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NEW INSIGHTS ON THE ENIGMATIC OTTERS FROM THE LATE MIOCENE OF TUSCANY: *TYRRHENOLUTRA MAREMMANA* NOV. COMB. (LUTRINAE, MUSTELIDAE, CARNIVORA), WITH A PHYLOGENY OF BUNODONT OTTERS

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Abstract. Otters, subfamily Lutrinae (Mustelidae), are predators that thrive in aquatic environments, and have a semiaquatic to fully aquatic lifestyle. While modern otters are found across the globe, their fossil history is limited, primarily documented by fragmented dentognathic remains. In this work, we report on and describe new dental remains of a medium-sized Lutrinae from the Late Miocene of Baccinello and Casteani (Tuscany), improving the poor fossil record of the subfamily in Europe. *Tyrrhenolutra helbingi* Hürzeler, 1987 is a poorly known species, described on some dental remains from the Baccinello mines and a few other localities. Considering its peculiar morphology, it has often been overlooked in the scientific literature. Description of the material stored at the Naturhistorisches Museum, Basel and Museo di Geologia e Paleontologia dell'Università di Firenze offers new insights on the intraspecific variability and dental morphology of this taxon. The comparative study of these findings highlights several morphological and biometrical similarities between *T. helbingi* and *Paludolutra maremmana* Hürzeler, 1987, which allow us to redefine these taxa as *Tyrrhenolutra maremmana* nov. comb. We carried out a total-evidence cladistic analysis seeking support for morphometric and morphological similarities between *T.* "*helbingi*" and "*P.*" *maremmana*. The resulting parsimony analyses support the synonymy, excluding a close relationship of *T. maremmana* with *Paludolutra* of Italy and Spain, as previously thought. Furthermore, we confirm a long-forgotten hypothesis identifying *Limnonyx* Crusafont Pairó, 1950 as the possible continental ancestor of *Tyrrhenolutra*.

INTRODUCTION

The carnivore record of the Tusco-Sardinian paleobioprovince

The uppermost Miocene sedimentary record of the Italian peri-Tyrrhenian areas, specifically Tuscany and Sardinia, reveals the presence of a distinctive and unique paleobiogeographic region. This region is distinguished for its unique vertebrate ecosystem, showcasing strongly endemic characteristics that set it apart from the contemporary mammal faunas of Europe and Africa. This paleobiogeographic area is commonly referred to as the Tusco-Sardinian paleobioprovince. The Tuscany portion of the paleobioprovince has better docu-

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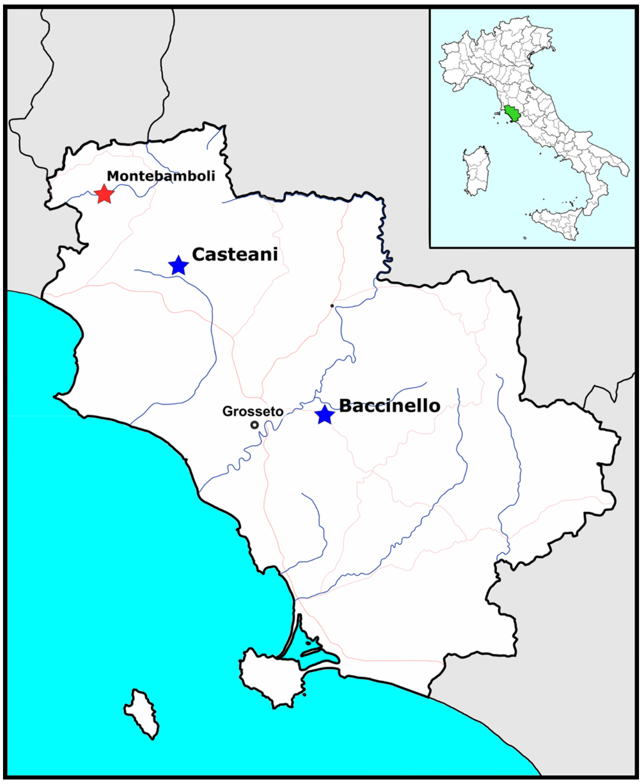

Fig. 1 - Map of the Grosseto province, indicating the position of V1 (blue star) and V2 (Red star) localities where otter remains where recovered.

mentation along the outcrops of the Baccinello-Cinigiano basin (BCB). The geology and paleontology of the Baccinello area are well known thanks to early research led by Johannes Hürzeler (1908-1995) from the Naturhistorisches Museum, Basel, which recovered abundant faunal remains (De Terra 1956; Gillet et al. 1965; Lorenz 1968; Rook 2012) and the late 1990s research undertaken by the Vertebrate Paleontology Research Group of the University of Florence (Benvenuti et al. 1994, 1999, 2001; Rook et al. 2000, 2006, 2011; Ligios et al. 2008; Benvenuti et al. 2015).

The relatively abundant fossil mammal remains recovered from this area are grouped into four distinct assemblages, called Baccinello V0, V1, V2, V3 (Lorenz 1968; Engesser 1989; Cirilli et al. 2016; Rook 2016). The Baccinello V1 and V2 faunas are characterised by unbalanced and impoverished faunas, with a predominance of specialized bovids with a tendency to hypsodonty, and some rodents with peculiar dental characteristics (Casanovas-Vilar et al. 2011b) and (in the case of dormice) a particularly large body size (Engesser 1983; Cirilli et al. 2016). These characteristics are all indicative of an endemic (insular) environment (Hürzeler & Engesser 1976; Sondaar 1977, 1986; Engesser 1989; Casanovas-Vilar et al. 2011a; Rook 2016). The high level of endemism exhibited by the V1 and V2 faunal assemblages in earlier studies of the BCB basin, has made biostratigraphic correlations with other European sites extremely difficult (Lorenz 1968; Hürzeler & Engesser 1976; Engesser 1989). A firmer chronological framework of the V0 to V3 faunal assemblages has been provided thanks to radiometric calibration (Rook et al. 2000) coupled with a magnetostratigraphic study of the BCB succession (Rook et al. 2011; Benvenuti et al. 2015). The Baccinello V1 fauna is magnetostratigraphically correlated with upper C4r and therefore has an age between 8.3 and 7.7 Ma. The V2 assemblage comes from sediments attributed to C3Ar and has an age bracketed between 7.1 and 6.7 Ma.

Even though insular faunas may contain relatively large numbers of endemic taxa, the terms “impoverished” and “unbalanced” indicate that the taxonomic diversity is poor at the higher levels, with many major groups often absent. Except for some rare cases (Lyras et al. 2010 and references therein), otters form great majority of fossil insular carnivores, while other carnivores are generally lacking from endemic insular faunas (Van Der Geer et al. 2010). Baccinello-Cinigiano Basin V1 fauna is not an exception, as the only carnivoran known from this fauna is the enigmatic otter *Tyrrhenolutra helbingi* Hürzeler, 1987. The V2 fauna carnivoran guild shows the arrival of new immigrants into the region [e.g., *Indarctos anthracitis* Weithofer, (1888); *“Mustela” majori*, Weithofer, 1888], hinting at temporary re-connection with Europe (Benvenuti et al. 2001), and the appearance of new otter species (*P. maremmana, Paludolutra campanii* Meneghini, 1862) possibly resulting from in situ evolution of local, endemic forms (Hürzeler 1987). A major reorganization in the palaeobiogeography of the Tyrrhenian area occurred during the Messinian. From a faunistic point of view, this time interval is characterised by a dramatic change. All the taxa belonging to the endemic faunal complex in BCB disappeared and were replaced by a new faunal assemblage (V3) including continental taxa with clear European affinities (Hürzeler & Engesser 1976; Rook et al. 1991; Rook & Rustioni 1991; Rook 1999; Abbazzi 2001; Rook & Martínez-Navarro 2004). In this renewed faunal assemblage, mustelids are present (i.e., *Plesi-*

ogulo crassa Kurtén, 1970) but no otter remains have been found thus far. Recently, Dominici & Benvenuti (2024) suggested an alternative scenario. In their hypothesis, all V1 and V2 fossil assemblages are coeval, therefore the Tusco-Sardinian paleobioprovince would be characterised by a single phase of insularism bracketed between two intervals of faunal interchange.

The intricate phylogeny of Lutrinae

Otters make up the subfamily Lutrinae of the family Mustelidae, which is one of the largest families of the order Mustelidae (Mason & Macdonald 2009). Currently, the subfamily Lutrinae includes 13 extant species of otters (De Ferran et al. 2022). Otters are characterised by a great adaptability, displaying a wide geographic distribution and being a common presence in all continents except for some areas such as Australia and some remote islands. Throughout this wide distribution, otters provide a unique look into the evolution of living aquatic mammals. This is because most extant marine mammals have been so highly modified by long periods of selection for life in the ocean that they bear little resemblance to their terrestrial ancestors. Otters, by contrast, are recent expatriates from terrestrial and freshwater habitats, and some species still live in both environments (Estes & Bodkin 2002). Another point of interest is the striking similarity between all the otter species, in appearance, ecology, and behaviour.

The phylogenetic position of the subfamily Lutrinae within Mustelidae has always been debated. De Muizon (1982) envisaged otters as a paraphyletic group, but included then known 'musteloid' taxa, such as phocids and mephitids, which are now known to belong to clades that have no close relationship with otters. The cladistic analysis of living mustelids by Bryant et al. (1993) placed Lutrinae as the sister group of the subfamily Melinae. This result possibly depended on the similarity between the upper teeth. However, this phylogeny has been contradicted by molecular phylogenies that place Lutrinae as the sister clade of the genus *Mustela* (Koepfli & Wayne 1998; Sato et al. 2003, 2012; Flynn et al. 2005; Koepfli et al. 2008a, 2008b; Law et al. 2018), as the sister clade of Ictonychinae (Dragoo & Honeycutt 1997; Koepfli & Wayne 2003; Wolsan & Sato 2010; Sato et al. 2012; Hassanin et al. 2021), or both (Koepfli et al. 2008b). Unfortunately, the limited number of genetic markers or short marker lengths can sometimes still fail to fully resolve the true evolutionary relationships among populations (Koepfli & Wayne 2003; Yu et al. 2008, 2011). The superficial similarity among otters in their morphology and ecology, makes the relationships among the 13 currently recognized extant species of lutrines equally unclear. When we take into account the fossil record, the relationships between different taxa and supraspecific taxonomy become even more complex as lutrine fossils are known to be rare, compared to some other carnivores (Willemsen 1992).

At least four subfamilies are differentiated in the Late Neogene of the Old World (and North America as well): Lutrini, Aonychini, Enhydrini, and Enhydriodontini (Pickford 2007) but the degree of uncertainty in the interpretation of the relationships between and within the groups is still high, due to the numerous lacunae in the fossil record and because of the presence of convergencies in dentognathic adaptations. Bunodont otters of various sizes were in fact widely distributed during the Late Miocene and Early Pliocene (Fig. 2), with records in North America (Repenning 1976; Berta & Morgan 1985; Tseng et al. 2017), Europe (Meneghini 1862; Pilgrim 1931, 1932; De Villalta Comella & Crusafont-Pairó 1945; Crusafont-Pairó 1950; Crusafont-Pairó & Golpe 1962, 1962; Willemsen 1983, 1992, 1999; Hürzeler 1987; Alcalá 1994), Asia (Falconer 1868; Lydekker 1884; Pilgrim 1931, 1932; Pickford 2007; Ji et al. 2013; Jablonski et al. 2014; Wang et al. 2018) as well as Africa (Stromer von Reichenbach 1931; Hendey 1974; Petter et al. 1991; Werdelin 2003a, 2003b; Morales et al. 2005; Morales & Pickford 2005).

The phylogenetic position and evolution of the Lutrinae from the Tusco-Sardinian paleobioprovince are uncertain. Meneghini (1862) was the first to describe the remains of the large-sized bunodont otter *P. campanii* from Montebamboli locality (Fig. 1) ascribing it, however, to the genus *Lutra* Brisson, 1762. It was later moved to *Enhydriodon* Falconer, 1868 by Forsyth Major (1872). A century later, Hürzeler (1987) reviewed all the Lutrinae material from the Grosseto province. Firstly, he moved the *Enhydriodon campanii* material to the new genus *Paludolutra* Hürzeler, 1987. Then he erected two new species. *Paludolutra maremmana* Hürzeler, 1987 was supposedly recovered from the older lignite beds in Montebamboli (Fig. 1) and possibly the direct ancestor or chronospecies of *P. campanii*. Both taxa were ascribed to BCB V2. A third *Paludolutra* species, *Paludolutra lluecai* (De Villalta

Comella & Crusafont-Pairó, 1945) is reported from a number of Turolian localities near Teruel in Spain (De Villalta Comella & Crusafont-Pairó 1945; Crusafont Pairó & De Villalta 1951; Crusafont-Pairó & Golpe 1962; Hürzeler 1987). *Paludolutra lluecai* is often considered the continental ancestor of the Tuscan species (Willemsen 1992). A few *Paludolutra* occurrences are reported by Vislobokova et al. (2001) and Sotnikova & Rook (2010) in Kholu (Russia) and Khirgis Nur 2 (Mongolia) from levels 11 and 20–22 m and from levels 37–40, 51–55, and 57 m, respectively. Unfortunately, these Asian occurrences cannot not be confirmed since no images are reported in the literature. A smaller and more slender form, known from limited and fragmented dentognathic remains from BCB V1, was attributed to *Tyrrhenolutra helbingi*. This taxon is the only otter-like mustelid known from the V1 fauna. Most of its remains were recovered in the Baccinello mines in the 20th century though it was also reported from the mine of Casteani, north of Grosseto (Fig. 1; Weithofer 1888; Azzaroli et al. 1986; Hürzeler 1987). Hürzeler (1987) suggested a tentative phyletic line from BCB V1 *T. helbingi* to BCB V2 *P. campanii*, through *P. maremmana*. No hypotheses were provided by Hürzeler (1987) regarding the possible origin of *Tyrrhenolutra*. After Hürzeler's (1987) pioneering work, virtually no study on European otters took them into consideration, particularly *Tyrrhenolutra*. The exact taxonomic placement of these species within the Mio-Pliocene radiation Lutrinae remains uncertain. *Tyrrhenolutra* has often been lumped together with the European bunodont lineage (e.g. Hürzeler 1987; Morales & Pickford 2005; Pickford 2007), but it is neither very large nor particularly bunodont, giving *Tyrrhenolutra* a somewhat unique position. During the Late Miocene Italy was characterised by another endemic fauna (Abruzzi-Apulia paleobioprovince) inhabited by a different otter, *Paralutra garganensis* Willemsen, 1983. The genus *Paralutra* is a typical member of the Middle-Late Miocene assemblages of Europe with three species *Paralutra jaegeri* Fraas, 1862, *Pr. transdanubica* Kretzoi 1951, and *Pr. garganensis*. The stratigraphic range of *Pr. jaegeri* covers from the Early Miocene (Pellecahus, France; MN 4; Roman & Viret 1934) to the early Late Miocene, as it has been found in Rudabánya (MN 9; Werdelin 2005). *Paralutra garganensis*, however, shows a very different morphology from its older relative and this led many authors to consider its generic attribution doubtful (Wang et al. 2018; Kargopoulos et al. 2022).

Recently, Wang et al. (2018) attempted cladistic analyses of extant and fossil Lutrinae including *Tyrrhenolutra*. In their work, *T. helbingi* appears basal to the endemic otter of Gargano *Pr. garganensis*, *Paludolutra,* and the North American genus *Enhydritherium* Berta & Morgan, 1985.

The present paper provides a detailed study of the known material of *Tyrrhenolutra* together with newly discovered cranial material, to shed light on this enigmatic taxon.

MATERIAL AND METHODS

The present study is based on the revision of key diagnostic features of the problematic species *Tyrrhenolutra helbingi* in comparison to other extant and fossil mustelids of the subfamily Lutrinae of Eurasia, Africa, and America.

The examined original fossil material comes from the Italian localities of Baccinello, Casteani and Montebamboli dated to the Tortonian (MN11-MN12, early Turolian, 8.3-7.1 Ma; Rook et al. 2011). The described fossils are housed at the NMB, MGPUF, MSNUP (see abbreviations below). As comparative fossil material we studied the collections of NMB, MGPUF, MNB and inspected all the relevant literature on Middle and Late Miocene Lutrinae. Extant specimens from NMB and MGPUF as well as data recovered from Morphosource (MorphoSource 2024), IMNH, AMNH, CMNH, FMNH, and L-AHR were also used for morphological and morphometric comparisons. The fossil comparative sample includes specimens of the genera: *Paludolutra* (see Hürzeler 1987; Willemsen 1992; Morales & Pickford 2005); *Limnonyx* Crusafont-Pairó, 1950 (see Tobien 1955; Willemsen 1992; Baskin 1998); *Paralutra* Roman & Viret, 1934 (see Roman & Viret 1934; Helbing 1936; Willemsen 1983; Villier et al. 2011); *Siamogale* Ginsburg et al., 1983 (see Grohé et al. 2010, 2020; Wang et al. 2018), *Vishnuonyx* Pilgrim, 1932(see Pickford 2007; Wang et al. 2018; Grohé et al. 2020; Kargopoulos et al. 2021); *Sivaonyx* Pilgrim, 1931 (see Morales & Pickford 2005; Pickford 2007; Peigné et al. 2008; Grohé et al. 2013); *Enhydriodon* (Matthew 1929; Geraads et al. 2011); *Enhydritherium* (see Berta & Morgan 1985; Lambert 1997; Tseng et al. 2017); *Lartetictis* Ginsburg & Morales, 1996 (see Valenciano et al. 2020).

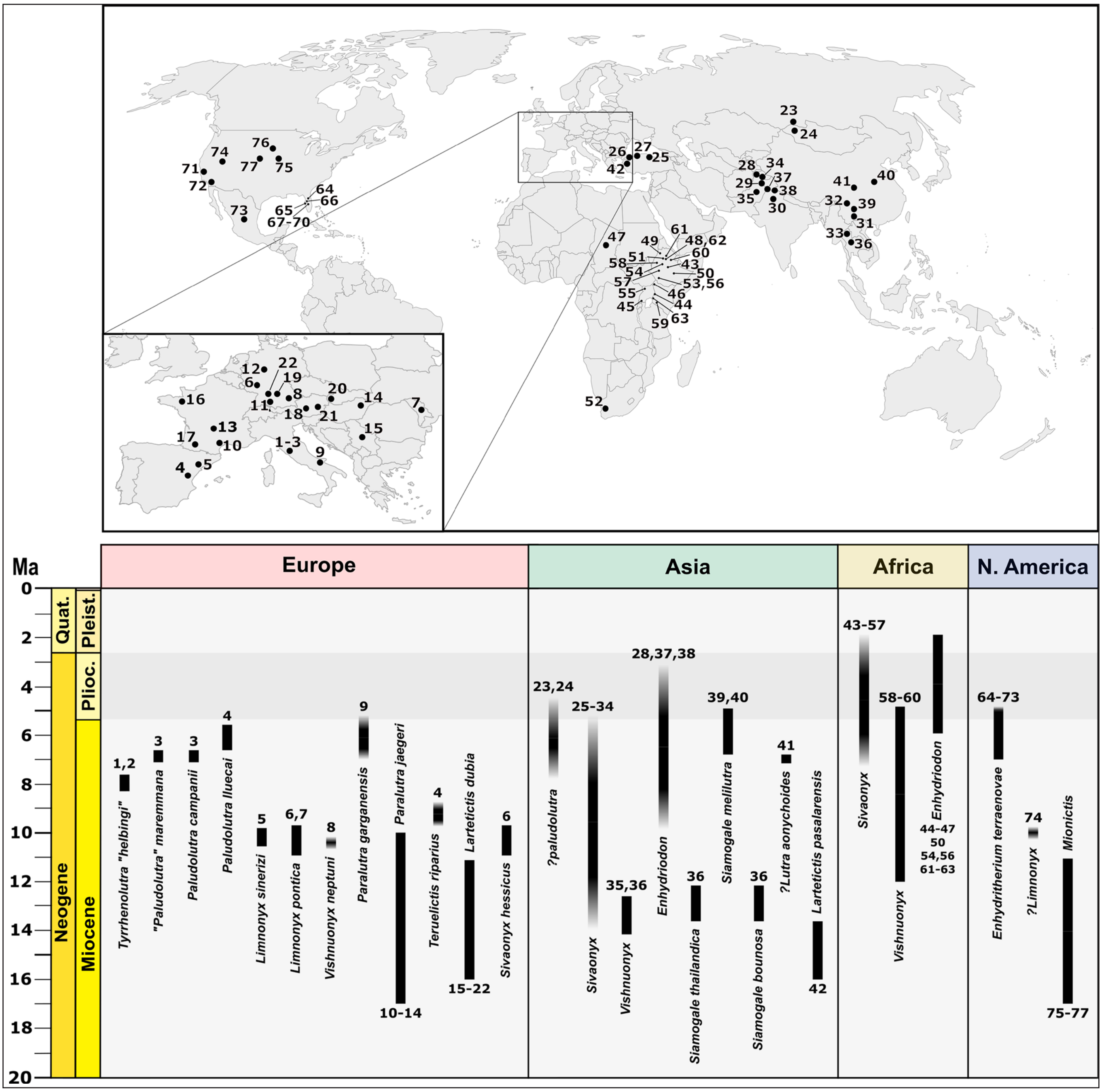

Fig. 2 - Stratigraphic and geographic occurrences showing the localities of the taxa analyzed herein. 1, Baccinello V1 (Italy); 2, Casteani (Italy); 3, Monte Bamboli (Italy); 4, Teruel basin (Spain); 5, Can Ponsich (Spain); 6, Eppelsheim (Germany); 7, Kishinev (Moldova); 8, Hammerschmiede (Germany); 9, "Terre Rosse" Gargano (Italy); 10, Pellechaus (France); 11, Ravensburg (Germany); 12, Steinheim (Germany); 13, La Grive (France); 14, Rubadánya (Hungary); 15, Mala Miliva (Serbia); 16, Faluns Anjou (France); 17, Sansan (France); 18, Göriach (Austria); 19, Goldberg (Germany); 20, Devinska Nova Ves (Slovakia); 21, Rosenthal bei Köpflach (Austria); 22, Mörgen (Germany); 23, Kholu (Russia); 24, Khirgis Nur 2 (Mongolia); 25, Çorakyerler (Turkey); 26, Küçükçekmece (Turkey); 27, Bayraktepe (Turkey); 28, Hasnot (Pakistan); 29, Potwar Plateaus (Pakistan); 30, Haritalyangar (India); 31, Lufeng (China); 32, Yuanmou (China); 33, Chiang Muan (Thailand); 34, Chorwali Katas (Pakistan); 35, Chinji (Pakistan); 36, Mae Moh (Thailand); 37, Siwalik Hills (India); 38, Himachel Pradesh (India); 39, Shuitangba (China); 40, Yushe Basin (China); 41, Locality 49, Yangmukou (China); 42, Paşalar (Turkey); 43, Adu-Asa (Ethiope); 44, Kanapoi (Kenya); 45, Kazinga (Uganda); 46, Kobi Foora (Kenya); 47, Koro Toro (Chad); 48, Hadar Denen Dora/Hadar Denen Pinnacle (Ethiopia); 49, Ailia Bay (Kenya); 50, Awash (Ethiopia); 51, Eshoa Kakurongori (Ethiopia); 52, Laangebanweg (South Africa); 53, Nachukui (Ethiopia); 54, Nakoret (Ethiopia); 55, Nkondo (Uganda); 56, Omo Shungura Fm./ Omo Fm. (Ethiopia); 57, Lukeino (Ethiopia); 58, Lothagam Lower Nawata (Ethiopia); 59, Ngorora (Tanzania); 60, Haradaso (Ethiopia); 61, Woranso Milie (Ethiopia); 62, Baringo (Tanzania); 63, Dikika (Ethiopia); 64, Moss Acre Racetrack (Florida); 65, Palmetto (Florida); 66, Withlacocee (Florida); 67, Fort Green Mine (Florida); 68, Rockland Mine (Florida); 69, Gardinier Mine (Florida); 70, Payne Creek (Florida); 71, Kettleman Hills (California); 72, Lawrence Canyon (California); 73, El Resbalon (Mexico); 74, Truckee Fm. (Nevada); 75, Lower Snake Creek Beds (Nebraska); 76, Canyon Little White River (South Dakota); 77, 17 Miles South Agate (Nebraska). Stratigraphic ranges of the European taxa based on Willemsen (1983; 1992); Hürzeler (1987); Grohé et al. (2013); Salesa et al. (2013); Valenciano et al. (2020); Kargopoulos et al. (2022). Stratigraphic ranges of the Asian taxa based on Vislobokova et al. (2001); Grohé et al. (2010, 2013, 2022); Wang et al. (2018); Valenciano et al. (2020, 2020); Kargopoulos et al. (2021). Stratigraphic ranges of the African taxa based on Werdelin & Sanders (2010); Kargopoulos et al. (2021); Grohé et al. (2022). Stratigraphic ranges of the North American taxa based on Prassack (2016); Tseng et al. (2017); Valenciano et al. (2020).

Dentognathic measurements were taken with digital calipers to the nearest 0.1 mm. Mandibular measurements follow Argant (2004) with minor modifications (see abbreviations below). Dental nomenclature and abbreviations are reported in Fig. 3.

We performed a centered Principal Components Analysis (PCA) on selected log-transformed continuous upper and lower dentition measurements in order to ascertain the morphometric similarities between various Lutrinae species, both extinct and extant. The extinct comparative sample includes the following taxa: *Enhydritherium terranovae* Berta & Morgan, 1985*, Lartetictis dubia* (de Blainville, 1841)*, Paludolutra campanii, Paralutra jaegeri, Siamogale melilutra* (Wang et al., 2018)*, Siamogale thailandica* Ginsburg et al., 1983*, Sivaonyx bathygnathus* (Lydekker, 1884)*, Sivaonyx gandakasensis* Pickford, 2007*, Teruelictis riparius* Salesa et al., 2013*, Vishnuonyx maemohensis* Grohé et al., 2020*, Vishnuonyx neptuni* Kargopoulos et al., 2021. The extant one includes: *Lutra lutra* Linnaeus, 1758*, Lontra canadensis* (Schreber, 1776)*, Lontra longicaudis* (Olfers, 1818)*, Lontra felina* (Molina, 1782)*, Lutrogale perspicillata* (Geoffroy Saint-Hilaire, 1826)*, Hydrictis maculicollis* (Lichtenstein, 1835)*, Enhydra lutris* (Linnaeus, 1758)*, Pteronura brasiliensis* (Zimmermann, 1780)*, Aonyx capensis* (Schinz 1821)*, Amblonyx cinereus* (Illiger, 1815)*, Aonyx congicus* (Lönnberg, 1910).

The following upper dentition variables were selected for the PCA: P2L, P2W, P3L, P3W, P4L, P4W, M1L, M1W. The following lower dentition variables were selected for the PCA: p2L, p2W, p3L, p3W, p4L, p4W, m1L, m1W.

A cladistic analysis was carried out, based on fossil and extant genera of lutrines from all over the World. We used the freeware software Mesquite version 3.81 (Maddison & Maddison 2023) to build and modify the character matrix. We used the analyses and matrix by Wang et al. (2018) as a basis and added eleven characters to their 37 craniodental characters, for a final matrix of 48 craniodental characters (plus molecular ones coded by Wang et al. 2018; Supplementary file 1) for 24 Operational Taxonomic Units (OTUs): sixteen fossil taxa (genera and species) and six extant otter species (i.e., *Pteronura brasiliensis, Lontra canadensis, Lontra felina, Enhydra lutris, Lutra lutra, Aonyx capensis*). *Martes americana* (Turton, 1806) and *Galictis cuja* (Molina, 1782) were used as outgroups for the analysis. The final supermatrix includes a total of 11,922 characters. Adding to the Wang et al. (2018) analysis we not wed scored five new Operational Taxonomic Units (OTU): *Paludolutra maremmana*, *Paludolutra campanii*, *Paludolutra lluecai*, *Limnonyx pontica*, *Limnonyx sinerizi*. The scoring of Wang et al. (2018) of *Tyrrhenolutra* and *Paludulotra* spp. has been revised according to our direct study of the material. Supporting our observations of the specimens of the added OTUs, we used descriptions from the relevant literature, e.g., Morales & Pickford (2005) for *P. lluecai*, and Crusafont Pairò (1950), Tobien (1955), Willemsen (1992) for *Limnonyx*. The character descriptions and the resulting data matrix are provided in Appendix B of the Supplementary Material. The analysis used TNT version 1.6 (Goloboff & Catalano 2016) to provide the tree using the traditional search setting (2000 random addition sequences and the TBR algorithm). Mesquite 3.81 was used to manage the tree resulting from the analysis and to export it in a graphic format.

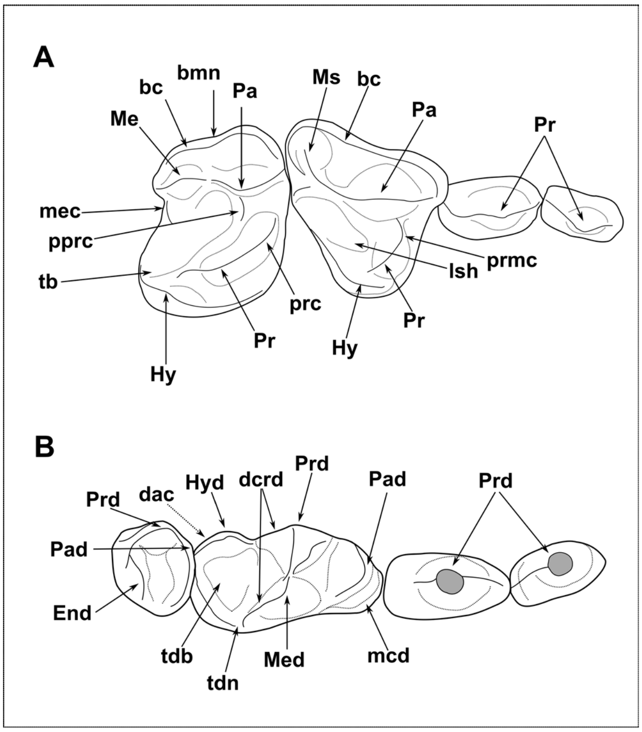

Fig. 3 - Schematic representation of the dental nomenclature used in this work (based on *Tyrrhenolutra*). Abbreviations, alphabetical order: bc, buccal cingulum; bmn, buccal medial notch; dac, distal accessory cuspule; dcrd, distal cristid; End, entoconid; Hy, hypocone; Hyd, hypoconid; lsh, lingual shelf; mec, metaconule; Med, metaconid; mcd, mesial cingulid; Ms, metastyle; Pa, paracone; Pad, paraconid; Pr: protocone; prc, protoconule; Prd, protoconid; pprc, preprotocrista; prmc, protocone medial crest; tb, talon basin; tdb, talonid basin; tdn, talonid notch.

Institutional abbreviations

AMNH, American Museum of Natural History (USA); **CMNH**, Cleveland Museum of Natural History (USA); **FMNH**, Field Museum of Natural History (USA); **IMNH**, Idaho Museum of Natural History (USA); **NMB**; Naturhistorisches Museum Basel (Switzerland); **MGPUF**; Museo di Geologia e Paleontologia dell'Università di Firenze (Italy); **MSNUP**; Museo di Storia Naturale dell'Università di Pisa (Italy); **MNB**; Museum für Naturkunde Berlin (Germany), **L-AHR**, Laboratory of Adam Hartstone-Rose (USA).

Fossil Collections abbreviations

Bac, Collections Baccinello (Tuscany, Italy) from the Naturhistorisches Museum Basel; **IGF**, Museo di Geologia e Paleontologia dell'Università di Firenze (former "Istituto di Geologia e Paleontologia di Firenze", Italy).

Nomenclatural abbreviations

***L.**, Lutra; **Lg.**, Lutrogale; **Lo.**, Lontra; **La.**, Lartetictis; **Li.**, Limnonyx; **E.**, Enhydra; **En.**, Enhydritherium; **P.**, Paludolutra; **Pt.**, Pteronura; **Pr.**, Paralutra; **A.**, Aonyx; **Am.**, Amblonyx.*

Measurement abbreviations

<u>Dentition</u> **L**, mesiodistal length; **W**, buccolingual width; **M1Lext**; metacone-paracone length of M1; **m1Ltrig**, length of the trigonid of m1; **m1Ltal**, length of the talonid of m1.

Description

Skull (Fig. 4)

The cranial material preserved in the NMB is all poorly preserved, mainly crushed and fragmented (Fig. 4F, L). The identification as belonging to *Tyrrhenolutra* was possible only thanks to the presence of some teeth in place. The few fragments still anatomically identifiable are a few pieces of the zygomatic arch and of the orbit in NMB.Bac.SCM-0902a (Fig. 4F). Unfortunately, their flattening and breakage hinder any further comments on them.

Upper teeth (Tab.1, Fig. 4)

The upper teeth from Baccinello V1 and Casteani are almost all well preserved except for a broken canine and two partial M1. Very few teeth show signs of wear and, if present, it is observable mostly on the incisal edges of the incisors and the first three premolars. Neither I1 nor I2 of *T. helbingi* were identified or are known from the literature but several I3 (Fig. 4A, M; NMB.Bac.51, NMB.Bac.SCM-0895, NMB.Bac.SCM-0903a, NMB.Bac.SCM-0900a) are reported from the Baccinello material. The I3 are all larger or even much larger (Fig. 4M; NMB.Bac.SCM-0903a) than the lower incisors. A single main cusp is flanked on the lingual side by a distinct cingulum that thickens toward the base to form a small lingual shelf. Two distinct crests can be observed connecting the tip of the crown with the cingulum. The first one is located on the distolabial surface of the tooth, while the second is shorter and runs on the lingual face orthogonally intersecting the cingulum. Although there is a general uniformity, some variability can be observed in the I3. NMB.Bac.SCM-0903a I3 (Fig. 4M) is noticeably more robust and stouter than the I3 of the holotype (Fig. 4A; NMB.Bac.51) and NMB.Bac.SCM-0895, where the tip of the crown is more slender and the lingual shelf is wider. The upper canines are sharp and weakly curved distally (Fig. 4H, I, L, M. They show a crimped and wrinkled enamel and a strongly denticulated cingulum decreasing on the buccal side. As observed for I3, C also shows a certain degree of variability. The canines of IGF11755 and NMB.Bac.SCM-0903e (Fig. 4H, M) are, in fact, much stouter and longer than the others. There is apparently no P1, although damage to NMB.Bac.51 prevents a definitive assessment; nor can we be sure if this is due to an evolutionary loss or to an individual variation. The P2 and P3 are very similar; they both have a single cusp (typical of many arctoid carnivorans) and prominent mesial and distal ridges connecting the cusp with a distinct cingulum that bounds the tooth. In both teeth, the cingulum is more distolingually marked. The P3, apart from being larger than the P2, is also proportionally buccolingually wider in its distal portion. The P4 is three-rooted and has a triangular occlusal outline. The paracone is by far the tallest cusp and in NMB.Bac.SCM-0903d (Fig. 4E) shows a certain degree of wear. A faint mesial crest arises near the apex of this cusp and connects with the strong protocone crest enclosing the lingual shelf. A high carnassial blade, not indented by a carnassial notch, distally connects the paracone with a lower but prominent metastyle. A tall crest-shaped hypocone lies distal to the protocone, connected with this cusp through a faint notch. A weak cingulum surrounds the labial and mesial sides of the tooth, fading distally. The M1 have low paracone and metacone compared to P4. The metacone is the tallest cusp and is much larger than the paracone. However, the paracone is surrounded by a much larger parastyle and buccal cingulum that often dwarf the paracone and can reach heights close to that of the metacone. The paraconule and protocone are both crest-like and oriented mesiobuccally-distolingually. The two crests are separated by a weak notch. A weak and straight preprotocrista runs from the base of the paracone to the notch between paraconule and protocone. A weak hypoconule is present on the distolingual bor-

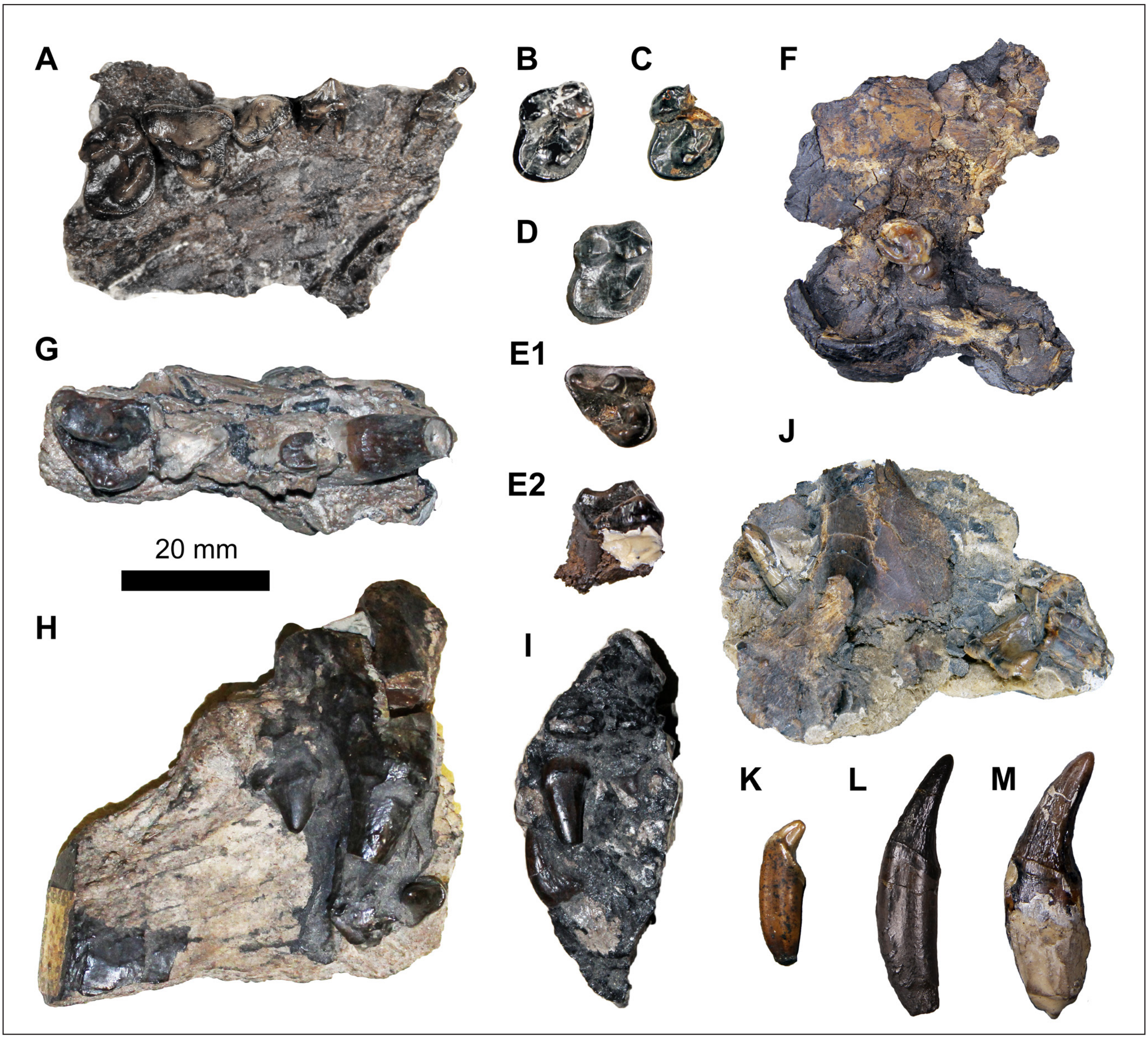

Fig. 4 - Cranial and upper teeth material of *Tyrrhenolutra maremmana* nov. comb. from Baccinello V1, Casteani and Montebamboli. A) NMB.Bac.51 (holotype), upper palate with right P2-M1 and I3. B) NMB.Bac.SCM-0903c, left M1 (mirrored). C) NMB.Bac.SCM-0903d, partial right M1. D) NMB.Bac.SCM-0938b, right M1. E) NMB.Bac.SCM-0903d, right P4 in occlusal (E1) and lingual (E2) view. F) NMB.Bac.SCM-0902a, skull fragments with right m2 and partial right M1. G) MSNUP N.2, maxilla fragment with C, P2, P4. H) IGF 11756b, left maxilla fragment with P2, P3. I) IGF 11756a, skull fragment with right C, c, p2 and left P2 and p2. J) NMB.Bac.SCM-0938a, skull fragments with C, P3, P4. K) NMB.Bac.SCM-0895a right I3. L) NMB.Bac.SCM-0902b, right C. M) NMB.Bac.SCM-0903e (mirrored).

der of the metacone. In all upper teeth the enamel of the cingulum and above it is distinctly wrinkled.

Mandible (Fig. 5)

The hemimandibles from Baccinello V1 and Casteani all show some sort of deformation or damage that hinders certainty in the description of the shape of the distal part of the jaw. The less deformed and more complete mandible of *T. helbingi* is NMB.Bac.54 (Fig.5A, B, C). The mandibular corpus is moderately high and rather short with a straight ventral margin, giving a rather robust appearance to the jaw. The masseteric fossa is wide and deep reaching m2 and indicative of a great development of the masseteric muscle. The vertical ramus is high with a slightly inclined rostral border caudally. The angular process and the condyle are poorly preserved in all specimens. Two mental foramina are present, the largest one is located below the p2, in a large fossa; caudal to this there is a

Species	Site	Ref.	C1L	C1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1Lext	M1W
Tyrrhenolutra helbingi	Casteani	IGF11756a	7,3		-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Casteani	IGF11755	10,7	8,6	-	-	9,3	6	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.51 (holotype)	-	-	6,4	3,7	8,6	5,7	12	12,7	9,9	9,4	13,6
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0938b	-	-	-	-	-	-	-	-	9	8,5	12,5
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0938a	-	-	-	-	-	-	10,7*	-	-	-	-
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0903c	-	-	-	-	-	-	-	-	9,7	8,7	11,7
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0903d	-	-	-	-	-	-	11	10,6	-	-	-
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0903b	8,1	6,2	-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0903e	10,1	8	-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello miniera	NMB.Bac.SCM-0903f	-	-	-	-	8	5,3	-	-	-	-	-
Paludolutra maremmana	Monte Bamboli	MNSUP N.2	10,8	8,7	-	-	-	-	14,3*	12,8	-	-	-
Paludolutra campanii	Monte Bamboli	NMB.Bac.1257	13,1	11,1	8,7	5,5	11	8,1	15,6	14,1	14,3	12,9	18,9

Tab. 1 - Upper teeth measurements of otters from the Tusco-Sardinian paleobioprovince.

much smaller foramen, located at the level of the mesial part of p3.

Lower teeth (Tab. 2, Fig. 5)

The lower dentition of *T. helbingi* is entirely known. The teeth are set close together and are oriented mesiobuccally from the canine to the p3. The incisors are very small, especially the i1. The i2 and i3 are slightly larger. The i1 and i2 have laterally flattened crowns, whereas i3 shows a more "spatula-like" shape. The lower canine is robust (more so than the upper canine), buccolingually compressed and distally curved. The surface of the crown of the canines is finely but markedly wrinkled. The p1 is absent. The premolars have a simple morphology with a single cuspid. The p2 is slightly smaller than p3 while p4 is much bigger than the other two. They show a stout cingulid surrounding the entire crown and sharp mesial and distal cristids. In all premolars, the cuspid is mesially placed and while p2 and p3 show an oval outline in occlusal view, p4 has a more triangular outline due to a distal buccolingual expansion of the crown. The m1 is mesiodistally elongated and robust. Specimen NMB.Bac.54 (Figs. 5A, B, C; 6K, L) shows marked dental wear on its carnassial that has obliterated most of the cuspids. The trigonid is about half the length of the tooth but is narrower than the talonid, giving the tooth a drop-like shape in occlusal view. The protoconid is slightly higher than the paraconid and metaconid. The metaconid is as large and high as the paraconid and is located slightly distal to the protoconid. Both cuspids have a distal cristid that extends well into the talonid. The talonid is wide and low; the hypoconid is lower than the other cuspids and rounded, with a small distal accessory cuspulid. The talonid basin is moderately deep and slightly transversally elongated. Like the upper and lower canines, the m1 of IGF 11756c (Figs. 5J, K, L; 6M, N) from Casteani is larger and more massive than the others, highlighting the intraspecific variability of the species. The m2 is round and relatively large, with two strong cuspids (protoconid and paraconid) and a large mesial shelf. As with the upper teeth, the enamel of the lower teeth is also wrinkled.

Milk dentition

In the NMB collections it is also present a juvenile mandible that preserves a dp4 together with the erupting m1. The dp4 appears as a miniature and more delicate version of m1. The trigonid cuspids appear proportionally more pronounced and sharper. Furthermore, the trigonid occupies most of the tooth surface while the talonid appears strongly reduced, giving the tooth a more "carnivore"-like appearance.

Comparison

Morphological comparison

The material of *T. helbingi* exhibits considerable differences compared to all extant taxa of Lutrinae. The first striking difference is without doubt the strong and diffuse wrinkling of the enamel. This character is completely absent in extant species, while is almost ubiquitous in Miocene forms. The upper premolars are tightly placed, unicuspid and with sharp mesial and distal cristids in all extant otters (except for the extremely specialized *E. lutris*) and in *T. helbingi*. The P2 of *T. helbingi* is, proportionally, buccolingually more compressed, and the P3 is much more robust. The P4 of *T. helbingi* differs from the extant taxa in its shelf-like morphology. In *T. helbingi* the protocone and hypocone crests are proportionally more developed, creating a tall mar-

Species	Locality	Ref.	c1L	c1W	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1Ltrig	m1Ltal	m1W	m2L	m2W
Tyrrhenolutra helbingi	Casteani	IGF 11756c	-	-	-	-	8,2	4,9	-	-	14,3*	10,4	5,3*	9,1	6,7	6,6
Tyrrhenolutra helbingi	Casteani	IGF 11755	-	-	-	-	7,9	5*	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.51 (holotype)	-	-	-	-	7,4	4,3	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.52	-	-	5,1	3,4	7,2	4,4	8,8	5,1	13,3	9,1	4,1	7,5	5,4	6,2
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.54	-	-	-	-	7,2	3,9	9,1	5,2	13	8,6	4,2	7,8		
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.53	-	-	-	-	-	-	9,2	4,6	13,1	8,9	4,3	6,8	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac55	7,9	6,2	5,5	3,9	7,1	4,3	9	5,2	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0894	8,40	6,50	-	-	-	-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0894	8,40	6,80	-	-	-	-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0895a	-	-	-	-	7,4	4,6	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0900b	-	-	-	-	-	-	-	-	-	-	-	-	5,3	6,1
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0900d	-	-	5,3	3,4	-	-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0903c	8,3	6,3	-	-	-	-	-	-	-	-	-	-	-	-
Tyrrhenolutra helbingi	Baccinello	NMB.Bac.SCM-0903f	8,8	5,9	-	-	-	-	-	-	-	-	-	-	-	-
Paludolutra maremmana	Montebamboli	MNSUP N.1	11,5	8,05	-	-	8,7	6,5	12,3	7,4	-	-	-	-	-	-

Tab. 2 - Lower teeth measurements of otters from the Tusco-Sardinian paleobioprovince.

gin that defines the lingual margin of the tooth. In addition, the two crests are separated by a clearly visible notch, a character absent in extant species. Among the extant species, only *Lutrogale* shows similarly developed lingual crests. Another clear difference possessed by *T. helbingi* is the slightly concave shape of the distolingual margin of P4, connecting the hypocone to the hypoconule. Compared to *T. helbingi,* existing taxa have a proportionally wider lingual shelf. The morphology of M1 appears more similar to that of *A. capensis* than to other extant taxa; they both have a mesiodistally enlarged molar with a tall and curved protocone-protoconule crest, absence of an incision on the lingual margin of the tooth, and a well-developed talon basin. Some differences can still be observed: the M1 of *T. helbingi* is proportionally more elongated buccolingually, and has a more developed metacone, and a more rounded distal margin of the talonid.

The mandible of *T. helbingi* appears more robust and with a straighter ventral margin than most of the extant otters (e.g., *Lutra, Lontra, Hydrictis* and *Lutrogale*). Its proportions are more similar to those of *A. capensis*, *Am. cinereus,* and *Pt. brasiliensis,* although not reaching the extreme morphology of *E. lutris.* The number of mandibular foramina appears variable in the subfamily Lutrinae: *L. lutra* is the only taxon to often have four; *Pt. brasiliensis*, *Lg. perspicillata* have three distinct foramina; lastly, *A. capensis, Am. cinereus, E. lutris,* and *H. maculicollis* have, similarly to *T. helbingi*, only two foramina. In *A. capensis* and *Am. cinereus,* the foramina are placed under p2 and p4, while in *T. helbingi* and *H. maculicollis* they are placed at the level of p3 and p4. The deformation of the vertical ramus in all *T. helbingi* specimens does not allow for a clear comparison. *T. helbingi* appears to have a rostrocaudally wider masseteric fossa than *L. lutra*, *Lg. perspicillata,* and *Pt. brasiliensis*, and a very rounded dorsal margin of the vertical ramus similar to the extant *A. capensis.*

The lower dentition of *T. helbingi* is characterised by proportionally high and robust premolars, completely different from the reduced premolars of *A. capensis* and *Am. cinereus*. Their height and robustness appear more similar to those of *Pt. brasiliensis* and *Lg. perspicillata* but, unlike the latter species, no distal accessory cuspulid can be observed on the p4. The m1 of *T. helbingi* is proportionally mesiodistally shorter and stouter than the m1 of *L. lutra*, *Lo. canadensis*, *Lg. perspicillata*, and *H. maculicollis*. These species are also characterised by taller and pointier paraconid and protoconid and a more defined carnassial notch. The m1 talonid basin of *T. helbingi* is buccally enclosed by a tall and sharp hypoconid; such a feature can be observed only in *Pt. brasiliensis* and *Lg. perspicillata*. However, in these two taxa, the talonid notch on the lingual margin is much deeper than in *T. helbingi. A. capensis* m1, when compared to *T. helbingi,* is slightly more mesiodistally elongated, the paraconid is proportionally smaller, and the metaconid distal cristid is fainter and shorter, defining a shallower talonid notch. *Am. cinereus* m1 is buccally bounded by a very prominent cingulid; this feature is absent in *T. helbingi*. The m2 of *T. helbingi* is proportionally larger and rounder than the m2 of most extant Lutrinae species; only *Pt. brasiliensis*, *Lg. perspicillata* and *Lo. canadensis* have an equally large m2.

Other than *T. helbingi*, between the late Middle and the Late Miocene of Europe, the subfamily Lutrinae is represented by the genera *Paludolutra, Sivaonyx*, *Limnonyx*, *Vishnuonyx*, *Lartetictis*, *Teruelictis* and *Paralutra* (Fig. 2). These genera show a wide range

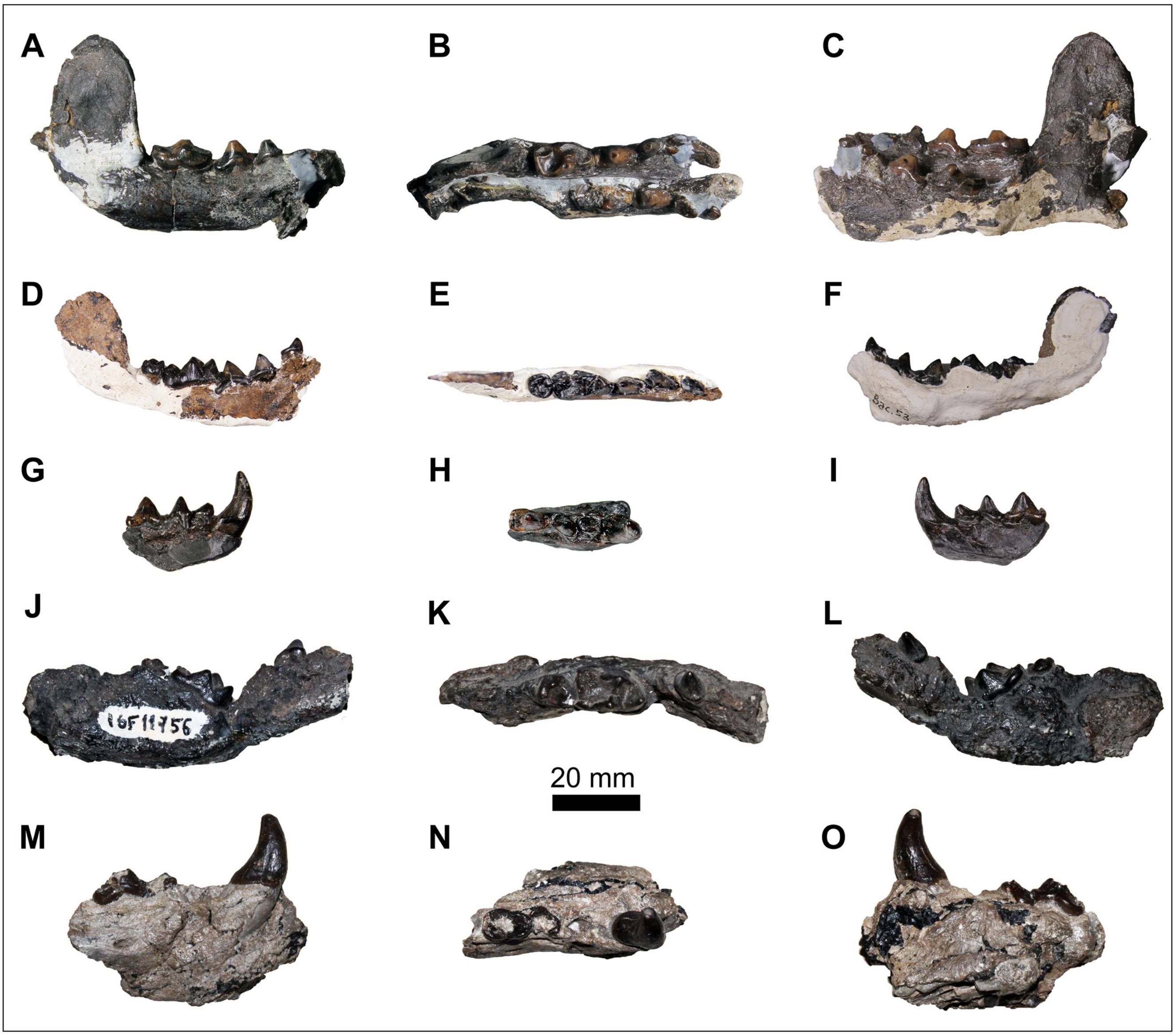

Fig. 5 - Mandibles of *Tyrrhenolutra maremmana* nov. com. from Baccinello V1, Casteani and Montebamboli. A-C) NMB.Bac.54, left and right hemimandible with right p2-m1 and left p2-m1, A: right buccal view; B: occlusal view; C: left buccal view. D-F) NMB.Bac.52, left hemimandible with p2-m2, D: buccal view (mirrored); E: occlusal view; F: lingual view (mirrored). G-H) NMB.Bac.55, right hemimandible fragment with c-p4, G: buccal view; H: occlusal view; I: lingual view. J-K) IGF 11756c, left mandible with p2, m1 and m2, J: buccal view (mirrored); K: occlusal view; L: lingual view (mirrored). M-O) MSNUP N.1, right mandible fragment with c, p3, p4, M: buccal view; N: occlusal view; O: lingual view.

of morphologies. The late Middle Miocene *Lartetictis* spp., *T. riparius* and *Pr. jaegeri* are characterised by more primitive morphologies. They all possess broad P4 with a hypocone and a significant distolingual expansion on the M1, but they differ from *Tyrrhenolutra* in, e.g., a reduced mesiodistal expansion of the P4 trigon shelf, a shorter, narrower M1 with more asymmetrical buccal cusps, and a more slender m1 with a narrower and more trenchant talonid. Interestingly, *Pr. jaegeri* and *T. helbingi* share the development of the P4 hypocone and protocone crests and the presence of a well-defined notch dividing them. *Paralutra garganensis* was recorded in the Late Miocene 'Terre Rosse' faunal complex, Gargano, Italy (Willemsen 1983; Villier et al. 2011). *Paralutra garganensis* appears much more robust than *Pr. jaegeri* and shows an even more robust morphology than *T. helbingi*. Compared to *T. helbingi*, *Pr. garganensis* P4 has a wider trigon shelf with a much more developed protoconule cusp, while M1 has a wider talon basin and is mesiobuccally surrounded by a very thick cingulum. *Vishnuonyx neptuni* is the only species of this genus found in Europe. The material attributed to this species exhibits considerable differences from *T. helbingi* in its entire dentition. Among the numerous differences are, e.g., a smaller P4 trigon shelf that does not reach the metastyle, a smaller, almost rectangular M1 without any expansion of the talon, p4 with a protoconid accessory cusp and a well-defined carnassial notch on m1. The genus *Sivaonyx* is represented in Europe by the species *Sivaonyx hessicus* (Lydekker, 1890), but its upper carnassial is unknown. However, other members of the genus show a much more developed lingual shelf with a very prominent cingulum surrounding the tooth. The M1, on the other hand, is mesiodistally compressed, lacking any talon expansion, and with very asymmetric labial cusps. The m1 of *Sivaonyx* spp. is much more robust than that of *T. helbingi*, with lower cusps and a wider talonid. The genus *Limnonyx* is known only from its lower dentition and a few specimens. Despite this, two Lower Vallesian (11.6–9.0 Ma) species of *Limnonyx* are present in the literature: *Limnonyx sinerizi* Crusafont-Pairó, 1950 and *Limnonyx pontica* (Nordmann, 1858), respectively, from Spain and Germany. Compared to *T. helbingi*, *Li. sinerizi* is characterised by a much more robust mandible with a curved ventral margin, while *Li. pontica* has a horizontal ventral border and a similar thickness to the Baccinello specimen. The p4 and m1 of *Limnonyx* spp. and *T. helbingi* show strong morphological resemblances. In all three taxa the p4 has a triangular outline in occlusal view while the m1, in particular in *Li. pontica,* is characterised by a broad talonid with a large hypoconid, paraconid and protoconid of similar height, and a long cristid distally extending from the metaconid into the talonid. The other otter genus found in the Tusco-Sardinian palaeobioprovince is *Paludolutra*. This genus is currently represented by three species (*P. maremmana*, *P. campanii* and *P. lluecai*). While *P. lluecai* and *P. campanii* share several characteristics and appear clearly distinct from *T. helbingi*, *P. maremmana* appears, surprisingly, very similar to *T. helbingi* (Fig. 6). *P. maremmana* P4 (Fig. 6C, D) resembles *T. helbingi* (Fig. 6A, B) in having a triangular inner shelf with a slightly concave distal margin, high and crest-like hypocone that delimits the lingual margin of the tooth and a weak cingulum that surrounds the labial and mesial sides of the tooth, fading distally. The protocone of *P. maremmana* (Fig.6C) is only partially preserved but it appears similarly crested and divided from the hypocone by a notch. Furthermore, *T. helbingi* and *P. maremmana* have robust but laterally compressed upper and lower canines. The P4 of *P. campanii* (Fig. 6E-H) and *P. lluecai*, have a much robust and bunodont appearance. They are characterised by a shorter and lower carnassial blade, a wider and rounder inner shelf in which a prominent and rounded protocone stands out. Furthermore, both *P. campanii* and *P. lluecai* P4 are surrounded by a thick and prominent cingulum that on the distal margin of the tooth joins a prominent hypoconule. Notably, the mesial position of the P4 protocone in *Paludolutra* is also seen in *Pr. garganensis*. The M1 of *P. campanii* (Fig. 6E-H), similarly to the P4, is much more robust and with a wider talon basin than *T. helbingi*; furthermore, in *P. campanii* M1 the paracone and metacone have similar size and the tooth is surrounded by a thick cingulum. *P. lluecai* and *P. campanii* actually show more similarities with the *Enhydritherium* from the early Pliocene of North America (Berta & Morgan 1985; Lambert 1997) than with *T. helbingi* and *P. maremmana*, as *Enhydritherium* also possesses a discrete protocone and hypocone on the P4, a well-developed labial cingulum on the P4 and a M1 with similar sized paracone and metacone. In Asia, bunodont otters are also represented by the genus *Siamogale* Ginsburg, Ingavat & Tassy, 1983. The three currently defined species, *Siamogale thailandica* Ginsburg, Ingavat & Tassy, 1983, *Siamogale bounosa* Grohé et al., 2020 and *Siamogale melilutra* Wang et al., 2018 appear clearly different from *T. helbingi* in having a much more developed M1 talon and lingual cingulum, and a lingual M1 cuspule that is absent in *Tyrrhenolutra*. The P4 morphology also differs from the crest-like protocone in *Siamogale*. In *Tyrrhenolutra* the protocone and hypocone are closer to each other and positioned lingual to the paracone.

Morphometric comparison

The results of a Principal Component Analysis (PCA) of the upper dentition are reported in Fig. 7A and the Supplementary online material (Supplementary file 1: Table S1). PC1 accounts for 69.47% of the variance, whereas the PC2 accounts for 13.69% and the PC3 accounts for 8.34%. PC1 has similar and negative loadings for all original variables analysed, thus being mainly influenced by size; the width of M1 and the dimensions of P3 and of the upper carnassial are the measurements with the highest negative values. All the extant and fossil small-sized taxa (e.g. *Lutra*, *Lontra* ssp., *Aonyx* ssp.,

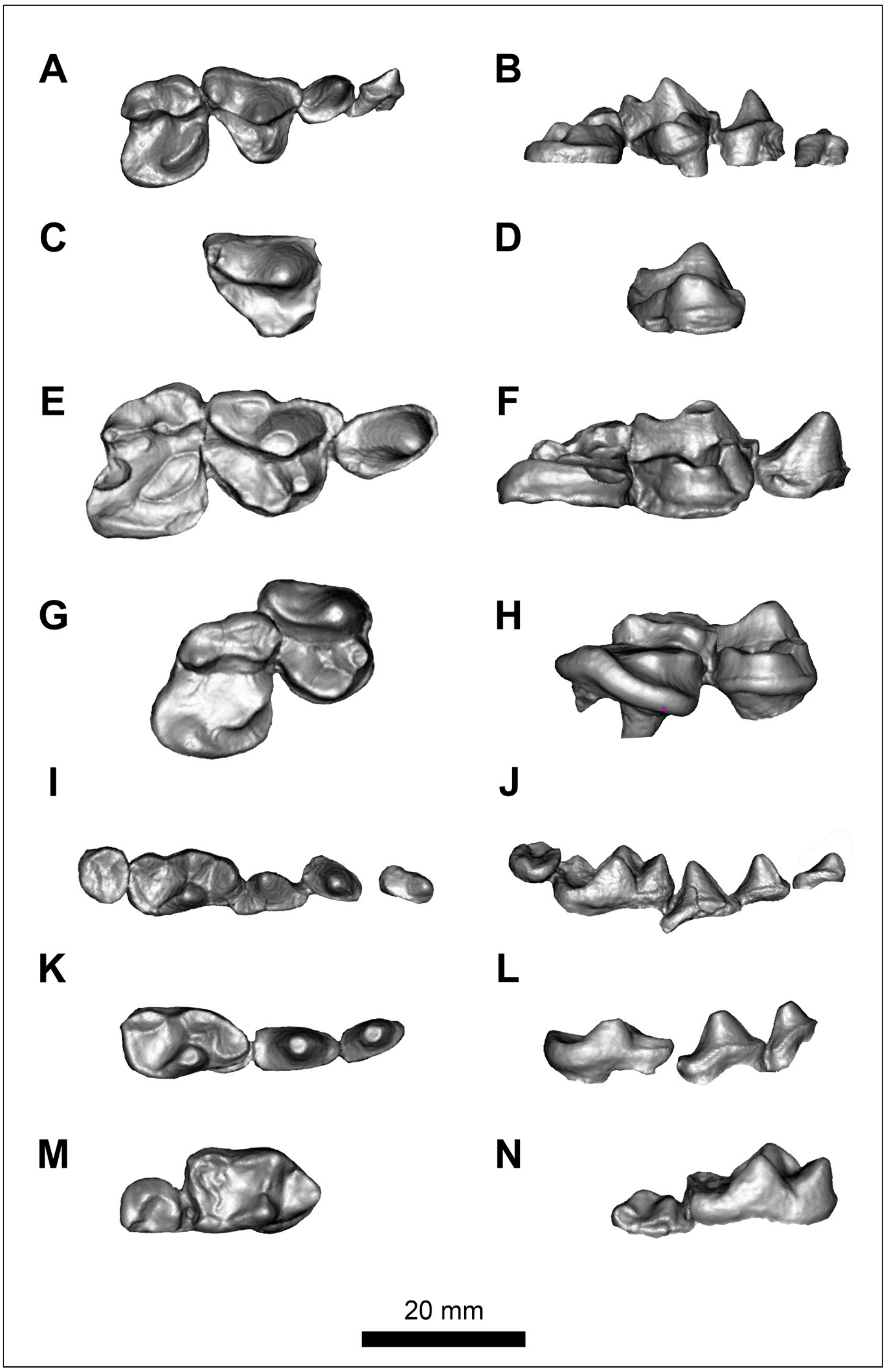

Fig. 6 - Comparison of upper and lower dentition of the otters of the Tusco-Sardinian paleobioprovince. Screenshots of their 3D model. A-B) *Tyrrhenolutra "helbingi"* NMB.Bac.51, A: occlusal view; B: lingual view. C-D) *"Paludolutra" maremmana* MSNUP N.2, C: occlusal view; D: lingual view. E-F) *Paludolutra campanii* NMB.Bac.1257, E: occlusal view; F: lingual view. G-H) *Paludolutra campanii* NMB.Bac.1258, G: occlusal view; H: lingual view. I-J) *Tyrrhenolutra "helbingi"* NMB.Bac.52, I: occlusal view; J: lingual view. K-L) *Tyrrhenolutra "helbingi"* NMB.Bac.54 mandible, K: occlusal view; L: lingual view. M-N) *Tyrrhenolutra "helbingi"* IGF 11756c, M: occlusal view; N: lingual view.

Paralutra, *Siamogale thailandica*) overlap to a large extent for PC1 and lie on the positive end of the axis. The extant and fossil large-sized taxa are gradually distributed on the negative end of the axis from *Enhydra* to *Pteronura* to *Siamogale* and *Paludolutra*. These last two taxa show, overall, very similar proportions. *Tyrrhenolutra* is placed in an intermediate position between large and small taxa, close to *A. capensis* and *Lg. perspicillata*. PC2 is positively dominated by the length of P2 and negatively influenced by the dimensions of M1. Most taxa overlap to a large extant on this axis; the few exceptions are *Pr. jaegeri* on the positive end for its proportionally longer P2, and *E. lutris* on the negative end for its highly specialised M1. PC3 is positively dominated by the length of the labial margin of M1, while it is negatively influenced by the widths of P3 and P4. PC3 separates *Siamogale*, *Paludolutra,* and several *A. capensis* (on the positive end) for its enlarged M1, and *E. lutris*, *Lo. felina*, *Lo. longicaudis*, *Pr. jaegeri* (on the negative end) for the compressed labial margin of M1 and the width of the premolars. Overall, taking into account all three PCAs, *T. helbingi* is placed in a somewhat isolated position closer to the proportions of extant medium-small fish-eating otters, in particular *Lg. perspicillata*. *Paludolutra campanii*, on the contrary, shows proportions of the upper dentition different from any current species, showing a clear resemblance to *S. melilutra*.

The results of the PCA on the lower dentition are reported in Fig. 7B and the Supplementary Online Material (Supplementary file 1: Table S2). PC1, accounts for 74.59% of the variance, while PC2 accounts for 16.36% and PC3 for only 3.49%. As in the case of the lower dentition, PC1 has negative and similar loadings for all analysed original variables, and thus is mainly influenced by size. The length of p4 and the width of p3 are the measurements with the highest values. Similarly to the upper dentition, PC1 segregates smaller-sized extant and fossil taxa, which overlap to a large extent, from large-sized taxa such as *Pteronura*, *Enhydra*, *Siamogale,* and *Enhydritherium*. *Tyrrhenolutra*, in this case, falls within the large group of medium-to-small sized otters. PC2 is positively dominated by the length of p2, and negatively influenced by the width of m1 and p4. Most of the taxa overlap to a large extent on this axis; the few exceptions are *E. lutris* and *Am. cinereus* on the negative end of the axis, due to their large lower carnassial. Overall, *T. helbingi* once again shows dental proportions very similar to those of *Lg. perspicillata*.

DISCUSSION

Tyrrhenolutra: intraspecific variability and taxonomic validity

The fragmentary nature of extinct bunodont otter-like mammals (Fig. 2) is what has caused confusion and heated debates on the taxonomy and attribution of the scanty material of these animals. The endemic otters of the Miocene lignite mines of Tuscany (Fig. 1) are no exception, as they have always intrigued paleontologists and naturalists since the XIX century (Meneghini 1862; Lydekker 1884; Schlosser 1887; Weithofer 1888, 1889; Ristori 1890; Stehlin 1909; Matthew 1929; Pilgrim 1931, 1932; Helbing 1936; Hürzeler & Engesser 1976; Willemsen 1992, 1999; Morales & Pickford 2005; Pickford 2007; Wang et al. 2018). Their limited geographic distribution and peculiar morphology have always been an obstacle to understanding their relationship with other fossil otters. The discovery of new fossil material provides an opportunity to reassess this group of aquatic mammals. The new otter material from the Baccinello mine (V1) is here referred to *Tyrrhenolutra*. The taxonomic attribution of the new remains to this genus is unequivocally supported by its strong morphologic and morphometric affinities with the other material of *T. helbingi* described in the past (Hürzeler 1987). Otter remains from the Casteani mine were listed but not described or figured by Weithofer (1888) and Hürzeler (1987). This material is figured for the first time in this work (Figs. 4, 5), their morphology undoubtedly resembles the material from Baccinello and their attribution to *Tyrrhenolutra* is therefore confirmed. Hürzeler (1987) erected the genus *Tyrrhenolutra* for the lutrine material from Baccinello level V1 (MN 11, 8.3 – 7.7 Ma) and included it within the *Aonyx*-group, but also proposing a direct relation with *Paludolutra*. Willemsen (1992) included this genus in the tribe Enhydrini, but while he confidently recognised a clear affinity between *P. lluecai* and *Paludolutra* from Tuscany, he did not resolve the systematic position of *Tyrrhenolutra*. Lastly, Pickford (2007) included *Tyrrhenolutra* in the tribe Aonychini based on the dimensions of the m1, suggesting a diet based on shellfish. The PCA of the upper and lower dentition show, however, dental proportions more akin to *Lg. perspicillata*, which is a mouth-oriented feeder and feeds primarily on fish with minor supplements of a variety of prey including snakes, rats and birds (Khan et al. 2010; Hussain 2013; Abdul-Patah et al. 2014; Timm-Davis et al. 2015).

Indeed, *Tyrrhenolutra* has a very peculiar dental morphology. It combines several bunodont traits (a large m1 with a basined and buccolingually expanded talonid; a tall horizontal ramus of the mandible with a straight ventral margin) with an inner shelf of the P4 that is not particularly wide and a not very robust and distally expanded M1 (Fig. 5A, B).

In general, the dental remains of *T. helbingi* highlight a high degree of morphometric variability; several dental remains (Fig.4; IGF 11755; IGF 11756; NMB.Bac.SCM-0903e), while maintaining a similar morphology, are clearly larger and more robust than the rest.

In modern otters intraspecific variability is strictly connected to sexual dimorphism and geo-

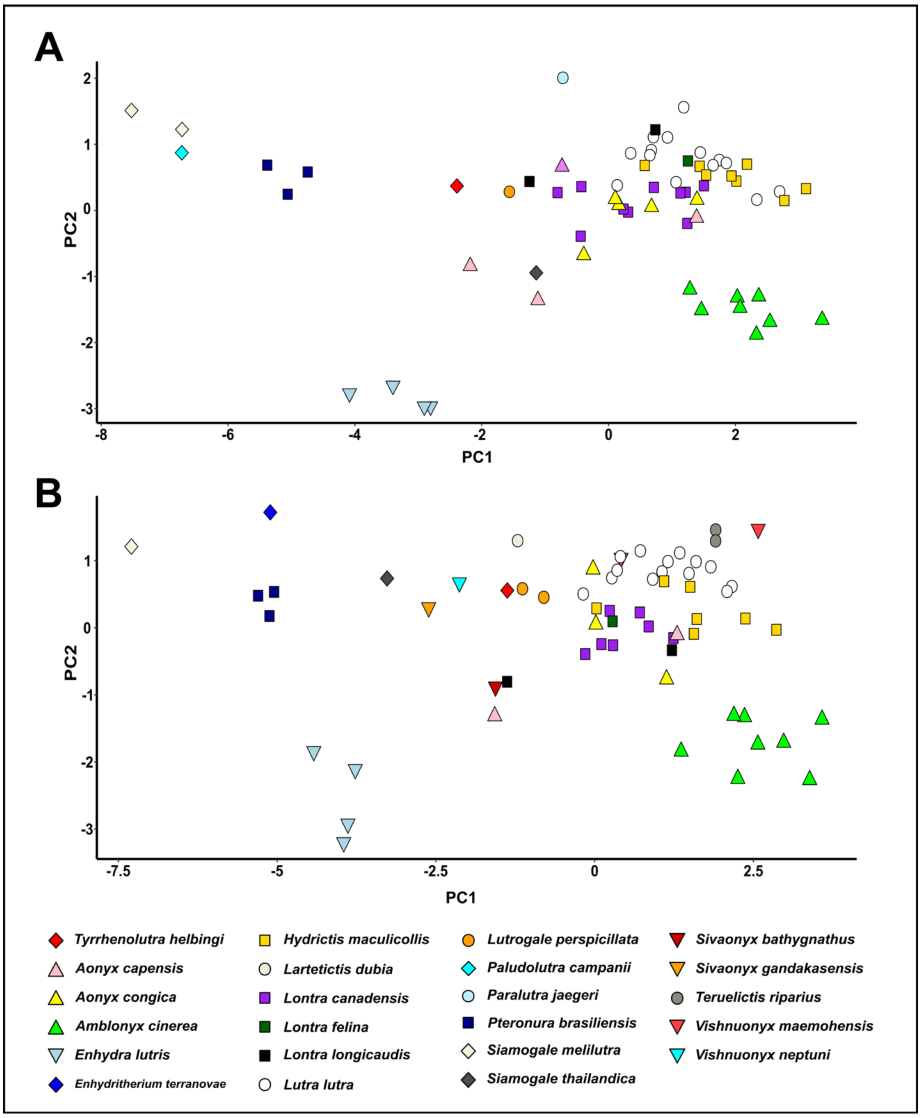

Fig. 7 - Principal Components Analysis (PCA) based on selected dentognathic variables of actual and fossil otters. A) Principal Component (PC) 1 versus PC2 of upper teeth. B) Principal Component (PC) 1 versus PC2 of lower teeth.

graphical distribution of the populations (e.g., Lynch & O'Sullivan 1993; Kruuk 2006; Baryshnikov & Puzachenko 2012; Hernández-Romero et al. 2015, 2018; Pontieri et al. 2023). Although sexual size dimorphism is found in all 13 otter species (Kruuk 2006), only a few studies have investigated patterns of sexual dimorphism in the skulls of otters. *Lutra lutra, Lo. longicaudis, E. lutris* are the taxa to have been examined more in detail, and morphometric analyses indicate that all three species exhibit cranial size dimorphism in which males are larger (Lynch & O'Sullivan 1993; Kruuk 2006; Baryshnikov & Puzachenko 2012; Hernández-Romero et al. 2015; Law et al. 2016; Hernández-Romero et al. 2018). Sexual size dimorphism in otters is often attributed to sexual selection in which males with larger body sizes and cranial morphologies are presumably able to gain bigger and better-quality territories for increased reproductive success (Moors 1980; Kruuk 2006). Nevertheless, according to the niche divergence hypothesis, male otters have been seen to eat larger prey items, often as a response to a resource-poor environment (Kruuk & Moorhouse 1990; Elliott Smith et al. 2015). Since the remains of *T. helbingi* are only found in a few localities that are geographically very close to each other, we can link the strong intraspecific variability observed in Baccinello and Casteani material to sexual dimorphism. The large-sized C (Fig. 4O; NMB.BacSCM-0903e), maxilla (Fig. 4H; IGF 11755) and mandible (Fig. 5J-L; IGF 11756) from Baccinello and Casteani may therefore be attributed to large male individuals.

Comparison of dentognathic characters with fossil bunodont otters has revealed significant similarities between P4 of *T. helbingi* and *P. maremmana* (Fig. 6) such as: a triangular inner shelf with a slightly concave distal margin; high and crest-like protocone and hypocone divided by a notch that delimits the lingual margin of the tooth; a weak cingulum that surrounds the labial and mesial sides of the tooth, fading distally. Hürzeler & Engesser (1976) erected the genus *Paludolutra* for the species *Enhydriodon campanii* from the Late Miocene locality of Montebamboli. Hürzeler (1987) added the species *P. maremmana* to the genus. Willemsen (1999), however, reduced the rank of *Paludolutra,* making it a subgenus of *Enhydriodon,* but the differences in dental morphology are sufficient to indicate full generic differentiation (Pickford 2007). Morales & Pickford (2005) proposed a synonymy between *Paludolutra* and *Sivaonyx*, but also in this case morphological differences are more than sufficient to suggest a clear separation between the two genera (Pickford 2007). Some authors reported a marked resemblance between *P. maremmana* and *P. lluecai* (Willemsen 1992; Morales & Pickford 2005), yet such a similarity cannot be confirmed here. Instead, *P. lluecai* appears clearly more similar to *P. campanii* as they both show a much more advanced bunodont morphology. Both *P. campanii* and *P. lluecai* have a shorter and lower carnassial blade and a wider and rounder inner shelf in which a prominent and rounded protocone stands out and is surrounded by a thick and prominent cingulum that on the distal margin of the tooth joins a prominent hypoconule.

Regarding the genus *Paralutra,* while *Pr. jaegeri* is characterised by a more primitive morphology (relatively restricted lingual shelf of P4, significant width difference between the paracone and the metacone in M1), *Pr. garganensis* shows much more advanced characteristics toward clear bunodont adaptations (strong cingulum around M1; distally projecting talon). *Paralutra garganensis* has a more robust morphology than *T. helbingi* with a wider trigon shelf and a much more developed cingulum. The otter from Gargano appears morphologically more similar to *Paludolutra*, representing a possible ancestor and, as some authors have pointed out, it *w*ould require a taxonomic revision and the assignment of the species to a new genus (Wang et al. 2018).

Another interesting genus, often overlooked, is *Limnonyx*. The origin of this genus is unclear. It appears in Europe in MN 9 with two taxa: *Li. pontica* in Eppelsheim (Tobien 1955) and Kishinev (Willemsen 1992) and *Li. sinerizi* in Spain (Crusafont-Pairó 1950). There are no putative European ancestors. Only a few mandibular fragments with a lower dentition are known, but the genus has always been included in the Aonychini, mainly due to a lower carnassial characterised by a broad talonid with a large hypoconid. The comparison of *Limnonyx* with *Tyrrhenolutra* highlighted several similarities between the two genera: a p4 with a triangular outline in occlusal view; an m1 with enlarged hypoconid; paraconid and protoconid of similar height, a long cristid distally extending from the metaconid into the talonid, and a moderately developed lingual cingulum. Although the remains of *Limnonyx* are few, the morphological similarity and the geographical and temporal proximity suggest that this genus could be the continental ancestor of *Tyrrhenolutra*.

Otters are a common occurrence in endemic insular faunas. This is due to their obvious swimming abilities. Extinct island otters have been reported from several Pleistocene islands (Van Der Geer et al. 2010). Despite their success in colonising islands, little is known about extinct island otters. This is because fossils of otters are rarely found and are often represented only by a few specimens. Furthermore, without knowing who their continental ancestor was, it is difficult to determine what effects the insular conditions had on the animal. This is the case for the two genera of otters present in the Tusco-Sardinian paleobioprovince. *Paludolutra campanii* was a larger otter, with a more complex tooth morphology, than the continental congeneric species *P. lluecai*. These differences could be a consequence of development in an isolated environment, or this may be a phylogenetic factor. *Tyrrhenolutra* is an even more enigmatic genus. A possible phylogenetic relationship with *Limnonyx* has been previously hypothesised (Pickford 2007) and is confirmed in this work, but the fossil remains of the genus are too scarce for further discussion of evolution in an insular environment of *Tyrrhenolutra*.

Cladistic analysis and phylogenetic implications

Currently, the family Mustelidae, which includes the otter subfamily (Lutrinae) is subdivided into eight subfamilies (Kim & Jo 2021). In turn, the subfamily Lutrinae includes 13 extant species of otters (De Ferran et al. 2022). The systematics and taxonomy of otters has been an enigmatic issue in the family Mustelidae, providing various inconsistent classification frameworks at broad levels of taxonomic rank (family, subfamily, tribe, genus, species, or subspecies; Wang et al. 2018; De Ferran et al. 2022). DNA sequences can be used to resolve the problems encountered in systematic and taxonomic studies of closely related lineages where which morphological differences are slight; however, the limited numbers of genetic markers or short marker lengths can sometimes still hinder the full resolution of the evolutionary relationships within the family.

As observed by several authors (Finarelli & Flynn 2006; Schnitzler et al. 2017), excluding fossil taxa from phylogenetic analyses may rule out useful information. Including both modern biological data and fossil information may be necessary to fully understand patterns and dynamics of organismal evolution. Wang et al. (2018) presented the first combined morphological and molecular (nuclear and mitochondrial DNAs) character matrices of fossil and living otters and despite the fragmentary nature of fossil record they obtained satisfactory results.

Starting from the matrix created by Wang et al. (2018), we expanded it with new characters and new fossil species to better investigate the relationships between Late Miocene Tuscan species. In the parsimony analysis, we found 1 tree of 1690 steps, consistency index (CI) = 0.77 and retention index (RI) = 0.52. The resulting tree is shown in Figure 8. The monophyly of Lutrinae is well supported in the strict consensus tree of the parsimony analysis with a bootstrap value of 90%. The first difference observed compared to the Wang et al. (2018) majority consensus tree is that *Pr. jaegeri* is the most basal otter (Clade 1, Fig. 8) as it lacks some of the otter synapomorphies (Wang et al. 2018), such as a distally expanded P4 lingual shelf (character 24, state 1, reversed state also in *Vishnuonyx*) and a P4 distolingual cingulum (character 46, state 1 or 2). *Paralutra jaegeri* is closely related to *Pt. brasiliensis* (Clade 2, Fig. 8) as it is the most basal extant otter which is itself closely related to the clade comprising *Lontra* species. Finally, *Enhydra* is the most morphologically derived extant otter. The *Lontra* clade is the sister clade of all the other extant and fossil species. In this large clade, the *Lutra-Aonyx* clade is the most primitive. The strict consensus tree shows relationships between extant species largely consistent with those obtained by Koepfli et al. (2008a), who used the same set of gene sequences, and de Ferran et al. (2022). The only difference observed is the more basal position of *Enhydra* in both Koepfli et al. (2008a) and de Ferran et al. (2022). As observed in the morphological comparison, *T. helbingi* is closely related to *P. maremmana* with which it shares, among other things, a high P4 hypocone (character 26; state 2), a weak P4 distolingual cingulum (character 46; state 1), a straight distal cingulid of p4 (character 40; state 2), and the presence of crenulation on the canines (character 43; state 1, convergent with *P. campanii*). Additionally, the European *Limnonyx sinerizi* and *Limnonyx pontica* are basal to these Italian otters as they share a distal metaconid ridge on m1 (character 34; state 1; convergent with *P. campanii*, *P. lluecai, En. terranovae, Siamogale* spp.), the absence of the metastylid on m1 (character 35; state 0), and a straight distal cingulid of p4 (character 40; state 2). The two other known species of *Paludolutra* are not related to the *T. helbingi* and *P. maremmana* clade (Clade 14, Fig. 8), but appear more closely related to the North American taxon *Enhydritherium* (Clade 10, Fig. 8) with which they share a low-crowned P4 hypocone (character 26, state 1, convergent with *Enhydra*), a strong P4 distolingual cingulum (character 46; state 2), and a cuspule lingual to the metacone on M1 (character 31, state 2). Additionally, in the strict consensus tree of the parsimony analysis the clade 14 of Figure 8 is more closely related to clade 7 of Figure 8 (including *Vishnuonyx* – *Sivaonyx* – *Enhydriodon* – *Enhydra*) than to *Tyrrhenolutra* – *Paludolutra maremmana* (Clade 14, Fig. 8). Clade 7 of Figure 8 shares the absence of crenulation on M1 (character 30, state 0), the presence of an M1 cuspule lingual to the metacone (character 31, state 2, convergent with *Enhydritherium, Paludolutra lluecai, Paludolutra campanii*), and a distinct p4 distal accessory cusp (character 32, state 1, convergent with *Lontra* and *Enhydra*). In this clade *Enhydra* represents the earliest branch as it differs from the other taxa in a reduced number of mental foramina (character 44, state 0), and a mesiodistally compressed m2 (character 42, state 1). In the Wang et al. (2018) majority consensus tree, *Enhydriodon* was basal to *Vishnuonyx* and *Sivaonyx*. As the authors noted this was unexpected given the degree of bunodonty and the stratigraphical occurrence of those genera in the Siwaliks of the Indian subcontinent. In our tree (Fig. 8), *Sivaonyx* is closely related to *Enhydriodon* (Clade 9, Fig. 8) with *Vishnuonyx* being ancestral to the two genera. This result appears more plausible considering the stratigraphical occurrences of these genera and is in line with the

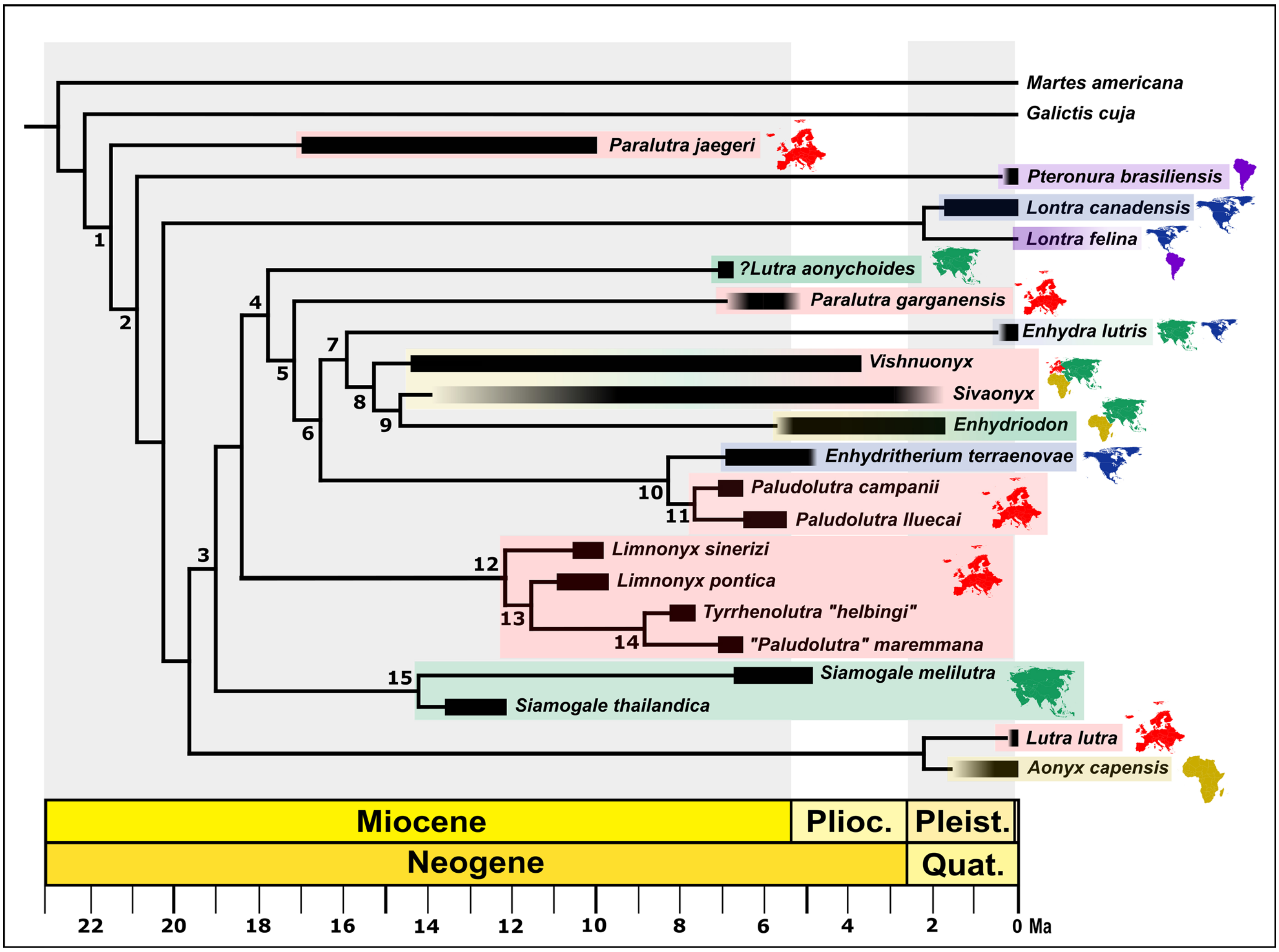

Fig. 8 - Results of the phylogenetic analyses of fossil and extant otters. Strict consensus tree produced with a cladistic analysis in TNT. Thick black bars indicate the stratigraphical distribution of fossil taxa. Colored boxes indicate the geographical distribution of the taxa.

interpretations given by several authors (Willemsen 1992; Pickford 2007; Peigné et al. 2008; Geraads et al. 2011; Valenciano & Govender 2020; Grohé et al. 2022). As observed by Wang et al. (2018), *Paralutra* does not constitute a monophyletic group; while *Paralutra jaegeri* is basal to all lutrines, "*Paralutra*" *garganensis* is strictly related to the bunodont otter lineage comprising the 10 and 11 clades. Finally, the enigmatic *Lutra aonychoides* is basal to *Paralutra garganensis* and the previously mentioned clades. A variety of methods have been developed to quantify the processes that have shaped the evolutionary history of a clade, to assess rate variation among lineages, and, more recently, to investigate rate variation through time (Rabosky 2006; Rabosky & Lovette 2008; Alfaro et al. 2009; Etienne et al. 2011, 2023; Stadler 2011; Etienne & Haegeman 2012; Rabosky et al. 2014; Laudanno et al. 2020, 2021). The incredible ecological and phenotypic diversity in Mustelidae is often attributed to adaptive radiation (Koepfli et al. 2008a, 2008b; Sato et al. 2009, 2012). The rapid diversification of mustelids took place approximately 14-9.5 Ma, immediately following the Mid-Miocene Climate Transition. This period marked the emergence of six out of the eight existing subfamilies within the Mustelidae (Koepfli et al. 2008a, 2008b). The subfamily Lutrinae formed during this evolutionary burst. Various authors propose different divergence times but always between 13 Ma and 7.5 Ma: 10.2-7.5 Ma for Koepfli et al. 2008a; 13.09-10.12 Ma for Law et al. 2018; 11.38-9.77 Ma for De Ferran et al. 2022. Despite a slight uncertainty in dating, it seems clear that the divergence times appear much more recent than those seen in the fossil record. *Pr. jaegeri*, for example, is reported since the Early Miocene (Pellecahus, France; MN 4; Roman & Viret 1934) and assuming the divergence times proposed by the molecular phylogenies, this taxon cannot be considered a "true" otter. Similar considerations can be made for the genera *Lartetictis*

Fig. 9 - Restoration of *Tyrrhenolutra maremmana* based on the cranial material from the Late Miocene of Tuscany. Artwork by Sara Scheggi.

and *Mionictis* Matthew, 1924. These two genera are currently included in the lutrines (Ginsburg 1999; Salesa et al. 2013; Valenciano et al. 2020) but in the past were often described as Melinae, related to the Eurasian badgers (Ginsburg & Morales 1996). Following the molecular data these genera could be considered, as already proposed by Heizmann and Morlo (1998), semiaquatic 'mustelines' with a dentition convergent with that of lutrines. Furthermore, the divergence time for *Pt. brasiliensis* (the most basal extant otter) is reported to be between 10.5-7.6 Ma (Koepfli et al. 2008a; Law et al. 2018; De Ferran et al. 2022); as a result, the systematic position of some older genera, such as *Siamogale*, *Vishnuonyx* and *Sivaonyx*, are at least doubtful since they should have diversified before the Brazilian giant otter.

Conclusions

The discovery of new material attributable to *Tyrrhenolutra* has improved the description of the hypodigm for the first time since its discovery (Hürzeler 1987). New material from Baccinello and Casteani, the latter of which was depicted for the first time, provided insight into the intraspecific variability of the species. *Tyrrhenolutra* material shows a great degree of variability with several remains being considerably larger and more robust that the others. In extant species male individuals are characterised by larger size and more robust dentition, both as a function of sexual selection but also to feed on larger prey and occupy different ecological niches (e.g., Lynch & O'Sullivan 1993; Kruuk 2006; Baryshnikov & Puzachenko 2012; Hernández-Romero et al. 2015, 2018; Pontieri et al. 2023). It is logical to assume that similar dynamics could have regulated the intraspecific variability of a taxon such as *Tyrrhenolutra* that lived in a resource-poor environment, such as an island ecosystem can be (Kruuk & Moorhouse 1990; Elliott Smith et al. 2015). The similarities observed between *T. helbingi* and *P. maremmana* and the differences from other species of the genus *Paludolutra* allow us to confidently attribute *P. maremmana* to the genus *Tyrrhenolutra*. If this was the case, the monospecificity of the genus would lapse (*T. helbingi* and *Tyrrhenolutra maremmana*). However, considering the great size variability within *T. helbingi* observed in the dentognathic material from Baccinello and Casteani, the slightly different morphology and larger dimensions of *P. maremmana* could still be regarded as intraspecific variability of a single species. Such a difference could be related to sexual dimorphism and/or the slightly different ages of the referred samples. This considered, we propose to synonymize the two taxa described by Hürzeler (1987) into a single species of otter that roamed the Tusco-Sardinian paleobioprovince in both BCB V1 and V2. Considering the numerous distinctive features of *Tyrrhenolutra* in comparison to the species *P. campanii* and *P. lluecai* but the similarity of "*P.*" *maremmana*, it seems plausible to ascribe the latter species to the genus *Tyrrhenolutra*.

Nevertheless, following the International Commission on Zoological Nomenclature (1999, Art. 23 and 24) the specific name "*P. maremmana*" has taxonomic priority relative to "*T. helbingi*" (respectively Hürzeler 1987 p. 38 and 1987 p. 40), and thus we suggest referring the material previously attributed to *Tyrrhenolutra "helbingi"* and *"Paludolutra" maremmana* to *Tyrrhenolutra maremmana* comb. nov. In addition, to reinforce the hypothesis of the close affinity between *T. helbingi* and *P. maremmana*, the phylogeny, morphological similarity, and geographical and temporal proximity has shown how the most probable continental ancestors of *T. maremmana* belonged to the genus *Limnonyx* and were not closely related to the genus *Paludolutra* as was thought in the past (Hürzeler 1987; Willemsen 1992; Pickford 2007). Following this scenario, the endemic Tuscan lutrine record is characterised by two separate immigration events. In the first phase the genus *Limnonyx* differentiated (probably from an Asian ancestor; Morlo et al. 2020) in eastern Europe at the end of the Serravallian, rapidly expanding its range from Germany to Spain and only in the Tortonian reaching the endemic domain of the Tusco-Sardinian paleobioprovince with the genus *Tyrrhenolutra*. The genus *Paludolutra*, instead, probably differentiated in western Europe (Spain) during the Late Miocene (Tortonian) and expanded its geographic range into the Tusco-Sardinian paleobiogeographic domain, benefiting from a temporary terrestrial connection that led to the transition from the V1 to the V2 faunal unit.

Data availability

The data generated and analyzed in the contribution are available in Supplementary Files 1 to 2.

Author contributions

A.F., S.B.-L. prepared the first draft and definitive version of the manuscript. L.R., reviewed and improved the first draft. A.F. took photos and 3D. A.F. data collection. A.F. and S.B.-L. performed the analyses, A.F. prepared the figures. All authors have read and agreed to the definitive version of the manuscript.

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APPENDIX

Systematic Palaeontology

Order **Carnivora** Bowdich, 1821
Family Mustelidae Batsch, 1788
Subfamily Lutrinae Bonaparte, 1838
Genus *Tyrrhenolutra* Hürzeler, 1987
Type species: *Tyrrhenolutra maremmana* Hürzeler, 1987 comb. nov.
Tabs. 1-2; Figs. 4-5

Revised Diagnosis: Medium-large sized otter about the size, or slightly larger, than the African clawless otter, with wrinkled enamel and premolars without accessory cuspids. The P4 is three-rooted and has a triangular outline with a slightly concave distal margin. The P4 inner shelf is characterised by a crestiform hypocone distal to the protocone, connected with this cusp through a faint notch. The M1 has low paracone and metacone; the metacone is the tallest cusp and is far larger than the paracone, the paracone is surrounded by a much larger parastyle and buccal cingulum that often dwarf the paracone. The paraconule and the protocone are both crestiform, separated by a notch and oriented mesiobuccally-distolingually. A weak hypoconule is present on the distolingual border of the metacone. The mandibular corpus is moderately high and rather short with a straight ventral margin; two mental foramina are present, the largest and anterior one is located below the p2. The p4 has a triangular outline in occlusal view due to a distal buccolingually expansion of the crown. The m1 is long and robust; The trigonid is about half the length of the tooth but is less wide than the talonid, giving the tooth a drop-like shape in occlusal view; the protoconid is slightly higher than the paraconid and metaconid; a long cristid distally extends from the metaconid into the talonid.

Referred specimens: NMB.Bac.51 (holotype), upper palate with right P2-M1 and I3 and a p3; IGF 11756a, skull fragment with right C, c, p2 and left P2 and p2; NMB.Bac.SCM-0902a, skull fragments with right m2 and a partial right M1; NMB.Bac.SCM-0902c, skull fragment with P2; NMB.Bac.SCM-0938a, skull fragments with C, P3, P4; IGF 11755, fragment of maxilla with left P2, C and p2; IGF 11756b, left maxilla fragment with P2, P3; MSNUP N.2, maxilla fragment with C, P2, P4; NMB.Bac.SCM-0895a right I3; NMB.Bac.SCM-0900a, left I3; NMB.Bac.SCM-0903a, left I3; NMB.Bac.SCM-0902b, right C; NMB.Bac.SCM-0903b, right C; NMB.Bac.SCM-0903e, left C; NMB.Bac.SCM-0903f, left P3; NMB.Bac.SCM-0903d, right P4; NMB.Bac.SCM-0903c, left M1; NMB.Bac.SCM-0938b, M1; NMB.Bac.SCM-0903d, right M1 broken; NMB.Bac.SCM-0902c, right M1 fragment; NMB.Bac.54, almost complete left and right hemimandible with right p2-m1 and left p2-m1; IGF 11756c, left mandible with p2, p4, m1 and m2; MSNUP N.1, mandible fragment with c, p3, p4; NMB.Bac.52, right hemimandible with p2-m2; NMB.Bac.55, right hemimandible fragment with c-p4; NMB.Bac.53, fragmentary juvenile left and right hemimandible with left d3 and d4; NMB.Bac.55bis, four isolated left teeth i1, i2, i3; NMB.Bac.SCM-0895b, left i2; NMB.Bac.51bis, two isolated teeth i3, p3; NMB.Bac.SCM-0900c, right c; NMB.Bac.SCM-0894, right and left c; NMB.Bac.SCM-0903f, lower left c fragment; NMB.Bac.SCM-0900d right p2; NMB.Bac.SCM-0895a, right p3; NMB.Bac.SCM-0900b, left m2.

Occurrence: Casteani (Weithofer 1888), Baccinello and Montebamboli (Hürzeler 1987).

Stratigraphy and Age: The peculiar late Miocene palaeogeographic configuration of emerged lands in the central Mediterranean area gave rise to a specific continental vertebrate palaeobioprovince (Rook et al. 1996, 2011; Abbazzi et al. 2008). Four vertebrate-bearing faunal assemblage zones have been distinguished in the first synthem of the Baccinello-Cinigiano Basin, referred to as V0, V1, V2, and V3 faunas (Lorenz 1968; Cirilli et al. 2016). The Baccinello mines V1 fauna (MN11, early Turolian), from which most of the material of *T. maremmana* comes, occurs in a lignite layer and is considered equivalent to the faunas recovered in lignite mines of southern Tuscany (Casteani, Montemassi, Acquanera and Ribolla; Hürzeler & Engesser 1976). The material previously attributed to *Paludolutra maremmana* instead comes from the Montebamboli mines. In this locality the lignite seam is slightly younger (MN12, V2 fauna).

References

Abbazzi L. (2001) - Cervidea and Moschidae (Mammalia, Artiodactyla) from the Baccinello V-3 Assemblage (late Miocene, Late Turolian, Grosseto, Italy). *Rivista Italiana Di Paleontologia e Stratigrafia*, 107(1): 107-123.

Abbazzi L., Delfino M., Gallai G., Trebini L. & Rook L. (2008) - New data on the vertebrate assemblage of Fiume Santo (north-west Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinian palaeobioprovince. *Palaeontology*, 51(2): 425-451.

Abdul-Patah P., Nur-Syuhada N., Md-Nor S., Sasaki H. & Md-Zain B.M. (2014) - Habitat and food resources of otters (Mustelidae) in Peninsular Malaysia In: AIP Conference Proceedings: 1614: 693-699. American Institute of Physics.

Alcalá L. (1994) - Macromamíferos Neógenos de la Fosa de Alfambra-Teruel. Instituto de Estudios Turolenses y Museo Nacional de Ciencias Naturales, Teruel, Spain, 554 pp.

Alfaro M.E., Santini F., Brock C., Alamillo H., Dornburg A., Rabosky D.L., Carnevale G. & Harmon L.J. (2009) - Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences*, 106(32): 13410-13414.

Argant A. (2004) - The Carnivores of the late Pliocene site of Saint-Vallier (Drome, France). *Geobios*, 37(Suppl. 1): S133-S182.

Azzaroli A., Boccaletti M., Delson E., Moratti G. & Torre D. (1986) - Chronological and paleogeographical background to the study of *Oreopithecus bambolii*. *Journal of Human Evolution*, 15(7): 533-540.

Baryshnikov G.F. & Puzachenko A.Y. (2012) - Craniometrical variability of the Eurasian otter (*Lutra lutra*: Carnivora: Mustelidae) from the Northern Eurasia. *Zoological Institute Russian Academy of Sciences*, 316(3): 203-222.

Baskin J.A. (1998) - Mustelidae In: Janis C.M. Scott K.M. & Jacobs L.L. (Eds.) - Evolution of Tertiary Mammals of North America: 152-173. Cambridge University Press, Cambridge, UK.

Batsch A.J.G.C. (1788) - Versuch einer Anleitung zur Kenntniss und Geschichte der Thiere und Mineralien : für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Academischen Buchhandlung, Jena, Germany, 528 pp.

Benvenuti M., Bertini A. & Rook L. (1994) - Facies analysis, vertebrate paleontology and palynology in the Late Miocene Baccinello-Cinigiano basin (Southern Tuscany). *Memorie Della Società Geologica Italiana*, 48: 415-423.

Benvenuti M., Moratti G., Sani F., Bonini M., Oms O.L., Papini M., Cavallina C. & Cavini L. (2015) - Messinian-earliest Zanclean tectonic-depositional dynamics of the Cinigiano-Baccinello and Velona basins (Tuscany, Italy). *Italian Journal of Geosciences*, 134(2): 237-254.

Benvenuti M., Papini M. & Rook L. (2001) - Mammal biochronology, UBSU and paleoenvironment evolution in a post-collisional basin; evidence from the late Miocene Baccinello Cinigiano Basin in southern Tuscany, Italy. *Bollettino Della Società Geologica Italiana*, 120(1): 97-118.

Benvenuti M., Papini M. & Testa G. (1999) - Sedimentary facies analysis in paleoclimatic reconstructions. Examples from the Upper Miocene-Pliocene successions of south-central Tuscany (Italy). In: Hominoid Evolution and climatic change in Europe. Vol 1: Climatic and environmental changes in the Neogene of Europe:355-377. Cambridge University Press.

Berta A. & Morgan G.S. (1985) - A New Sea Otter (Carnivora: Mustelidae) from the Late Miocene and Early Pliocene (Hemphillian) of North America. *Journal of Paleontology*, 59(4): 809-819.

Bonaparte C.L.G.L. (1838) - Synopsis vertebratorum systematis. *Nuovi Annali Delle Scienze Naturali*, 2: 105-133.

Bowdich E.T. (1821) - An Analysis of the Natural Classifications of Mammalia, for the use of Students and Travellers. J. Smith, Paris, France, 1 pp.

Brisson M.-J. (1762) - Regnum animale in classes IX. distributum, sive, Synopsis methodica : sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species : cum brevi cujusque speciei descriptione, citationibus auctorum de iis tractantium, nominibus eis ab ipsis & nationibus impositis, nominibusque vulgaribus:Editio altera auctior., 1-316. Apud Theodorum Haak, Lugduni Batavorum, 316 pp.

Bryant H.N., Russell A.P. & Fitch W.D. (1993) - Phylogenetic relationships within the extant Mustelidae (Carnivora): appraisal of the cladistic status of the Simpsonian subfamilies. *Zoological Journal of the Linnean Society*, 108(4): 301-334.

Casanovas-Vilar I., Alba D.M., Garcés M., Robles J.M. & Moyà-Solà S. (2011a) - Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences*, 108(14): 5554-5559.

Casanovas-Vilar I., van Dam J.A., Trebini L. & Rook L. (2011b) - The rodents from the Late Miocene *Oreopithecus*-bearing site of Fiume Santo (Sardinia, Italy). *Geobios*, 44(2-3): 173-187.

Cirilli O., Benvenuti M.G., Carnevale G., Vilar I.C., Delfino M., Furió M., Papini M., Villa A. & Rook L. (2016) - Fosso Della Fittaia: The Oldest Tusco-Sardinian Late Miocene Endemic Vertebrate Assemblages (baccinello-Cinigiano Basin, Tuscany, Italy). *Rivista Italiana Di Paleontologia e Stratigrafia*, 122(2): 13-34.

Crusafont Pairó M. & De Villalta J.F. (1951) - Los nuevos mamíferos del Neógeno de España. *Notas y Comunicaciones Del Instituto Geológico y Minero de España*, 22: 1-25.

Crusafont-Pairó M. (1950) - *Limnonyx* un nuevo lutrido del mioceno español. *Notas y Cominicaciones Del Instituto Geológico y Minero de España*, 20: 129-142.

Crusafont-Pairó M. & Golpe J.M. (1962) - Nuevos hallazgos de lútridos aonicoides (*Sivaonyx*, *Enhydriodon*) en el Pikermiense español (Cuenca de Teruel). *Notas y Comunicaciones del Instituto Geologico y Minero de España*, 67: 5-16.

de Blainville H.-M.D. (1841) - Ostéographie des Carnassiers, précédée de considerations sur l'histoire de la science à leur égard, les principes de leur classification, leur distribution géographique actuelle, et suivie de recherches sur leur ancienneté à la surface de la terre.:Vol. Tome Deuxième. J. B. Baillière et Fils, Libraires de l'Académie impériale de Médicine, Paris, France, 1000 pp.

De Ferran V., Figueiró H.V., De Jesus Trindade F., Smith O., Sinding M.-H.S., Trinca C.S., Lazzari G.Z., Veron G., Vianna J.A., Barbanera F., Kliver S., Serdyukova N., Bulyonkova T., Ryder O.A., Gilbert M.T.P., Koepfli K.-P. & Eizirik E. (2022) - Phylogenomics of the world's otters. *Current Biology*, 32(16): 3650-3658.e4.

de Muizon C. (1982) - Les relations phylogénétiques des Lutrinae (Mustelidae, Mammalia). *Geobios*, 15: 259-277.

De Terra H. (1956) - New Approach to the Problem of Man's Origin. *Science*, 124(3235): 1282-1285.

De Villalta Comella J.F. & Crusafont-Pairó M. (1945) - *Enhydriodon lluecai* nova sp. el primer Lútrido del Pontiense español. *Boletín de La Real Sociedad Española de Historia Natural. Actas*, 43: 383-396.

Dominici S. & Benvenuti M. (2024) - Two alternative ages for the Montebamboli *Oreopithecus* (Late Miocene, Tuscany). *Bollettino Della Società Paleontologica Italiana*, 63: 1-18.

Dragoo J.W. & Honeycutt R.L. (1997) - Systematics of Mustelid-Like Carnivores. *Journal of Mammalogy*, 78(2): 426-443.

Elliott Smith E.A., Newsome S.D., Estes J.A. & Tinker M.T. (2015) - The cost of reproduction: differential resource specialization in female and male California sea otters. *Oecologia*, 178: 17-29.

Engesser B. (1983) - Die jungtertiären Kleinsäuger des Gebietes der Maremma (Toskana, Italien). I: Gliridae (Rodentia, Mammalia). *Eclogae Geologicae Helvetiae*, 76(3): 763-780.

Engesser B. (1989) - The late Tertiary small mammals of the Maremma region (Tuscany, Italy): II Muridae ansd Cricetidae (Rodentia, Mammalia). *Bollettino Della Società Paleontologica Italiana*, 28(2-3): 227-252.

Estes J.A. & Bodkin J.L. (2002) - Otters In: William F. Perrin Bernd Würsing & J.G.M. Thewissen (Eds.) - Encyclopedia of marine mammals: First: 842-858. Academic Press, San Diego, CA.

Etienne R.S. & Haegeman B. (2012) - A Conceptual and Statistical Framework for Adaptive Radiations with a Key Role for Diversity Dependence. *The American Naturalist*, 180(4): E75-E89.

Etienne R.S., Haegeman B., Dugo-Cota Á., Vilà C., Gonzalez-Voyer A. & Valente L. (2023) - The Phylogenetic Limits to Diversity-Dependent Diversification. *Systematic Biology*, 72(2): 433-445.

Etienne R.S., Haegeman B., Stadler T., Aze T., Pearson P.N., Purvis A. & Phillimore A.B. (2011) - Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proceedings of the Royal Society B: Biological Sciences*, 279(1732): 1300-1309.

Falconer H. (1868) - On *Enhydriodon* (*Amyxodon*), a fossil genus allied to *Lutra* from the Tertiary strata of the Siwalik Hills In: Murchison C. (Ed.) - Palaeontological Memoirs and Notes of the late Hugh Falconer, A.M., M.D.: Vol. I. Fauna Antiqua Sivalensis, 331-338. Robert Hardwicke, 192 Piccadilly, London, UK.

Finarelli J.A. & Flynn J.J. (2006) - Ancestral State Reconstruction of Body Size in the Caniformia (Carnivora, Mammalia): The Effects of Incorporating Data from the Fossil Record. *Systematic Biology*, 55(2): 301-313.

Flynn J.J., Finarelli J.A., Zehr S., Hsu J. & Nedbal M.A. (2005) - Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology*, 54(2): 317-337.

Forsyth Major C.I. (1872) - La faune des vertébrés de Monte Bamboli (Maremmes de la Toscane). *Atti Società Italiana di Scienze Naturali*, 15: 290-303.

Fraas (1862) - Die tertiären Hirsche von Steinheim. *Jahreshefte Der Gesellschaft Für Naturkunde in Württemberg*, 18: 113-131.

Geoffroy Saint-Hilaire I. (1826) - Loutre. *Dictionnaire Classique d'Histoire Naturelle*, 9: 515-520.

Geraads D., Alemseged Z., Bobe R. & Reed D. (2011) - *Enhydriodon dikikae*, sp. nov. (Carnivora: Mammalia), a gigantic otter from the Pliocene of Dikika, Lower Awash, Ethiopia. *Journal of Vertebrate Paleontology*, 31(2): 447-453.

Gillet S., Lorenz H.G. & Woltersdorf F. (1965) - Introduction à l'étude du Miocène supérieur de Baccinello (environs de Grosseto, Italie). *Bulletin du Service de la carte géologique d'Alsace et de Lorraine*, 18: 31-42.

Ginsburg L. (1999) - Order Carnivora In: Rössner G.E. & Heissig K. (Eds.) - The Miocene Land Mammals of Europe:109-148. Verlag Dr Friedrich Pfeil, München, Germany.

Ginsburg L., Ingavat R. & Tassy P. (1983) - *Siamogole thailandica*, nouveau Mustelidae (Carnivora, Mammalia) neogene du Sud-Est asiatique. *Bulletin de la Société Géologique de France*, S7-XXV(6): 953-956.

Ginsburg L. & Morales J. (1996) - *Lartetictis* et *Adroverictis*, nouveaux genres de Melinae (Mustelidae, Carnivora, Mammalia) du Miocène de l'Ancien Monde. *Bulletin Du Muséum National d'Histoire Naturelle, 4ème Série – Section C – Sciences de la Terre, Paléontologie, Géologie, Minéralogie,* 18(4): 663-671.

Goloboff P.A. & Catalano S.A. (2016) - TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32(3): 221-238.

Grohé C., Chaimanee Y., de Bonis L., Yamee C., Blondel C. & Jaeger J.-J. (2010) - New data on Mustelidae (Carnivora) from Southeast Asia: *Siamogale thailandica*, a peculiar otter-like mustelid from the late middle Miocene Mae Moh Basin, northern Thailand. *Naturwissenschaften*, 97(11): 1003-1015.

Grohé C., de Bonis L., Chaimanee Y., Blondel C. & Jaeger J.-J. (2013) - The oldest Asian *Sivaonyx* (Lutrinae, Mustelidae): a contribution to the evolutionary history of bunodont otters. *Palaeontologia Electronica*, 16(3): 29A.

Grohé C., De Bonis L., Chaimanee Y., Chavasseau O., Rugbumrung M., Yamee C., Suraprasit K., Gibert C., Surault J., Blondel C. & Jaeger J.-J. (2020) - The Late Middle Miocene Mae Moh Basin of Northern Thailand: The Richest Neogene Assemblage of Carnivora from Southeast Asia and a Paleobiogeographic Analysis of Miocene Asian Carnivorans. *American Museum Novitates*, 2020(3952): 1.

Grohé C., Uno K. & Boisserie J.-R. (2022) - Lutrinae Bonaparte, 1838 (Carnivora, Mustelidae) from the Plio-Pleistocene of the Lower Omo Valley, southwestern Ethiopia: systematics and new insights into the paleoecology and paleobiogeography of the Turkana otters. *Comptes Rendus Palevol*, (30): 681-705.

Hassanin A., Veron G., Ropiquet A., Jansen Van Vuuren B., Lécu A., Goodman S.M., Haider J. & Nguyen T.T. (2021) - Evolutionary history of Carnivora (Mammalia, Laurasiatheria) inferred from mitochondrial genomes. *PLOS ONE*, 16(2): e0240770.

Heizmann E. & Morlo M. (1998) - Die semiaquatische *Lartetictis dubia* (Mustelinae, Carnivora, Mammalia) vom Goldberg/Ries (Baden-Württemberg). *Mainzer Naturwissenschaftliches Archiv, Beiheft*, 21: 141-153.

Helbing H. (1936) - Die Carnivoren des Steinheimer Beckens. A. Mustelidae. *Palaeontographica Supplement*, 8: 5-156.

Hendey Q.B. (1974) - The Late Cenozoic Carnivora of the South-Western Cape Province. *Annals of the South African Museum*, 63: 1-369.

Hernández-Romero P.C., Guerrero J.A. & Valdespino C. (2015) - Morphological variability of the cranium of *Lontra longicaudis* (Carnivora: Mustelidae): a morphometric and geographic analysis. *Zoological Studies*, 54(1): 50.

Hernández-Romero P.C., Gutiérrez-Rodríguez C., Valdespino C. & Prieto-Torres D.A. (2018) - The role of geographical and ecological factors on population divergence of the Neotropical otter *Lontra longicaudis* (Carnivora, Mustelidae). *Evolutionary Biology*, 45: 37-55.

Hürzeler J. (1987) - Die Lutrinen (Carnivora, Mammalia) aus dem" Grosseto-Lignit" der Toscana. *Schweizerische Paläontologische Abhandlungen*, 110: 28-48.

Hürzeler J. & Engesser B. (1976) - Les faunes de mammifères néogènes du Bassin de Baccinello (Grosseto, Italie). *Comptes Rendus - Academie Des Sciences, Serie II: Sciences de La Terre et Des Planetes*, 283: 333-336.

Hussain S.A. (2013) - Activity pattern, behavioural activity and interspecific interaction of smooth coated otter (*Lutrogale perspicillata*) in National Chambal Sanctuary, India. *IUCN Otter Specialist Group Bulletin*, 30(1): 5-17.

Illiger J.C.W. (1815) - Ueberblick der Säugethiere nach ihrer Vertheilung über die Welttheile. *Abhandlungen Der Physikalischen Klasse Der Königlich-Preussischen Akademie Der Wissenschaften Aus Den Jahren 1804–1811*, 1815: 39-159.

International Commission on Zoological Nomenclature (1999) - International Code of Zoological Nomenclature: 4th Edition. International Trust for Zoological Nomenclature, London, UK.

Jablonski N.G., Su D.F., Flynn L.J., Ji X., Deng C., Kelley J., Zhang Y., Yin J., You Y. & Yang X. (2014) - The site of Shuitangba (Yunnan, China) preserves a unique, terminal Miocene fauna. *Journal of Vertebrate Paleontology*, 34(5): 1251-1257.

Ji X., Jablonski N.G., Su D.F., Deng C., Flynn L.J., You Y. & Kelley J. (2013) - Juvenile hominoid cranium from the terminal Miocene of Yunnan, China. *Chinese Science Bulletin*, 58(31): 3771-3779.

Kargopoulos N., Valenciano A., Abella J., Kampouridis P., Lechner T. & Böhme M. (2022) - The exceptionally high diversity of small carnivorans from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany). *PLOS ONE*, 17(7): e0268968.

Kargopoulos N., Valenciano A., Kampouridis P., Lechner T. & Böhme M. (2021) - New early late Miocene species of *Vishnuonyx* (Carnivora, Lutrinae) from the hominid locality of Hammerschmiede, Bavaria, Germany. *Journal of Vertebrate Paleontology*, 41(3): e1948858.

Khan W.A., Qasim M., Ahmad E., Chaudhry A.A., Bhaagat H.B. & Akhtar M. (2010) - Status of smooth coated otter (*Lutrogale perspicillata sindica*) in Pakistan. *Pakistan Journal of Zoology*, 42(6).

Kim H.-N. & Jo Y.-S. (2021) - Complete mitochondrial genome sequencing of *Lutra lutra* (Linnaeus, 1758) (Carnivora: Mustelidae) and its phylogenetic status in Mustelidae. *Mitochondrial DNA Part B*, 6(7): 2066-2068.

Koepfli K.-P., Deere K.A., Slater G.J., Begg C., Begg K., Grassman L., Lucherini M., Veron G. & Wayne R.K. (2008a) - Multigene phylogeny of the Mustelidae: Resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology*, 6(1): 10.

Koepfli K.-P., Kanchanasaka B., Sasaki H., Jacques H., Louie K.D.Y., Hoai T., Dang N.X., Geffen E., Gutleb A., Han S., Heggberget T.M., LaFontaine L., Lee H., Melisch R., Ruiz-Olmo J., Santos-Reis M., Sidorovich V.E., Stubbe M. & Wayne R.K. (2008b) - Establishing the foundation for an applied molecular taxonomy of otters in Southeast Asia. *Conservation Genetics*, 9(6): 1589-1604.

Koepfli K.-P. & Wayne R.K. (1998) - Phylogenetic relationships of otters (Carnivora: Mustelidae) based on mitochondrial cytochrome b sequences. *Journal of Zoology*, 246(4): 401-416.

Koepfli K.-P. & Wayne R.K. (2003) - Type I STS markers are more informative than cytochrome b in phylogenetic reconstruction of the Mustelidae (Mammalia: Carnivora). *Systematic Biology*, 52(5): 571-593.

Kretzoi M. (1951) - The *Hipparion*-fauna from Csákvar. *Földtani Közlöny*, 81: 402-417.

Kruuk H. (2006) - Otters: ecology, behaviour and conservation. Oxford University Press, USA.

Kruuk H. & Moorhouse A. (1990) - Seasonal and spatial differences in food selection by otters *(Lutra lutra)* in Shetland. *Journal of Zoology*, 221(4): 621-637.

Kurtén B. (1970) - The neogene wolverine *Plesiogulo* and the origin of *Gulo* (Carnivora, Mammalia). *Acta Zoologica Fennica*, 131: 1-22.

Lambert W.D. (1997) - The osteology and paleoecology of the giant otter *Enhydritherium terraenovae*. *Journal of Vertebrate Paleontology*, 17(4): 738-749.

Laudanno G., Haegeman B. & Etienne R.S. (2020) - Additional Analytical Support for a New Method to Compute the Likelihood of Diversification Models. *Bulletin of Mathematical Biology*, 82(2): 22.

Laudanno G., Haegeman B., Rabosky D.L. & Etienne R.S. (2021) - Detecting Lineage-Specific Shifts in Diversification: A Proper Likelihood Approach. *Systematic Biology*, 70(2): 389-407.

Law C.J., Slater G.J. & Mehta R.S. (2018) - Lineage Diversity and Size Disparity in Musteloidea: Testing Patterns of Adaptive Radiation Using Molecular and Fossil-Based Methods. *Systematic Biology*, 67(1): 127-144.

Law C.J., Young C. & Mehta R.S. (2016) - Ontogenetic Scaling of Theoretical Bite Force in Southern Sea Otters (*Enhydra lutris nereis*). *Physiological and Biochemical Zoology*, 89(5): 347-363.

Lichtenstein K.M.H. (1835) - Ueber *Lutra maculicollis* Lichtenst. aus dem Kafferlande. *Archiv Für Naturgeschichte, Berlin*, 1(1): 89-92.

Ligios S., Benvenuti M., Gliozzi E., Papini M. & Rook L. (2008) - Late Miocene palaeoenvironmental evolution of the Baccinello–Cinigiano Basin (Tuscany, central Italy) and new autoecological data on rare fossil fresh-to brackish-water ostracods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 264(3-4): 277-287.

Linnaeus C. von (1758) - Systema Naturae per Regna Tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis:Editio Decima, Vol. Tomus I. Holmiae, Impensis Direct. Laurentii Salvii.

Lönnberg E. (1910) - A new subspecies of clawless otter (*Aonyx capensis congica*) from Lower Congo. *Arkiv För Zoologi*, 7: 1-8.

Lorenz H.G. (1968) - Stratigraphisches und mikropaläontologisches Untersuchungen des Braunkohlengebietes von Baccinello (Grosseto, Italien). *Rivista Italiana di Paleontologia e Stratigrafia*, 74: 147-270.

Lydekker R. (1884) - Siwalik and Narbada Carnivora In: Indian Tertiary and post Tertiary Vertebrata:Vol. II, part VI, 178-355. Geological Survey Office, Calcutta, India.

Lydekker R. (1890) - On a new species of otter from the lower Pliocene of Eppelsheim. *Proceedings of the Zoological Society of London*, 1890: 3-5.

Lynch J.M. & O'Sullivan W.M. (1993) - Cranial form and sexual dimorphism in the Irish otter *Lutra lutra* L. *Biology and Environment: Proceedings of the Royal Irish Academy*, 93B(2): 97-105.

Lyras G.A., van der Geer A.A.E. & Rook L. (2010) - Body size of insular carnivores: Evidence from the fossil record. *Journal of Biogeography*, 37(6): 1007-1021.

Maddison W. P. & D.R. Maddison (2023) - Mesquite: a modular system for evolutionary analysis. Version 3.81 http://www.mesquiteproject.org

Mason C.F. & Macdonald S.M. (2009) - Otters: Ecology and Conservation. Cambridge University Press, 256 pp.

Matthew W.D. (1929) - Critical observations upon Siwalik mammals. *Bulletin of the American Museum of Natural History*, 56: 437-560.

Matthew W.D. & Thomson A. (1924) - Third contribution to the Snake Creek fauna. *Bulletin of the American Museum of Natural History*, 50: 59-210.

Meneghini G. (1862) - Descrizione dei resti di due fiere trovati nelle ligniti mioceniche di Montebamboli. *Atti Della Società Italiana Di Scienze Naturali*, 4: 17-33.

Molina J.I. (1782) - Saggio sulla storia naturale del Chili / del signor Abate Giovanni Ignazio Molina. Stamperia di S. Tommaso d'Aquino, Bologna.

Moors P.J. (1980) - Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos*: 147-158.

Morales J. & Pickford M. (2005) - Giant bunodont Lutrinae from the Mio-Pliocene of Kenya and Uganda. *Estudios Geológicos*, 61: 233-246.

Morales J., Pickford M. & Soria D. (2005) - Carnivores from the Late Miocene and Basal Pliocene of the Tugen Hills, Kenya. *Revista de La Sociedad Geológica de España,* 18(1-2): 39-61.

Morlo M., Nagel D. & Bastl K. (2020) - Evolution of the carnivoran (Carnivora, Mammalia) guild structure across the Middle/Upper Miocene boundary in Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 553: 109801.

MorphoSource (2024) - Retrieved January 8, 2024, from https://www.morphosource.org/

Nordmann A. (1858) - Palaeontologie Südrusslands: *Felis*, *Hyaena*, *Canis*, *Thalassictis*, *Mustela*, *Lutra*, *Spermophilus*, *Arvicola*, *Spalax*, *Castor*, *Lepus* und *Equus*: vorgetragen in der finnischen Societät der Wissenschaften den 4 December 1854: Vol. 2. Friis.

Olfers I.F. von (1818) - Bemerkungen zu Illiger's Dberblick der Saugethiere nach ihrer Vertheilung tiber die Welttheile, rucksichtlich der Sudamericanischen Arten (Species). *In Neue Bibliothek Der Wichtigsten Reisebeschreibungen Zur Erweiterung Der Erd- Und Volkerkunde, Weimar. W. L. Eschwege's Journal von Brasilien*, 15(2): 192-237.

Peigné S., De Bonis L., Likius A., Mackaye H.T., Vignaud P. & Brunet M. (2008) - Late Miocene Carnivora from Chad: Lutrinae (Mustelidae). *Zoological Journal of the Linnean Society*, 152(4): 793-846.

Petter G., Pickford M. & Howell F.C. (1991) - La loutre piscivore du Pliocène de Nyaburogo et de Nkondo (Mammalia, Carnivora). *Comptes Rendus Des Séances de l'Académie Des Sciences de Paris*, 312: 949-955.

Pickford M. (2007) - Revision of the Mio-Pliocene bunodont otter-like mammals of the Indian Subcontinent. *Estudios Geológicos*, 63(1): 83.

Pilgrim G.E. (1931) - Catalogue of the Pontian Carnivora of Europe in the British Museum. Trustees of the British Museum (Natural History), London, UK, 174 pp.

Pilgrim G.E. (1932) - The Fossil Carnivora of India. *Memoirs of the Geological Survey of India*, XVIII: 1-258.

Pontieri F., Russo L.F., Raia P. & Loy A. (2023) - A surprising pattern of Sexual Dimorphism in the Eurasian otter (*Lutra lutra*) in Sweden. *Hystrix, the Italian Journal of Mammalogy*. 34(1): 14-18.

Prassack K.A. (2016) - *Lontra weiri*, sp. nov., a Pliocene river otter (Mammalia, Carnivora, Mustelidae, Lutrinae) from the Hagerman Fossil Beds (Hagerman Fossil Beds National Monument), Idaho, U.S.A. *Journal of Vertebrate Paleontology*, 36(4): e1149075.

Rabosky D.L. (2006) - LASER: A Maximum Likelihood Toolkit for Detecting Temporal Shifts in Diversification Rates from Molecular Phylogenies. *Evolutionary Bioinformatics*, 2: 117693430600200024.

Rabosky D.L., Donnellan S.C., Grundler M. & Lovette I.J. (2014) - Analysis and Visualization of Complex Macroevolutionary Dynamics: An Example from Australian

Scincid Lizards. *Systematic Biology*, 63(4): 610-627.

Rabosky D.L. & Lovette I.J. (2008) - Explosive Evolutionary Radiations: Decreasing Speciation or Increasing Extinction Through Time? *Evolution*, 62(8): 1866-1875.

Repenning C.A. (1976) - *Enhydra* and *Enhydriodon* from the Pacific coast of North America. *Journal of Research of the U. S. Geological Survey*, 4(3): 305-315.

Ristori G. (1890) - Sopra i resti di un coccodrillo scoperti nelle ligniti mioceniche di Montebamboli (Maremma Toscana), *Pubblicazioni del Reale Istituto di Studi Superiori Pratici e di Perfezionamento in Firenze, Sezione di Scienze Fisiche e Naturali:* 153-176.

Roman F. & Viret J. (1934) - La faune de mammifères du Burdigalien de La Romieu (Gers.). *Mémoires de La Société Géologique de France (Paleontologie)*, 21: 23-167.

Rook L. (1999) - Late Turolian *Mesopithecus* (Mammalia, Primates, Colobinae) from Italy. *Journal of Human Evolution*, 36(5): 535-547.

Rook L. (2012) - Basel–Tuscany, a long-lasting link. *Swiss Journal of Palaeontology*, 131(1): 7-9.

Rook L. (2016) - Geopalaeontological setting, chronology and palaeoenvironmental evolution of the Baccinello-Cinigiano Basin continental successions (Late Miocene, Italy). *Comptes Rendus Palevol*, 15(7): 825-836.

Rook L., Ficcarelli G. & Torre D. (1991) - Messinian carnivores from Italy. *Bollettino Della Società Paleontologica Italiana*, 30(17): 7-22.

Rook L., Gallai G. & Torre D. (2006) - Lands and endemic mammals in the Late Miocene of Italy: Constrains for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238(1-4): 263-269.

Rook L., Harrison T. & Engesser B. (1996) - The taxonomic status and biochronological implications of new finds of *Oreopithecus* from Baccinello (Tuscany, Italy). *Journal of Human Evolution*, 30(1): 3-27.

Rook L. & Martínez-Navarro B. (2004) - *Viverra howelli* n. sp., a new viverrid (Carnivora, Mammalia) from the Baccinello-Cinigiano basin (Latest Miocene, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 110(3): 719-723.

Rook L., Oms O., Benvenuti M.G. & Papini M. (2011) - Magnetostratigraphy of the Late Miocene Baccinello–Cinigiano basin (Tuscany, Italy) and the age of *Oreopithecus bambolii* faunal assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 305(1-4): 286-294.

Rook L., Renne P., Benvenuti M. & Papini M. (2000) - News and Views Geochronology of *Oreopithecus*-bearing succession at Baccinello (Italy) and the extinction pattern of European Miocene hominoids. *Journal of Human Evolution*, 39: 577-582.

Rook L. & Rustioni M. (1991) - *Tapirus* cf. *arvernensis* remains from the Late Turolian Baccinello V3 faunal assemblage (Grosseto, Tuscany). *Bollettino della Società Paleontologica Italiana*, 30: 325-327.

Salesa M.J., Antón M., Siliceo G., Pesquero M.D., Morales J. & Alcalá L. (2013) - A non-aquatic otter (Mammalia, Carnivora, Mustelidae) from the Late Miocene (Vallesian, MN 10) of La Roma 2 (Alfambra, Teruel, Spain): Systematics and functional anatomy. *Zoological Journal of the Linnean Society*, 169(2): 448-482.

Sato J.J., Hosoda T., Wolsan M., Tsuchiya K., Yamamoto M. & Suzuki H. (2003) - Phylogenetic relationships and divergence times among mustelids (Mammalia: Carnivora) based on nucleotide sequences of the nuclear interphotoreceptor retinoid binding protein and mitochondrial cytochrome b genes. *Zoological Science*, 20(2): 243-264.

Sato J.J., Wolsan M., Minami S., Hosoda T., Sinaga M.H., Hiyama K., Yamaguchi Y. & Suzuki H. (2009) - Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. *Molecular Phylogenetics and Evolution*, 53(3): 907-922.

Sato J.J., Wolsan M., Prevosti F.J., D'Elía G., Begg C., Begg K., Hosoda T., Campbell K.L. & Suzuki H. (2012) - Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). *Molecular Phylogenetics and Evolution*, 63(3): 745-757.

Schinz H.R. (1821) - Das Tierreisch von dem Herrn. *Ritter von Cuvier, Stuttgart*, 1: 211-214.

Schlosser M. (1887) - Die affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. *Beitrage Zur Palaeontologie Osterreich-Ungarns Und Des Orients*, 6: 1-224.

Schnitzler J., Theis C., Polly P.D. & Eronen J.T. (2017) - Fossils matter - Understanding modes and rates of trait evolution in Musteloidea (Carnivora). *Evolutionary Ecology Research*, 18(2): 187-200.

Schreber J.C.D. (1776) - Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen. Wolfgang Walther, Erlangen, Germany.

Sondaar P.Y. (1977) - Insularity and Its Effect on Mammal Evolution In: Hecht M.K. Goody P.C. & Hecht B.M. (Eds.) - Major Patterns in Vertebrate Evolution: 671-707. Springer US, Boston, MA.

Sondaar P.Y. (1986) - The island sweepstakes. *Natural History*, 95(9): 50-57.

Sotnikova M. & Rook L. (2010) - Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the Late Miocene to Early Pleistocene. *Quaternary International*, 212(2): 86-97.

Stadler T. (2011) - Mammalian phylogeny reveals recent diversification rate shifts. *Proceedings of the National Academy of Sciences*, 108(15): 6187-6192.

Stehlin H.G. (1909) - Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bulletin de la Société géologique de France* 19: 488-520.

Stromer von Reichenbach E. (1931) - Reste Süsswasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwestafrika). *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Bayerischen Akademie der Wissenschaften zu München*, 21(5): 17-47.

Timm-Davis L.L., DeWitt T.J. & Marshall C.D. (2015) - Divergent skull morphology supports two trophic specializations in otters (Lutrinae). *PloS One*, 10(12): e0143236.

Tobien H. (1955) - Neue und wenig bekannte Carnivoren aus den unterpliozänen Dinotheriensanden Rheinhessens. *Notizblatt Des Hessischen Landesamtes Für Bodenforschung Zu Wiesbaden*, 83: 7-31.

Tseng Z.J., Pacheco-Castro A., Carranza-Castañeda O., Aranda-Gómez J.J., Wang X. & Troncoso H. (2017) - Discovery of the fossil otter *Enhydritherium terraenovae* (Carnivora, Mammalia) in Mexico reconciles a palaeozoogeographic mystery. *Biology Letters*, 13(6): 20170259.

Turton W. (1806) - A general system of nature, through the three grand kingdoms of animals, vegetables, and minerals, systematically divided into their several classes, orders, genera, species, and varieties, with their habitations, manners, economy, structure and peculiarities. 1: 1-966.

Printed for Lackington, Allen, and Co., Temple of the Muses, Finsbury Square, London.

Valenciano A. & Govender R. (2020) - New insights into the giant mustelids (Mammalia, Carnivora, Mustelidae) from Langebaanweg fossil site (West Coast Fossil Park, South Africa, early Pliocene). *PeerJ*, 8: e9221.

Valenciano A., Mayda S. & Alpagut B. (2020) - First record of *Lartetictis* (Carnivora, Mustelidae, Lutrinae) in Turkey from the middle Miocene hominoid locality of Paşalar. *Historical Biology*, 32(10): 1361-1376.

Van Der Geer A.A.E., Lyras G.A., De Vos J. & Dermitzakis M. (2010) - Evolution of island mammals: adaptation and extinction of placental mammals on islands. Wiley-Blackwell, Hoboken, NJ, 479 pp.

Villier B., Pavia M. & Rook L. (2011) - New remains of *Paralutra garganensis* Willemsen, 1983 (Mustelidae, Lutrinae) from the Late Miocene "Terre Rosse" of Gargano (Apulia, Italy). *Bollettino della Società Paleontologica Italiana*, 50: 135-143.

Vislobokova I., Sotnikova M. & Dodonov A. (2001) - Late Miocene-Pliocene Mammalian faunas of Russia and neighbouring countries. *Bollettino della Società Paleontologica Italiana,* 40(2): 307-313.

Wang X., Grohé C., Su D.F., White S.C., Ji X., Kelley J., Jablonski N.G., Deng T., You Y. & Yang X. (2018) - A new otter of giant size, *Siamogale melilutra* sp. nov. (Lutrinae: Mustelidae: Carnivora), from the latest Miocene Shuitangba site in north-eastern Yunnan, south-western China, and a total-evidence phylogeny of lutrines. *Journal of Systematic Palaeontology*, 16(1): 39-65.

Weithofer K.A. (1888) - Alcune osservazioni sulla fauna delle ligniti di Casteani e di Montebamboli (Toscana). *Bollettino del Regio Comitato geologico d'Italia*, 5(3): 248-253.

Weithofer K.A. (1889) - Ueber die tertiären Landsäugethiere Italiens. *Jahrbuch Der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 31: 55-82.

Werdelin L. (2003a) - Carnivores from the Kanapoi hominid site, Turkana Basin, northern Kenya In: Harris J.M. & Leakey M.G. (Eds.) - Contributions in science - Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya. 498: 115-132.

Werdelin L. (2003b) - Mio-Pliocene Carnivora from Lothagam, Kenya In: Leakey M.G. & Harris J.M. (Eds.) - Lothagam - The Dawn of Humanity in Eastern Africa: 261-314. Columbia University Press.

Werdelin L. (2005) - The Carnivora of Rudabánya (MN 9, Late Miocene, Hungary). *Palaeontographia Italica*, 90: 163-180.

Werdelin L. & Sanders W.J. (2010) - Cenozoic Mammals of AfricaUniversity of California Press. University of California Press, Berkeley, California, USA, 986 pp.

Willemsen G. (1999) - Some remarks on the Enhydrini (Lutrinae) from the Siwaliks, Pakistan. *Deinsea*, 7(1): 411-418.

Willemsen G.F. (1983) - *Paralutra garganensis* sp. nov. (Mustelidae, Lutrinae): a new otter from the Miocene of Gargano, Italy. *Scripta Geologica*, 72: 1-8.

Willemsen G.F. (1992) - A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geologica*, 101: 1-115.

Wolsan M. & Sato J.J. (2010) - Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). *Cladistics*, 26(2): 168-194.

Yu L., Liu J., Luan P., Lee H., Lee M., Min M., Ryder O.A., Chemnick L., Davis H. & Zhang Y. (2008) - New insights into the evolution of intronic sequences of the β-fibrinogen gene and their application in reconstructing mustelid phylogeny. *Zoological Science*, 25(6): 662-672.

Yu L., Luan P.-T., Jin W., Ryder O.A., Chemnick L.G., Davis H.A. & Zhang Y. (2011) - Phylogenetic utility of nuclear introns in interfamilial relationships of Caniformia (order Carnivora). *Systematic Biology*, 60(2): 175-187.

Zimmermann E.A.W. von (1780) - Geographische Geschichte des Menschen und der allgemein verbreiteten vierfüßigen Tiere. Zweiter Band. Weygandschen Buchhandlung, Liepzig.