

NEW MATERIAL OF *LUTRA SIMPLICIDENS* (CARNIVORA, MUSTELIDAE, LUTRINAE), A KEY TAXON FOR UNDERSTANDING THE EVOLUTION OF EUROPEAN OTTERS

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Abstract. *Lutra lutra* (Linnaeus, 1758) is the only otter living in Europe today, but the palaeodiversity of this group during the Pleistocene was much higher. *Lutra simplicidens* Thenius, 1965 is one of the best-known taxa from the European Quaternary fossil record, having been reported in at least eight localities in Central Europe, Britain, Italy and the Azov Sea area, with a stratigraphic occurrence spanning the mid Early to the Middle Pleistocene. However, no cranial remains of this species have been described so far. Here I analyse some unpublished material of *L. simplicidens* from the early Middle Pleistocene site of Voigtstedt (Germany), which consists of the right and left P¹-M¹ of the same individual and a complete left humerus. The comparative study of these findings highlights a number of morphological and biometrical similarities between *L. simplicidens* and some Mediterranean Quaternary otters, such as *Lutraeximia umbra* Cherin et al., 2016 from central Italy, *Lutraeximia trinacriae* (Burgio & Fiore, 1988) from Sicily, *Sardolutra ichnusae* (Malatesta, 1977) from Sardinia and *Lutrogale cretensis* (Symeonides & Sondaar, 1975) from Crete. These species - together with the living *Lutrogale perspicillata* (Geoffroy Saint-Hilaire, 1826) - form a monophyletic clade, which most probably includes also *L. simplicidens*, as well as several other Eurasian extinct taxa only known by fragmentary remains. These results confirm the pivotal importance of *L. simplicidens* for the evolution of European otters and lead to doubts about its taxonomic status, which will be solved with the discovery of new material.

INTRODUCTION

A recent revision of the collection of fossil carnivores from Voigtstedt (Germany) housed in the Senckenberg Research Station of Quaternary Palaeontology in Weimar allows to identify some unpublished material of the extinct otter *Lutra simplicidens* Thenius, 1965, which is the subject of this article.

Lutra simplicidens is a taxon of particular interest since some previous works (Willemsen 2006; Cherin et al. 2016) highlighted its pivotal importance in the evolutionary history of Mediterranean Quaternary Lutrinae, which is still largely shrouded in mystery. This is mainly due to the relative rarity of otter remains in the Plio-Pleistocene fossil record. The Mediterranean otter record during the Villafranchian (i.e., mid-Piacenzian to mid-Calabrian; about 3.3-1.2 Ma) is particularly poor. *Lutra sinerizi* Villalta, 1952 from the early Villafranchian site of Villarroya (Spain) is a disputed taxon, probably

referable to *Enhydriactis* Forsyth-Major, 1901 (Viret 1954; Willemsen 1992). *Lutra bravardi* Pomel, 1843 from Les Étouaries (France) is another cryptic taxon. The holotype is lost (Willemsen 1992) and the other records are too scanty for a species-level attribution (see Heintz et al. 1974 for Saint Vallier; Kretzoi 1953 for Kisláng; Fejfar et al. 1990 for Hajnacka I/2).

Sotnikova et al. (2002) report *Lutra* sp. from Liventsovka (Russia), middle Villafranchian. *Lutra fatimazobrae* Geraads, 1997 from Ahl al Oughlam (Morocco) is also referred to the middle Villafranchian (earliest Pleistocene) and is represented by three incomplete mandibles, an isolated M₁ and a fragmentary femur (Geraads 1997). The late Villafranchian fossil material is still scarce but much better preserved. Recently, Cherin et al. (2016) described the new taxon *Lutraeximia umbra* Cherin et al. 2016 from the locality of Pantalla (Umbria, Italy). This site has yielded a number of exquisitely-preserved cranial materials of large mammals, including various Carnivora (Cherin et al. 2013a, 2013b, 2014a, 2014b). Among this material, the holotype

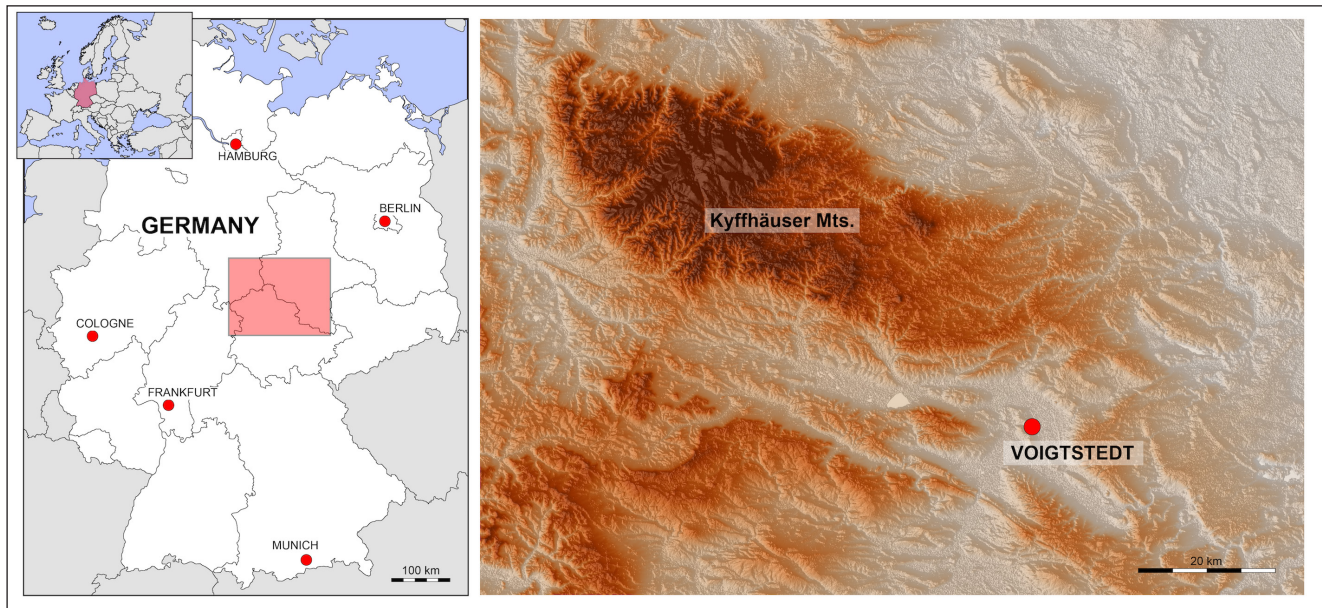


Fig. 1 - Location of the palaeontological site of Voigtstedt (Germany).

of *L. umbra* stands out, representing the only lutrine cranium discovered to date in the Quaternary of the Mediterranean area. Cherin & Rook (2014) report the earliest occurrence of *Lutra simplicidens* in the Upper Valdarno (Tuscany, Italy), more or less in the same stratigraphic interval of *L. umbra*. The richness of the *L. simplicidens* fossil record increases from the Epivillafranchian (*L. simplicidens tamanensis* from Chumbur Kosa, Azov Sea area; Sotnikova & Titov 2009) throughout the Middle Pleistocene (*L. simplicidens simplicidens* from Central Europe and Britain; Willemsen 1992). *Lutra simplicidens* is a medium-sized otter, weighting about 6.5-7.0 kg (Cherin et al. 2016), that is, little more than the lowest body mass of the extant Eurasian otter *Lutra lutra* (Linnaeus, 1758) (5.0-14.0 kg; Kruuk 2006). The post-cranial skeleton of *L. simplicidens* exhibits a suite of adaptations for the aquatic life more specialized than those of *L. lutra*. In particular, *L. simplicidens* shows (i) a strongly curved humerus (well designed to withstand the strains of strong flexing during swimming), (ii) well-developed grooves for the extensor muscle in the radius (strong lower arm extension is related to efficient dog-paddle swimming) and (iii) a short and stout femur (which facilitates the back-swing of the leg during swimming) (Willemsen 1992).

Prior to the present work, no cranial material of *L. simplicidens* was known. Here I describe for the first time the upper distal dentition (P_4-M_1) – as well

as a complete humerus – of *L. simplicidens* from the early Middle Pleistocene site of Voigtstedt (Kahlke 1965) (Fig. 1), and offer new insights on the taxonomy and the evolutionary importance of this species.

MATERIALS AND METHODS

The described material is stored in the Senckenberg Research Station of Quaternary Palaeontology in Weimar and consists in the right and left P_4-M_1 and in a left humerus.

For the dental material, the following cranial specimens belonging to extant Lutrinae were analysed: *Aonyx capensis* Schinz, 1821: HNHM 67.83.1; *Enhydra lutris* (Linnaeus, 1758): HNHM 87.67.1; *Lontra canadensis* (Schreber, 1777): HNHM 64.143.1; *Lontra longicaudis* (Olfers, 1818): MZUF 410, MZUF 411, MZUF 4091; *Lontra provocax* (Thomas, 1908): MZUF 1602; *Lutra lutra*: MZUF 12407, HNHM 60.110.1, HNHM 55.82.1, HNHM 78.49.1, HNHM 69.20.1; *Lutra sumatrana* Gray, 1865: HNHM 1800.53; *Pteronura brasiliensis* (Gmelin, 1788): MZUF 4052. Additional pictures of *Lontra canadensis* (specimen UMMZ 103352) were downloaded from the Animal Diversity Web database of the University of Michigan (<http://animaldiversity.org>; Creative Commons 3.0 Unported license). Pictures of the four remaining living species – *Lontra felina* (Molina, 1782), *Hydrictis maculicollis* (Lichtenstein, 1835), *Aonyx cinerea* (Illiger, 1815) and *Lutrogale perspicillata* (Geoffroy Saint-Hilaire, 1826) – were taken from Larivière (1998; 2002; 2003) and Ten Hwang & Larivière (2005), respectively. Regarding the extinct taxa, the holotypes of *Lutraeximia umbra* (SBAU 337654), *Lutraeximia trinacriae* (Burgio & Fiore, 1988) (MGGP SP1 to SP25) and *Lutra palaeindica* Falconer, 1868 (cranium NHM 37151) and the mandible of *Lutra simplicidens* from the Upper Valdarno (NHM M29688) were analysed. Data and images of other fossil taxa were taken from the literature, mostly Willemsen (1992) for *Lutra simplicidens*, *Lutra euxena* (Bate, 1935), *Lutra castiglioni* (Pereira & Salotti, 2000), *Algarolutra majori* (Malatesta, 1978) and *Megalenhydris barbaricina* Willemsen & Malatesta, 1987; Malatesta (1977) for *Sardolutra ichnusae* (Malatesta, 1977); Symeonides & Sondaar (1975) for *Lutrogale creten-*

sis (Symeonides & Sondaar, 1975); Teilhard de Chardin & Piveteau (1930) and Van Zyll de Jong (1972) for the Chinese *Lutra licenti* Teilhard de Chardin & Piveteau, 1930. For the comparative analysis of the humerus, bibliographic information was taken from Willemsen (1992).

Morphometric measurements were recorded to the nearest 0.1 mm with a digital calliper following Driesch (1976) and Willemsen (1992). Morphometric data published by Pohle (1919), Willemsen (1992) and Raghavan et al. (2007) were also considered.

Institutional abbreviations

AMZ, Azov Museum-reserve, Azov; **BM**, British Museum, London; **CM**, Cromer Museum, Cromer; **HNHM**, Hungarian Natural History Museum & Geological Institute of Hungary, Budapest; **IQW**, Senckenberg Research Station of Quaternary Palaeontology, Weimar; **KMBF**, Kreis-Museum, Bad Frankenhausen; **MGGP**, Museo Geologico-Paleontologico 'G.G. Gemellaro', Università di Palermo; **MZUF**, Museo di Storia Naturale, Sezione di Zoologia 'La Specola', Università di Firenze; **NHM**, Natural History Museum, London; **PIV**, Palaeontological Institute, University of Vienna; **SBAU**, Soprintendenza per i Beni Archeologici dell'Umbria, Perugia; **UMMZ**, University of Michigan Museum of Zoology.

Nomenclatural abbreviations

L., *Lutra*; **Le.**, *Lutraeximia*; **Lg.**, *Lutrogale*; **Lo.**, *Lontra*.

SYSTEMATIC PALAEONTOLOGY

Order **Carnivora** Bowdich, 1821

Family **Mustelidae** Fischer von Waldheim, 1817

Subfamily **Lutrinae** Bonaparte, 1838

Genus *Lutra* Brisson, 1762

Lutra simplicidens Thenius, 1965

Figs 2-3, Tabs 1-2

- 1891 *Lutra vulgaris* partim – Newton, p. 12
 1926 *Lutra* sp. – Soergel, p. 36
 1948 *Nesolutra* sp. – Thenius, p. 187
 1951 *Lutra euscena* partim – Thenius, p. 342
 1961 *Lutra* cf. *lutra* – Kahlke, p. 198
 1961 *Lutra* sp. – Kahlke, p. 135
 1962 *Lutra euscena* partim – Thenius, p. 78
 1981 *Lutra* sp. – Stuart, p. 158
 1982 *Lutra* sp. – Stuart, p. 111

Holotype: Left mandible with P₂-M₁ stored in the Palaeontological Institute of the University of Vienna (PIV Hdsh. VIII/36).

Type locality: Hundsheim, near Deutsch-Altenburg, Austria, Bed VIII of the fissure filling.

Stratigraphic occurrence: mid Early Pleistocene (early late Villafranchian) to Middle Pleistocene.

Referred material: Hundsheim (Austria): type mandible, right radius, right femur, left tibia, right calcaneus (PIV; Thenius 1948; 1951; 1965); Voigtstedt (Germany): right C^{max}, left dP³, right radius, left ulna, left II metatarsal, right calcaneus, right astragalus, II phalanx (IQW; Thenius 1965), right M₁ (KMBF; Heinrich et al. 1986); Süssenborn (Germany): fragmented mandible (IQW; Soergel 1926); Mosbach 2 (Germany): left humerus (NHM; Willemsen 1992), right mandible with M₁ (IQW; Willemsen 1992); East Runton (UK):

left mandible with M₁ (BM; Willemsen 1992); West Runton (UK): right mandibular fragment with M₁ (CM; Willemsen 1992), humerus and caudal vertebra (BM; Willemsen 1992); Upper Valdarno (Italy): right mandible with M₁-M₂ (NHM; Cherin & Rook 2014); Chumbur Kosa (Russia): left mandible with M₁ and fragment of P₄ (AMZ; Sotnikova & Titov 2009).

Additional material from Voigtstedt: Right P⁴-M¹ IQW 1966/7313 (Voi. 3525); fragment of left maxilla with P⁴-M¹ IQW 1966/7314 (Voi. 3532); left humerus IQW 1966/7349 (Voi. 3658+3659).

Emended diagnosis: Lutrinae with broad P₂ and P₃, short and narrow M₁ with no hypoconulid, ridge-shaped hypoconid forming the outer border of the rather flat talonid, inner cingulum only present at the mesial basis of the paraconid. P⁴ with mesiodistally enlarged talon, whose distal margin does not reach the distal margin of the metacone in occlusal view; characteristic distal convexity along the distal margin of the talon, about half length. Bean-shaped M¹, with paracone much larger than the metacone and well-developed, crest-like protocone and hypocone. Humerus with marked dorsoventral curvature of the shaft, supracondylar crest expanded laterally, large deltoid tuberosity, strong lateral curvature of the deltoid ridge and particularly broad distal epiphysis. Curved radius with small caput and robust distal part. Laterally compressed ulna with curved olecranon. Femur short and robust with strongly developed trochanters.

Description and comparison

Upper teeth. The dimensions (Tab. 1) and external appearance (e.g., state of fossilization, colour, wear virtually absent) of IQW 1966/7313 (Voi. 3525) and IQW 1966/7314 (Voi. 3532) suggest that they may belong to the same individual.

The P⁴ (Figs 2 and 5) shows two morphologically distinct portions, the trigon labially and the talon lingually. In the trigon, the high paracone is oriented almost vertically. The metacone is lower than the paracone and the crest that connects the two cusps are curved lingually. Mesially to the paracone, the parastyle is well defined and pointed mesially, very similar to that observed in *Le. umbra*. As in

		IQW 1966/7313 (Voi. 3525)	IQW 1966/7314 (Voi. 3532)
		right	left
P ⁴	Length	10.3	10.7
	Talon length	8.4	8.0
	Max breadth	8.1	7.9
M ¹	Labial length	8.4	7.9
	Lingual length	7.1	7.0
	Mesial breadth	10.1	10.3
	Distal breadth	9.0	8.9

Tab. 1 - Measurements (mm) of the P⁴ and M¹ of '*Lutra*' *simplicidens* Thenius, 1965 from Voigtstedt (Germany).

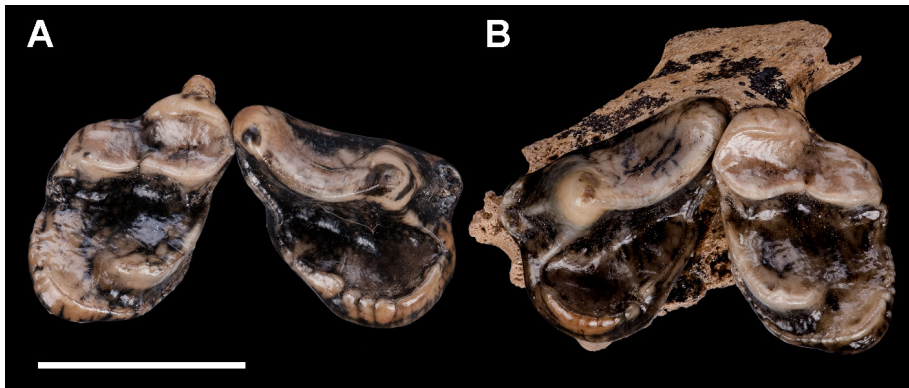


Fig. 2 - P⁴-M¹ of '*Lutra simplicidens*' Thenius, 1965 from Voigtstedt (Germany) in occlusal view. A) Right side, IQW 1966/7313 (Voi. 3525). B) Left side, IQW 1966/7314 (Voi. 3532). Scale bar 1 cm.

Le. umbra, the tip of the parastyle and the mesial wall of the paracone are connected by a distinct crest, which does not extend to the paracone tip. The talon is mesiodistally enlarged, but its distal margin does not reach the distal margin of the metacone in occlusal view. A P⁴ with a broad talon is present

in the extinct *Le. umbra*, *L. licenti*, *Lg. cretensis* and *M. barbaricina* and in the living *Lontra*, *Aonyx*, *Lutrogale* and *Pteronura*. The carnassial talon of *L. simplicidens* from Voigtstedt differs from that of the above taxa in showing a characteristic distal convexity along the distal margin, about half length. Mesiolingually, the protocone is strong and crest-like. It is connected to the paracone by a prominent preprotocrista. The latter character is recognized also in the extant *Lutra* and *Lutrogale*, as well as in the extinct *Le. umbra*, *Le. trinacriae*, *S. ichnusae*, *Lg. cretensis* and *L. licenti*. The distolingual cingulum is visible but very thin.

The bean-shaped occlusal outline of M¹ (Fig. 2) perfectly fits that of *Le. umbra*, and also resembles those of *L. lutra*, *L. sumatrana* and *L. licenti* (Fig. 4). Conversely, in the other Lutrinae the M¹ talon can be oriented mesially (*Le. trinacriae*), almost perpendicular to the tooth row (*S. ichnusae*), or mesiodistally expanded, resulting in an 8-shaped occlusal outline of the molar (*L. bravardi*, *Lontra*, *Pteronura*, *Lutrogale* and especially *Aonyx*). The paracone is much larger than the metacone, as observed in *Le. trinacriae*. The protocone is also well developed, connected to the paracone by a strong crest. The hypocone is on the



Fig. 3 - Left humerus of '*Lutra simplicidens*' Thenius, 1965 from Voigtstedt (Germany). A) Posterior view. B) Medial view. Scale bar 1 cm.

	IQW 1966/7349 (Voi.3658+3659)	BM 17895	NHM 1956/296
	left	left	left
Length	66.0	-	-
Length troch. maj. - lat. epicondyle	64.9	-	-
Min breadth diaphysis	6.0	6.4	8.0
Breadth proximal epiphysis	16.7	-	19.7
Ant-post length proximal epiphysis	16.3	-	21.0
Breadth distal epiphysis	21.2	-	-

Tab. 2 - Measurements (mm) of the humerus of '*Lutra simplicidens*' Thenius, 1965 from Voigtstedt (Germany), West Runton (UK) and Mosbach (Germany). Data for BM 17895 and NHM 1956/269 are from Willemsen (1992).

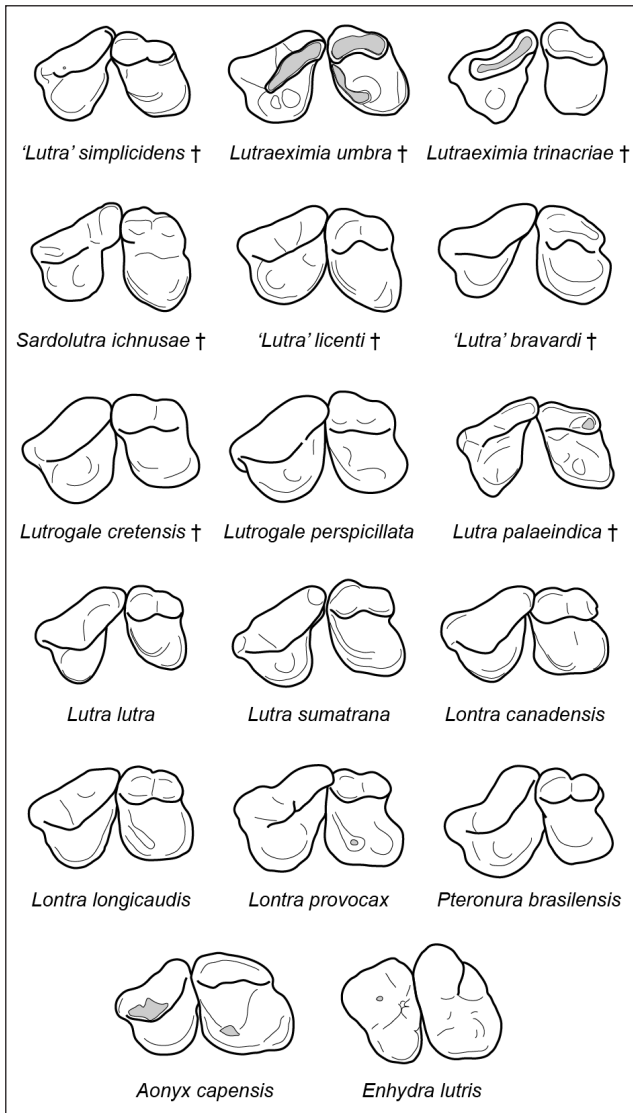


Fig. 4 - Occlusal view of the left P⁴-M¹ of selected extinct and extant Lutrinae, drawn not in scale. '*L.* *simplicidens*, IQW 1966/7314 (Voi. 3532), M¹ labial length (M¹LL): 7.4 mm; *L.* *umbra*, SBAU 337654, M¹LL: 9.3 mm; *L.* *trinacriae*, MGGP SP1, M¹LL: 8.0 mm; *S.* *ichnusae*, re-drawn from Malatesta (1977), M¹LL: 7.5 mm (Willemsen 1992); '*L.* *licenti*, drawn from Van Zyll de Jong (1972), M¹LL: 8.8 mm (Van Zyll de Jong 1972); '*L.* *bravardi*, re-drawn from Gervais (1859), M¹LL: 8.8 mm (Willemsen 1992); *Lg.* *cretensis*, re-drawn from Symeonides & Sondaar (1975), M¹LL: 7.5 mm (Symeonides & Sondaar 1975); *Lg.* *perspicillata*, drawn from Ten Hwang & Larivière (2005), M¹LL: ca. 8.2 mm; *L.* *palaeindica*, NHM 37151, M¹LL: 7.5 mm; *L.* *lutra*, MZUF 12407, M¹LL: 6.6 mm; *L.* *sumatrana*, HNHM 1800.53, M¹LL: 7.2 mm; *Lo.* *canadensis*, HNHM 64.143.1, M¹LL: 7.9 mm; *Lo.* *longicaudis*, MZUF 410, M¹LL: 7.5 mm; *Lo.* *provocax*, MZUF 1602, M¹LL: 7.6 mm; *P.* *brasiliensis*, MZUF 4052, M¹LL: 11.8 mm; *A.* *capensis*, HNHM 67.83.1, M¹LL: 12.7 mm; *E.* *lutris*, HNHM 87.67.1, M¹LL: 12.7 mm. Names of extinct taxa are followed by a dagger. Figure modified from Cherin et al. (2016).

distolingual corner of the talon and is crest-like, as in *L.* *umbra*. The central basin of the talon is concave.

From the dimensional point of view, both the P⁴ and M¹ are relatively small and their measure-

ments are close to those of *L.* *trinacriae* and *S.* *ichnusae* (Fig. 5).

Humerus. The humerus of *L. simplicidens* is known from two specimens discovered at Mosbach 2 (NHM 1956/296) and West Runton Freshwater Bed (BM 17895) (Willemsen 1992). Comparative measurements of the three specimens are reported in Tab. 2. Being almost complete, IQW 1966/7349 (Voi. 3658+3659) is the best preserved humerus of *L. simplicidens* described to date (Fig. 3). IQW 1966/7349 (Voi. 3658+3659), NHM 1956/296 and BM 17895 differ from the humerus of the living *Lutra* in the strong dorsoventral curvature of the shaft, in the supracondylar crest very expanded laterally, in the larger deltoid tuberosity and in the strong lateral curve of the deltoid ridge, which brings to a lateral expansion of the deltoid tuberosity. The above features make *L. simplicidens* resembling *S. ichnusae* from Sardinia and *L.* *trinacriae* from Sicily. Conversely, the distal epiphysis of *L. simplicidens* is wider than those of *S. ichnusae* and *L.* *trinacriae*.

DISCUSSION AND CONCLUSIONS

The new otter material from Voigtstedt is here referred to *L. simplicidens*. The taxonomic attribution of the humerus IQW 1966/7349 (Voi. 3658+3659) is unequivocally supported by its strong morphologic and morphometric affinities with the other humeri of *L. simplicidens* described so far (Willemsen 1992).

Although upper teeth of *L. simplicidens* had never been reported, I can state with reasonable certainty that IQW 1966/7313 (Voi. 3525) and IQW 1966/7314 (Voi. 3532) belong to this species for the following reasons:

- 1) *Lutra simplicidens* is the only otter taxon reported at Voigtstedt (Thenius 1965).
- 2) The taphonomic features (e.g., rust-brownish surface colour with blackish spots and stripes) of the upper teeth are perfectly comparable to those of the other skeletal remains that form the Voigtstedt sample of *L. simplicidens*.
- 3) The size of the upper teeth fits with the predictions based on the size of the lower teeth.

Tab. 3 shows the length of the upper and lower carnassial teeth of some extinct and extant otter species. The latter are selected to cover the range of dental morphotypes found in the Lutrinae, corresponding to different dietary adaptations (see 'fish

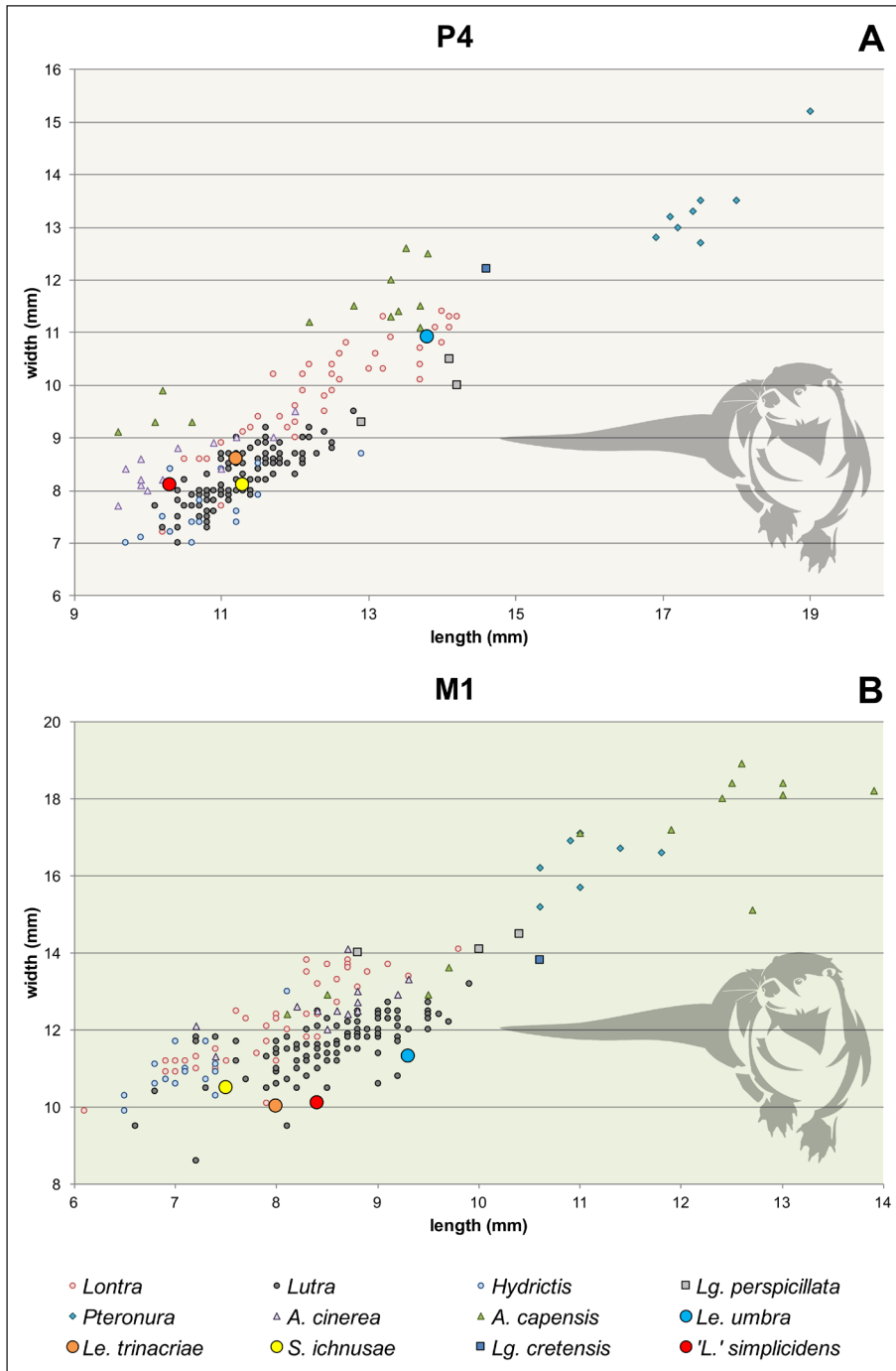


Fig. 5 - Plot of upper tooth measurements in '*Lutra*' *simplicidens* and other extant and extinct otter taxa. A) Plot of P⁴ length vs. maximum width. B) Plot of M¹ labial length vs. maximum width. Morphometric data are from Cherin et al. (2016).

specialist', 'dual purpose' and 'aonychoid' dentitions in Willemsen 1992 and Cherin et al. 2016; the '*Enhydra*' dentition is here excluded due to the aberrant dental anatomy of *E. lutris*.

Considering an average P⁴/M₁ length ratio of 0.855 (Tab. 3), and knowing that the M₁ length of *L. simplicidens* from Voigtstedt is 12.5 mm (Cherin & Rook 2014), the estimated length of the P⁴ results in 10.7 mm, which corresponds to the actual length of the left P⁴ described therein (Tab. 1).

The comparative analysis of the new material

of *L. simplicidens* from Voigtstedt reveals a number of morphological and biometrical features that this species shares with other Quaternary otters of the Mediterranean area. In particular, *L. simplicidens* resembles *Le. umbra* from central Italy in many characters of the upper teeth (P⁴ with well-defined and pointed parastyle, connected to the paracone by a mesial crest; mesiodistally enlarged carnassial talon; prominent preprotocrista; bean-shaped M₁ with crest-like hypocone). Some dental affinities are also observed in *Le. trinacriae*, such as the size difference

Taxon	P ⁴ length	M ₁ length	P ⁴ /M ₁ ratio
<i>Lo. canadensis</i>	11.10	13.2	0.841
<i>Lo. longicaudis</i>	12.8	14.4	0.889
<i>Lo. provocax</i>	12.8	15.6	0.821
<i>Lo. felina</i>	11.2	12.9	0.868
<i>S. ichnusae</i>	11.3	12.9	0.876
<i>Le. trinacriae</i>	11.2	13.1	0.855
<i>M. barbaricina</i>	14.8	17.7	0.836
Average ratio			0.855

Tab. 3 - Length (mm) of the P⁴ and M₁ of selected extant and extinct Lutrinae and ratio between the P⁴ and M₁ length. Mean values for *Lo. canadensis* (N=52), *Lo. longicaudis* (N=27), *Lo. provocax* (N=9) and *Lo. felina* (N=23) are from Van Zyll de Jong (1972). Values for *M. barbaricina* are from Willemsen (1992).

between paracone and metacone in the M¹ and the preprotocrista in the P⁴. The preprotocrista occurs also in *S. ichnusae* and *Lg. cretensis*, as well as in the Chinese *L. licenti*. Finally, the latter species shares with *L. simplicidens* also the enlarged carnassial talon and the bean-shaped M¹. Although the humerus is not known for most of the Plio-Pleistocene fossil otters, the morphology and dimensions of the specimen from Voigtstedt are very similar to those of the humerus of *Le. trinacriae* and *S. ichnusae*.

The phylogenetic analysis performed by Cherin et al. (2016) allows to identify a monophyletic clade that includes the living *Lg. perspicillata* and the extinct *Lg. cretensis* (Crete), *S. ichnusae* (Sardinia), *Le. trinacriae* (Sicily) and *Le. umbra* (Umbria). Although the smooth-coated otter *Lg. perspicillata* today occurs mainly in South and Southeast Asia, the presence of the isolated subspecies *Lg. p. maxwelli* in Iraq (Ten Hwang & Larivière 2005) supports the hypothesis that the Pleistocene distribution of this genus was broader than today and possibly reached the Mediterranean area (Willemsen 1980). The genus *Lutrogale* represents the sister taxon to the three Italian Pleistocene taxa, *S. ichnusae* and the pair formed by *Le. umbra* and *Le. trinacriae* (Cherin et al. 2016). The close phylogenetic relationships between *Lg. cretensis*, *S. ichnusae*, *Le. trinacriae* and *Le. umbra* support the information from the palaeontological record, which indicates that the Pleistocene diversity of Mediterranean Lutrinae had to be much richer than today, when only *L. lutra* survived. In fact, many other taxa from the Mediterranean Pleistocene were not considered in the analysis by Cherin et al. (2016) due to their fragmentary fossil record: *L. euxena* from Mal-

ta, *L. castiglioniis*, *A. majori* and *M. barbaricina* from Sardinia and Corsica, *L. fatimazobrae* from Morocco and especially *L. simplicidens*. For the same reasons, the Authors excluded the Chinese taxon *L. licenti*, which however shares a number of craniodental similarities with *Le. umbra* (Cherin et al. 2016). Some past works speculate on the crucial importance of *L. simplicidens* for the evolutionary history of Mediterranean otters. According to Willemsen (2006), *L. simplicidens* may be ancestral to most of the Middle Pleistocene to Holocene endemic otters of the Mediterranean islands, including *L. euxena*, *Le. trinacriae*, *S. ichnusae*, *L. castiglioniis*, *A. majori* and *M. barbaricina*. Considering the close phylogenetic relationships between *Le. trinacriae*, *S. ichnusae* and *Le. umbra*, Cherin et al. (2016) also hypothesize an affinity between the latter species and *L. simplicidens*. Similarly, Cherin & Rook (2014) point out a probable relationship between *L. simplicidens* and *L. fatimazobrae*.

The present work allows recognizing a number of anatomical similarities in the upper teeth and humerus between *L. simplicidens* and other European Quaternary otters, especially *Le. umbra* and *Le. trinacriae*. This strongly suggests that *L. simplicidens* may be part of the same clade. Unfortunately, this cannot be supported by cladistic data until sufficiently complete cranial material of *L. simplicidens* are discovered. The same goes for the Chinese *L. licenti* and the remaining species from the Mediterranean islands (*L. euxena*, *L. castiglioniis*, *A. majori* and *M. barbaricina*).

New discoveries can also help to clarify the taxonomic status of many of these extinct forms. Most of the taxonomic determinations of Eurasian fossil taxa have been proposed decades ago, when for instance the distinction between *Lutra* and *Lontra* was still not accepted (species of these two genera were traditionally referred to *Lutra*, but the pioneering work by Van Zyll de Jong 1972 and the molecular studies by Koepfli & Wayne 1998 and Koepfli et al. 2008 demonstrated that the morphological and genetic differences between these species justify separate generic attributions). For these reasons, most of the Eurasian species previously assigned to *Lutra* (i.e., '*L. licenti*', '*L. euxena*', '*L. castiglioniis*', '*L. fatimazobrae*' and especially '*L. simplicidens*') would certainly require a taxonomic revision. At the state of the art, in the light of the observed similarities with *Le. umbra* and *Le. trinacriae*, the possible attribution of '*L. simplicidens*' to the genus *Lutraeximia* is plausible, but further discoveries are needed to test this hypothesis.

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REFERENCES

- Bate D.M.A. (1935) - Two new mammals from the Pleistocene of Malta, with notes on the associated fauna. *Proc. Zool. Soc. London*, 1935: 247-264.
- Bonaparte C.L. (1838) - Synopsis Vertebratorum Systematis. *Nuovi Ann. Sci. Nat. Bologna*, 2: 105-133.
- Bowdich T.E. (1821) - An analysis of the Natural Classification of Mammalia for the use of students and travellers. J. Smith, Paris, 115 pp.
- Brisson M.J. (1762) - Regnum animale in classes IX distributum sive synopsis methodica. Editio altera auction. Th. Haak, Leiden, 296 pp.
- Burgio E. & Fiore M. (1988) - *Nesolutra trinacriae* n. sp., lontra quaternaria della Sicilia. *Boll. Soc. Paleontol. It.*, 27: 259-275.
- Cherin M. & Rook L. (2014) - First report of *Lutra simplicidens* (Carnivora, Mustelidae, Lutrinae) in the Early Pleistocene of the Upper Valdarno (Italy) and the origin of European otters. *Ital. J. Geosci.*, 133: 200-203.
- Cherin M., Bertè D.F., Sardella R. & Rook L. (2013a) - *Canis etruscus* (Canidae, Mammalia) and its role in the faunal assemblage from Pantalla (Perugia, central Italy): comparison with the Late Villafranchian large carnivore guild of Italy. *Boll. Soc. Paleontol. It.*, 52: 11-18.
- Cherin M., Iurino D.A. & Sardella R. (2013b) - New well-preserved material of *Lynx issiodorensis valdarnensis* (Felidae, Mammalia) from the Early Pleistocene of Pantalla (central Italy). *Boll. Soc. Paleontol. It.*, 52: 103-111.
- Cherin M., Bertè D.F., Rook L. & Sardella R. (2014a) - Redefining *Canis etruscus* (Canidae, Mammalia): A new look into the evolutionary history of Early Pleistocene dogs resulting from the outstanding fossil record from Pantalla (Italy). *J. Mamm. Evol.*, 21: 95-110.
- Cherin M., Iurino D.A., Sardella R. & Rook L. (2014b) - *Acinonyx pardinensis* (Carnivora, Felidae) from the Early Pleistocene of Pantalla (Italy): predatory behavior and ecological role of the giant Plio-Pleistocene cheetah. *Quat. Sci. Rev.*, 87: 82-97.
- Cherin M., Iurino D.A., Willemsen G. & Carnevale G. (2016) - A new otter from the Early Pleistocene of Pantalla (Italy), with remarks on the evolutionary history of Mediterranean Quaternary Lutrinae (Carnivora, Mustelidae). *Quat. Sci. Rev.*, 135: 92-102.
- Driesch A. von den (1976) - A guide to the measurement of animal bones from archaeological sites. *Bull. Peabody Mus. Nat. Hist.*, 1: 1-137.
- Falconer H. (1868) - Fauna Antiqua Sivalensis. XVII. On *Enhydriodon* (*Amyxodon*), a fossil genus allied to *Lutra*, from the tertiary strata of the Siwalik Hills. *Falconer Palaeont. Mem.*, 1: 331-338.
- Fejfar O., Heinrich W.D. & Heintz E. (1990) - Neues aus dem Villafranchium von Hajna cka bei Filakovo (Slowakei, cssr). *Quartärpaläontologie*, 8: 47-70.
- Fischer von Waldheim G. (1817) - Adversaria Zoologica. *Mém. Soc. Imp. Nat. Moscou*, 5: 368-428.
- Forsyth-Major C.I. (1901) - On *Enhydriodictis galictoides*, a new fossil from Sardinia. *Proc. Zool. Soc. London*, 2: 625-628.
- Geoffroy Saint-Hilaire I. (1826) - Loutre. *Dict. Class. Hist. Nat.*, 9: 515-520.
- Geraads D. (1997) - Carnivores du Pliocene terminal de Ahl al Oughlam (Casablanca, Maroc). *Geobios*, 30: 127-164.
- Gervais P. (1859) - Zoologie et paléontologie française. Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres régions du globe. A. Bertrand, Paris, 628 pp.
- Gmelin J.F. (1788) - Caroli a Linné systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima tertia, aucta, reformata. Impensis Georg. Emanuel. Beer., Leipzig, 500 pp.
- Gray J.E. (1865) - Revision of the genera and species of Mustelidae in the British Museum. *Proc. Zool. Soc. London*, 1865: 100-154.
- Heinrich W.D., Fejfar O. & Schäfer D. (1986) - Nachweis eines Otters (Mammalia: Carnivora) in der paläolithischen Travertinfundstätte von Weimar-Ehringsdorf in Thüringen. *Ausgrabungen Funde*, 31: 199-203.
- Heintz E., Guérin C., Martin R. & Prat F. (1974) - Principaux gisements villafranchiens de France: listes fauniques et biostratigraphie. *Mem. Bureau Rech. Geol. Minières*, 78: 169-182.
- Illiger J.K.W. (1815) - Ueberblick der Säugethiere nach ihrer Vertheilung über die Welttheile. *Abb. Phys. Klas. Kön.-Preuss. Akad. Wissen. Jabr. 1804-1811*, 1815: 39-159.
- Kahlke H.D. (1961) - Revision der Säugetierfaunen der klassischen deutschen Pleistozän Fundstellen von Süßenbom, Mosbach und Taubach. *Geologie*, 10: 493-532.
- Kahlke H.D. (Ed.) (1965). Das Pleistozän von Voigtstedt. *Pal. Abb. A*, 2/3: 211-692.
- Koepfli K.P. & Wayne R.K. (1998) - Phylogenetic relationships of otters (Carnivora: Mustelidae) based on mitochondrial cytochrome b sequences. *J. Zool.*, 246: 401-416.
- Koepfli K.P., Deere K.A., Slater G.J., Begg C., Begg K., Grassman L., Lucherini M., Veron G. & Wayne R.K. (2008) - Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biol.*, 6: 10.
- Kretzoi M. (1953) - Jelentés a kislángi Kalabriai (Villafrankai)

- fauna feltárásáról. *Magy. Állami Földtani Intézet Évi Jelentése*, 1: 213-264.
- Kruuk H. (2006) - Otters: Ecology, Behavior and Conservation. Oxford University Press, New York, 265 pp.
- Larivière S. (1998) - *Lontra felina*. *Mamm. Species*, 575: 1-5.
- Larivière S. (2002) - *Lutra maculicollis*. *Mamm. Species*, 712: 1-6.
- Larivière S. (2003) - *Amblonyx cinereus*. *Mamm. Species*, 720: 1-5.
- Lichtenstein K.M.H. (1835) - Ueber *Lutra maculicollis* Lichtenst. aus dem Kafferlande. *Archiv für Naturgeschichte*, 1: 89-92.
- Linnaeus C. (1758) - Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. L. Salvii, Holmiae, 824 pp.
- Malatesta A. (1977) - The skeleton of *Nesolutra ichnusae* sp. n., a Quaternary otter discovered in Sardinia. *Geol. Romana*, 16: 173-209.
- Malatesta A. (1978) - On the genus *Cyrnaonyx* Helbing, 1935 (Mustelidae, Lutrinae) and its type species. *Quaternaria*, 20: 109-116.
- Molina G.I. (1782) - Saggio sulla storia naturale del Chili. Aquino, Bologna, 368 pp.
- Newton E.T. (1891) - The Vertebrata of the Pliocene deposits of Britain. HM Stationery Office, London, 137 pp.
- Olfers I.F. von (1818) - Bemerkungen zu Illiger's Überblick der Säugethiere nach ihrer Vertheilung über die Welttheile, rücksichtlich der Südamericanischen Arten (Species). *W.L. Eschwege's Journal von Brasilien*, 15: 192-237.
- Pereira E. & Salotti M. (2000) - *Cyrnolutra castiglioni*, une nouvelle forme de loutre (Mustelidae, Lutrinae), dans un depot du Pléistocène moyen "Castiglione 3CG" (Oletta, aute-Corse). *C. R. Acad. Sci. II A*, 331: 45-52.
- Pohle H. (1919) - Die Unterfamilie der Lutrinae. *Arch. Naturgeschichte*, 85A: 1-247.
- Pomel A. (1843) - Note sur une espèce fossile du genre Loutre, dont les ossements ont été recueillis dans les alluvions volcaniques de l'Auvergne. *Bull. Soc. Géol. France*, 1: 168-171.
- Raghavan P., Pickford M., Patnaik R. & Gayathri P. (2007) - First fossil small-clawed otter, *Amblonyx*, with a note on some specimens of *Lutra*, from the Upper Siwaliks, India. *Estud. Geol.*, 63: 135-146.
- Schinz H.R. (1821) - Das Tierreich von dem Herrn. Ritter von Cuvier, 1: 211-214.
- Schreber J.C.D. (1777) - Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen. Wolfgang Walther, Erlangen, 314 pp.
- Stuart A.J. (1981) - A comparison of the Middle Pleistocene mammal faunas of Voigtstedt (Thuringia, GDR) and West Runton (Norfolk, England). *Quartärpaläontologie*, 4: 155-163.
- Stuart A.J. (1982) - Pleistocene vertebrates in the British Isles. Longman, London & New York, 212 pp.
- Soergel W. (1926) - Der Fischotter aus den Kiesen von Süßenborn. *Beitr. Geol. Thür.*, 2: 35-38.
- Sotnikova M. & Titov V. (2009) - Carnivora of the Tamanian faunal unit (the Azov Sea area). *Quat. Int.*, 201: 43-52.
- Sotnikova M., Baigusheva V.S. & Titov V. (2002) - Carnivores of the Khapry faunal assemblage and their stratigraphic implications. *Stratigr. Geol. Correl.*, 10: 375-390.
- Symeonides N. & Sondaar P.Y. (1975) - A new otter from the Pleistocene of Crete. *Ann. Geol. Des. Pays Helliniques*, 27: 11-24.
- Teilhard de Chardin P. & Piveteau J. (1930) - Les mammifères fossiles de Nihowan (Chine). *Ann. Paleontol.*, 19: 1-134.
- Ten Hwang Y. & Larivière S. (2005) - *Lutrogale perspicillata*. *Mamm. Species*, 786: 1-4.
- Thenius E. (1948) - Fischotter und Bisamspitsmaus aus dem Altquartär von Hundsheim in Niederösterreich. *S.B. Österr. Akad. Wiss., math.-naturwiss. Kl.*, 157: 187-196.
- Thenius E. (1951) - Die neuen paläontologischen Ausgrabungen in Hundsheim (NO). *Anz. Österr. Akad. Wiss., math.-naturwiss. Kl.*, 1951: 341-343.
- Thenius E. (1962) - Die Großsäugetiere des Pleistozäns von Mitteleuropa. *Z. Säugetierk.*, 27: 65-83.
- Thenius E. (1965) - Die Carnivoren-Reste aus dem Altpleistozän von Voigtstedt bei Sangerhausen in Thüringen. *Paläont. Abh. A*, 2: 539-564.
- Thomas O. (1908) - On certain African and South American otters. *Ann. Mag. Nat. Hist.*, 14: 57-61.
- Van Zyll de Jong C.G. (1972) - A systematic review of the nearctic and neotropical river otters (Genus *Lutra*, Mustelidae, Carnivora). *R. Ont. Mus. Life Sci. Contrib.*, 80: 1-104.
- Villalta J.F. (1952) - Contribución al conocimiento de la fauna de mamíferos fósiles del Plioceno de Villarroya (Logroño). *Boll. Inst. Geol. Min. España*, 64: 1-203.
- Viret J. (1954) - Le loess à banc durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. Avec une analyse granulométrique. *Nov. Arch. Mus. Hist. Nat. Lyon*, 4: 1-200.
- Willemsen G.F. (1980) - Comparative study of the functional morphology of some Lutrinae, especially *Lutra lutra*, *Lutrogale perspicillata* and the Pleistocene *Isololutra cretensis*. *Proc. Koninklijke Nederl. Akademie van Wetenschappen B*, 83: 289-326.
- Willemsen G.F. (1992) - A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scr. Geol.*, 101: 1-115.
- Willemsen G.F. (2006) - *Megalenhydris* and its relationships to *Lutra* reconsidered. *Hellenic J. Geosci.*, 41: 83-87.
- Willemsen G.F. & Malatesta A. (1987) - *Megalenhydris barbaricina* sp. nov., a new otter from Sardinia. *Proc. Kon. Nederl. Akad. Wetens. B*, 90: 83-92.

