Paralutra garganensis sp. nov. (Mustelidae, Lutrinae), a new otter from the Miocene of Gargano, Italy

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A new lutrine species, *Paralutra garganensis*, is described from the Miocene of the Gargano area, Italy. The material consists of a maxillary fragment with P^4 and M^1 and a calcaneum. There is a clear resemblance with *P. jaegeri* (Fraas), but the talon of the P^4 is larger in the Gargano species. Also, the latter species was larger. It is concluded, that *P. jaegeri* was ancestral to *P. garganensis*, and that the latter probably fed on shellfish to a greater extent than the former.

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Introduction

In 1969, the upper Miocene fissure fillings in the Gargano area (province Foggia, Italy) were discovered by Drs C. Beets, M. Freudenthal and H.J.W.G. Schalke. A large number of vertebrate remains has been collected and is stored at the Rijksmuseum van Geologie en Mineralogie at Leiden. The vertebrates belong to the

following groups: Amphibia, Reptilia, Aves (Ballmann, 1973, 1976), Insectivora (Freudenthal, 1971, 1972; Butler, 1981), Rodentia (Freudenthal, 1971, 1976), Lagomorpha (Freudenthal, 1976), Carnivora, and Artiodactyla (Freudenthal, 1971; Leinders, in press). The fauna has an unbalanced character and quite a few endemic forms occur. Several endemic birds have been described. The giant insectivore *Deinogalerix koenigswaldi* Freudenthal, 1972 (see also Butler, 1981) is also an endemic form and even an entire endemic family of ruminants is known, the Hoplitomerychidae (Leinders, in press). The only known carnivore is the otter to be described in this paper. From the character of the fauna Freudenthal (1971) concluded that the Gargano Peninsula must have been an island during the late Miocene. Geological data show that the area became separated from the mainland during the middle Miocene (Jacobacci, 1962).

Acknowledgements

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Taxonomic description

Family Mustelidae Swainson, 1835
Subfamily Lutrinae Baird, 1857
Tribe Lutrini Sokolov, 1973
Genus *Paralutra* Roman & Viret, 1934

Paralutra garganensis sp. nov.
Pl. 1, figs. 2, 3.

Holotype – Part of maxilla sin. with P^4 and M^1 in situ, stored in the Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands, RGM 261 151.
Type locality – Fina H, Gargano, prov. Foggia, Italy.
Age – Late Miocene.
Derivatio nominis – From Gargano, where the fossil was found.
Material – The holotype (see above) and a calcaneum dex., RGM 261 152.
Diagnosis – Lutrine, larger than both *Lutra lutra* L., 1758 and *Paralutra jaegeri* (Fraas, 1862). The P^4 has a very large paracone, the metacone is much lower. The protocone is a small, separate cusp, situated lingually from the paracone. A large talon extends to the posterior edge of the trigone. The large talon of the P^4 forms the most striking difference with *P. jaegeri*. The M^1 has a large talon, extending backward as a kind of lobe; the lingual length of the tooth is considerably greater than the buccal length. The protocone is much elongated. A real hypocone is absent. The tooth resembles very much that of *P. jaegeri*, but it is relatively less wide in comparison to its antero-posterior length.

Table 1. Tooth measurements, in millimetres. *Paralutra jaegeri* after Helbing (1936). RGM = Rijksmuseum van Geologie en Mineralogie, Leiden; RMNHL = Rijksmuseum van Natuurlijke Historie, Leiden.

		Paralutra garganensis RGM 261 151	*Lutra lutra* RMNHL 12 915	*Paralutra jaegeri* Darmstadt IN 936	*Paralutra jaegeri* Stuttgart 4082
P^4	buccal length	12.6	10.8	10.9	12.8
	talon max. length	ca. 10.8	7.0	–	10.1
	width	12.0	8.5	8.0	–
	paracone heighth	8.3	–	6.3	8.6
M^1	buccal length	9.4	8.2	6.0	–
	lingual length	10.9	7.2	6.7	–
	width	13.4	12.1	10.3	–

DESCRIPTION OF THE MATERIAL

Left maxillary fragment with P^4 and M^1 in situ, holotype (RGM 261 151, Pl. 1, fig. 3)

Measurements are given in Table 1.

P^4 – The paracone is much higher than the other cusps. The difference between the paracone and the metacone is much greater than in the *Lutra lutra* specimen used for comparison. The posterior slope of the paracone forms, together with the metacone, a slightly concave cutting edge. Anteriorly, a very small parastyl is present. Lingually from the paracone lies the protocone as a seperate cusp. The talon is relatively large, larger than in both *L. lutra* and *P. jaegeri*, and extends to the posterior edge of the trigone covering the entire lingual side of the tooth. It forms a hollow basin, surrounded by a cingulum. Anteriorly, the cingulum continues on the buccal side backward to halfway the paracone. The P^4 is three-rooted, with two roots on the outer side and one on the inner.

M^1 – The paracone and the metacone are much lower and not as sharp as in our *Lutra* specimen. The parastyl is low and not as strongly developed as in *Lutra*. It touches the P^4 metacone, which is also very low. Both cusps are about equally high. The protocone is much elongated and forms a ridge, beginning at the base of the parastyl and extending inward and backward. Between this ridge and the paracone-metacone a hollow basin is present. The talon extends as a lobe further backward than the trigone. The inner cingulum is well developed. A real hypocone is not present as a separate cusp, but as a slight protuberance in the cingulum. The tooth is, in comparison to its antero-posterior length, not as wide as in *P. jaegeri* specimens (Helbing, 1936). The M^1 has two small roots on the outer side and a large one on the inner side.

Table 2. Calcaneum measurements, in millimetres. RGM = Rijksmuseum van Geologie en Mineralogie, Leiden; RMNHL = Rijksmuseum van Natuurlijke Historie, Leiden.

	Paralutra garganensis RGM 261 152	*Lutra lutra* RMNHL 12915
length (part of tuber absent!)	31.1	–
smallest width of tuber	6.9	5.0
smallest height of tuber (dorsoventrally)	11.5	9.3
transversal breadth of cuboid facet	10.9	9.2
dorso-ventral breadth of cuboid facet	9.6	8.1
smallest breadth of groove between the astragalar facets	2.7	2.4

Right calcaneum (RGM 261 152, Pl. 1, fig. 2)

Measurements are given in Table 2.

The calcaneum looks typical lutrine (see Stains, 1976), but is much larger than in *L. lutra*, and therefore the assignment to *P. garganensis* seems warranted. It lacks the posterior part of the tuber. The astragalar facets are relatively larger than in *L. lutra*. In a dorsal view, the lateral astragalar facet covers the entire width of the tuber, which is not the case in our *L. lutra* specimen. The medial astragalar facet has a trapezoid shape. The tuber is not very broad, as in *Enhydra*, but slender, as in *Lutra*. The peroneal tubercle, which is grooved for the tendon of the peroneus longus, is hardly perceptible. The cuboid facet is less circular than in *L. lutra*.

Discussion

Comparing the Gargano otter with other Miocene lutrines from Europe, such as *Potamotherium miocenicum* (Peters, 1868), *Enhydriodon* Falconer, 1868 and *Paralutra*, it becomes clear, that there are close affinities with *Paralutra*. The structure of the P^4 and the M^1 of *Potamotherium* is quite different from our specimen: the protocone of the P^4 is not present as a seperate cusp and the metacone of the same tooth forms, in an occlusal view, a sharp angle with the paracone; the M^1 of *Potamotherium* is triangular and has a structure not found in any other lutrine (see Pohle, 1919; Thenius, 1949; Savage, 1957). This characteristic structure is also found in the Oligocene species *Potamotherium valletoni* Geoffroy, 1833.

Enhydriodon and some close relatives (*Sivaonyx* Pilgrim, 1932 and *Vishnuonyx* Pilgrim, 1932) were described from the Siwaliks (Falconer, 1868; Lydekker, 1884; Pilgrim, 1932). Later, they have also been reported from other places. From Europe, Pilgrim described *E. latipes* from Pikermi. Only remains of the hind leg are known, and since such remains are not known from the Siwalik otters, it is difficult to judge whether this is really an *Enhydriodon*. *E. campanii* (Meneghini, 1863) from the Sarmatian of Monte Bamboli, Toscana, Italy, is known by an upper tooth row. The teeth are very massive, a normal characteristic of the genus, and the more or less quadrangular P^4 possesses four large cusps. *E. lluecai* Villalta Comella & Crusafont Pairó, 1945 from the Pontian of Spain is represented by a lower jaw and tooth row. The structure of the P^4 in the genus *Enhydriodon* is very characteristic and it is quite clear that the Gargano otter represents a different lutrine stock.

From the Pontian of Eppelsheim *Lutra hessica* Lydekker, 1890 has been described, based on an M_1 only. Pohle (1919) includes it in *Aonyx* Lesson, 1827.

Paralutra jaegeri (Fraas, 1862) (synonym: *Lutra lorteti* Filhol, 1879) is the type species and only species described sofar, of the genus *Paralutra*. It is known from several places in Europe, such as La Grive-St Alban, Ravensburg and Steinheim (Helbing, 1936; Ginsburg, 1968). The mandibular fragment from Pellecahus (France), described by Roman & Viret (1934), does not belong to this species but to *Mionictis artenensis* Ginsburg, 1968 (which is not a lutrine) according to Ginsburg. The shape of the M^1 of *Paralutra* is very characteristic. It has a much elongated protocone and, at the lingual side, the talon extends backward as a kind of lobe. Comparing the M^1 of the Gargano otter with the plates and figures in Helbing (1936), a great resemblance is apparent. Also the P^4 resembles the one of *P. jaegeri*, though the large talon of the Gargano specimen forms a striking difference. Undoubtedly the Gargano otter is a *Paralutra*.

P. jaegeri is variable in size (Helbing, 1936) but the Gargano form is larger than the largest measurements given by Helbing. This, together with the morphological differences described above, fully justifies the creating of a new species for this form.

P. garganensis probably was an endemic form on the Late Miocene island Gargano. Its ancestor was, most probably, *P. jaegeri* from the mainland. Whether *P. garganensis* was a relic on the island from before the separation from the mainland, adapting itself to local conditions and thus diverging from *P. jaegeri* after its isolation, or an immigrant from the mainland, diverging from its ancestor after its arrival on the island, is unknown.

As stated in the introduction, the fauna on the Gargano island was a typically unbalanced one. Such faunas are known from the Pleistocene of many Mediterranean islands (Sondaar, 1977; Dermitzakis & Sondaar, 1978). Almost always, large carnivores are absent from these faunas. Of the large mammals only good swimmers, such as deer, elephants and hippopotamuses, managed to reach the islands. The only carnivores found on several such islands are otters, which, of course, are good swimmers (from the Pleistocene of Malta, though, a bear is known). Otters are, however, rare, compared with other mammalian remains. Isolated on the island, endemic forms may evolve, adapted to the local ecological conditions. From Crete, *Isolalutra cretensis* Symeonides & Sondaar, 1975 was described. The extant Asian genus *Lutrogale* probably was ancestral to this endemic form (Willemsen, 1980). From Sardinia and Corsica, a large otter has

been described as *Cyrnaonyx majori* Malatesta, 1978. Also from Sardinia, a small species, *Nesolutra ichnusae* Malatesta, 1977, is known. From Malta, postcranial remains have been described as *Nesolutra euxena* Bate, 1935.

Some of these island forms became more adapted to a marine environment, such as *Nesolutra ichnusae* (see Malatesta, 1977), others to a more terrestrial way of life, as is the case with *Isolalutra cretensis* (Willemsen, 1980). The remains of *Paralutra garganensis* are too few to say much about its ecology. The dentition, however, gives some information on the feeding habits of a lutrine. Especially the P^4 is important. In living species, forms with a small talon, such as *Lutra lutra*, feed mainly on fish. Forms with a large talon and relatively massive teeth, such as *Aonyx*, feed on shellfish mainly. *Lutrogale perspicillata* Geoffroy, 1826, has close affinities with *Lutra*. The P^4 has an expanded talon, however, and it is known to feed on shellfish to a greater extent than *L. lutra* (Willemsen, 1980). From the large talon it can be inferred that *P. garganensis* fed on shellfish to a greater extent than its ancestor, *P. jaegeri*.

It is difficult to say much about the possible terrestrial or marine habits of *P. garganensis*. Some conclusions may be drawn from the calcaneum. In *Enhydra lutris* (L., 1758), the Sea Otter, and in phocids, the tuber calcanei, to which the achilles tendon is attached, is broad and the peroneal tubercle large and grooved. The same is the case in *Potamotherium valletoni*. In *Enhydra* and in phocids, the m. peroneus longus and other extensors of the foot are well developed. In *Enhydra*, the lateral astragalar facet is flat, smooth and facing dorsally rather than toward the lateral side. It is relatively small (see Stains, 1976). In *P. garganensis*, the tuber is relatively slender, as in *Lutra*, the peroneal tubercle is less developed than in *Lutra*, and the lateral astragalar facet is more like it is in *Lutra* than in *Enhydra*. I think it improbable that *P. garganensis* was as highly aquatic as *Enhydra* or *Potamotherium*, but, of course, one has to be very careful in drawing conclusions from so little material. Whether it was semiaquatic, like *Lutra*, ore more terrestrial, like, to some extent, *Lutrogale*, and, to a far greater extent, *Aonyx*, remains unknown until more material is found.

It is clear, that *Paralutra* is related to *Lutra* and its allies, the tribe Lutrini of Sokolov (1973). As Malatesta (1977) pointed out, *Paralutra* cannot be considered ancestral to *Lutra*, since in *P. jaegeri* no P^1 is present, contrary to *Lutra* and *Lutrogale*. Malatesta (1977) considers *Paralutra* to be ancestral to *Nesolutra ichnusae*. There are indeed some similarities in the structure of the P^4 and the M^1. On the other hand, the typical posterior expansion of the M^1 and the elongated protocone are absent in *N. ichnusae*. A descendance of *N. ichnusae* from *Paralutra* is certainly possible, but far from proved at the moment.

Conclusions

Paralutra garganensis was an endemic species on the Miocene island of Gargano. It probably fed on shellfish to a greater extent than its ancestor, *P. jaegeri*, which was probably a fish-eater like *Lutra lutra*. On the basis of the material presently available, it is unlikely that *P. garganensis* was a highly aquatic form like *Enhydra* or *Potamotherium*.

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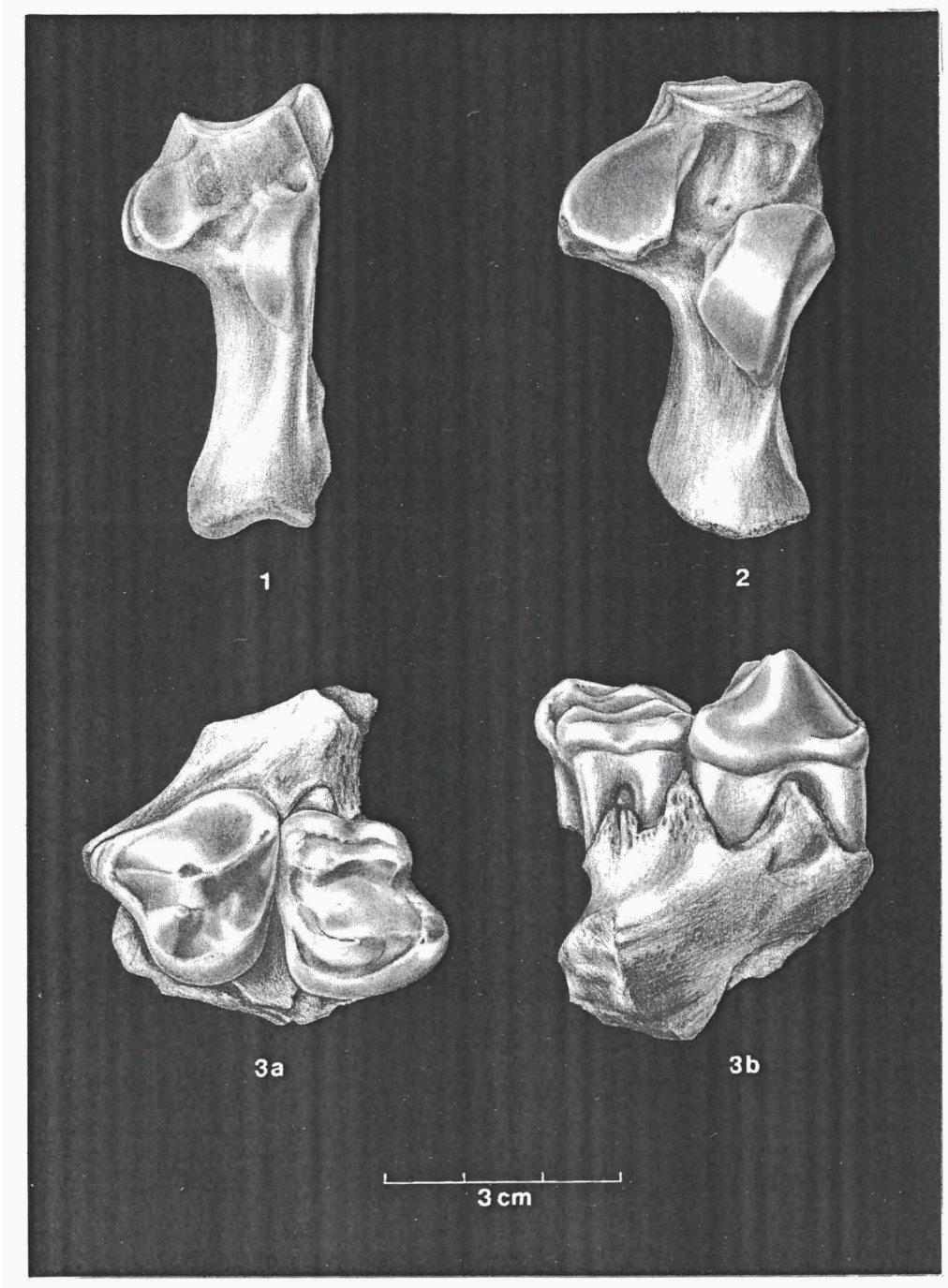
Plate 1



1. *Lutra lutra*, RMNHL 12 915, right calcaneum.
2. *Paralutra garganensis*, RGM 261 152, right calcaneum.
3. *Paralutra garganensis*, RGM 261 151, left maxillary fragment with P^4 and M^1, a: occlusal view; b: lingual view.