



Rediscovering *Lutra lutra* from Grotta Romanelli (southern Italy) in the framework of the puzzling evolutionary history of Eurasian otter

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Abstract

A river otter hemimandible has been rediscovered during the revision of the historical collections of G.A. Blanc from Grotta Romanelli, complementing the ongoing multidisciplinary research fieldwork on the site. The specimen, recovered from the level G (“terre rosse”; early Late Pleistocene or late Middle Pleistocene), is here assigned to *Lutra lutra*. Indeed, morphological and morphometric comparisons with other Quaternary Lutrinae fossils from Europe allow to exclude an attribution to the relatively widespread and older *Lutra simplicidens*, characterized by distinctive carnassial proportions. Differences with *Cyrnaonyx antiqua*, which possessed a more robust, shellfish-feeding dentition, support the view of a successful niche repartition between the two species during the late Middle to Late Pleistocene of Europe. The occurrence of *Lutra lutra* from the “terre rosse” of Grotta Romanelli suggests deep modifications of the landscapes due to the ecological adaptation of the taxon, and indicates that the Eurasian otter spread into Europe at the Middle–Late Pleistocene transition.

Keywords Pleistocene · Mediterranean · Carnivora · Body mass · Lutrinae

Introduction

Otters (Lutrinae), subfamily of Mustelidae, constitute a widely distributed carnivoran group (13 extant species), which evolved morphological adaptations for living and hunting in aquatic environments (Wilson and Mittermeier 2009; Nowak 1999). Despite earlier insights from morphological analysis (Van Zyll de Jong 1972, 1987), river otters have been traditionally ascribed only to *Lutra*, until genetic

data highlighted the substantial molecular divergence between the Eurasian and American branches of Lutrinae evolutionary tree, now assigned to *Lutra* and *Lontra*, respectively (Koepfli and Wayne 1998; Koepfli et al. 2008).

However, if *Lontra* occurred in North American deposits since the Pliocene (Prassack 2016), placing the first appearance of *Lutra* in a chronological framework is on the contrary complicated by the use of the genus either as a waste-basket taxon, or in sensu lato, to allocate specimens of uncertain affinities and/or *Lutra*-like morphology (Willemssen 1992; Geraads et al. 2015; Cherin et al. 2016). In

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fact, the earliest “*Lutra*” species, *Lutra affinis* Gervais 1859, is only known from three sites close to the Miocene–Pliocene boundary: Venta del Moro (Spain), Maramena (Greece) and Montpellier (France). However, the whereabouts of the never-figured type material from Montpellier are unknown (Willemsen 1992). Furthermore, the fragmentary remains from the other localities markedly differ in size (Koufos 2011; Montoya et al. 2011) and have been suggested to represent different taxa (Cherin et al. 2016). Several putative *Lutra* species have been described from the Pliocene to the Early Pleistocene of Europe (Gervais 1859; Pohle 1919; Kurtén 1968; Willemsen 1992; Fejfar and Sabol 2004), but none of them provides conclusive evidence of their generic status (Cherin et al. 2016).

A long gap characterized the Lutrinae record during the late Pliocene and the beginning of the Early Pleistocene, until the earliest occurrence of *Lutra simplicidens* and *Lutraeximia umbra* from the late Villafranchian Upper Valdarno (Tuscany) and Pantalla (Umbria), respectively (Cherin and Rook 2014; Cherin et al. 2016). The latter taxon is only known from the holotype cranium, whereas the former is relatively widespread in the early Middle Pleistocene and is regarded as ancestral to several endemic otters of the Mediterranean islands (Willemsen 2006): “*Lutra*” *euxena* from Malta, *Lutraeximia trinacriae* from Sicily, and *Sardolutra ichnusae*, “*Lutra*” *castiglionis*, *Algarolutra majori* and *Megalenhydrys barbaricina* from Sardinia and Corsica, even though these fossil samples often include few and fragmentary remains (Willemsen 1992; Cherin et al. 2016). Nonetheless, the extant Eurasian river otter, *Lutra lutra*, is considered not related to these European species and its origin is placed in the Asian continent, probably deriving from the fossil species *Lutra palaeoindica* (Willemsen 1992; Raghavan et al. 2007). This scenario has received indirect support from the first description of *L. simplicidens* maxillary dentition, which led Cherin (2017) to doubt of the species generic attribution, remarking the similarities with *Lutraeximia umbra* (Cherin et al. 2016). Alternatively, Fejfar and Sabol (2004) argued for a derivation of the extant *Lutra sumatrana* from *Lutra bravardi* Pomel 1843, but excluding a close relationship with *L. lutra* of the latter species, which is difficult to reconcile with molecular data that consistently find a close relation between *L. lutra* and *L. sumatrana* (Koeplli et al. 2008; Hung and Law 2016).

L. lutra is the most widely distributed otter species, with extant populations occurring throughout Asia, Europe and northern Africa. Historically, this carnivoran was also widespread in Japan, Portugal, arctic region of Asia and Europe and southern Indonesia (Foster-Turley et al. 1990). Up to now, fossils of the species are mainly known from Holocene deposits (Sommer and Benecke 2004), even if it was also reported from the late Middle Pleistocene of Grotta Maggiore di San Bernardino (Cassoli and Tagliacozzo 1994c)

and the Late Pleistocene sites of Geographical Society Cave (Russian Far East) (Baryshnikov 2015), Pilisszántó 1 (Jánossy 1986) and Skjonghelleren Cave (Larsen et al. 1987). Indeed, Baryshnikov and Puzachenko (2012) suggested that the river otter could have survived during the cold phases of the Last Glacial in southern European refugia, from where it redispersed during the Early Holocene. Another otter species, *Cyrnaonyx antiqua*, is reported from several late Middle to Late Pleistocene European localities and is characterized by a more robust, shellfish-feeding type of dentition (Kurtén 1968; Willemsen 1992).

The otter fossil from Grotta Romanelli (southern Italy), belonging to the historical collection of Gian Alberto Blanc and never figured or described, is here presented for the first time. In addition, morphological and morphometric comparisons with other Lutrinae fossils coming from the Early Pleistocene to Middle Holocene sites of Europe and with extant specimens of European otter are taken into account to evaluate their morphological and body size variability.

Materials and methods

Grotta Romanelli (40° 00′ 58.33″ N, 18° 25′ 59.36″ E) is a costal cave located in the administrative territory of the Castro (Lecce) municipality, at the south-eastern extremity of Apulia (southern Italy) (Fig. 1a–d). The cave lies within the area of the Regional Natural Park “Costa Otranto—Santa Maria di Leuca and Bosco di Tricase”. From the beginning of the twentieth century, Grotta Romanelli was considered a key site for Mediterranean Quaternary studies, due to its remarkable importance as the first evidence of the Upper Paleolithic period in the Italian Peninsula and the first record of rock art in the Euro-Mediterranean area (Graziosi 1973; Sardella et al. 2018, 2019). The deposit was discovered in 1874 by Ulderigo Botti (Botti 1874), but only during the earlier 1900s, Paolo Emilio Stasi realized the first excavation campaigns (Stasi and Regalia 1904). In 1914, Gian Alberto Blanc began a pioneering excavation campaign, during which the first systematic archeological/paleontological and stratigraphic study using scientific methods was carried out (Blanc 1920, 1928) (Fig. 1e–g). Nowadays, Grotta Romanelli is recognized as a key site for the Mediterranean Pleistocene for its archeological and paleontological content and the relative stratigraphical, geomorphological and radiometric data (Sardella et al. 2018, 2019).

The infilling deposit was described by Blanc (1920) which identified two main stratigraphical complexes: the upper complex, called “terre brune” (levels A–E), bearing Upper Paleolithic artifacts and vertebrate fauna; the lower complex (G–K) formed by a deposit called “terre rosse” (level G), bearing Middle Paleolithic artifacts and vertebrate fauna, a stalagmitic layer (level H), a bone breccia

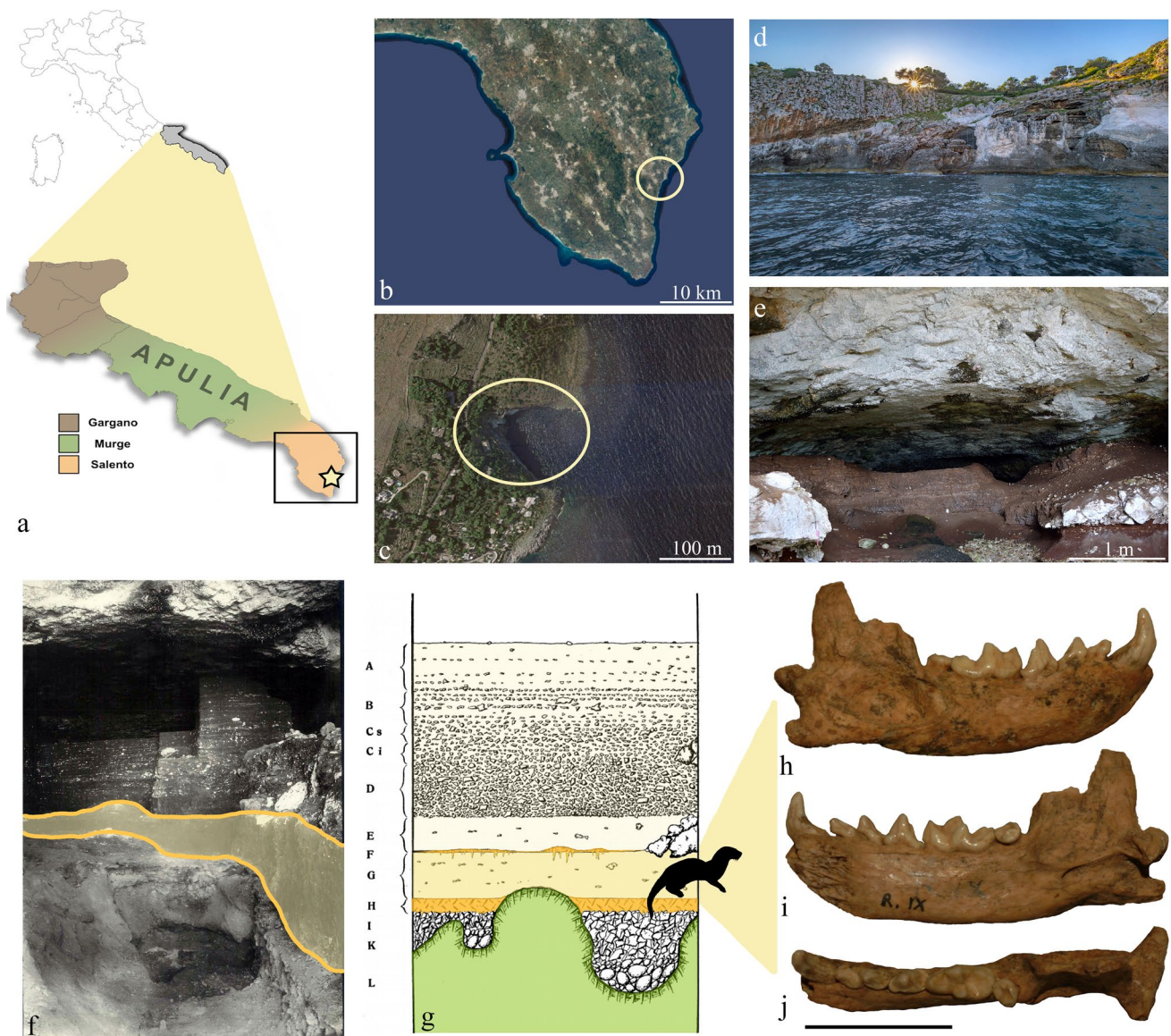


Fig. 1 Geographical position of Grotta Romanelli (a–c). External (d) and internal (e) views of the cave. Stratigraphy of the deposit as described by Blanc (f), the level where the fossil otter was found is

highlighted in light orange. Schematic log of the sedimentary succession (modified by Blanc 1920). Fossil *Lutra lutra* from Grotta Romanelli in labial (h), lingual (i) and occlusal (j) views

(level I), and a beach deposit (level K) referred to the Tyrrhenian Stage (Marine Isotopic Stage 5) (Blanc 1920, 1928) (Fig. 1f, g). These two complexes were separated by a thick stalagmitic layer (called level F) (Blanc 1920, 1928) (Fig. 1g). The upper complex was referred to the end of the Late Pleistocene and Early Holocene on the basis of radiocarbon datings performed since the end of 1950 (Bella et al. 1958; Vogel and Waterbolk 1963; Alessio et al. 1964, 1965). The two speleothems (levels H and F) were also dated with the $^{230}\text{Th}/^{234}\text{Th}$ method: level H yielded an apparent age of < 69,000 years BP, and level F was dated to $40,000 \pm 3250$ years BP (Fornaca-Rinaldi 1968a, b; Fornaca-Rinaldi and Radmilli 1968; Sardella et al. 2018). During the

1950s and 1960s, the excavation campaigns were directed by Cardini with the support of the Italian Institute of Human Paleontology (IsIPU) (Sardella et al. 2018).

In 2015, new multidisciplinary research fieldwork began, coordinated by Sapienza University of Rome together with other research institutions and with the authorization of Soprintendenza Archeologia Belle Arti e Paesaggio di Brindisi, Lecce e Taranto, with the aim to provide an updated stratigraphic and chronological scheme as well as to describe the fossil remains and artifacts (Giustini et al. 2018; Sardella et al. 2018, 2019), which is also triggering a revision of the large mammal faunas from the region (Sardella et al. 2014; Mecozzi et al. 2017, 2018, 2019; Iannucci et al. 2020; Iurino

et al. 2020). The research team had to face the consequences of more than 40 years of inactivity in the site and the combined effects of erosion and illegal excavations that took place during last decades (Conti et al. 2017; Giustini et al. 2018; Sardella et al. 2018). Recently, the age of the “terre brune” has been reassessed, with new fossil remains submitted for ^{14}C dating using the accelerator mass spectrometry radiocarbon (AMS14C) dating techniques (Calcagnile et al. 2019; Sigari et al. 2021). The results expand and refine the previous chronology, with a time span for levels D and B, respectively, from 13,976–13,545 ^{14}C cal BP to 9135–8639 ^{14}C cal BP (Calcagnile et al. 2019), whereas the level E was dated between 13,087–12,839 and 13,408–13,153 (Sigari et al. 2021). As reported by Sardella et al. (2018), one of the main unexplained aspects, which needs to be investigated, concerns the age of the lower deposits due to the apparent contradiction between the supposed archaic nature of the Mousterian artifacts and the position of the vertebrate fauna being situated above the supposed MIS 5.5 terrace.

New analyses on the fauna and lithic tools from the lower complex suggest a possible late Middle Pleistocene to early Late Pleistocene age (Sardella et al. 2018), but more data need to define the updated chronostratigraphy of the infilling deposit.

The fossil remains described in this work were collected from the “terre rosse” (level G), but no information about the exact stratigraphical position is available (Blanc 1920, 1928) (Fig. 1h–j). Other mammal species found in the level G are: *Elephas antiquus* (= *Palaeoloxodon antiquus*), *Rhinoceros merckii* (= *Stephanorhinus kirchbergensis*), *Hippopotamus* sp. *amphibius*, *Hippopotamus* sp. *pentlandi*, *Bos taurus* var. *primigenius* (= *Bos primigenius*), *Cervus elaphus*, *Cervus elaphus* var. *corsicanus* (= *Cervus elaphus corsicanus*), *Dama dama*, *Capreolus capreolus*, *Equus caballus*, *Hyaena crocuta* var. *spelaea* (= *Crocuta crocuta spelaea*), *Canis lupus*, *Canis aureus*, *Meles taxus* (= *Meles meles*), *Oryctolagus cuniculus* and *Pelagius monachus* (= *Pelagius monachus*) (Blanc 1920). The wolf and rhino remains from level G have recently been revised by Sardella et al. (2014) and Pandolfi et al. (2017), who referred them to *Canis lupus* and *Stephanorhinus hemitoechus*, respectively.

The fossil material from Grotta Romanelli is housed in the collection of the “Museo delle Civiltà” (ex. Museo Preistorico ed etnografico Luigi Pigorini), labeled with a progressive number MUCIV-GR1935 (Fig. 1h–j).

According to von den Driesch (1976) and Willemsen (1992), 16 mandibular and dental variables have been considered: total length (TI), length from the anterior border of the C_1 to posterior border of the M_2 (LC_1M_2), height of the mandibular corpus above M_1 (HM_1), length and breadth of the lower teeth (C_1L , C_1W , P_2L , P_2W , P_3L , P_3W , P_4L , P_4W , M_1L , M_2L , M_2W) length of trigonid (M_1Ltri), breadth of the trigonid (M_1Wtri) and talonid (M_1Wtal). Craniodental

morphometric measurements were recorded to the nearest 0.1 mm with a digital caliper.

Literature data on fossil river otters from the Early Pleistocene to Early Holocene (Late Villafranchian to Aurelian) sites (Table 1) as well as extant specimens of *L. lutra* have been used. Comparisons are also based on fossil material found in the late Neolithic site of Tosina di Monzambano (Mantova—Italy) (Bona 2014; Poggiani Keller 2014) and extant specimens housed in the PaleoFactory laboratory, Department of Earth Sciences, Sapienza, University of Rome.

We performed body mass estimates of the fossil sample following regression equations based on the length of the lower carnassial (Van Valkenburg 1990) (Table 1). Size and proportions of the lower carnassial of the specimen from Grotta Romanelli were compared with literature data on Pleistocene–Holocene otters through standard bivariate plot. In mustelids, these teeth enable determining masticatory performance and bite force and their morphology and size are linked to diet (e.g., Baryshnikov et al. 2003; Madurell-Malapeira et al. 2011a, b).

Systematic Paleontology

Class **Mammalia** Linnaeus, 1758

Order **Carnivora** Bowdich, 1821

Family **Mustelidae** Fischer von Waldheim, 1817

Subfamily **Lutrinae** Bonaparte, 1838

Genus **Lutra** Brisson, 1762

Lutra lutra Linnaeus, 1758

Figure 1h–j

Material. Right hemimandible (MUCIV-GR1935; measurements in Table 2).

Locality and level. Grotta Romanelli; “terre rosse”—G.

Description. MUCIV-GR1935 is a finely preserved mandible, lacking only of a portion of the vertical ramus. In labial view, it shows three mental foramina: one located to the mid length of the C_1 ; one posteriorly to the distal border of the P_2 ; and one to the mid length of the P_3 . The anterior portion of the masseteric fossa reaches the level of the distal portion of the M_1 . The ramus is high and straight with respect to the corpus axis and the angular process is elongated dorsally. In dorsal view, the mandibular condyle has a straight posterior border and is inclined in posterolateral direction. The ventral outline of the mandibular corpus is almost straight, but anteriorly, at the level of the alveolus of the P_2 , it sharply rears upwards. The toothrow is relatively straight and the longitudinal axis of each

Table 1 Literature data on fossil otters from the Early Pleistocene to Holocene sites of Eurasia

Species	Site	Catalog number	Age	References	M ₁ L (mm)	Body size (kg)
<i>Lutra lutra</i>	Grotta Romanelli	MUCIV-GR1935	late Middle–early Late Pleistocene	This work	12.8	6.5
<i>Lutra lutra</i>	Primorskii Territory	ZIN 37285–1	Late Pleistocene	Baryshnikov (2015)	13.7	8.2
<i>Lutra lutra</i>	Ellewoutsdijk	RGM 146662	Holocene	Willemsen (1992)	12.4	5.8
<i>Lutra lutra</i>	Kapel-Avezaath	RGM 147002	Holocene	Willemsen (1992)	13.4	7.6
<i>Lutra lutra</i>	Maasvlakte	Ke RM238	Holocene	Willemsen (1992)	13.3	7.4
<i>Lutra lutra</i>	Maasvlakte	Ke RM2974	Holocene	Willemsen (1992)	12.5	6.0
<i>Lutra lutra</i>	Maasvlakte	Ke RM 4109	Holocene	Willemsen (1992)	13.6	8.0
<i>Lutra lutra</i>	Weesp	IPP We2/1	Holocene	Willemsen (1992)	13.2	7.2
<i>Lutra lutra</i>	Vlaardingen	IPP G20d/B7	Holocene	Willemsen (1992)	13.0	6.9
<i>Lutra lutra</i>	Vlaardingen	IPP 121c/B4	Holocene	Willemsen (1992)	12.6	6.2
<i>Lutra lutra</i>	Vlaardingen	IPP F20b/B2	Holocene	Willemsen (1992)	13.0	6.9
<i>Lutra lutra</i>	Leidschendam	IPPL387/8	Holocene	Willemsen (1992)	11.9	5.0
<i>Lutra lutra</i>	Tosina	Tos 6813	Holocene	This work	13.6	8.0
<i>Lutra lutra</i>	Tosina	Tos 7128	Holocene	This work	13.1	7.0
<i>Lutra simplicidens</i>	Chumbur Kosa	AMZ/OP-966	Early Pleistocene	Sotnikova and Titov (2009)	13.1	7.0
<i>Lutra simplicidens</i>	Upper Valdarno	NHM M296688	Early Pleistocene	Cherin and Rook (2014)	12.6	6.2
<i>Lutra simplicidens</i>	Breccia di Soave	Na	Middle Pleistocene	Pasa (1947)	12.0	5.2
<i>Lutra simplicidens</i>	Hundsheim	PIV Hsh VII/26	Middle Pleistocene	Thenius (1965)	12.8	6.5
<i>Lutra simplicidens</i>	East Runton	BM 6089	Middle Pleistocene	Willemsen (1992)	12.0	5.2
<i>Lutra simplicidens</i>	West Runton	CM CR4 984	Middle Pleistocene	Willemsen (1992)	12.7	6.3
<i>Lutra simplicidens</i>	Mosbach	SMF PA/F8718	Middle Pleistocene	Willemsen (1992)	12.9	6.7
<i>Lutra simplicidens</i>	Voigtstedt	KMBF I-711K	Middle Pleistocene	Willemsen (1992)	12.6	6.2
<i>Cyrraonyx antiqua</i>	Lunel Viel	LPM LUV 68	Middle Pleistocene	Serres et al. (1839)	14.0	8.9
<i>Cyrraonyx antiqua</i>	Saalfeld	MNB MBMa8069	Late Pleistocene	Willemsen (1992)	14.0	8.9
<i>Cyrraonyx antiqua</i>	Ehringsdorf	Na	Late Pleistocene	Willemsen (1992)	14.0	8.9
<i>Cyrraonyx antiqua</i>	Maasvlakte	Ke RM 226	Late Pleistocene	Willemsen (1992)	14.8	10.8
<i>Cyrraonyx antiqua</i>	Tornetown Cave	BM M 34371	Late Pleistocene	Willemsen (1992)	13.5	7.8
<i>Cyrraonyx antiqua</i>	Tornetown Cave	BM M 34372	Late Pleistocene	Willemsen (1992)	13.2	7.2
<i>Cyrraonyx antiqua</i>	Tornetown Cave	BM M 50708	Late Pleistocene	Willemsen (1992)	14.1	9.1
Extant <i>Lutra lutra</i>	Italian Peninsula	882		This work	13.4	7.6
Extant <i>Lutra lutra</i>	Italian Peninsula	882		This work	13.5	7.8
Extant <i>Lutra lutra</i>	Italian Peninsula	883		This work	13.8	8.4

tooth diverges, with the C₁, P₃ and M₁ axes almost aligned. The posterior part of the P₄ crown slightly overlaps with the anterior margin of the M₁. No incisors are preserved. The C₁ is mesodistally elongated, with a smooth crown. No diastema separates the C₁ from the P₂. The P₂ is a two-rooted and buccolingually compressed tooth with a small and mesially projected protoconid, and with a crest connecting the weak distal cingulum to the protoconid. The P₃ is buccolingually compressed and has the high, straight and anteriorly located protoconid, and a weak crest connecting the mesial cingulum to the protoconid. It has weak lingual and labial cingula. The P₄ is also buccolingually compressed, with the high protoconid, a marked distal accessory cusp, and a marked basal cingulum.

In the lower carnassial (M₁) the talonid is wider than the trigonid. The paraconid is well developed and high

as the metaconid. The protoconid is the highest cusp and two distinct grooves separate it from the paraconid and the entoconid. The entoconid and hypoconid are reduced and aligned with the metaconid and the paraconid, respectively. Along the distal rim of the talonid, there are two very reduced cusps, buccally the entoconulid and lingually the hypoconulid. The talonid basin is concave. The basal distal cingulum is well developed, whereas anteriorly tends to be less marked.

The M₂ displays a circular outline, with four cusps. The less developed cuspids, the paraconid and the hypoconid, occupy the anterior and posterior portion of the tooth, respectively; whereas, the metaconid and the protoconid are more developed.

Table 2 Mandibular and lower teeth measurements (mm) of *Lutra lutra* from Grotta Romanelli

Measurements	Grotta Romanelli MUCIV-GR1935
TL	66.5
HM ₁	14.5
C ₁ -M ₂	40.3
M ₁ -M ₂	17.0
C ₁ L	8.0
C ₁ W	4.9
P ₂ L	4.8
P ₂ W	3.1
P ₃ L	5.4
P ₃ W	3.5
P ₄ L	7.6
P ₄ W	4.5
M ₁ L	12.8
M ₁ Ltri	7.5
M ₁ Wtri	5.7
M ₁ Wtal	6.3
M ₂ L	4.8
M ₂ W	5.3

Comparison. MUCIV-GR1935 possesses a typical *Lutra*-like appearance. Morphologically, the lower carnassial of the specimen from Grotta Romanelli shares several features with *L. lutra* (Fig. 2f–l): talonid wider than trigonid; concave talonid; hypoconulid present; strong and continuous lingual cingulum (Willemsen 1992). Opposite characters were observed in *L. simplicidens* from Hundsheim, Sussenborn, Mosbach, East Runton and West Runton (Fig. 2a–d): trigonid wider than talonid; flat talonid; hypoconulid absent; less developed and incomplete lingual cingulum (Willemsen 1992). However, the specimen NHM M29688 from the Upper Valdarno ascribed to *L. simplicidens* possesses a continuous cingulum, which extends all around the paraconid, and the trigonid and talonid are equal in width (Cherin and Rook 2014) (Fig. 2a). Similarly, in the specimen AMZ/OP-966 from the Chumbur Kosa (Azov Sea area), classified as *L. simplicidens tamanensis*, trigonid and talonid are equal in width (Sotnikova and Titov 2009) (Fig. 2d). The studied specimen differs from *L. palaeindica* from the Upper Siwalik in that it possesses a larger trigonid than talonid (Fig. 2e). MUCIV-GR1935 shares several features with the extant *L. sumatrana* (Fig. 2m, n), such as the talonid larger than trigonid and the concave talonid basin.

According to Willemsen (1992), the lower carnassial of *Cyraonyx antiqua* differs from *L. lutra* in the following features: larger paraconid; metaconid more closely connected to the other two cuspids of the trigonid and smaller than the other two cuspids; talonid wider than trigonid; labial

cingulum more developed; larger hypoconid (Fig. 2o, p). MUCIV-GR1935 from Grotta Romanelli resembles *C. antiqua* for the large paraconid and the talonid wider than trigonid.

In the extant specimens of *L. lutra*, the morphology of the M₂ is highly variable, with three main morphotypes recognized, characterized by a progressive complication of crown morphology: A1, with only protoconid and metaconid; A2, with protoconid, metaconid, paraconid and hypoconid; A3, with all the four cuspids on the grinding surface and an additional element, a projection on the lingual side of tooth crown (Gimranov and Kosintsev 2012). Following this, MUCIV-GR1935 can be referred to the A2 morphotype. The only M₂ of *L. simplicidens* from the Upper Valdarno differs from MUCIV-GR1935 in the absence of the paraconid and in possessing a more centrally placed protoconid (Cherin and Rook 2014).

Results

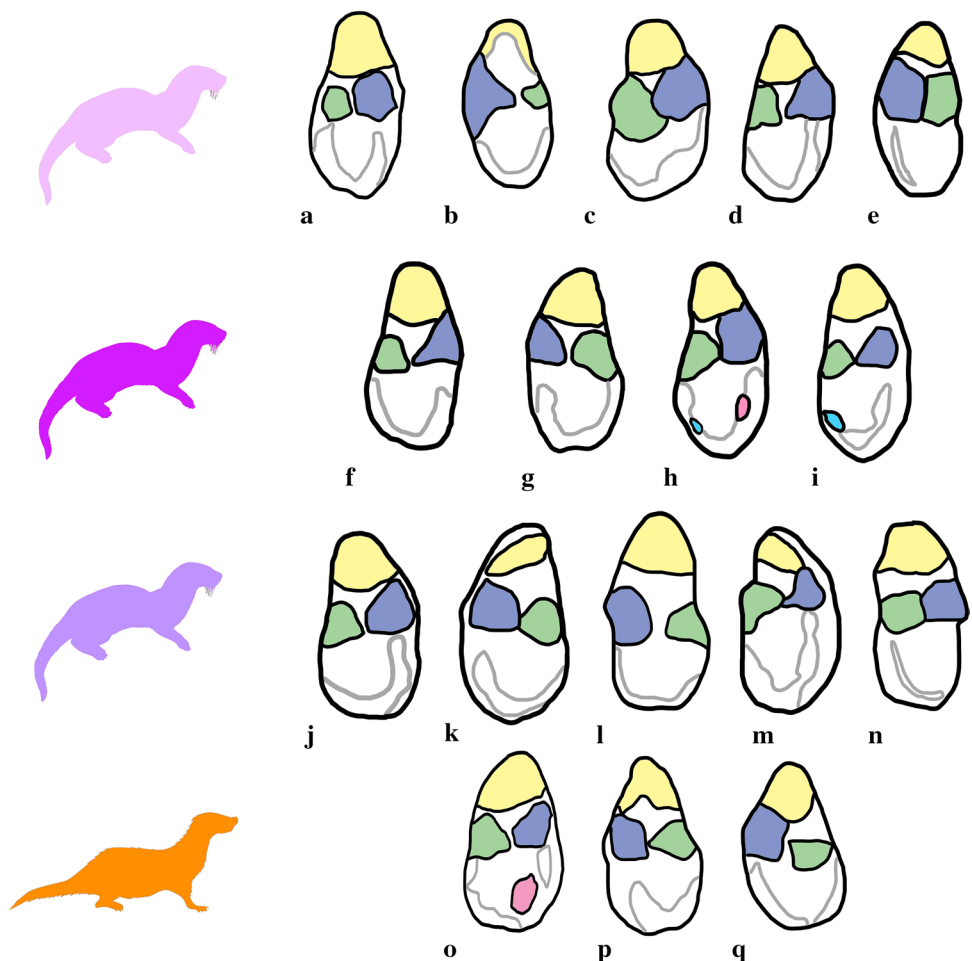
Morphometric comparison

Standard bivariate plots of talonid width (M₁WTal) vs length (M₁L) of the lower carnassial show a distinctively small size for the genus *Lutra* (Fig. 3a). Within the *Lutra* group, the specimen from Grotta Romanelli and those of *L. simplicidens* fall in the broader variability of *L. lutra*. The *C. antiqua* material is instead characterized by a large size of the lower carnassial, well distinct in the M₁WTal (Fig. 3a). Considering the M₁WIndex (calculated as M₁Wtal–M₁Wtri), other differences can be observed (Fig. 3b). Two groups can be distinct based on the M₁WIndex: the material with positive values (above the dotted line), which has a larger talonid; and those specimens with negative values (below the dotted line), which have a larger trigonid. Generally, *C. antiqua* and *L. lutra* occupy the upper part of the graphs, whereas *L. simplicidens* occupies the lower part (Fig. 3b). However, a few specimens of *Lutra* show a talonid and trigonid equal in width (located on the dotted line) (Fig. 3b).

Body mass

Body size in extant otters is hugely variable, reflecting the diverse ecological niches this group occupies (Conroy et al. 2000; Kruuk 2006): small-sized piscivore (c. 5–10 kg), medium-sized cancrivore (c. 11–12 kg) and large-sized molluscivore (c. 22–25 kg) (Raghavan et al. 2007). Therefore, in the fossil record, reconstructing the body size could represent an important proxy to evaluate possible ecological niche differentiation (Conroy et al. 2000). The Eurasian otter is a dimorphic species, with males 50% larger than females (Larivière and Jennings

Fig. 2 Comparative morphological sketch of the lower carnassial of the fossil and extant otter taxa in occlusal view (drawn not in scale). *Lutra simplicidens*: **a** NHM M29688 from Upper Valdarno (Cherin and Rook 2014); **b** BM 6089 from West Runton (Willemssen 1992); **c** SMF PA/F 8718 from Mosbach (Willemssen 1992); **d** KP-27075/OP-966 from Chumbur Rosa (Sotnikova and Titov 2009). *Lutra palaeindica*: **e** BM37152 from Upper Siwalk (Matthew 1929). Fossil *Lutra lutra*: **f** MUCIV-GR1935 from Grotta Romanelli; **g** ZIN 37,285–1 from Geographical Society Cave (Baryshnikov 2015); **h, i** Tos 6813 and Tos 7128 from Tosina di Monzambano (Mantova—Italy). Extant *Lutra lutra*: **j, k** 882 and 883; **l** n/a (Pohle, 1919). *Lutra sumatrana*: **m** n/a (Pohle 1919); **n** ZM CN4494 (Zyll de Yong, 1972). *Cyrsaonyx antiqua*: **o–q** BM M 34,378 and BM M 50,709 from Tornetown Cave (Willemssen 1992); **p** Ke RM 226 from Maasvlakte (Willemssen 1992)



2009). According to Conroy et al. (2000), the body mass of males is of 5.45–11.4 kg, whereas that of females is of 3.36–7.6 kg. Conversely, values reported by Kruuk (2006) range from 5.0 to 14.0 kg, but no sex distinction was made. Considering the fossil sample, the M_1L predicts a reduced body-size variation for the Early–Middle Pleistocene *L. simplicidens*, with values between 5.2 and 7.0 kg (Table 1). The *L. lutra* sample possesses slightly larger, but not different body mass, with estimated values ranging from 5.0 to 8.2 kg (Table 1). Finally, the highest body size values are obtained for the sample of *C. antiqua*, whose estimates are between 7.8 and 10.8 kg (Table 1).

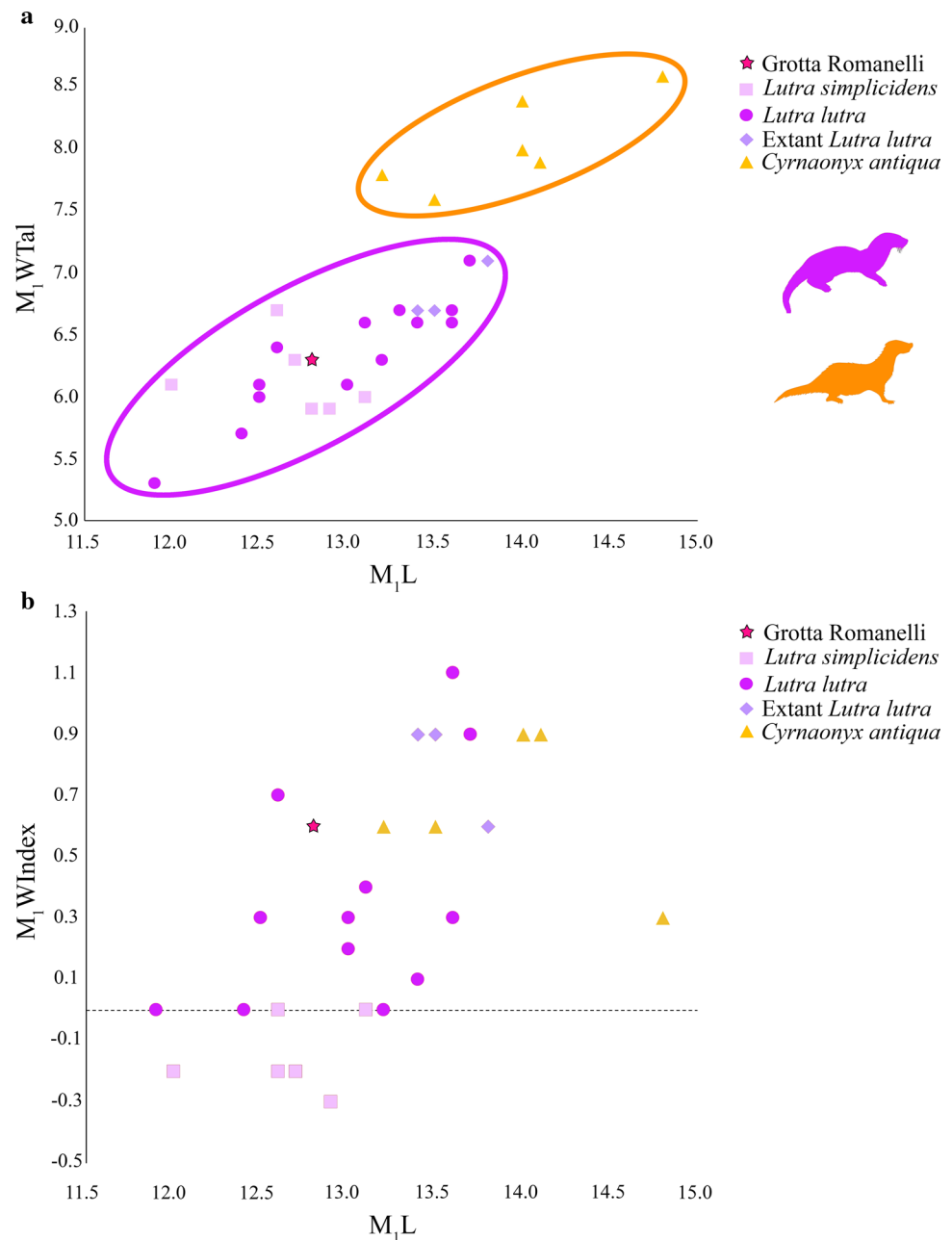
The estimated values on fossil otters reveal a reduced body size variation among groups, with slight difference in the average values and wide overlap in distribution ranges. Taking into account the body mass range of the extant Eurasian otter, the difference among the fossil groups is even less significant, since all their body size values fall into the extant variation range.

Discussion

Eurasian quaternary otters

Blanc (1920, 1928) reported for the first-time the presence of *L. lutra* from the level G of Grotta Romanelli. Since then, the Eurasian otter from this archeological site was cited by paleontologists (e.g., Willemssen 1992; Pennacchioni and Cassola 1986), but no operational diagnosis was available, thus preventing its morphological and/or biometric comparison. The lack of these data sometimes sparked debates on taxonomy of some specimens belonging to these collections, as for instance happened for the canid collection recovered from the level G of Grotta Romanelli (see Sardella et al. 2014 for discussion). Morphological analysis reveals that the features of the fossil specimen from Grotta Romanelli clearly fit with an attribution to the extant *L. lutra*, confirming what Blanc (1920, 1928) reported.

Fig. 3 Plot of lower carnassial: **a** length of M_1 vs. width of M_1 talonid; **b** length of M_1 vs. width of M_1 W index (calculated as M_1 W talonid– M_1 W trigonid)



Despite several fossil otters have been referred to *Lutra* over the years, many of them are now reassigned to other genera, whereas “*Lutra*” is retained mainly for ease of reference for taxa of uncertain taxonomy (Willemsen 1992; Cherin et al. 2016), recognizing its paraphyletic nature (Geraads et al. 2015). *L. simplicidens* has a relatively abundant fossil record, compared to other Pleistocene Lutrinae. However, it is almost entirely known from isolated mandibular and postcranial remains (Willemsen 1992), which are not directly comparable with the recently described *Lutraeximia umbra*, only known for the holotype cranium. It is worth noticing that Cherin (2017), providing the first description of the maxillary dentition of *L. simplicidens*, recognized a

close relationship between this species, *Lutraeximia umbra*, *Lutraeximia trinacriae* and other Mediterranean Quaternary otters likely forming a monophyletic clade (Cherin et al. 2016). If new discoveries are needed to substantiate the attribution of *L. simplicidens* to *Lutraeximia* (Cherin 2017), nonetheless there is general agreement in recognizing as hardly conceivable a derivation of *L. lutra* from *L. simplicidens* (Willemsen 1992, 2006). Our data agree in evidencing morphometric differences between the two species, providing further support for a different derivation of *L. lutra*.

Willemsen (1992) hypothesized an Asian origin for *L. lutra*, probably from *L. palaeindica*. However, the latter taxon is only known from the type sample (Falconer 1868;

Pohle 1919; Matthew 1929), and possibly from another specimen (Raghavan et al. 2007), recovered from the Upper Siwalik. Similarly, no cranial material of *L. simplicidens* has been described so far, which highlights the strongly restricted knowledge on the morphological variability of these species. Nevertheless, in dental morphology, *L. palaeindica* shares many features with *L. simplicidens*. In the P⁴: the metacone lower than the paracone with a crest that connects the two cusps curved lingually, the parastyle well defined and the talonid mesiodistally elongated, triangular-shaped in occlusal view (though more pronounced in *L. palaeindica*) (Fig. 4); and in the M₁: the trigonid larger the talonid and a relatively reduced metaconid (Fig. 2). Compared to *C. antiqua*, these two taxa instead possess marked differences in the upper and lower carnassial morphology, especially in the P⁴, where the profile in occlusal view is trapezoidal (Fig. 4j–m).

Setting our results in chronological framework, it seems that *L. lutra* dispersed into Europe from Asia at the beginning of the Late Pleistocene or, possibly, during the late Middle Pleistocene, replacing *L. simplicidens*. In this scenario, the taxonomic attribution of two Middle Pleistocene specimens needs to be considered. The first is the hemimandible from Cengelle BB classified as *L. lutra* by Pasa (1947). According to his description, the specimen displayed clear *Lutra* features, among which is a trigonid larger than talonid in the lower carnassial. It is worth noting that *L. simplicidens* was instituted by Thenius (1965), and thus the name was not available to Pasa (1947). According to Willemsen (1992), the trigonid larger than talonid character has a high taxonomic value, which allows an unquestionable

attribution of the specimen from Cengelle BB to *L. simplicidens*. The second specimen was a P⁴ recovered from Hoxne and ascribed to *Lutra* sp. by Willemsen (1992). The author recognized the strong resemblance with *L. lutra*, but given the absence of coeval maxillary Lutrinae material, he could not rule out an attribution to *L. simplicidens*, preferring an evolutionary hypothesis in which *L. lutra* appears during the Early Holocene. Recently, Cherin (2017) described for the first time the morphology of the maxillary dentition of *L. simplicidens*. The comparison of the P⁴ shows slightly but significative morphological differences between the Hoxne specimen and Voigtstedt ones (Fig. 4a, b, d; Table 3). Notably, *L. simplicidens* possesses a characteristic talon profile, with a convexity along the distal margin, about half length, in occlusal view (Cherin 2017) (Fig. 4a, b). In the P⁴ from Hoxne, the profile of the distal margin is straight, not convex, which allows to refer it to *L. lutra*.

Paleoecological implications

Despite its fossil record is less abundant if compared to other Mustelidae taxa (e.g., *Meles meles*, Mecozzi et al. 2019), otters are largely distributed across the Eurasian continent over a long stratigraphical interval. Currently, this carnivoran inhabits a large variety of aquatic habitats, including highland and lowland lakes, rivers, streams, marshes, swamp forests and coastal areas independent of their size, origin or latitude (Mason and Macdonald 2009; Hung and Law 2016). It can be found in brackish waters from sea level up to 4120 m (Mason and Macdonald 2009). Similarly to other European carnivorans, the extant populations of *L. lutra* suffer the

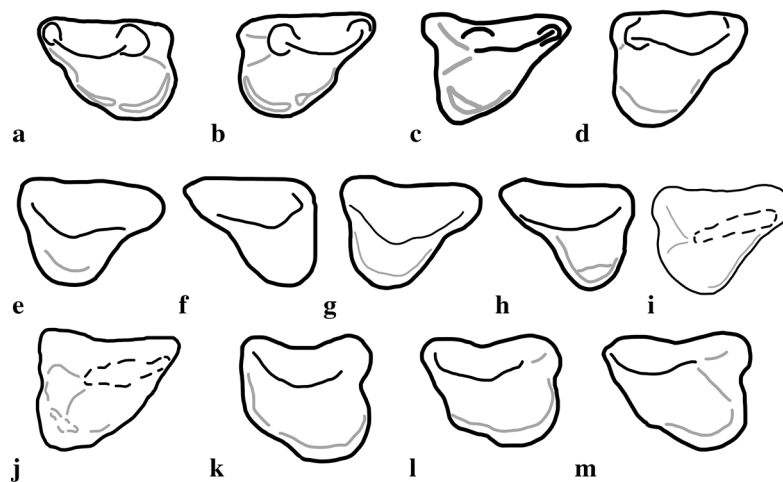


Fig. 4 Upper fourth premolar of fossil and extant otter in occlusal view (drawn not in scale). *Lutra simplicidens*: **a** IQW 1966/7313 (Voi. 3525) from Voigtstedt; **b** IQW 1966/7314 (Voi. 3532) from Voigtstedt (Cherin 2017). *Lutra palaeindica*: **c** BM37151 from Upper Siwalik (Matthew 1929). *Lutra* sp.: **d** BM4936 from Hoxne (Willemsen 1992). *Lutra lutra*: **e** n/a (Zyll de Jong 1972). **f** n/a (Pohle 1919).

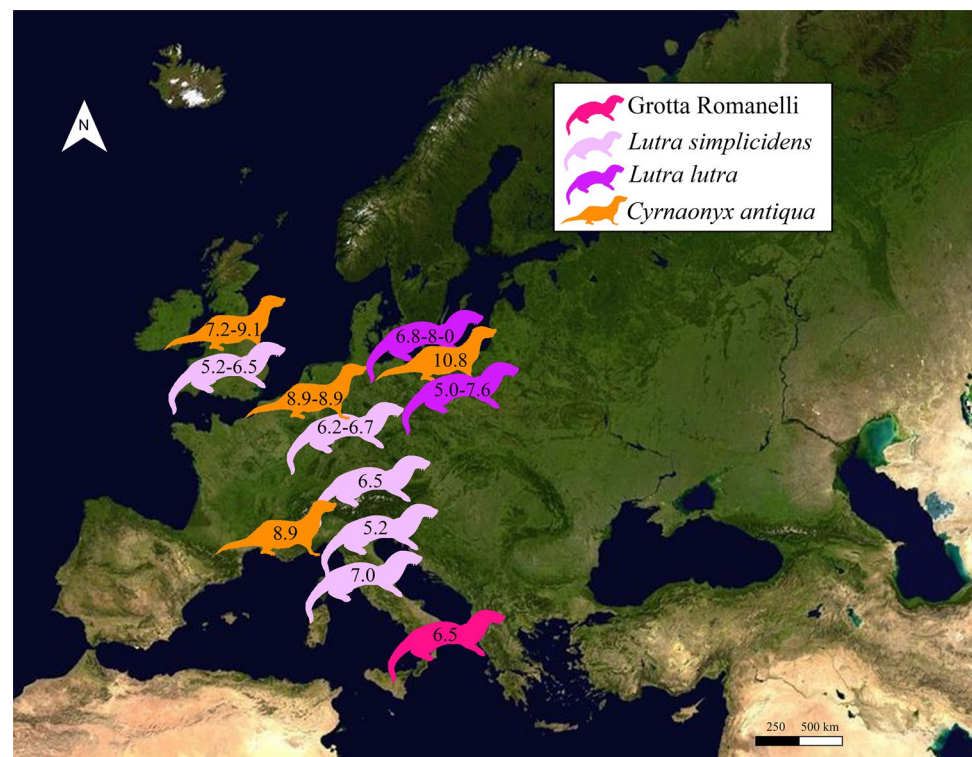
Lutra sumatrana: **g** CN4494 (Zyll de Jong 1972); **h** n/a (Pohle 1919). *Lutraeximia umbra*: **i** SBAU 337,654 from Pantalla (Cherin et al. 2016). *Cyraonyx antiqua*: **j** 7 M from Cengelle (Pasa 1947); **k–m** BM34371, BM50707 and BM34373 from Tornetown Cave (Willemsen 1992)

Table 3 Literature data on the upper fourth premolar of fossil otters from the Early Pleistocene to Holocene sites of Eurasia

Species	Site	Specimen number	References	P ⁴ L (mm)
<i>Lutraeximia umbra</i>	Pantalla	SBAU 337654	Cherin et al. (2016)	13.8
<i>Lutraeximia umbra</i>	Pantalla	SBAU 337654	Cherin et al. (2016)	13.9
<i>Lutra simplicidens</i>	Voigtstedt	IQW 1966/7313 (Voi. 3525)	Cherin (2017)	10.3
<i>Lutra simplicidens</i>	Voigtstedt	IQW 1966/7314 (Voi. 3532)	Cherin (2017)	10.7
<i>Lutra palaeindica</i>	Upper Siwalik	NHM M 37151	Raghavan et al. (2007)	11.5
<i>Lutra lutra</i>	Hoxne	BM4936	Willemsen (1992)	12.3
<i>Cyrnaonyx antiqua</i>	Tornewton Cave	BM M 34370	Willemsen (1992)	11.2
<i>Cyrnaonyx antiqua</i>	Tornewton Cave	BM M 34373	Willemsen (1992)	11.3
<i>Cyrnaonyx antiqua</i>	Tornewton Cave	BM M 34374	Willemsen (1992)	11.6
<i>Cyrnaonyx antiqua</i>	Tornewton Cave	BM M 50707	Willemsen (1992)	11.0
<i>Cyrnaonyx antiqua</i>	Verona	M7	Willemsen (1992)	11.8

strong human pressure, which mainly reflects the habitat loss (Toschi 1965; Prigioni 2003). In the Italian Peninsula, the presence of the Eurasian otter is nowadays confined in the southern regions, with stable populations reported also in northern Apulia (Toschi 1965; Prigioni 2003). Thus, the occurrence of *L. lutra* from Grotta Romanelli is surprisingly, since the geographical position of the site falls outside the range of the extant species. Moreover, its ecological profile indicates a strong relation to large freshwater bodies (rivers or lakes), which are no longer present in the southern part of the Apulia (Mastronuzzi and Sansò 2017). Therefore, its presence strongly supports a more diversified hydrographic network in this territory during the late Quaternary.

Body mass estimates reveal a large overlap between *L. lutra* and *L. simplicidens* (Fig. 5), which also share a fish-feeding type of dentition, making difficult to envision a possible coexistence. On the contrary, *C. antiqua* has similar but slightly larger values of estimated body mass but occupied a different trophic niche. In fact, given its robust dentition with broader teeth, several authors aligned it with *Aonyx* (e.g., Malatesta 1978; Pennacchioni and Cassola 1986), whose paleobiological interpretation points to a more important role of shellfish in its diet (Willemsen 1992). Following this, a sympatric coexistence scenario of the fish-feeding *L. simplicidens* and *L. lutra* with *C. antiqua* could be possible, with different craniodental features which reflect the

Fig. 5 Geographical distribution of the body size estimates

diversification of ecological niches. The other fossil European otter, *Lutraeximia umbra*, according to Cherin et al. (2016) had a strong preference for hard prey (molluscs), but possessed intermediate features between fish specialist and hard invertebrates dentition.

Finally, several scholars detected geographic-related body size differences in extant otters, which have been explained according to Bergmann's ecogeographical rule (Yom-Tov et al. 2006; Meiri et al. 2007), or advocating a detrimental effect of environmental pressures and food availability (Yom-Tov et al. 2010). Despite the paucity of the otter sample prevents definitive conclusions, body size estimates of the fossil specimens would show no dimensional clines across Europe, neither geographic, nor chronological (Fig. 5).

Homo-otter interactions

The finding of the fossil otter in the deposit of Grotta Romanelli opens another question that requires attention. Although the studied specimen lacks both exact stratigraphical and taphonomic information, in level G lithic artifacts referred to Mousterian (Middle Paleolithic) were also found, which document the human occupation of the cave. The potential *Homo-Lutra* interactions during Pleistocene are indeterminate, and in need of an in-depth emphasis from both paleoecological and archaeozoological points of view. Man exploited carnivorans for a wide range of purposes, among which food and fur, but even for bone artifact industry, symbolism, and ornamental purposes (Mallye 2007, 2011). The *Homo* medium-to-small-sized carnivoran interactions are difficult to investigate due to the fragility of the skeletal bones (Kurtén 1968). Indeed, the majority of the carnivoran records from archeological deposits are represented by fragmentary craniodental, metapodial and phalange remains. This is probably due to selective human exploitation, since the skull and distal portion of the limbs have lesser nutritional return. In addition, the carnivoran species are usually rare in archeological deposits, as for instances Riparo Mochi (2.9%, Tagliacozzo et al. 2012), Arene Candide (27.7%, Cassoli and Tagliacozzo 1994a), Riparo Fumane (16.8%, Cassoli and Tagliacozzo 1994b), Grotta Maggiore di San Bernardino (26.5%, Cassoli and Tagliacozzo 1994c) and upper complex (level E–A) of Grotta Romanelli (26.9%, Tagliacozzo 2003). However, the presence of carnivorans and *Homo* in the same deposit not necessarily indicates that these taxa were hunted. Cassoli and Tagliacozzo (1994a), analyzing the fossil remains from the long sedimentary succession of Arene Candide, suggested that the majority of the carnivoran fossil remains do not show cut mark and often were found in anatomical connection. The authors also identified bite marks in a few carnivoran specimens,

as well as some ungulate ones, suggesting therefore that this cave was also seasonally frequented by large carnivorans (leopard or hyaena) or more stable occupied by bear, where the prevalence of young individuals has been interpreted as its possible den. Recently, a natural accumulation of an abundant sample of *L. lutra* from Bliznets Cave (Russian Far East) has been described, testifying that otters can visit caves as well as perish in them (Alekseeva and Baryshnikov 2020). In this scenario, who hunted the *L. lutra* from Grotta Romanelli cannot be ascertained, even if the abundance of the Middle Paleolithic artifacts from level G points to the Neanderthal as possible responsible, which could have included otter in its diet.

Conclusion

The Eurasian otter from the late Middle Pleistocene of Grotta Romanelli represents one of the earliest evidences of the species, previously known only since the Holocene onwards. The comparison analyses allow to exclude an attribution to *L. simplicidens* and *C. antiqua*. *L. simplicidens* and *L. lutra* have a similar size and share a fish-feeding type of dentition, but they are distinct by the proportions of their lower carnassial teeth and morphological features of the upper carnassial. *C. antiqua* has a shellfish-feeding dentition, broader and more robust than that of *L. lutra*. However, here, we recognize that the two species overlap in chronological distribution, which urges to exercise caution in the attribution of isolated remains.

The occurrence of the Eurasian otter from the “terre rosse” of Grotta Romanelli provides valuable paleoecological information. *L. lutra*, nowadays, is mainly living in fresh and clear running waters or lakes, and a certain degree of adaptation to brackish water is possible. Most likely, a hydrographic network could have been occurred in the area in front of the cave, at present under the sea level.

Unfortunately, taphonomic data are not enough to reconstruct who buried the mandible and how, at present the only bone referable to the species, in the “terre rosse”. Anyway, the occurrence of *L. lutra* at Grotta Romanelli suggests that the taxon spreads into Europe earlier than supposed before, at least at the beginning of the Late Pleistocene or during the late Middle Pleistocene, replacing *L. simplicidens* and coexisting with *C. antiqua*.

Genetic evidence resume *L. lutra* as closely related with the extant *L. sumatrana* (Hung and Law 2016), and it has been suggested that both derived from the Upper Siwalik *L. palaeindica* (Willemsen 1992). However, despite the lack of cranial material prevents conclusive comparisons, our analyses reveal strong morphological affinities between *L. palaeindica* and *L. simplicidens*.

Further discoveries will shed new light on systematics and evolution of these carnivorans in the Quaternary of Europe.

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