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Late Pleistocene and Holocene distribution history of the Eurasian beaver in Italy

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Abstract: The genus *Castor* first appeared in the Palaearctic region during the Late Miocene, while the current species, *Castor fiber*, is widely accepted to have emerged in the Early Pleistocene. In the Last Glacial Maximum (Late Pleistocene), the beaver disappeared from most of the Western Palaearctic, only surviving in a few relic areas including the south-eastern Alpine Chain as shown by new data. After the subsequent extended repopulation in the warmer phases of the Lateglacial and in the early Holocene, the species once again disappeared locally from several countries, including Italy, between the 17th and the 20th centuries. Direct or indirect persecution by humans seems to be the main cause of beaver extinction in Europe. In Low Medieval Italy, it is more likely that the disappearance of the beaver between the 16th and 17th centuries was due to habitat alteration and human population pressure. Numerous reclamations have been carried out since the late Middle Ages, mostly in the easternmost area of the Po Valley, the last beaver refuge in Italy. Eurasian beaver was common in the northern and widespread in the central part of Italy, but always absent in southern Italy, probably due to unfavourable hydrological conditions of watercourses in the latter.

Keywords: *Castor fiber*; Holocene; Italy; Late Pleistocene; palaeobiogeography.

Introduction

The original distribution of the Eurasian beaver, *Castor fiber* Linnaeus, 1758, the largest Eurasian rodent, once comprised a large portion of the Palaearctic region, from Great Britain and the westernmost Iberian Peninsula to the Balkans and Scandinavia, Mongolia, Siberia and north-western China, throughout the deciduous and coniferous forest zones, and in suitable riparian areas, in tundra and in steppe (Djoshkin and Safonov 1972, Halley and Rosell 2003, Halley et al. 2012, Batbold et al. 2016). Currently, eight or nine subspecies of *C. fiber* are known, but their boundaries and resultant synonymies are unclear and obscured by historical translocations and reintroductions (Gabryś and Ważna 2003, Halley and Rosell 2003, Helgen 2005).

According to several authors (e.g. Halley and Rosell 2002, Batbold et al. 2016), the species underwent a decline in historical times mainly caused by overhunting for fur and meat, combined with loss of habitats and the long-lasting demand for *castoreum*, a secretion from the scent glands that was particularly appreciated in medieval times and renowned in the pharmacopoeia since antiquity (Batbold et al. 2016, De Grossi Mazzorin 2016).

Between the 16th and 19th centuries, a cooler climatic phase called the Little Ice Age coincided with a well-known slaughter of beavers for their fur, particularly in North America but also in Europe. The demand for this valuable good increased especially for the production of fashionable hats (Varekamp 2006).

Later on, between the end of the 19th and the beginning of the 20th century, a significant reduction occurred with populations outside of Italy scattered into enclaves not exceeding 1200 individuals (Halley and Rosell 2002, Halley et al. 2012).

The ecology of the species is heavily reliant on riparian woodland ecosystems (Rosell et al. 2005, Marr et al. 2018). Beavers are adapted to a semi-aquatic life, using a variety of freshwater bodies, preferably surrounded by woodland, but may also be found in agricultural land or even suburban and urban areas (Tattersall 1999, Halley and Rosell 2002, Batbold et al. 2016): for instance, the vicariant Nearctic species, the American beaver, *Castor canadensis* Kuhl, 1820, returned on its own in 2007 to the River Bronx, the last remaining freshwater river of New York City, after more than 30 years of cleaning and restoration (Sanderson 2009).

Moreover, southern Europe was largely populated by Eurasian beavers up to the 17th century, when the advent of efficient steel traps and accurate firearms began to drastically reduce their populations. The 19th century saw

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rash extinction episodes for reasons mentioned earlier combined with drainage of many of the marshland areas home to the species (Batbold et al. 2016). The south-westernmost populations of Eurasian beavers occurred in a few localities in the Iberian Peninsula (Halley and Rosell 2003), as well as in the southern course of the River Rhone and its mouth (Rouland 1997), where a relic stock of the species still survives and was declared protected in France in 1968. Later on, protection measures, natural expansion and reintroductions allowed beavers to re-colonize large parts of their former range (Rouland and Migot 1990, Dewas et al. 2011).

Although the south-eastern distribution of *Castor fiber* seems to have been halted by the Himalayas, the species' south-western Palaearctic distribution reaches much farther southern latitudes (Batbold et al. 2016). Beyond the barrier constituted by the Mediterranean Sea, the distribution of the beaver never reached the North African Atlas region, probably due to the excessive width of the Strait of Gibraltar (14 km), impossible for beavers to cross without human assistance. In former times, their distribution also expanded into the Near East: the rivers whose sources in the eastern Anatolian mountains reached the alluvial plains of Mesopotamia allowed the establishment of one of the southernmost populations of the species in the whole Palaearctic up to very recent times. Their former occurrence in this area is documented by the recovery of fossil remains in archaeological contexts (Patterson 1937, Kumerloeve 1967, Legge and Rowley-Conwy 1986, Becker 2005, Siracusano 2010). *Castor fiber* was discovered in the rivers Euphrates and Khabur in 1835 (Ainsworth 1838), and may have continued to exist until the late 19th–early 20th centuries in Anatolia and Syria (Danford and Alston 1880, Harrison 1972). It disappeared from Iraq at a much earlier time, possibly as a result of deforestation and general human population pressure (Hatt 1959).

The aim of the present work is to investigate the distribution history of Eurasian beavers in the southernmost areas of its Palaearctic distribution with particular attention to Late Pleistocene and Holocene Italy, up to its regional extinction. As also observed by De Grossi Mazzorin (2016), the remains of this species in Italy are key to understand the dynamics that led to its extinction in an important part of the southernmost area of its distribution.

Materials and methods

The reconstruction of the past distribution of *Castor fiber* in Italy was carried out through a literature search compiling the main vertebrate deposits and archaeological contexts referred to the Late Pleistocene and Holocene. Around 1000 sites were examined, among which less than 10% yielded remains of beavers.

The presence of Eurasian beaver remains, site type, altitude and existing radiometric dating of the sites were considered. When available, the cranial and post-cranial skeletal elements and possible cut-marks, and the occurrence or absence of bone remains of other so-called fur animals (e.g. hare, marmot and wild carnivores) were also noted.

Because of the uncertainties of the records and due to major changes in excavation techniques and/or dating methods, the literature pre-dating the Second World War (e.g. Strobel 1875, Clerici 1887, De Stefani 1916, Boule 1919, Fabiani 1919, Dal Piaz 1929) was excluded. Furthermore, the bone remains generally referred to the Quaternary or the Holocene, and were recovered from river erosion outcrops, collected from roadwork excavations or from post-glacial peat bogs which are relatively numerous in the Po Valley and Veneto (e.g. Anelli 1947, Martinis 1948, Malvolti 1950, Accordi 1952). These were not considered as their dating was not deemed reliable.

The Pleistocene chronostratigraphy used in this work follows Gibbard et al. (2010), while Orombelli and Ravazzi (1996), supplemented by Ravazzi (2003), were followed for the Holocene. Some Latin classics and zoological texts dated to the 14th–17th centuries were also consulted.

Results and discussion

Origin and early records of the genus *Castor*

Beaver remains are relatively common in the European fossil record, but often represented by only a few specimens. The origin of the genus *Castor* Linnaeus, 1758 is debated, but it probably first appears across Europe at the beginning of the Late Miocene with the species *Castor neglectus* Schlosser, 1902; *Castor praefiber* Depéret, 1890 then appears in the latest Miocene (Barisone 2004, Rekovets et al. 2009) and is present throughout the Pliocene. The extant species, *Castor fiber*, is known since the beginning of the Early Pleistocene (Barisone 2004, Barisone et al. 2006, Kotsakis 2008, Rekovets et al. 2009).

In Italy, the genus occurs in the latest Miocene with fossils of *Castor praefiber*, while *Castor fiber* appears in the first part of the Early Pleistocene (Kotsakis et al. 2003, Barisone 2004). During the Early Pleistocene, a local cronosubspecies, *Castor fiber plicidens* Bosco, 1898,

evolved in central Italy and became extinct at the end of the Early Pleistocene, replaced by populations similar to the current *C. fiber* (see Barisone et al. 2006, Kotsakis 2008).

Early Pleistocene fossils of *Castor fiber* were found in numerous sites of central and northern Italy (Kotsakis et al. 2003, Argenti 2004, Barisone et al. 2006). Remains of the species were also found in several Middle Pleistocene sites in central Italy, often in association with Acheulean lithic artefacts (Biddittu and Celletti 2001, Kotsakis et al. 2003, Sala 2006), and in a few localities in northern Italy (Kotsakis et al. 2003). Conversely, Late Pleistocene and Holocene remains of Eurasian beavers are more numerous in northern Italy.

Late Pleistocene records of beavers

Fossil remains of *Castor fiber* have been reported from many Late Pleistocene sites across Europe (e.g. Chaline 1972, Aalto et al. 1989, Antunes 1989, Simionescu 1990, Sesé and Sevilla 1996, Kolfschoten 2000, Baryshnikov 2002, Bachura and Kosintsev 2007, Rekovets et al. 2009, Bogićević et al. 2011, Wilczyński et al. 2012) and in some localities in the Near East (Legge and Rowley-Conwy 1986).

In Italy (Figure 1, Table 1), beaver remains attributed to the early part of the Late Pleistocene come from Units IV–V of Grotta Maggiore di San Bernardino (Berici Hills), Veneto, and refer to the Marine Isotope Stage (MIS) 5c-a. In this cave, fossils of *Castor fiber* also occur in late Middle Pleistocene layers (MIS 7 and transition MIS 6/5) and in MIS 3. Associated with Mousterian artefacts, these beaver remains are strongly fragmented and are constituted mostly of metapodial bones, carpal and tarsal bones, phalanges and caudal vertebrae, including some juvenile elements, some of which display cut-marks (Table 1; Lubrano et al. 2018).

In southern Latium, Eurasian beaver remains come from the Mousterian sites of Valle Radice and Carnello, Liri-Garigliano basin (Table 1). According to Segre et al. (1984), the two deposits are contemporary and date to the beginning of the last glaciation episode (MIS 5a; see also Caloi and Palombo 1994, Petronio et al. 2011). However, the faunal assemblages seem to reveal different habitats which is especially highlighted in the recorded bird taxa: in Carnello, avian aquatic species are more frequent, while in Valle Radice species adapted to rocky habitats and high altitudes predominate. In Carnello beaver remains are more abundant, while in Valle Radice they are relatively rare and associated with marmot, giant deer, bison and ibex remains (Segre et al. 1984, Pandolfi and Tagliacozzo 2015). The occurrence of these species suggests a colder setting in Valle Radice than in Carnello. Therefore, the Valle Radice faunal assemblage could be rather referred to the full MIS 4.

As far as is presently known, the fossil remains from Grotta Reali, upper Volturno basin, Molise (Table 1), associated with Mousterian industry and referred to a temperate-fresh interstadial phase of MIS 3, represent the southernmost occurrences (41°35′48″ N) of *Castor fiber* in Italy.

Further fossils of beavers of MIS 3 age are from Grotta di Equi (Apuane Alps), Grotta del Bandito (Gesso Valley), the Aurignacian layers A2 and D1c of Riparo di Fumane and the Aurignacian layer 1fg of Riparo del Broion (Adige basin) (Table 1).

Eurasian beaver fossils referred to MIS 2 were found in several sites of the Adige basin in north-eastern Italy (southern Alpine foothills); these are dated before, during and after the Last Glacial Maximum (LGM). Layers 1cde (Gravettian) and 1ab (ancient Epigravettian) of Riparo del Broion as well as the Gravettian layer of Grotta del Buso Doppio del Broion date to the LGM, whereas the Epigravettian layers 12–10 of Riparo Tagliente date to Bølling (Table 1). Other Lateglacial remains of the species from Allerød and/or Dryas III layers were found in other Epigravettian sites of north-eastern Italy (Table 1), mainly in plain and hilly areas, but also in the mountains. In each of these sites, records of beavers consist only of one or very few remains, and frequently as isolated teeth. Two sites are located at 1070 and 1240 m a.s.l. (Cogola and Dalmeri shelters; Table 1), higher than the current altitudinal distribution limit (850 m a.s.l.; see Batbold et al. 2016). However, it cannot be excluded that the beaver was hunted at lower altitudes, in the valleys, and then carried to these high-altitude shelters.

Holocene records of beavers (prehistory and protohistory)

In the early Holocene, Eurasian beaver remains were found in several European sites. In the Alpine region, in the Rhone Valley and in the Danube basin, beavers rarely represent more than 5% of the total identified mammal remains (Wierer and Boscato 2006, Kind 2009, 2013). North-Central Europe provides, instead, Mesolithic sites with high abundances of beavers, such as Rottenburg Siebenlinden 3 (Germany) (Kind 2003), Lammasmägi and Pärnu (Estonia) (Lõugas 1997, Veski et al. 2005), Hardinxveld (Netherlands) (Louwe Kooijmans 2003) and Dabki (Poland) (Sobociński 1986, Schmölcke

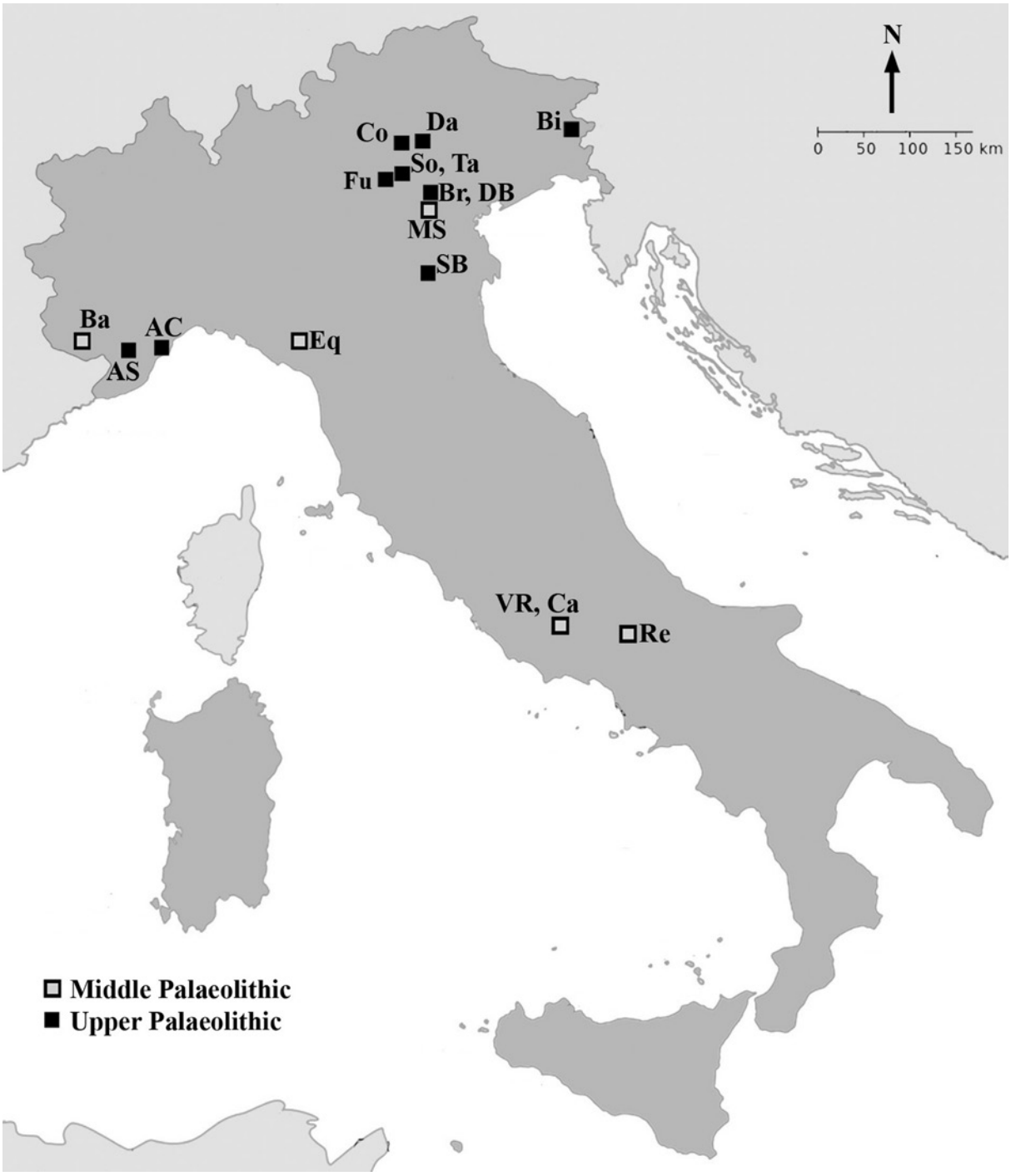

Figure 1: Geographical distribution of Italian sites with Eurasian beaver remains referred to the Palaeolithic (alphabetical order). Middle Palaeolithic: Ba, Grotta del Bandito; Eq, Grotta di Equi; MS, Grotta Maggiore di San Bernardino; Re, Grotta Reali; VR, Ca, Valle Radice and Carnello. Upper Palaeolithic: AC, Caverna delle Arene Candide; AS, Arma dello Stefanin; Bi, Riparo di Biarzo; Br, RD, Riparo del Broion and Grotta del Buso Doppio del Broion; Co, Riparo Cogola; Da, Riparo Dalmeri; Fu, Riparo di Fumane; SB, Settepolesini di Bondeno; So, Ta, Riparo Soman, Riparo Tagliente.

and Nikulina 2015), where the number of bone fragments of *Castor fiber* reaches 30–60% of the mammal remains. It may be that Mesolithic hunters practiced some sort of specialized beaver hunting in the vicinity of these sites, such as can be seen in the Russian Zamostje 2, north of Moscow, in the upper Volga (Chaix 2003, 2004). Layer 8 of Zamostje 2 (7380 ± 60 years BP) yielded a mammal assemblage with a predominance of *C. fiber* (825 remains

Table 1: List of Late Pleistocene sites of Italy with *Castor fiber* remains, their age and geographic area.

Site	Region	Alt. a.s.l.	Site type	Industry	Radiometric dating BP (ka)	n	%	References
Settepolesini di Bondeno	Emilia Romagna	6	Peat bog		13.2–13.4			Gallini and Sala 2001
Riparo di Biarzo	Friuli Venezia Giulia	160	Rockshelter	Epigravettian	11.1	12	1.28	Romandini and Bertolini 2010, Bertolini et al. 2012
Carnello	Latium	~300	Cave	Mousterian				Segre et al. 1984
Valle Radice	Latium	326	Cave	Mousterian		4		Biddittu et al. 1967, Segre et al. 1984
Arma dello Stefanin (layer V)	Liguria	440	Cave	Epigravettian	<12.7	7	0.28	Barker et al. 1990
Caverna Arene Candide (layer M2)	Liguria	90	Cave	Epigravettian	10.9	1	0.06	Cassoli and Tagliacozzo 1994b
Grotta Reali (US 1)	Molise	515	Cave	Mousterian		2	0.51	Sala et al. 2012, Thun Hohenstein and Bertolini 2012
Grotta Reali (US 2abc)	Molise	515	Cave	Mousterian	33.5	2	1.50	Sala et al. 2012, Thun Hohenstein and Bertolini 2012
Grotta del Bandito	Piedmont	726	Cave					Zunino and Pavia 2005
Riparo Cogola (layer 18)	Trentino Südtirol	1070	Rockshelter	Epigravettian	9.8	1	0.87	Fiore and Tagliacozzo 2004, 2005
Riparo Dalmeri	Trentino Südtirol	1240	Rockshelter	Epigravettian	11.1–11.2	17	0.20	Cassoli et al. 1999, Fiore and Tagliacozzo 2005
Grotta di Equi	Tuscany	258	Cave	Mousterian				Ghezzo et al. 2014
Grotta del Buso Doppio del Broion	Veneto	150	Cave	Gravettian		2	3.70	Nannini and Romandini 2015
Grotta Maggiore San Bernardino (Unit II)	Veneto	135	Cave	Mousterian	33 ± 5–38 ± 5	25	4.20	Cassoli and Tagliacozzo 1994a, López-García et al. 2017
Grotta Maggiore San Bernardino (Units IV–V)	Veneto	135	Cave	Mousterian	83 ± 18–108 ± 15	5	2.12	Cassoli and Tagliacozzo 1994a, López-García et al. 2017
Grotta Maggiore San Bernardino (Unit VI)	Veneto	135	Cave	Mousterian	133 ± 43	14	5.20	Cassoli and Tagliacozzo 1994a, López-García et al. 2017
Riparo del Broion (layer 1ab)	Veneto	135	Rockshelter	Epigravettian	17.8	2	2.41	Gurioli et al. 2010
Riparo del Broion (layer 1cde)	Veneto	135	Rockshelter	Gravettian	25.9	1	5.00	Gurioli et al. 2010
Riparo del Broion (layer 1fg)	Veneto	135	Rockshelter	Aurignacian	26.0–32.1	1	0.93	Gurioli et al. 2010
Riparo di Fumane (layer A2)	Veneto	350	Rockshelter	Aurignacian	30.6–32.1	1	0.10	Cassoli and Tagliacozzo 1991
Riparo di Fumane (layer D1c)	Veneto	350	Rockshelter	Aurignacian	<30.700	1	0.72	Cassoli and Tagliacozzo 1991
Riparo Soman (transition)	Veneto	100	Rockshelter	Epigravettian – Mesolithic		10	0.93	Tagliacozzo and Cassoli 1992
Riparo Soman (phase II)	Veneto	120	Rockshelter	Epigravettian	10.4–10.5	1	0.27	Tagliacozzo and Cassoli 1992, Fiore and Tagliacozzo 2005
Riparo Tagliente (cut 10)	Veneto	250	Rockshelter	Epigravettian	12.6–13.3	2	0.07	Capuzzi and Sala 1980, Rocci Ris et al. 2005
Riparo Tagliente (cuts 12–11)	Veneto	250	Rockshelter	Epigravettian	12.0–13.4	1	0.77	Capuzzi and Sala 1980, Fiore and Tagliacozzo 2005

Alt. a.s.l., Altitude above sea level; radiometric dating (ka BP) is not calibrated; n, number of beaver remains; %, percentage of beaver remains.

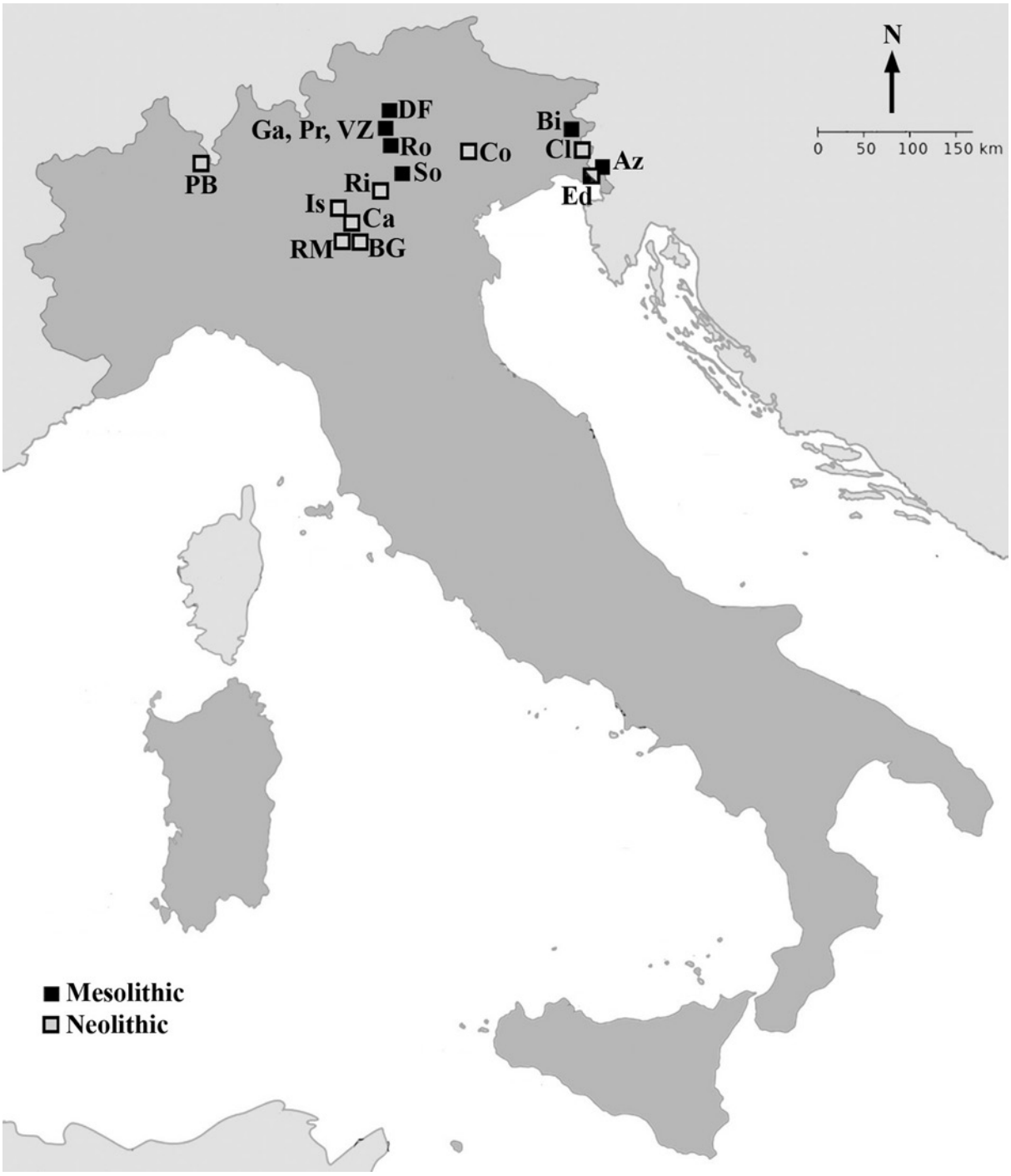

Figure 2: Geographical distribution of Italian sites with Eurasian beaver remains referred to the Mesolithic and Neolithic (alphabetical order).
Mesolithic: Az, Grotta Azzurra di Samatorza; Bi, Riparo di Biarzo; DF, Riparo Dos de la Forca – Galgenbühel; Ed, Grotta dell'Edera; Ga, Pr, VZ, Riparo Gaban, Riparo Pradestel e Vatte di Zambana; Ro, Rparo di Romagnano III; So, Riparo Soman. Neolithic: BG, Belforte di Gazzuolo; Ca, Casalmoro; Cl, Cladrecis; Co, Cornuda; Ed, Grotta dell'Edera; Is, Isorella; PB, Pizzo di Bodio; Ri, Rivoli Veronese; RM, Rivarolo Mantovano.

making 52% of the total and with at least 80 individuals); processing marks on the bones presumably indicate food exploitation, as well as the use of these animals for pelts and tool production, such as scissors and chisels. Intensive beaver exploitation continued in the Neolithic (Chaix 2003, 2004).

In Italy, remains of the species associated with Mesolithic industry were found in sites located both in the

Table 2: List of Holocene Italian sites with *Castor fiber* remains, their age and geographic area.

Site	Region	Alt. a.s.l.	Site type	Culture/industry	n	%	References
Grotta Azzurra di Samatorza	Friuli Venezia Giulia	270	Cave	Mesolithic	14	0.88	Cannarella and Cremonesi 1967
Grotta dell'Edera (layer 3c)	Friuli Venezia Giulia	234	Cave	Mesolithic	5	0.32	Boschin and Riedel 2010
Riparo di Biarzo	Friuli Venezia Giulia	160	Rockshelter	Mesolithic	1	0.54	Rowley-Conwy 1996
Galgenbühel – Dos de la Forca	Trentino Südtirol	225	Rockshelter	Mesolithic	327	39.54	Wierer and Boscato 2006, Wierer et al. 2016
Riparo Gaban	Trentino Südtirol	260	Rockshelter	Mesolithic	9	0.80	Thun Hohenstein et al. 2016
Riparo Pradestel	Trentino Südtirol	250	Rockshelter	Mesolithic	300	18.82	Boscato and Sala 1980
Riparo Romagnano III	Trentino Südtirol	190	Rockshelter	Mesolithic	47	3.82	Boscato and Sala 1980, Boscato et al. 1992
Riparo Soman	Trentino Südtirol	120	Rockshelter	Mesolithic	11	5.16	Tagliacozzo and Cassoli 1992
Vatte di Zambana	Trentino Südtirol	210	Rockshelter	Mesolithic	7	3.63	Boscato and Sala 1980
Cladrecis	Friuli Venezia Giulia	216	Cave	Neolithic	1	0.10	Riedel 1984a
Grotta dell'Edera (layers 2–2a)	Friuli Venezia Giulia	234	Cave	Neolithic	20	1.22	Boschin and Riedel 2000
Belforte di Gazzuolo	Lombardy	25	Open settlement	Neolithic	14	1.83	Guerreschi et al. 1986
Casalmoro di S. Maria Segreta	Lombardy	50	Gravel quarry	Neolithic	1	1.75	Clark 1984
Isorella	Lombardy	55	Pit in the field	Neolithic	4	2.27	Bon et al. 2005a
Pizzo da Bodio	Lombardy	240	Open settlement	Neolithic	3	1.40	Sorrentino 2010
Rivarolo Mantovano	Lombardy	27	Open settlement	Neolithic	9	5.56	Catalani 1984
Cornuda	Veneto	350	Landslide material	Neolithic	1	0.12	Riedel 1988
Rivoli Veronese	Veneto	192	Open-air settlement	Neolithic	1	0.10	Jarman 1976
Parma – aeroporto	Emilia Romagna	45	Natural canal bottom	Copper Age	1	0.14	Bon et al. 2005b
Acquaviva	Trentino Südtirol	240	Rockshelter	Copper Age	1	0.83	Riedel 1982
Isera – La Torretta	Trentino Südtirol	247	Hilltop settlement	Copper Age	7	0.30	Riedel and Rizzi 1997
Riparo Soman	Trentino Südtirol	200	Rockshelter	Copper Age	3	4.00	Tagliacozzo and Cassoli 1992
Bazzano	Emilia Romagna	104	Hilltop settlement	Bronze Age	1		Maini 2012
Calerno presso l'Enza	Emilia Romagna	50	Hut	Bronze Age			De Grossi Mazzorin 2014
Grotta del Farneto	Emilia Romagna	90	Cave	Bronze Age	1	0.14	Sala 1980
Monte Castellaccio	Emilia Romagna	54	Hilltop settlement	Bronze Age	1	0.16	De Grossi Mazzorin 1996a
Barche di Solferino	Lombardy	138	Pile dwelling	Bronze Age	2	0.07	Riedel 1976
Albanbuhel	Trentino Südtirol	850	Hilltop settlement	Bronze Age	1	0.01	Riedel and Rizzi 1995
Colombo di Mori	Trentino Südtirol	220	Hilltop settlement	Bronze Age	1	0.13	Bonardi et al. 2000
Adria – Via Amolaretta	Veneto	~16	Open-air settlement	Bronze Age	1	0.26	Gambacurta et al. 2012
Campestrin di Grignano Pol	Veneto	5	Open-air settlement	Bronze Age	1	0.31	Bertolini and Thun Hohenstein 2016
Canàr di S.Pietro Polesine	Veneto	7	Open-air settlement	Bronze Age	55	0.26	Riedel 1998
Tombola di Cerea	Veneto	15	Pile dwelling	Bronze Age	2	0.17	Zanini et al. 2016
Bologna Via del Pratello	Emilia Romagna	60	Oper-air settlement	Bronze/Iron	1		Farello 1995
Bologna – Via Foscolo	Emilia Romagna	64	Open-air settlement	Iron Age	1	0.26	Farello 2002
Mirandola Barchessone	Emilia Romagna	20	Open-air finds	Iron Age	1	1.32	Farello 1993
S. Martino Spino	Emilia Romagna	12	Settlement	Iron Age	1	1.35?	Farello 1995
Spina	Emilia Romagna	0	Harbour settlement	Iron Age			Farello 2006
Centes di Gradiscutta	Friuli Venezia Giulia	15	Hilltop settlement	Iron Age	2	0.69	Riedel et al. 2005
Ficana 3b–c	Latium	50	Hilltop settlement	Iron Age	1	0.00	De Grossi Mazzorin 1996b
Vadena II	Trentino Südtirol	170	Settlement	Iron Age	7	0.40	Riedel 2002
San Rocchino (VII–VI BC)	Tuscany	0	Settlement	Iron Age	56	8.50	Wilkens 2003

Table 2 (continued)

Site	Region	Alt. a.s.l.	Site type	Culture/industry	n	%	References
San Rocchino (IV BC)	Tuscany	0	Settlement	Iron Age	76	8.26	Wilkens 2003
San Rocchino (IV–III BC)	Tuscany	0	Settlement	Iron Age	35	7.66	Wilkens 2003
San Rocchino (not dated)	Tuscany	0	Settlement	Iron Age	176	9.92	Wilkens 2003
Colognola ai Colli	Veneto	173	Settlement	Iron Age	8	0.40	Riedel 1984b
Concordia Sagittaria	Veneto	3	Settlement	Iron Age	1	0.09	Pino Uria and Tagliacozzo 2001
Oppeano	Veneto	29	Settlement	Iron Age	1	0.14	Minniti 2010
Terranegra di Legnago	Veneto	~12	Settlement	Iron Age	2	0.10	Depellegrin and Tecchiati 2016
Modena – Ghirlandina	Emilia Romagna	~43	Urban centre	Roman Age			De Grossi Mazzorin 2016
Podere Ortaglia	Tuscany	178	Sanctuary	Roman Age	14	0.81	Betetto 2005
Adria (V AD)	Veneto	~4	Urban centre	Roman Age			Asta et al. 2014
Canale del Cornio Venezia	Veneto	~0	Natural canal bottom	Roman Age	3		Asta et al. 2014
Roma – Crypta Balbi	Lazio	~29	Monastery	Middle Ages	1	0.03	Minniti 2005
Tarquinia – P. Vitelleschi (pit 181)	Lazio	~33	Noble palace	Middle Ages	17	0.34	Clark 1989
San Vincenzo al Volturno	Molise	~530	Monastery	Middle Ages	4		Clark 1997
Firenze – P.za Signoria (US 114)	Toscana	~60	Urban centre	Middle Ages	1	0.09	Corridi 1995
Nogara Veronese	Veneto	~18	Urban centre	Middle Ages	1	0.47	Baker 2007
Verona	Veneto	~60	Urban centre	Middle Ages			Riedel 1994

Alt. a.s.l., Altitude above sea level; n, number of beaver remains; %, percentage of beaver remains.

plains and in the mountains of the north-eastern regions (Figure 2, Table 2).

At the Galgenbühel rockshelter (Table 2, Figure 2), the beaver is the predominant species by number of remains (39.6%), which increases in “phase 3” (46.5%) and especially in “phase 2” (52.3%) where it is associated with many fossil fragments of other fur animals (21.6%). These are present in just slightly lesser quantities than the ungulates (25.3%). *Castor fiber* is represented by skeletal elements from the entire body, with a predominance of cranial bones (mandibles and teeth) and extremities (metapodial bones and phalanges), with several cut-marks on the former as well as on post-cranial bones. All these cut-marks are usually related to skinning and butchery activities indicating the exploitation of the beaver for fur and food.

Castor fiber is also well represented at the Pradestel rockshelter (Table 2, Figure 2) with 18.8% of mammal remains, and shows a peak of 48.7% in layers L1–L4 which is only slightly lower than the ungulates (49.4%). The beaver remains are mostly fragmented and attributable to all age classes, spanning from very young individuals with deciduous teeth to senile ones with fully worn occlusal surfaces. Other fur animals, such as hare and various species of carnivores, are always present with relevant percentages.

According to Wierer and Boscato (2006), in both Pradestel and Galgenbühel, some Mesolithic human groups living in the middle River Adige Valley were probably specialized in the hunt of these rodents, exploited together with other fur animals either for dietary purposes or for their hide.

Other Mesolithic sites in the Adige Valley, such as the rockshelters of Romagnano III, Gaban, Soman and Vatte di Zambana, show a fair percentage of beaver remains, ranging between 3.6 and 5.2% (Table 2). By contrast, in the sites of the Trieste Karst (Grotta Azzurra di Camatorza and layer 3c of Grotta dell’Edera) and Isonzo basin (layer 4 of Riparo di Biarzo), the remains of the species never exceed 1% (Table 2).

Even after the transition from a predation to a production economy in the Neolithic, the Eurasian beaver continues to be the object of hunting activity by humans. Remains of this species have been collected in many archaeological contexts across Europe (e.g. Komosa et al. 2007, Duval et al. 2011, Danukalova et al. 2014, Bejenaru et al. 2015) and in some sites in the Near East (Legge and Rowley-Conwy 1986, Becker 2005, Siracusano 2010).

In the Italian Neolithic sites examined, *Castor fiber* occurs with few finds, often only as a few teeth, with percentages lower than 2.5% apart from Rivarolo Mantovano

(Table 2). The highest occurrence of the species is found in the central part of northern Italy in Lombardy between the River Po and its tributaries and the Lake of Varese. Other sites are in north-eastern Italy, but there is no evidence of the occurrence of the species south of the River Po (Figure 2).

This scenario changes in the latest phases of prehistory, with sites yielding beaver remains almost in every region of north-eastern and central Italy. Perhaps, during the Metal Ages (Copper, Bronze and Iron Age), an interest for beaver-hunting reappeared in these regions, as testified by the higher number of remains, while an actual expansion of the populations might have also occurred south of the River Po due to more suitable climatic and environmental conditions. However, apart from a few exceptions, the percentage of finds in the mammal assemblages of each archaeological site is below 1% (Table 2).

Despite the aforementioned Neolithic trend, only one site (the Bronze Age pile dwelling of Barche di Solferino, Lake Garda) revealed the presence of *Castor fiber* in Lombardy (Figure 3). Conversely, beaver remains are found between the north-east regions of the peninsula and the Po Plain in several sites dated to the Copper and Bronze Age (III–II millennium BC). The Bronze Age pile dwelling of Canàr di San Pietro Polesine in Veneto, near the River Po Delta, is one rare example of an abundant beaver assemblage (55 elements; Table 2).

During the Iron Age, *Castor fiber* remains are mostly found in the Po Plain, in the Adige basin, in Friuli Venezia Giulia and even in central Italy (Figure 3, Table 2). In Tuscany, the site of San Rocchino on the shores of the Massaciuccoli Lake yielded the impressive amount of about 350 beaver bones, reaching between 8 and 10% of the mammal assemblage. An intensive exploitation of *C. fiber* in this site is also shown by the cut-marks and fire marks on the bones. According to Wilkens (2003), this might have been a specialised beaver-hunting station. Such assumption is also corroborated by the examination of the increasingly selective killing choices, which appear more oriented towards the adults during the later phases of occupation, due to the maximum yield of secondary products in that age class.

Records of beavers in historical times in Italy

In historical times, a Tuscan site showing interesting beaver remains is the Etruscan sanctuary of Podere Ortaglia (Table 2), i.e. the only case of a ritual context with *Castor fiber* in Italy. This sacred area, holding over 4000 intentionally deposited faunal remains, was probably dedicated to a goddess of the hunt, such as Artemis (Sorrentino and Landini 2015).

Few fossil remains of beavers are known in the Roman Age, such as the jaws and the humerus found in the sediments dated between the 2nd century BC and the 1st century AD of Canale del Cornio, in the Venice Lagoon. Remains of the rodent are also recorded among the faunistic findings of the Late Antiquity levels identified below the Ghirlandina in Modena, whereas finds from the late Roman period in Adria come from the layers attributed to the 5th century AD (Table 2). Among the literary testimonies, Varro (1st century BC) reports the presence of "*fiber*" in the rivers of Latium and provides an etymology for this name (*De Lingua Latina* 5.79; see Kent 1938); Pliny the Elder (1st century AD) describes the behaviour of an aquatic animal, named *fiber* and identifiable with the beaver (*Naturalis Historia* 8.47; see Rackham 1940), and describes various medicinal properties of the *castoreum* (*Naturalis Historia* 20.53, 26.46, 26.70–78, 32.13; see Jones 1951, 1956, 1963).

Records of beavers from medieval Italy are not numerous. However, in Late Antiquity and the Middle Ages, evidence seems to confirm the plains of northernmost Italian provinces as areas where the species persisted, along with some isolated areas in central Italy (Table 2, Figure 4). Remains of this rodent have been found at Nogara in the "Basso Veronese" (12th–13th centuries) and in a waste pit (13th century) of the urban centre of Verona in northern Italy, but also at Palazzo Vitelleschi in late Medieval Tarquinia (12th–15th centuries), Latium. Beaver bones are also among the faunistic findings of the Crypta Balbi (Rome) dated to the 7th and 8th century, and probably relating to the monastic complex of San Lorenzo in Pallacinis (Table 2). Similarly, the discovery of the 8th–9th centuries beaver bones of San Vincenzo al Volturno in Molise (Table 2) likely relate to the monastic diet that relegated this animal, as in the case of otters, turtles and coots, among the so-called *aquatilia* that could be consumed without breaking the precepts dictated by the Church (De Grossi Mazzorin and Minniti 1999). In the Middle Ages, the tail of the beaver was believed to have a nature comparable to that of the fish (Figure 5) and, consequently, this part of the animal could be eaten even in the days of liturgical penitence. A fragment of *Castor fiber* humerus was found in the early medieval levels of Piazza della Signoria in Florence (Table 2). It should however be noted that the presence of the rodent in the contemporary faunal horizons of Tuscany is rather unique and is perhaps linked to the trade of furs.

Alongside medieval findings, there are also literary references. For instance, Pratesi (2001) and Bon et al. (1991) are of the opinion that the beaver persisted in 14th century Italy, and particularly in the eastern Po forests,

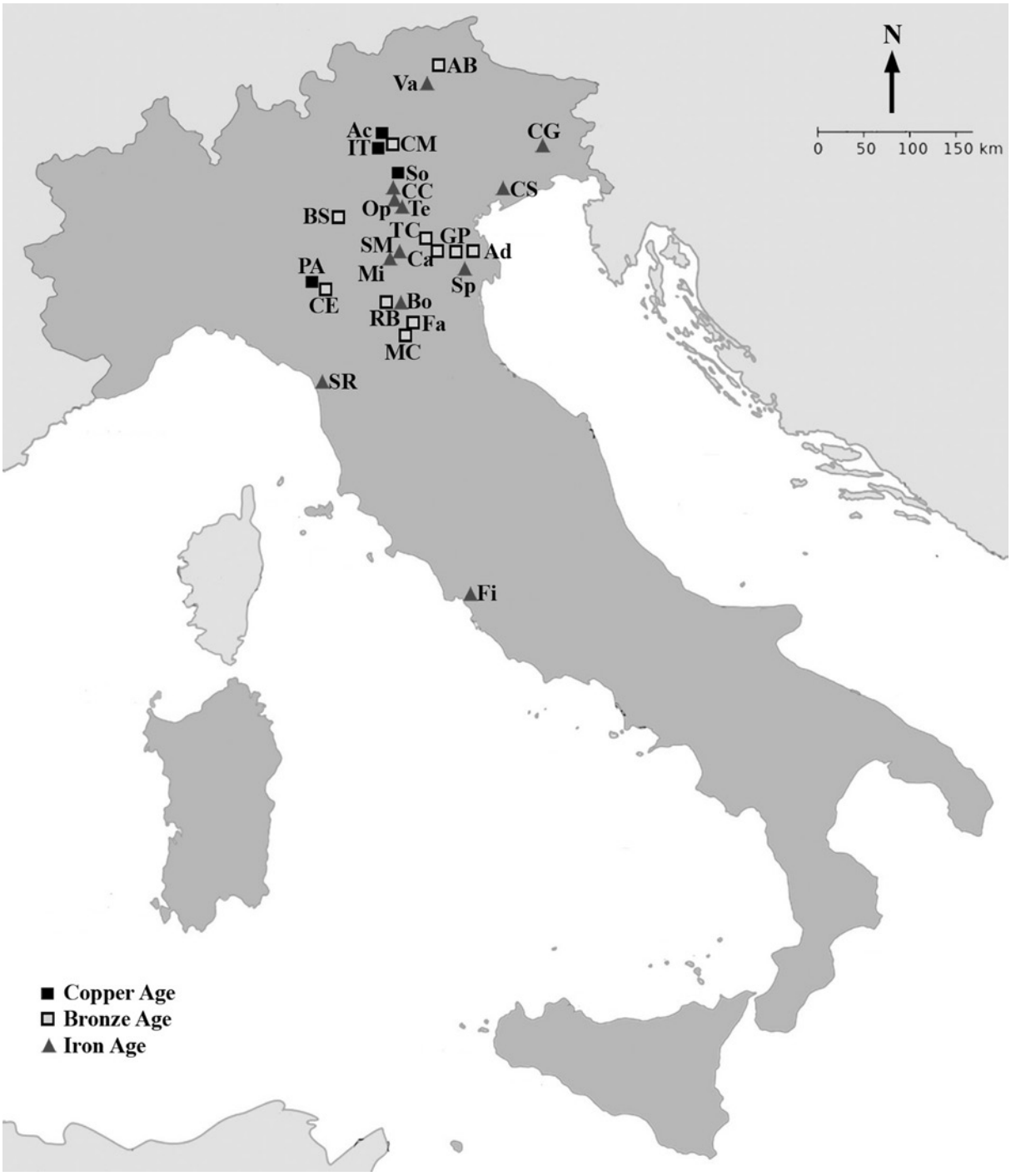

Figure 3: Geographical distribution of Italian sites with Eurasian beaver remains referred to the Metal Ages (alphabetical order). Copper Age: Ac, Acquaviva; IT, Isera Torretta; PA, Parma Aeroporto; So, Riparo Soman. Bronze Age: AB, Albanbuhel – Bressanone; Ad, Adria; BS, Barche di Solferino; Ca, Canàr di S. Pietro Polesine; CE, Celerno presso l'Enza; CM, Colombo di Mori; Fa, Grotta del Farneto; GP, Campestrin di Grignano Polesine; MC, Monte Castellaccio; RB, Rocca di Bazzano; TC, Tombola di Cerea. Iron Age: Bo, Bologna; CC, Colognola ai Colli; CG, Centes di Gradiscutta; CS: Concordia Sagittaria; Fi, Ficana; Mi, Mirandola; Op, Oppeano; SM, San Martino di Spino; Sp, Spina; SR, San Rocchino; Te, Terranegra di Legnago; Va, Vadena.

due to its mentioning in the *Dittamondo*, a didactic poem by Fazio degli Uberti, who died in Verona in 1368. Speaking of the town of Ferrara and its surroundings, the latter scholar describes a curious aquatic animal, "beast and fish", called *bevero*, "which goose has the foot, and fish tail" (Fazio Degli Uberti 1501, p. 156). The archaic Italian term *bevero*, or *bivara*, reveals an identical origin with the English *beaver*, the German *Biber* and the ancient French

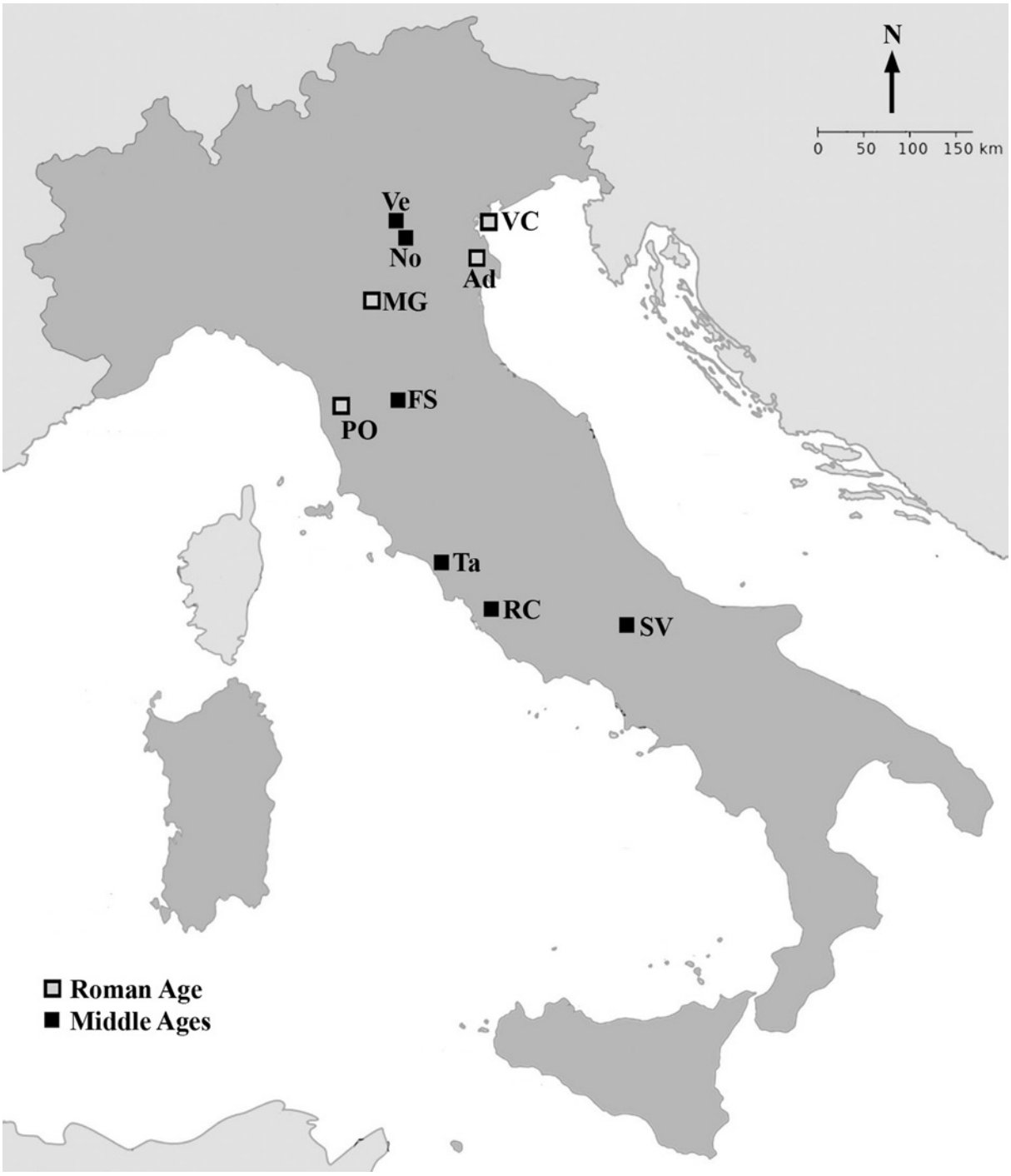

Figure 4: Geographical distribution of Italian sites with Eurasian beaver remains referred to the historical times (alphabetical order). Roman Age: Ad, Adria; MG, Modena – Ghirlandina; PO, Podere Ortaglia; VC, Venice – Canale del Cornio. Middle Ages: FS, Florence – Piazza della Signoria; No, Nogara Veronese; RC, Rome – Crypta Balbi; Ta, Tarquinia; SV, San Vincenzo al Volturno; Ve, Verona.

bièvre, with which the beaver is referred to in the respective languages. In the 16th century, Gesner (1558, p. 337) also reported the presence of beavers near the mouth of the River Po: "[…] *ut inquit Strabo. Item in Italia, ubi Padus in mare se exonerat*". In the following century, Aldrovandi (1637, p. 282, and Figure 6), referring to this last quotation, affirms that he is not able to confirm or deny it: "[…] *quod si fit verum nec nè, nondùm certiores facti sumus*". Therefore, it is probable that at the beginning of the 17th century (Aldrovandi died in 1605), the beaver was already extinct or very rare in the easternmost Po Plain, and thus in Italy.

A little known quotation, which could confirm the presence of the species in the area of 16th century Po Delta, is that of Amatus Lusitanus (1553, p. 187) which

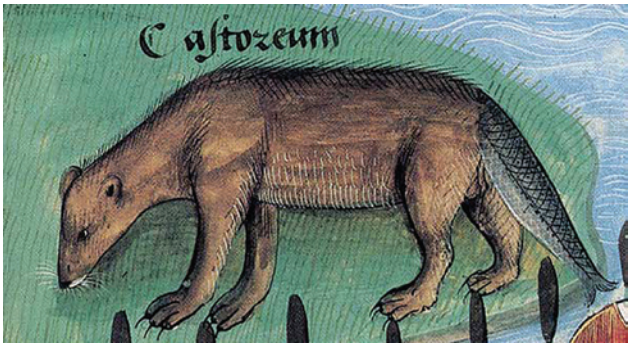

Figure 5: Representation of a Eurasian beaver, *Castor fiber*, from the *Liber de simplici medicina* (Livre des simples médecines, ca. 1480 – Paris, Biblioteque Nationale, Département des manuscrits, Français 12322, f. 188) by Matheus Platearius (Salerno, 12th century). Available from Wikipedia commons, https://fr.wikipedia.org/wiki [08 August 2018].

Figure 6: Representation of a Eurasian beaver, *Castor fiber*, from the *Plates of animals* (Quadrupedia vivipara, plate I, a, c.97) of Ulisse Aldrovandi (Bologna, 1522–1605) (courtesy of the University Library of Bologna).

describes the dissection of a beaver specimen made in Ferrara in 1541: "[…], *id anno 1541, nos quoque experti sumus, quum Ferrariae in officina Nicolai Nicolutri pharmacopolaea Pinea, integrum castorem habuimus, et eum circa testes dissecuimus* […]".

Concluding remarks

The extant beaver populations in the Western Palaearctic are the result of post-glacial repopulation and subsequent demographic expansions, followed by a decline in historical times that led to multiple local extinctions.

In the LGM (between 23 and 16 ka BP; see Sommer and Nadachowski 2006), *Castor fiber* seems to have disappeared from most of Europe, surviving in some relic areas from which the species would later repopulate the rest of the continent. According to Sommer and Nadachowski (2006), it survived only in the Balkans (Hungary, Croatia and Greece), but more recently beaver fossils referred to the LGM were also found in Italy (Gurioli et al. 2010, Nannini and Romandini 2015) and probably in Moldova (David and Pascari 2013). Other relic areas in the LGM were probably located near the mouth of the River Rhone, in the Iberian Peninsula, and between the Caucasus and southern Urals, but confirming data is still missing. However, in these regions, beaver remains dating to the Lateglacial, between the Dryas I and the Bølling (Bridault et al. 2000, Davis 2002, Bachura and Kosintsev 2007) have already been found; as such it is more likely that these remains belonged to autochthonous animals rather than immigrants from the Balkans.

According to the fossil record, from the abovementioned relic areas, the beaver would have reached the Garonne and the Loire basins (France) between the Dryas II and the Allerød (Poulain 1972, Fosse 1999), the Rhine and the Elbe basins (Germany), Denmark and southern Sweden in the Allerød (Street and Baales 1997, Teichert 1999, Aaris-Sørensen 2000), England and Estonia in the Dryas III (Currant 1986, Veski et al. 2005), Finland and Norway in the early Holocene (Ukkonen 1993, Aaris-Sørensen 2000) and Russian territory north of the Urals only in the late Holocene (Ponomarev et al. 2013).

In historical times, the presence of the beaver in Europe is well documented up to the Middle Ages, when the species appears to become extinct in Denmark. The progressive extinctions in many European nations, between the 15th and the first half of the 20th century, are summarized in Halley et al. (2012, Table 2); this can be supplemented with the data from Slovenia (17–18th centuries; Kryštufek et al. 2006) and Spain (19th century; Ferrández Verdú et al. 2017). The renewed interest in beaver hunting for fur procurement might have had an impact on the species' extinction in the Little Ice Age (16th–19th centuries), although this is better documented for the North American continent (Verekamp 2006). At the beginning of the 20th century, only small, isolated relic populations had survived in south Norway wetlands and along the Rhone in France, the Elbe in Germany, the Neman and the Dnepr in Belarus and Ukraine, the Don in Russia, the Konda, the Sosva and the Yenisei in Siberia and the Ulungur, between China and Mongolia (Nolet and Rosell 1998, Halley et al. 2012). From the second half of the last century, the species was reintroduced in many countries and new populations

are still expanding (Halley and Rosell 2002, 2003, Halley et al. 2012, Kiss et al. 2013, Batbold et al. 2016, Trbojević and Trbojević 2016).

In Italy, Kotsakis (2008) and Masseti (2008) are of the opinion that the species inhabited the Italian territories until the Renaissance. The local extinction of *Castor fiber* was reported either during the 16th century (Warren 1927, Bon et al. 1991, Véron 1992, Halley et al. 2012) or at the beginning of the 17th century (Pratesi 2001).

According to the archaeozoological record, the most recent finds are comprised between the 12th and the 15th centuries (Clark 1989, Riedel 1994, Baker 2007). A few literary references, mainly Amatus Lusitanus (1553) and Aldrovandi (1637), suggest that the last Italian beaver populations resisted in Polesine (the easternmost area of the Po Plain) between the mid 16th century and the beginning of the 17th century.

The extinction of the Eurasian beaver is generally attributed to human hunting activity for the exploitation of fur and the *castoreum*, combined with loss of wetland habitats (e.g. Halley and Rosell 2002, Batbold et al. 2016). However, both the archaeozoological studies of Duval et al. (2011) and Bejenaru et al. (2015) have strongly scaled back the role of overhunting as a cause of demographic decline and/or local extinction, in France and Romania, respectively. The present study on the occurrence of beaver remains in Italy shows that probable specialised beaver-hunting sites are only recorded during the Mesolithic and in one isolated case during the Iron Age. In historical times, when the extinction of beaver occurs, there is no evidence of any specialised hunting site. Given the constant limited presence of *Castor fiber* through the rest of the periods under study, the strong decrease of remains of the species in the late Middle Ages and Renaissance does not seem to be biased by the lack of archaeozoological data. Therefore, at least for Italy, beaver extinction should be mainly attributed to the alteration of the habitat and general human population pressure. In particular, the last beaver refuges have seen a high increase in deforestation, land reclamations and hydraulic arrangements of the lower Adige Valley, the Po Delta area and the Venice Lagoon between the 14th and the 16th centuries, until the opening of the Taglio di Porto Viro, in the northern part of the Po Delta, in the years 1600–1604 (Cantù 1838, Tumiatti 2005). These intensive changes to the landscape and, consequently, to the wetland ecosystems preferred by *C. fiber*, were made by the ruling Este family in the Duchy of Ferrara and by the Serenissima Republic of Venice in Veneto (see Cantù 1838, Almagià 1961).

Regarding the ecology and the biogeography of the species, it is interesting to note that no beaver remains have ever been found in southern Italy. The southernmost finds are those of Molise and southern Latium, about 41°N, in the basins of the rivers Volturno and Liri-Garigliano, both flowing into the Tyrrhenian Sea. Moreover, in central Italy, there is no record of beaver associated with the river basins leading to the Adriatic Sea. The occurrence of *Castor fiber* in historical times in Anatolia and Mesopotamia up to the latitude of Baghdad, about 33°N, suggests that the absence of the same species in the central Adriatic and in southern Italy should not depend on the latitude or peculiar climatic conditions. Beaver does not favour low temperatures, even if its current geographical distribution could indicate it (reaching northern Scandinavia). In general, *C. fiber* is a species adaptable to different climatic conditions and should be able to live in almost any freshwater habitat where there are trees, or even shrubs, and the bank slope is not steep. Patterns of recolonisation demonstrate a clear preference for still or slow, laminar water flows (Halley and Rosell 2002, Batbold et al. 2016). Therefore, the absence of beaver remains in the central Adriatic and in southern Italy is probably connected to the hydrological regime of watercourses, strongly influenced by seasonality (Turri 1987, DIAM 2015), and to the lack of rivers in these regions that can guarantee a constant perennial water regime.

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