

# Megalenhydris and its relationship to *Lutra* Reconsidered\*

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**ABSTRACT:** The morphology of *Megalenhydris barbaricina* is compared to other lutrines. *Cyrnolutra castiglioni* is transferred to *Lutra*, it is concluded that this is the most probable ancestor of *Megalenhydris*. Since *L. simplicidens* is the probable ancestor of *L. castiglioni*, the former radiated into several species with different ecologies on Sardinia/Corsica. It is further concluded that *Megalenhydris* must be classified in the tribe Lutrini.

**Key-words:** Lutrinae, systematics, ecology, Sardinia / Corsica.

**ΠΕΡΙΛΗΨΗ:** Η μορφολογία του *Megalenhydris barbaricina* συγκρίνεται με άλλα Lutrinae. Προκύπτει ότι το *Cyrnolutra castiglioni* είναι ο πιθανότερος πρόγονος του *Megalenhydris*. Από τη στιγμή που το *L. simplicidens* είναι ο πιθανός πρόγονος του *L. castiglioni*, το πρώτο εξελίχθηκε σε διάφορα είδη με διαφορετικές οικολογίες στη Σαρδηνία/ Κορσική. Συμπεραίνεται περαιτέρω ότι το *Megalenhydris* πρέπει να ταξινομηθεί στα Lutrinae.

**Λέξεις-κλειδιά:** Lutrinae, συστηματική ταξινόμηση, οικολογία, Σαρδηνία/ Κορσική.

## INTRODUCTION

In 1987, a new endemic lutrine from Sardinia was described: *Megalenhydris barbaricina* WILLEMSSEN & MALATESTA 1987. The fossil was discovered at Ispiginoli Cave near Dorgali (ANONYMOUS, 1977; SONDAAR, 1978). I have tentatively classified the species as belonging to the tribe Aonychini (WILLEMSSEN, 1992). This spelling introduced by DAVIS, 1978 is a proper emendation on linguistic grounds of Sokolovs (1973) Aonyxina, which would give Aonyxini.) New findings and reconsideration of earlier described material seem to indicate a closer relationship with *Lutra*.

## MATERIAL

The only specimen of *Megalenhydris barbaricina* is the holotype, preserved at the Museo Civico Di Archeologia e Speleologia in Nuoro, Sardinia. It is a partly preserved skeleton, including a left mandible with dentition, a P4 and M1 and a humerus. Part of the axial skeleton and some hind limb bones are embedded in the sediment and partly covered by calcite. The fossil was found in an abyssal cave on the cave floor, covered by calcite. It is therefore impossible to put it into a stratigraphical context, but it may be of Late Pleistocene age or younger. The material was described in WILLEMSSEN & MALATESTA (1987) and in WILLEMSSEN (1992) and does not need to be repeated. Though, I want to point out that the description of the m1 in WILLEMSSEN & MALATESTA (1987) was not correct. The

description was corrected in WILLEMSSEN (1992).

The m1 talonid has a large lingual extension. But the talonid is less wide than the trigonid. In all Aonychini the talonid is considerably wider. In *Lutra lutra* the ratio of trigonid width and talonid width is varying between 1.00 and 1.28 (13 specimens, recent and subfossil). In *Lutra simplicidens* it is 0.99 in four specimens. In *Lutra fatimazohrae* it is even smaller and in *Lutra trinacriae* and *Sardolutra ichnusae* it is 1.00 (see Table 1). Also, the external cingulum of the talonid is not very well developed in *Megalenhydris barbaricina*. The hypoconid has the form of a crest as in Lutrini, whereas it is a cuspid in Aonychini. The hypoconulid is absent, unlike *Lutra lutra*. The same condition is found in *Lutra trinacriae*, *Cyrnolutra castiglioni*, *Sardolutra ichnusae*, *Lutra simplicidens* and

TABLE 1

Ratio of talonid width and trigonid width of m1.

|                                  |                               |
|----------------------------------|-------------------------------|
| <i>Lutra lutra</i>               | 1,00 – 1,28 (n=15, mean 1,10) |
| <i>Lutra fatimazohrae</i>        | 0,93-0,96 (n=2)               |
| <i>Lutra simplicidens</i>        | 0,97 (n=4)                    |
| <i>Lutra trinacriae</i>          | 1,00 (n=1)                    |
| <i>Sardolutra ichnusae</i>       | 1,00 (n=1)                    |
| <i>Megalenhydris barbaricina</i> | 0,99 (n=1)                    |
| <i>Algarolutra majori</i>        | 1,00 (n=1)                    |
| <i>Cyrnaonyx antiquus</i>        | 1,04 – 1,13 (n=6, mean 1,10)  |

\* Αναθεώρηση του γένους *Megalenhydris* και της σχέσης του με το γένος *Lutra*.

*Lutra fatimazohrae* (WILLEMSSEN, 1992; PEREIRA & SALOTTI, 2000; GERAADS, 1997).

The upper dentition is robust, P4 is broad and has a large talon. Some Lutrini (*Lutrogale* and *Pteronura*) have large P4 talons, but the tooth is relatively wider in *Megalenhydris barbaricina*, having dimensions like in *Aonyx capensis*. On the other hand, the tooth is not as blunt as in that species.

The most unique character of *Megalenhydris barbaricina* is the dorsoventrally flattened condition of the first five caudal vertebra which are preserved. The condition of the sacrum is difficult to assess. PEREIRA & SALOTTI (2000) report a rather flattened caudal part of the sacrum in *Cyrnolutra castiglioni*, unlike the otherwise in many respects similar *Sardolutra ichnusae*. Both species had a very strong tail, used in swimming, to a larger extent than other lutrines.

**DISCUSSION**

A number of endemic lutrines have been described from the Mediterranean islands. The first one to be described was *Lutra euxena* (BATE, 1935) from Tal Gnien in Malta. This species is known only by some limb bones, a canine and an incisor. It is probably of Middle Pleistocene age (WILLEMSSEN, 1992). From Sicily, the Middle Pleistocene *Lutra trinacriae* (BURGIO & FIORE, 1988) was described. Only the holotype, an almost complete skeleton, is known. Both species show great similarities to *Lutra simplicidens* (WILLEMSSEN, 1992). From Sardinia and Corsica (which can be treated as one area, since faunal exchange was quite possible during large parts of the Plei-

stocene), four species have been described. *Sardolutra ichnusae* (MALATESTA, 1977) is known by one skeleton from the Würm/Weichselian of Nettuno Cave, Sardinia. *Algarolutra majori* (MALATESTA, 1978; see also MALATESTA & WILLEMSSEN, 1986) is known from Corsica and Sardinia. The findings from Dragonara Cave, Sardinia are probably Würm/Weichselian (WILLEMSSEN, 1992), the findings from Corsica cannot be dated. The species is very incompletely known: some upper molars as well as a few limb bones described by GLIOZZI (1985). The third species is *Cyrnolutra castiglioni* PEREIRA & SALOTTI, 2000 from the Middle Pleistocene from Castiglione Cave, Corsica. It is reported from a level called Cast 3CG and SALOTTI *et al.* (1997) report an absolute date for a cervid bone of 157500 BP (+22200/-17300), which is the late Middle Pleistocene. The fourth species from Sardinia/Corsica is *Megalenhydris barbaricina*. From Crete, *Lutrogale cretensis* (SYMEONIDES & SONDAAR, 1975) has been described. The species is known by one almost complete skeleton as well as some more specimens, all from Liko Cave on the island of Crete (SYMEONIDES & SONDAAR, 1975; WILLEMSSEN, 1980, 1992, 1996). *Algarolutra majori* fossils were found in a level called Liko Ba. REESE *et al.* (1996) dated Liko B to 105000 years BP ± 20% by amino acid racemization. This would mean the last interglacial, corresponding to the Eemian.

The common species of River Otter during the Middle Pleistocene in Europe seems to have been *Lutra simplicidens* Thenius, 1965. This species is known from a number of localities throughout Europe. The material is not abundant, as lutrine fossils never tend to be, but the geographic and stratigraphic distribution suggests that the

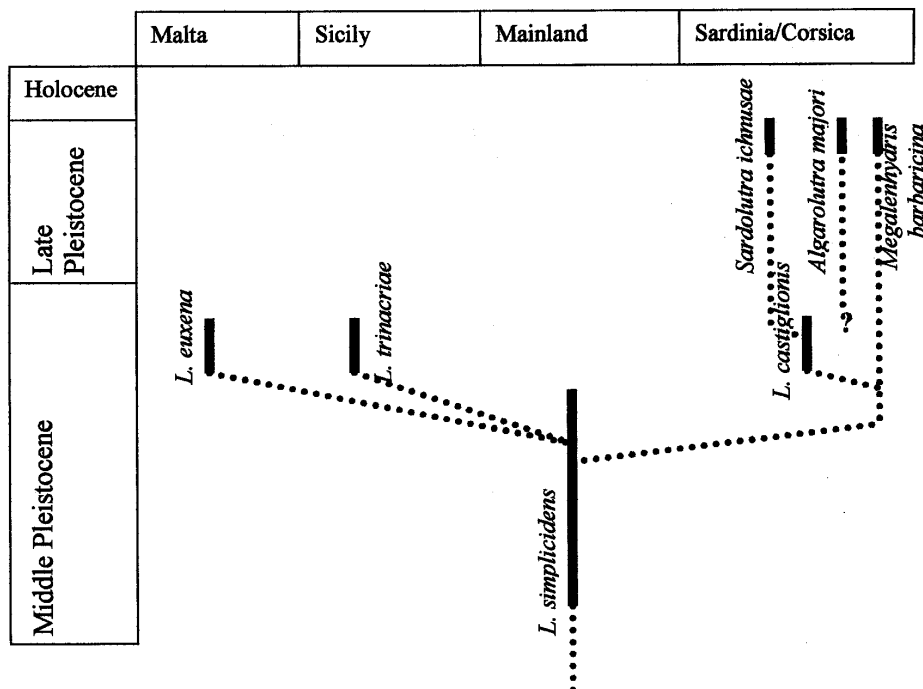


Fig. 1. The endemic lutrines from the Mediterranean islands.

species lived in a large part of Europe during the Middle Pleistocene. The species is known from localities from Central Europe (Voigtstedt, Mosbach, Hundsheim, Süßenborn, perhaps also from Uppony in Hungary) and from Britain (East Runton, West Runton and Eastern Bavents) (for an overview see WILLEMSEN, 1992).

The extant European Otter *Lutra lutra* (L., 1758), which is present throughout the largest part of Eurasia today, cannot be derived from *L. simplicidens*. The latter has a postcranial skeleton which is more derived in its adaptation to an aquatic way of life. A direct phylogenetic relationship is therefore improbable (THENIUS, 1965; WILLEMSEN, 1992). As I have pointed out before, *L. lutra* as well as *L. sumatrana* GRAY, 1865 from South-East Asia are closely related to *L. palaeindica* FALCONER, 1868 from the Upper Siwalik in Pakistan. Probably, there is a close phylogenetic relationship between the three species and it is quite conceivable that *Lutra palaeindica* was ancestral to *L. lutra* and *L. sumatrana*.

I consider *L. lutra* to be an immigrant from Asia to Europe during the Late Pleistocene/Early Holocene. There is no certain fossil record of the species in the European Pleistocene. Pleistocene mentionings of the species have to be considered with care, since they turned out to be *L. simplicidens* in all cases where I had opportunity to check the material (WILLEMSEN, 1992).

The ancestry of *Lutra simplicidens* is unknown. The genus is badly known from before the Middle Pleistocene. From some of the older descriptions from Europe, such as *L. affinis* and *L. bravardi*, the holotypes nor any other material are available today and the descriptions are quite insufficient. *L. lybica* STROMER, 1914 from Wadi Natrun (Pliocene, Egypt) is not very well described either. It can be seen however that the specimen (a mandible with p2-m1) is rather aberrant. Its lower carnassial has a very short and triangularly shaped talonid, unlike any other known *Lutra*.

The only older species which shows resemblance to *Lutra simplicidens* is *Lutra fatimazahrae* GERAADS, 1997. The species was found in Upper Pliocene deposits from Ahl Algarolutra majori Oughlam, Morocco. The similarity was noted by GERAADS (1997), who gives a good description of the material (two parts of mandibles, an isolated lower carnassial and a femur fragment). The *Lutra fatimazahrae* material is strikingly like *Lutra simplicidens*. Similarities are the m1 talonid being narrower than the trigonid (see Table 1), the lack of a hypoconulid on the m1 and the in comparison with *Lutra lutra* more medially placed trochanter minor on the femur. *Lutra fatimazahrae* differs from *Lutra simplicidens* by its larger size, the higher mandibular ramus and the more developed m1 metaconid. GERAADS (1997) may be right in ruling out *Lutra fatimazahrae* as ancestor to *Lutra simplicidens*, but a close phylogenetic relationship between the species is beyond doubt.

We may conclude that *Lutra simplicidens* represents a

lineage of Lutrini which has been present in the region for some time and was widely spread during the Middle Pleistocene.

*Lutrogale cretensis* does clearly have a phylogenetic relationship with *Lutrogale perspicillata* (WILLEMSEN, 1980), which represents an Asiatic genus, not known from the European mainland. I have earlier pointed out similarities of *Lutra euxena*, *Lutra trinacriae* and *Sardolutra ichnusae* with mainland *Lutra simplicidens* and presumed the latter to be ancestral to the mentioned three species (WILLEMSEN, 1992). I choose to put *Sardolutra ichnusae* in a separate genus because of a number of unique characters: the lack of P1, the fused 2nd and 3rd spine of the sacrum, the proximally fused tibia and fibula and the peculiar and very large baculum.

*Cyrnolutra castiglioni* was described by PEREIRA & SALOTTI (2000). Unfortunately, they did not make direct comparisons to *Lutra simplicidens*. It is clear from their description however, that *Cyrnolutra castiglioni* shows many similarities to both *Lutra simplicidens* and to the island species *Lutra euxena*, *Lutra trinacriae* and *Sardolutra ichnusae*. As far as the parts are known, the structure of both humerus and femur are similar. The humerus is not keeled, has a stronger curvature than in *Lutra lutra* and the deltoid ridge shows an outward curve in all four species, contrary to *Lutra lutra*. The radius also resembles the other island species and *Lutra simplicidens*. It is strong and has well developed muscular insertions. The structure of the m1 is also similar, having a rather narrow talonid. Both *Cyrnolutra castiglioni*, *Lutra trinacriae* and *Lutra simplicidens* lack a hypoconulid. This is however present in *Sardolutra ichnusae*.

*Cyrnolutra castiglioni* has one unique character in common with *Sardolutra ichnusae*: the fused second and third sacral spine. This points at a more close phylogenetic relationship between those two species. On the other hand, The sacrum of *Cyrnolutra castiglioni* does differ from *Sardolutra ichnusae* in that the caudal part (3rd vertebra) is dorsoventrally flattened. Considering the other characteristics of *Sardolutra*, the baculum is not extremely large as in the latter and m1 does not have a hypoconulid. Whether the fibula and tibia are fused proximally or not, is unknown. The metapods do not indicate a foot as large as in *Sardolutra ichnusae*. The very large baculum is connected to a marine way of life (facilitating mating in open sea) and *Cyrnolutra castiglioni* was therefore probably living in fresh water, as PEREIRA & SALOTTI (2000) pointed out.

The flattening of the caudal part of the sacrum, which is a rather peculiar character for a lutrine, do not make a direct ancestry of *Cyrnolutra castiglioni* to *Sardolutra ichnusae* probable. But the fused sacral spines as well as overall resemblance indicate a very close relationship between *Cyrnolutra castiglioni* and the direct ancestor of *Sardolutra* (Fig 1). I think that *Cyrnolutra castiglioni* resembles the other species to an extent, that it could be

included in the genus *Lutra* together with the Sicilian and Maltese lutrines, and the species should then be named *Lutra castiglioni*. As PEREIRA & SALOTTI (2000) state themselves, *Lutra simplicidens* is the most probable ancestor for this species.

The finding of *Lutra castiglioni* casts new light on the relationships of *Megalenhydris barbaricina*. The large talons in the P4 and M1 in the latter, suggested to me a relationship to the Aonychini (WILLEMSSEN, 1992). In that case, one could think of some relationship to the continental aonychine *Cyrnaonyx antiquus*. On the other hand the m1 is more like the Lutrini, especially the relatively narrow talonid and the lack of cuspids on the talonid. This condition seems to indicate that the species in fact is related *Lutra*, and especially to *Lutra simplicidens* and *Lutra castiglioni*. Even in *Megalenhydris barbaricina*, a hypoconulid is not present in m1. The enlarged talons of P4 and M1 are then a secondary adaptation to a diet comprising bottom-dwelling fish as well as crustaceans, rather than motile fish as most *Lutra* are feeding on. The flattening of part of the sacrum in *Lutra castiglioni* and the flattening of the first five caudal vertebrae of *Megalenhydris barbaricina* (the condition of the sacrum cannot be assessed) point also towards a phylogenetic relationship. In both cases it reflects a much stronger tail, which was more important in propulsion in an aquatic environment than in other lutrines. The humerus of *Megalenhydris barbaricina* is somewhat less curved than in *Lutra lutra* and the deltoid tuberosity is not enlarged in the same way as in *Lutra castiglioni* and *Sardolutra ichnusae*. This also may reflect the fact that the tail has become much more important in propulsion than the fore limbs. So the most probable Middle Pleistocene ancestor of *Megalenhydris barbaricina* is *Lutra castiglioni*. As a consequence, the species must definitively be included in the Lutrini.

Somewhat isolated stands *Algarolutra majori*. Even here, P4 has an enlarged talon, compared to *Lutra*. The m1 however has a rather narrow talonid, as in *Lutra simplicidens* and the hypoconid forms a ridge. GLIOZZI (1985) described some postcranial bones, a humerus, some metapodials and a phalange. The humerus is less curved than in *Lutra lutra*, which is contrary to *Lutra simplicidens* and the island *Lutra* species, but like *Megalenhydris barbaricina*. Remains of *Algarolutra majori* are far too fragmentary to give us possibility to say much about the phylogenetic position of the species, but from what we know now, some relationship to the other Sardinian and Corsican lutrines is the most plausible.

## CONCLUSIONS

We may conclude that *Lutra simplicidens* reached Sardinia/Corsica, Sicily and Malta during the early Middle Pleistocene or even before. On all islands, an endemic species evolved. On Sardinia/Corsica at least two closely related forms evolved, one of them being *Lutra*

*castiglioni*, and in the Late Pleistocene several species, adapted to different environments, had evolved: the small, marine *Sardolutra ichnusae*, feeding on highly motile fish, the very large *Megalenhydris barbaricina*, feeding on large fish and shellfish and crustaceans and *Algarolutra majori*, feeding on fish and crustaceans.

Regarding taxonomy, we may conclude that *Megalenhydris barbaricina* has to be classified as a Lutrini, *Cyrnaolutra castiglioni* is transferred to the genus *Lutra*.

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