica (red square in Fig. 7A). Such an area (comprised between 400 and 600 meters above sea level) corresponds to a mean annual temperature

(MAT) that varies between 12.4 and 9.8ºC and very high mean annual precipitation (MAP) comprised between 1320 and 1340 mm.

If we closely compare Ilirska Bistrica and Rivoli Veronese modern values (1982-2002; Tab. 2), the Early Pleistocene climate deduced for Rivoli Veronese would have been characterized as cold and with a very high atmospheric temperature range, temperate summer and cold winter (Figure 7B; Tab. 3). Rainfall was very abundant, with a regular distribution over the year and with the highest amount occurring during winter and to a lesser extent, spring. No dry month is evidenced, thus characterizing the climate as mountainous humid to very humid, according to the Aridity Indexes (Tab. 3). In comparison with the current climatic data from Rivoli Veronese area, the MER-estimated MAT would have been somewhat colder (-0.8ºC) than at present (Tab. 2). Such colder climatic conditions during the Early Pleistocene are linked with a decrease in temperature during the spring and summer months (between -1.1ºC and -1.9ºC), but not during the winter, which is warmer (+0.2ºC and +2.0ºC). The total amount of rainfall would have been much higher (+488 mm) than at present in the Rivoli Veronese area. The frequency of precipitation would also have been much higher than the modern-day climate, especially during the fall and winter months (from September to January). Such higher humidity is confirmed by the De Martonne Index (Tab. 3).

To confirm these results, a second overlap is undertaken, excluding from the analysis the genus *Pseudopus*, a large anguid lizard currently absent from Italy, as it was the taxon that strongly constrained the previous one-UTM square overlap. According to the MER method, when a taxon is removed from the analysis, the resulting overlap is supposed to be still valid even if less precise. When removing *Pseudopus* from the assemblage, the obtained overlap is much larger, comprising a total of 90 UTM squares (black and red squares on Fig. 7A). These UTM 50 x 50 km squares mainly correspond to mountainous areas and are distributed from the western borders of Romania and Bulgaria, the eastern border of Hungary in the East, and up to the western-central part of France in the West. It also encompasses the south of Austria and Switzerland, northernmost Italy and a large area of central-eastern France. Such an overlap corresponds to a mean annual temperature of 10.6 ± 1.7ºC and a mean annual precipitation of 839 ± 233 mm. This further verifies a cold (-1.8ºC compared to present conditions in Rivoli Veronese) and humid (similar to present values in that case) pattern for the palaeoclimatic reconstruction of the Early Pleistocene site.

5. Discussion

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

Within the biochronological range given by the rodent assemblage from Rivoli Veronese (Kotsakis et al., 2003; Sala and Masini, 2007) that suggest a late Villanyan (MN17) age, which has also been constrained by palaeomagnetism studies (Bellucci et al., 2014) that is between 2.13 and 2.0 Ma, our palaeoherpetofaunal based climate reconstruction suggests that fossil remains found at Rivoli Veronese may have been deposited during a cold phase (i.e. MIS 78, 76 or 74) of the late Gelasian. Similar to the conditions evidenced by the pollen record in the Appennine side of the Po Plain (Bertini, 2010; Fauquette and Bertini, 2003), the climate in Rivoli Veronese during this cold phase was characterized by a rather strong degree of humidity (Tab. 3). This confirms the climatic peculiarity of Northern Italy during the Gelasian when compared with the drier glacial phases of the rest of the peninsula. The presence of either temporary or permanent water bodies is further evidenced by the high number of water-linked taxa recognised in the herpetofauna, particularly *Natrix* and all other amphibians. Given the absence of both palynological and palaeobotanical data from the locality, an estimate of the probable vegetation must be indirectly inferred from the usual environmental preferences of the identified taxa. On the whole, the amphibians and reptiles assemblage includes taxa that are indicative of a forested environment (see Speybroeck et al., 2016, for a brief summary of their ecological requirements). Extant *I. alpestris* and plethodontids of the genus *Speleomantes*, for example, frequent water bodies and intersticies, crevices and caves that are surrounded by forests respectively. *Zamenis longissimus* is also considered a forest-dweller (even though alternating with more open basking areas). *Hyla* gr. *H. arborea*, cf. *Zootoca vivipara* and

Coronella might support the presence of open environments near the edge of the forest (Speybroeck et al., 2016), but the few remains confidently attributed to these taxa might suggest that open areas were not the dominant environment in the vicinity of the karst fissures of Rivoli Veronese. In any case, these open meadows might have been also used by *Lacerta* gr. *L. viridis* for basking. Generalist taxa such as *B. bufo* and *Rana* were also present, neither confirming nor contradicting the palaeoenvironmental indications as given by the rest of the herpetofauna. A humid and forested environment is also consistent with the mammal remains, due to the finding of hygrophilous insectivores and flying squirrels (Sala et al., 1994; Fanfani and Masini, 1997).

As noted by Delfino and Sala (2007), such a humid environment contrasts with the past common view of Neogene and Quaternary allocaudates being dry-adapted taxa, and is more consistent with Gardner and Böhme’s (2008) hypothesis of a group with wider habitat tolerances, but with a preference for moist and forested karstic areas. Given these ecological preferences, questions might be raised as to why they went extinct after the Early Pleistocene. Such humid and forested conditions were still present in the Southern Alps during the Calabrian, despite some possible and brief drier period with more open vegetation (Ravazzi and Rossignol Strick, 1995). It can be argued that whilst these periods may have had a negative impact on the survival of allocaudates in Northern Italy, an even stronger change in environmental conditions from a forested to a grassland/steppe environment had had virtually no effects on *A. pannonicum* in its type locality, Csarnóta 2 (Venczel and Gardner, 2005). The burrowing lifestyle of allocaudates has been suggested as the likely reason behind the low impact of the environmental changes at Csarnóta 2, and so this hypothesis might also hold true for those living in Northern Italy. Yet these organisms still went extinct. It is interesting to note that another interstitial amphibian found in Rivoli Veronese, *Speleomantes*, also disappeared from the area after the Gelasian. Therefore it seems likely that the cause of their disappearance could still overcome the resilience provided by their interstitial habits.

It is commonly thought that glacial phases during the first part of the Early Pleistocene were of a rather low amplitude, with the first major glaciation occurring during the Marine Isotope Stage (MIS) 22 (0.87 Ma; Muttoni et al., 2003, 2007). According to Muttoni and colleagues (2007), the magnitude of this glacial event was comparable to that of the Last Glacial Maximum, and it is possible that during this period, the ice cap covering the Alps were also similarly expanded towards the southern margin of the mountain range. Reconstructions of the Last Glacial Maximum place the ice cap margin very close to, if not covering, the area of Rivoli Veronese (see fig. 1 in Muttoni et al., 2003, and fig. 1a in Muttoni et al., 2007). It is therefore possible that the proximity of the ice cap might have made the karstic fissures unsuitable for both *Albanerpeton* and *Speleomantes*, which were not able to either migrate further south or recolonize the area during the following interglacial. Following the reconstructions reported in Muttoni et al. (2003, 2007), Rivoli Veronese was encircled by two different extensions of the ice cap during the Last Glacial Maximum, both from the Lake Garda and the Adige River sides. If a similar pattern is also valid for the MIS 22 glaciation, the Rivoli Veronese amphibians and reptiles may have found themselves trapped, with low possibilities of moving away from the glacier margin. In any case, if this part of Northern Italy acted as an Early Pleistocene refugium for allocaudates (as it seems suggested by the absence of other coeval or younger findings), it appears that the loss of suitable conditions resulted in, or at the very least pushed them towards, their extinction..

Herpetofaunal extinction or extirpation events during the Pleistocene are also well known in the two other European peninsulae facing the Mediterranean (namely, the Iberian and the Balkan Peninsulae). In both cases, the disappearance of taxa followed a southward trend, with their distributional ranges showing a contraction towards the southern portions of the two peninsulae over time (see e.g., varanids in Greece, Georgalis et al., 2017, and agamids in Spain, Delfino et al., 2008b; Blain et al., 2016a). It is interesting to note how the disappearance of “exotic” amphibians and reptiles in Iberia seems to be geographically linked with particular moments in time (Blain et al., 2016a): i.e., the Olduvai palaeomagnetic event in the northern part of the country and the

Jaramillo event in the southern part. However, it must be stressed that these extirpations concern mainly thermophilous reptiles (with the only exception of the green toad, *Bufotes viridis* s.l.), whose disappearance is usually linked with the cooling associated with glaciation events (even if competitive exclusion caused by other taxa could have also played a role). Given that, it is most likely that their local disappearance, and that of the cold-tolerant *Albanerpeton* and *Speleomantes* in the northern side of the Po Plain, might not be linked to the same causes.

5.2. Amphibians and reptiles from Rivoli Veronese and the Pleistocene herpetological assemblages of Italy

Albanerpeton is not the only peculiar taxon present in the rather diverse herpetological assemblage of Rivoli Veronese. The occurrence of *Speleomantes* is rather interesting too. Currently, this cave-dwelling plethodontid has a rather restricted distribution, limited to Sardinia, Liguria and the Appennines in Italy and to the southeastern corner of France (Lanza et al., 1995, 2006). Introduced populations are reported from Southern France and the eastern border of Northern Italy (*Speleomantes strinatii*; Sillero et al., 2014), as well as from Lower Saxony in Germany (probably *Speleomantes italicus*; Alexander Kupfer, pers.comm. to AV). Given this, the presence of an undetermined species of *Speleomantes* in Rivoli Veronese is identified as one of the very few fossil occurrences of this genus outside the current distributional range. Indeed, the very poor fossil record of *Speleomantes* is largely limited to the Pliocene to Holocene discoveries coming from localities inside areas inhabited by its extant representatives (for a summary, see Böhme and Ilg, 2003, Delfino, 2004, and Delfino et al., 2005). A single occurrence, other than Rivoli Veronese, is located far outside from this range: the middle Miocene trunk vertebra from Devínska Nová Ves, in Slovakia, attributed to a possible new species of *Hydromantes* (*Speleomantes*) by Venczel and Sanchiz (2005). The Rivoli Veronese finding testifies for a wider distribution of the genus during the Pleistocene. Neverheless, it cannot shed clear lights on its evolutionary dynamics in Europe, due to the presence of older occurrences that are already established in the current range and the absence of late Miocene- or Pliocene-aged extralimital fossils that might give clues on possible colonization routes.

All others amphibians found in Rivoli Veronese, except *I. alpestris*, have a rich fossil record (Böhme and Ilg, 2003). *Ichthyosaura alpestris* or morphologically-related forms, on the other hand, have been found in a few sites. These are: one locality from the Oligocene/Miocene boundary of Germany (Böhme and Ilg, 2003), one locality from the early Pliocene of Slovakia (Hodrová, 1984; Ivanov, 2007), one locality from the Early Pleistocene of Italy (Delfino and Bailon, 2000), four localities from the Middle Pleistocene of England (Gleed-Owen, 1998), France (Hanquet et al., 2010), Germany (Böhme, 1997; Holman, 1998) and Russia (Böhme and Ilg, 2003) and one locality from the Late Pleistocene of Spain (Holman, 1998). Including the single vertebra found in Rivoli Veronese, these remains represent only a handful of fossil occurrences of a species that was present in Europe since the beginning of the Neogene. It is interesting to note that the Middle Pleistocene was a period of large diffusion of this caudate into the continent, with a range that was far more extended than the current one (see Sillero et al., 2014) spreading from England and Southeastern France in the West to European Russia in the East. Rivoli Veronese represents only the second fossil occurrence of this species in mainland Italy, and the first one inside its current Italian range. The other remains, identified only tentatively as *Ichthyosaura* cf. *I. alpestris*, come from the slightly younger (Calabrian) fissure fillings of Cava dell’Erba, in the Pirro Nord karst network in Apulia (Delfino and Bailon, 2000). More remains are required from Central and Southern Italy to understand whether this species once had a stable and continuous distribution in the Appennine Peninsula, or the Pirro Nord fossils and the extant isolated populations in Calabria (Sindaco et al., 2006; Lanza et al., 2007; Sillero et al., 2014) are just the results of sporadic dispersal events.

A high number of taxa (at least five) composes the lizard assemblage from the Early Pleistocene of Rivoli Veronese. If not taking into account the third, small and undetermined lacertid, all these taxa but *Pseudopus*, are still present in the Verona province today. The current range of the genus *Pseudopus* has its western limit near the border between Slovenia and Italy (Sillero et al., 2014), where it is represented by the sole extant species, *Pseudopus apodus*. Nevertheless, the genus is also reported at sites in the Appennine Peninsula, occurring in deposits since the late Miocene (Böhme and Ilg, 2003), and has its youngest Italian occurrences right in the Verona province (Delfino, 2002; Delfino et al., 2008a). The *Pseudopus* osteoderm reported from the Calabrian site of Pirro Nord by Delfino and Bailon (2000) is now considered as an intrusion of an older (Neogene) fossil in the Early Pleistocene sample (Delfino and Atzori, 2013). Apart from Rivoli Veronese, *Pseudopus* remains in the Verona area have been found in the Early Pleistocene of Monte La Mesa, the Middle Pleistocene of Cengelle, Viatelle and Zoppega 2 and the Late Pleistocene of Grotta della Volpe (Delfino, 2002; Delfino et al., 2008a). These remains were at first attributed to the extinct *Pseudopus pannonicus* (Delfino, 2002), but later reallocated to an undetermined *Pseudopus* species (Delfino et al., 2008a). Given that, it is not possible to clearly state whether they represent a residual occurrence of *P. pannonicus* in Italy (and then also one of the oldest occurrences of the species in Europe; Böhme and Ilg, 2003) or rather a western expansion of *P. apodus* during the Pleistocene. Nevertheless, it appears clear that *Pseudopus* inhabited the area during the whole Pleistocene, eventually disappearing before the beginning of the Holocene.

Among others lizards identified in Rivoli Veronese, cf. *Zootoca vivipara* is the first report in Italy of a fossil form morphologically similar to the viviparous lizard, whose fossil record is known only from countries in the northern part of Europe (Gleed-Owen, 1998; Holman, 1998; Böhme and Ilg, 2003). Moreover, this is one of the oldest occurrences of this lizard, together with findings reported from the Early Pleistocene of Bad Deutsch-Altenburg, in Austria (Rauscher, 1992). Both *Lacerta* gr. *L. viridis* and *Anguis* gr. *A. fragilis*, on the other hand, were already reported from Italian sites, and they also have a more widespread fossil record in Europe (Holman, 1998; Böhme and Ilg, 2003). Still, those from Rivoli Veronese are the oldest remains of the slow worm currently known in Italy (Delfino, 2002; Böhme and Ilg, 2003; Delfino et al., 2008a).

Snakes are represented in Rivoli Veronese by taxa that are known from a number of other Italian Pleistocene localities, often as part of the same assemblages (Delfino, 2002; Böhme and Ilg, 2003; Delfino et al., 2008a). All of these are also currently present in the area (Sillero et al., 2014). As far as *Coronella* and *Z. longissimus* are concerned, they represent the oldest occurrences of the respective taxa known thus far in Italy. It is worth to note the apparent absence of *Hierophis viridiflavus*, which otherwise, is rather common at other Quaternary sites located in the Veneto region (Delfino et al., 2008a). Given the high adaptability of this snake, it is likely that this absence is not environmentally controlled. In any case, it is not possible to exclude that unrecognised *H. viridiflavus* vertebrae may have been included in the high number of trunk vertebrae identified only as undetermined “colubrines”, whose morphological differences suggest the possible presence of unrecognised colubrine taxa other than *Coronella* and *Zamenis*.

The Gelasian herpetofauna of Rivoli Veronese appears to have been rather diverse then, including at least 16 different taxa (probably more, taking into account the possible presence of other, unrecognised colubrines). Except for a few occurrences (namely, *Albanerpeton*, *Speleomantes* and *Pseudopus*), all the identified taxa are still present in the area, indicating that the extant amphibians and reptiles association was already setting up during the Early Pleistocene. If compared with the other well-known Early Pleistocene Italian site of the karst network at Pirro Nord, which is considered to be slightly younger (Calabrian) in age (Arzarello et al., 2007, 2009; López-García et al., 2015), the assemblage of Rivoli Veronese is slightly less diverse (18 taxa found in the fissure fillings of Pirro Nord versus 16 in the herein studied locality; Delfino and Bailon, 2000; Delfino and Atzori, 2013; Blain et al., 2016b). Apart from a certain similarity in the snake component, the rest of the herpetofauna from Pirro Nord is distinctly different from that of Rivoli Veronese, including an amphisbaenian and a rather diverse chelonian fauna (three different co-occurring taxa; Delfino and Bailon, 2000), notably missing from the Northern-Italian site. This difference might be linked to a dryer and warmer, Mediterranean climate in Southern Italy during the Calabrian, but also to the trans-Adriatic influence of Balkan faunistic elements colonizing the area by the beginning of the Pleistocene (e.g., *Pelobates syriacus*; Blain et al., 2016b). Moreover, the involvement of some kind of taphonomic bias in the lack of larger taxa such as turtles from the palaeoherpetofauna of the Northern-Italian site must be also taken into account, given that the Rivoli Veronese fissure is filled with fine-grained sediments and large faunal elements (e.g., large mammals) are lacking as a whole.

6. Conclusions

The analysis of fossil remains of amphibians and reptiles coming from Rivoli Veronese has resulted in the identification of a highly diverse herpetofauna that shares numerous taxa with the extant herpetological population of the same area. Moreover, the Early Pleistocene assemblage includes important findings, such as one of the very few extralimital occurrences of *Speleomantes*, the first record of the viviparous lizard from Italy (even though only tentatively recognised), as well as the oldest occurrence of the slow worm, the smooth snake and the Aesculapian snake in the country. These add to the fact that the sites hosted the youngest remains of allocaudates that are globally known.

The palaeoclimatic and palaeoenvironmental reconstruction indicates a cold and humid climate and a forested environment, possibly with less represented, more open areas in the surroundings. The Po Basin is considered peculiar in the frame of the Gelasian climate of Italy because of the presence of forested glacial phases, but until recently, evidence showing this came mainly from the southern margin of the basin. Our analysis confirms that the northern side of the Po Plain was characterized by environmental conditions similar to those present in the south (that is, a forested, cold and humid environment), as well as new evidence supporting the hypothesized preference for humid environmental condition by *Albanerpeton*.

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Figure captions

Figure 1. Map of Northern Italy, showing the position of Rivoli Veronese. [planned for single column width]

Fig. 1

Figure 2. cf. *Albanerpeton* sp. from Rivoli Veronese. A: left dentary (RV-H-027) in medial view. B: right dentary (RV-H-234) in medial view. Scale bar = 1 mm. [planned for single column width]

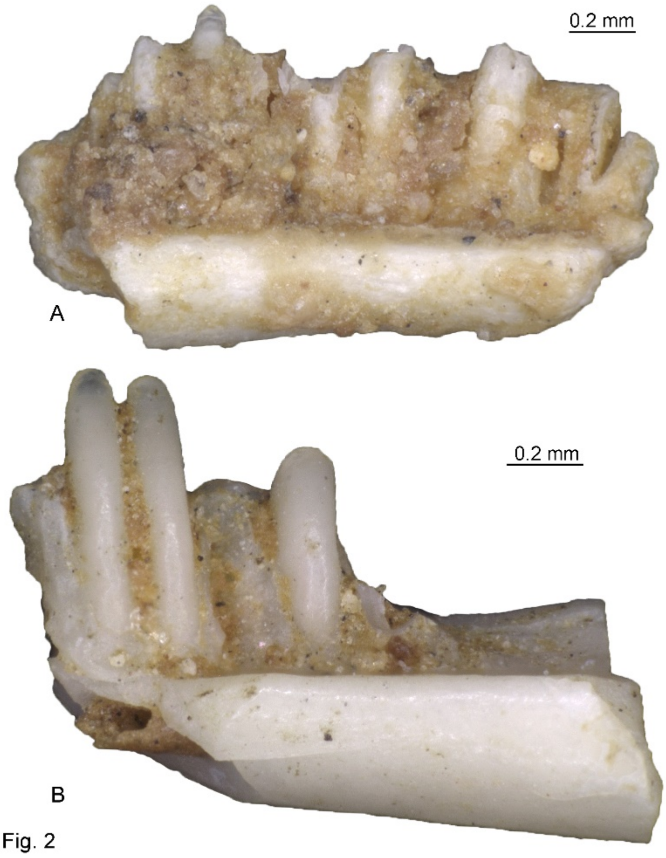

Fig. 2

Figure 3. Caudates from Rivoli Veronese. A-C: *Speleomantes* sp., presacral vertebra (RV-H-003) in dorsal (A), ventral (B) and left lateral (C) views. D-F: *Ichthyosaura alpestris*, presacral vertebra (RV-H-004) in dorsal (D), ventral (E) and right lateral (F) views. G-H: Caudata indet., caudal vertebra (RV-H-257) in right lateral (G) and dorsal (F) views. Scale bars equals 1 mm (A-F) and 0.5 mm (G-H). [planned for single column width]

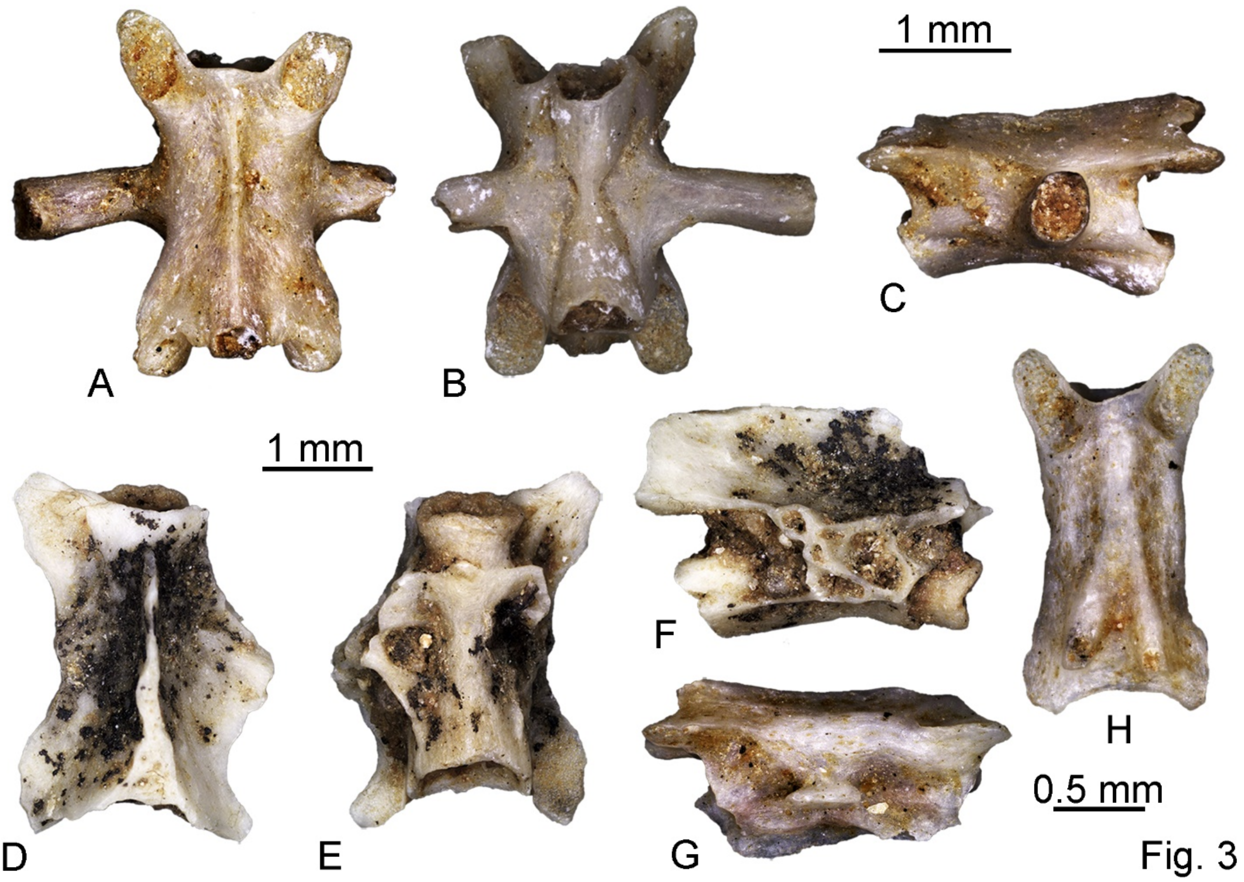

Figure 4. Anurans from Rivoli Veronese. A-B: *Bombina* sp., left humerus (RV-H-010) in ventral (A) and lateral (B) views. C-D: *Bufo bufo*, right scapula (RV-H-001) in ventral (C) and dorsal (D) views. E: *Bufo bufo*, left ilium (RV-H-107) in lateral view. F-G: *Hyla* gr. *H. arborea*, trunk vertebra (RV-H-135) in dorsal (F) and anterior (G) views. H-I: *Rana* sp., left humerus (RV-H-006) in ventral (H) and medial (I) views. J: Ranidae indet., right ilium (RV-H-005) in lateral view. K-L: Ranidae indet., left ilium (RV-H-042) in lateral (K) and dorsal (L) views. Scale bars equals 1 mm (A-E, H-J) and 0.5 mm (F-G, K-L). [planned for double column width]

Fig. 4

Figure 5. Lizards from Rivoli Veronese. A-B: *Lacerta* gr. *L. viridis*, right frontal (RV-H-143) in dorsal (A) and ventral (B) views. C-D: cf. *Zootoca vivipara*, fused frontals (RV-H-144) in dorsal (C) and ventral (D) views. E-F: Lacertidae indet., parietal (RV-H-165) in dorsal (E) and ventral (F) views. G-H: Lacertidae indet., premaxilla (RV-H-156) in anterior (G) and posterior (H) views. I: *Anguis* gr. *A. fragilis,* left dentary (RV-H-034) in medial view. J-L: *Anguis* gr. *A. fragilis*, trunk vertebra (RV-H-036) in dorsal (J), ventral (K) and left lateral (L) views. M-N: ?*Anguis* sp., left dentary (RV-H-235) in medial (M) and ventromedial (N) views; the arrow marks the fused intramandibular septum. O: cf. *Pseudopus* sp., fragment of dentary (RV-H-033) in medial view. P-R: cf. *Pseudopus* sp., caudal vertebra (RV-H-030) in right lateral (P), dorsal (Q) and ventral (R) views. Scale bars equals 1 mm (A-D, I-N, P-R) and 0.5 mm (E-H, O). [planned for double column width]

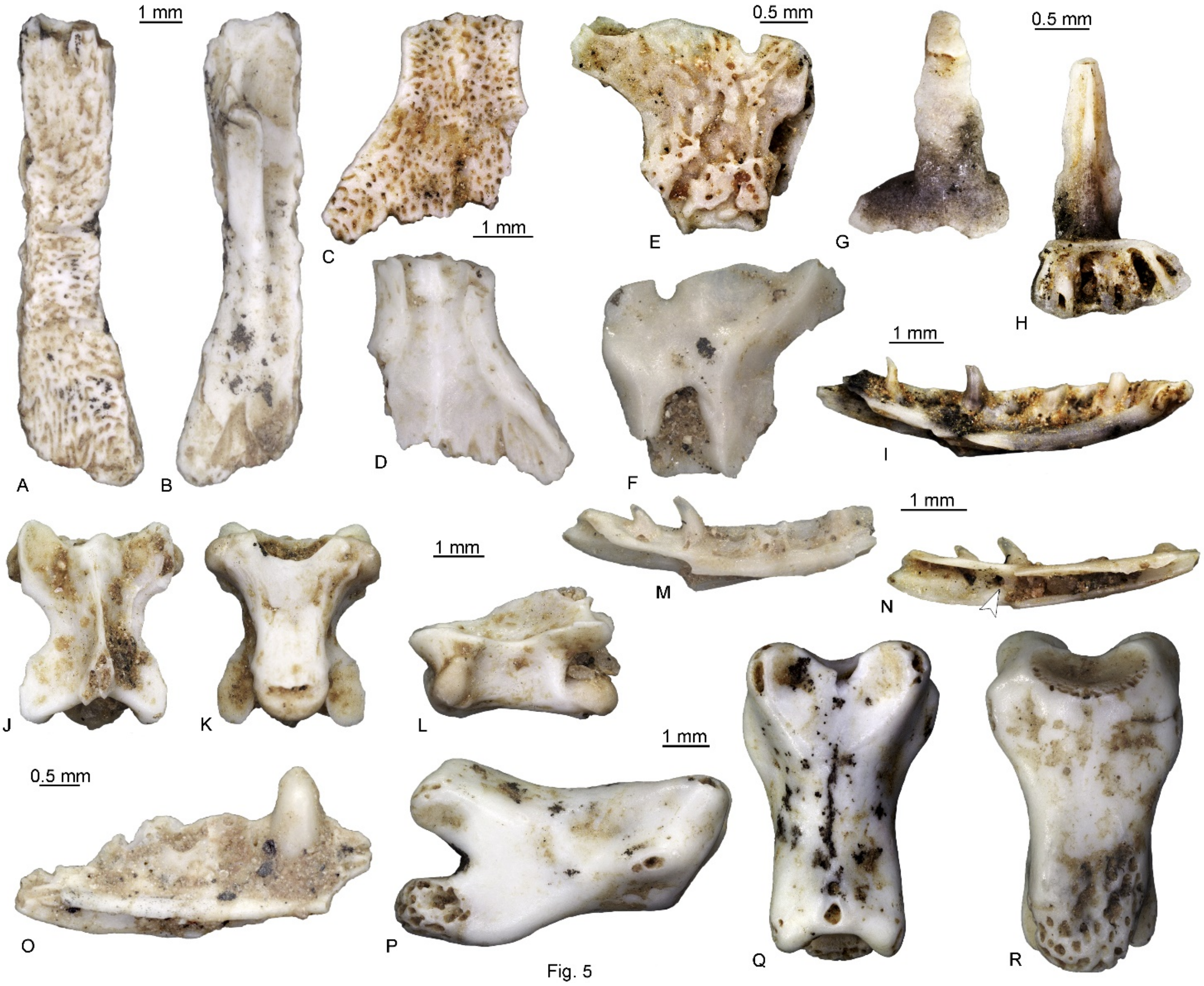

Figure 6. Snakes from Rivoli Veronese. A-D: *Coronella* sp., trunk vertebra (RV-H-011) in dorsal (A), anterior (B), left lateral (C) and ventral (D) views. E-H: *Zamenis longissimus*, trunk vertebra (RV-H-255) in dorsal (E), anterior (F), left lateral (G) and ventral (H) views. I-L: *Natrix* sp., trunk vertebra (RV-H-076) in dorsal (I), anterior (J), left lateral (K) and ventral (L) views. M-P: *Vipera* gr. *V. aspis*, trunk vertebra (RV-H-009) in dorsal (M), anterior (N), left lateral (O) and ventral (P) views. Scale bars equals 1 mm (E-P) and 0.5 mm (A-D). [planned for double column width]

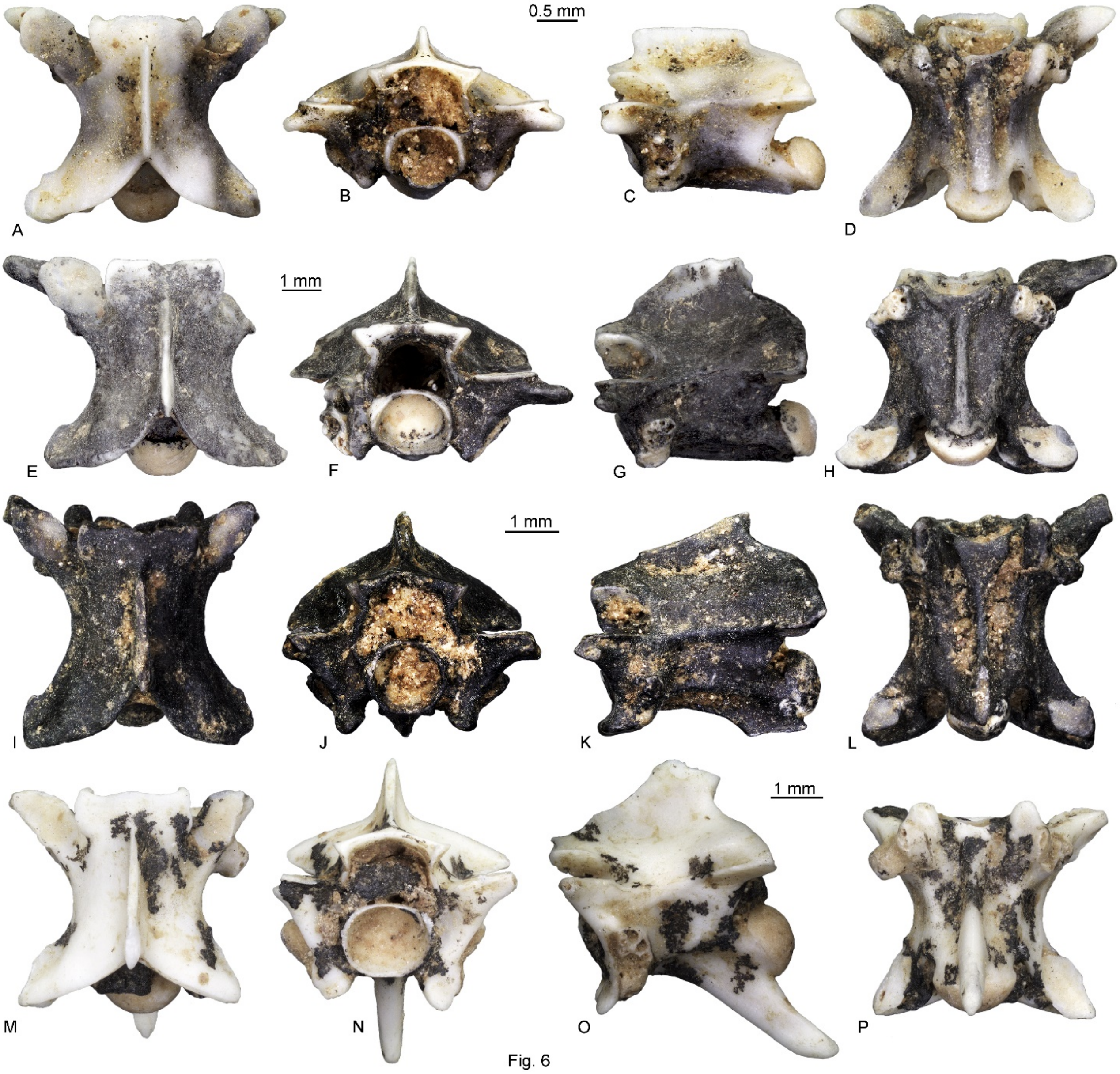

Fig. 6

Figure 7. Monthly palaeoclimatic reconstructions for Rivoli Veronese based on its fossil herpetofaunal assemblage. A: overlaps of the current distribution done in 50 × 50 km UTM squares without *Speleomantes* (red square) and without *Speleomantes* and *Pseudopus* (black and red squares). B: climatograms from Ilirska Bistrica (southwestern Slovakia; red square) that would represent the Early Pleistocene paleoclimate occurring at Rivoli Veronese according to the MER method compared with current data of Rivoli Veronese. (Colour online) [planned for double column width]

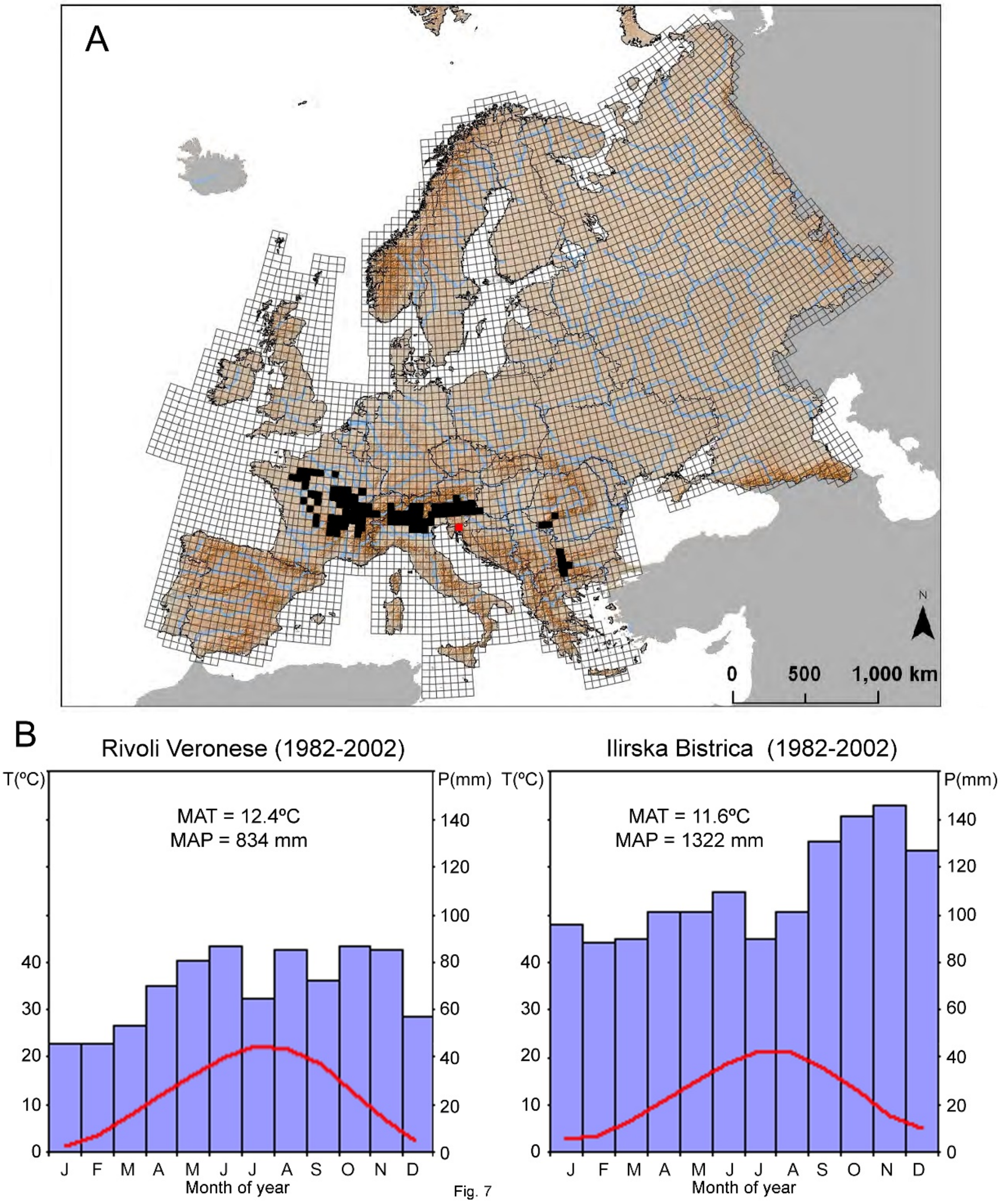

Fig. 7

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.

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

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