

New remains of *Paralutra garganensis* Willemsen, 1983 (Mustelidae, Lutrinae) from the Late Miocene “Terre Rosse” of Gargano (Apulia, Italy)

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KEY WORDS - *Paralutra garganensis*, *Mikrotia fauna*, Late Miocene, Gargano, Italy.

ABSTRACT - A short account is presented here of the discovery of new material attributable to *Paralutra garganensis* Willemsen, 1983, the only carnivore species documented from the Late Miocene endemic “Terre Rosse” faunal complex (also referred to as the “*Mikrotia fauna*”). Although thousands of fossil remains of the “*Mikrotia fauna*” have been collected during extensive sampling campaigns carried out since the 1970s, *Paralutra garganensis* was to date only represented by the type specimens. The recent revision of material belonging to the “*Mikrotia fauna*” housed in Museum collections in Firenze and Torino (Italy) and Leiden (Netherlands) has allowed the identification of the specimens described herein and, furthermore, has highlighted new evidence regarding the ecology of the species. The latter findings in turn broaden our understanding to date of the ecological structure of the “*Mikrotia fauna*”.

RIASSUNTO - [Nuovi resti di *Paralutra garganensis* Willemsen, 1983 (Mustelidae, Lutrinae) dai depositi a “Terre Rosse” del Miocene Superiore del Gargano (Puglia, Italia)] - In questa breve nota vengono descritti nuovi resti attribuibili a *Paralutra garganensis* Willemsen, 1983, l'unica specie di mammifero carnivoro conosciuta all'interno del complesso faunistico del Miocene Superiore delle “Terre Rosse” del Gargano (noto anche come “Fauna a *Mikrotia*”). Tra le molte migliaia di resti attribuiti alla “Fauna a *Mikrotia*” raccolti a partire dalla fine degli anni 1970, *Paralutra garganensis* era rappresentato solo dalla serie-tipo. La recente revisione dei materiali conservati a Firenze, Torino e Leiden ha permesso l'identificazione del nuovo materiale descritto nel presente lavoro, con ulteriori indicazioni sull'ecologia della specie. Questi nuovi dati permettono anche di aumentare le conoscenze sulla struttura ecologica della “Fauna a *Mikrotia*”.

INTRODUCTION

Fossil insular faunas are generally referred to in the paleontological literature as unbalanced impoverished faunas (MacArthur & Wilson, 1963; Sondaar, 1977). Even through insular faunas may contain relatively large numbers of endemic taxa, the term “impoverished” indicates that taxonomic diversity is poor at the higher levels with many major groups absent. In addition, insular faunas are usually referred to as “unbalanced” because of the absence of large terrestrial carnivores. As a matter of fact, otters form by far the majority of the fossil insular carnivores, while other carnivores are generally lacking from endemic insular faunas (Van der Geer et al., 2010). As an exception to this general rule, mustelids, hyaenids and canids are among the taxa sporadically occurring in insular endemic fossil assemblages (Rook et al., 2004; Theodorou et al., 2007; Lyras et al., 2010). The aim of the present note is to report on new carnivore specimens from the endemic insular Late Miocene “Terre Rosse” faunal complex (also known as “*Mikrotia fauna*”) in the Gargano area, southern Italy (Masini et al., 2010).

CARNIVORE RECORD IN THE GARGANO “TERRE ROSSE” FAUNAL COMPLEX

Rich vertebrate bearing karst fissure infillings, outcropping thanks to an intense quarrying activity in

the area between Apricena and Poggio Imperiale in the western part of the Gargano, are well known in the literature since the late 1970s (Freudenthal, 1971; Abbazzi et al., 1996; Masini et al., 2010). The vertebrate fossil-bearing infillings of the extensive karst system network (Abbazzi et al., 1996; Pavia et al., 2010) document two different population phases, a Late Miocene endemic faunal association (the so called “*Mikrotia fauna*”) and a late Villafranchian continental faunal assemblage, a fauna in literature referred to as “Pirro”, or “Dell’Erba”, from the family names of different quarry owners, or “Pirro Nord” (Abbazzi et al., 1996; Arzarello et al., 2007, 2009; Pavia et al., 2011).

For the purpose of the present note, we limit our attention to the Late Miocene population phase. The “*Mikrotia fauna*” is named after one of the most representative elements, the endemic stephanodont murid of the genus *Mikrotia*. Faunal elements belonging to this faunal assemblage display highly developed endemic characteristics and record evolutionary radiations indicating that there were only sporadic communications (testified by new immigrants) with the continental mainland (De Giuli et al., 1985, 1990; Rook et al., 2006; Van den Hoek-Ostende et al., 2009; Freudenthal & Martín-Suárez, 2010).

Practically all mammals of the “*Mikrotia fauna*” show marked endemic features and most of the genera are restricted to this endemic paleo-bioprovince (like the galericine *Deinogalerix*, the murid *Mikrotia*, the glirid

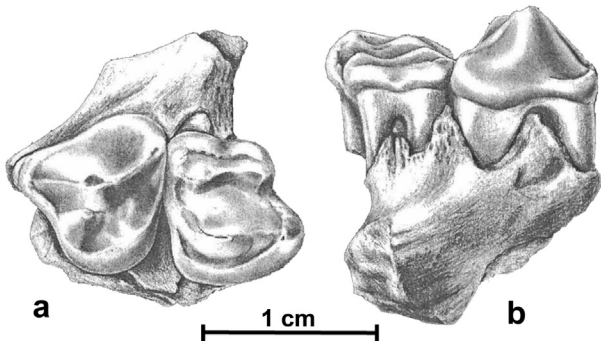


Fig. 1 - The holotype (left maxillary fragment bearing P⁴ and M¹) of *Paraluutra garganensis* (RGM 261151): a) occlusal view. b) buccal view. From Willemsen (1983).

Stertomys, the hamster *Hattomys*, and the five-horned ruminant *Hoplitomeryx* (Freudenthal, 1976, 1985; Butler, 1980; Leinders, 1984; Daams & Freudenthal, 1985), while a number of endemic species belongs to genera with a wider distribution (e.g. several species of the ochotonids *Prolagus*, the glirid *Dryomys* and the otter *Paraluutra*) (Freudenthal, 1971; Willemsen, 1983; Mazza, 1987; Freudenthal & Martín-Suárez, 2006; Masini et al., 2010), finally a very limited number of species are not endemic (e.g. *Apodemus* present in all sampled localities, and *Cricetulodon* restricted to the oldest fissure fillings) (Freudenthal, 1976, 1985). Among thousands of fossil remains from the extensive sampling carried out since the 1970's by different research groups, the only known carnivore within the "Mikrotia fauna"

was till now represented by a left maxillary fragment with M¹ and P⁴ (Figs 1, 2a) and a right calcaneum (Fig. 4a), constituting the type series of the species described by Willemsen (1983) as *Paraluutra garganensis*. The revision of the collections stored at the Università di Firenze allowed the identification of a new specimen of *Paraluutra garganensis*. Moreover, the revision of the Leiden collections, and the recent (2000) field work by a team from the Università di Torino, allowed us to identify the occurrence of more fossils representing additional carnivore material. Despite the lack of comparative material of European Miocene Lutrinae for most of these remains, we attributed these new specimens to *Paraluutra garganensis*, the only carnivore present in the "Mikrotia fauna" assemblage.

MATERIALS AND METHODS

Abbreviations

TRF - "Terre Rosse" collection of the Dipartimento di Scienze della Terra, Università di Firenze (collections of 1980's field work by the team directed by the late Claudio De Giuli). RGM - Rijksmuseum van Geologie en Mineralogie of Leiden (now Netherlands Centre of Biodiversity, Naturalis; collections of 1970's field work by Mathijs Freudenthal team). PU - Museo di Geologia e Paleontologia, Università di Torino (2000-2010 field work by Giulio Pavia team). CCC - Centre de Conservation du Musée des Confluences, Lyon. LGR - "La Grive Saint-Alban" collection of the CCC. FSL - Collection of Université Claude Bernard, Lyon 1.

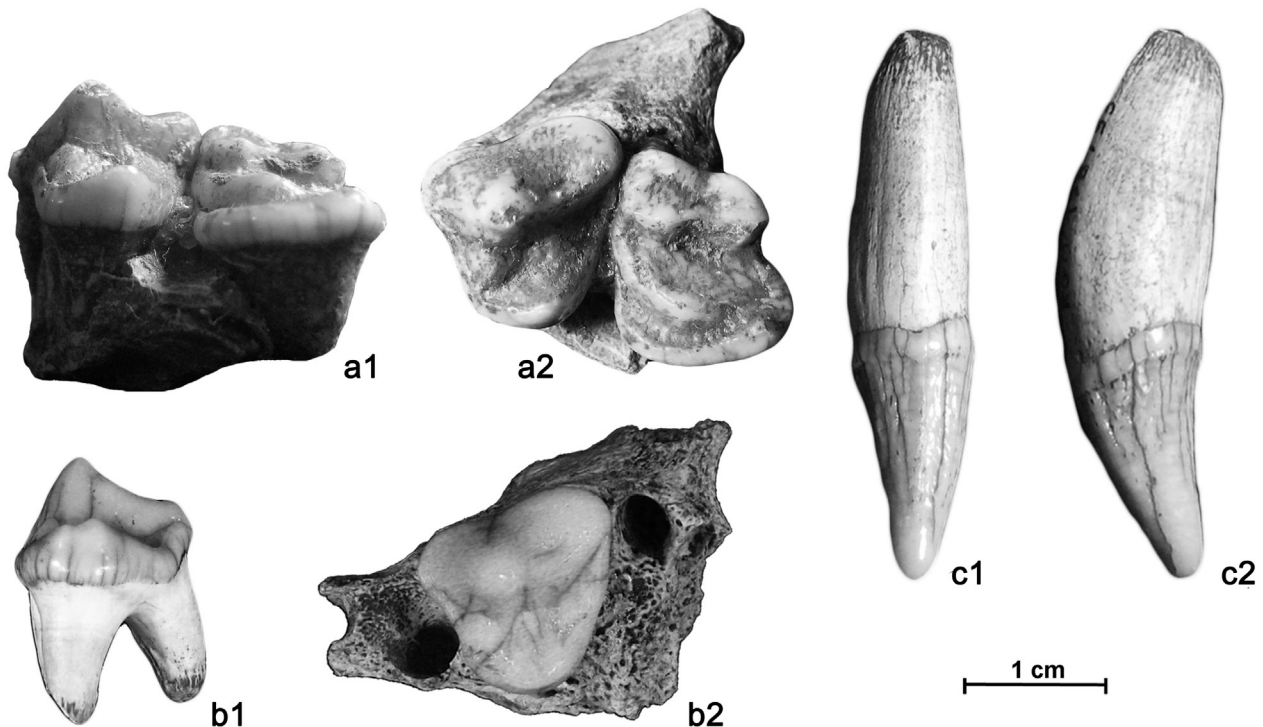


Fig. 2 - *Paraluutra garganensis* dentition. a) Holotype left maxillary fragment with M¹ and P⁴ RGM 261151, in buccal (a1) and occlusal (a2) views. b) Left maxillary bone with P⁴ TRF001F9, tooth extracted from alveoli in lingual view (b1) and inserted in its maxillary bone in occlusal view (b2). Note the relative position of P³ and M¹ alveoli, respectively. c) Left upper canine RGM 178193, in distal (c1) and buccal (c2) views.

Comparative Material

We compared our material with the holotype of *Paralutra garganensis* (RGM 261151). According to Willemsen (1983), *Paralutra jaegeri* (Fraas, 1862), a species described from Steinheim (Germany; Helbing, 1936) and reported from La Grive Saint-Alban (France; Roman & Viret, 1934) is the nearest continental relative to Gargano lutrines, thus why we extended the comparisons to fossils from “La Grive Saint-Alban” (CCC collections) and “Steinheim crater” (FSL collections). Unfortunately all the dental material (but the lower canines CCC LGR 4186 and CCC LGR4187) from “La Grive Saint-Alban” disappears from the collections after various relocations, at this regard we are therefore forced to compare TRF001F9 only with the available illustrations and descriptions (Viret, 1951; Willemsen, 1983, 1992). We also compare our dental material with the Italian Late Miocene lutrines from Monte Bamboli and Baccinello (*Paludolutra campanii*, *P. maremmana* and *Tyrrhenolutra helbingi*; Hürzeler, 1987) and with *Paludolutra lluecai* from the “Cuenca de Turel” in Spain (Crusafont-Pairó & Golpe, 1962b; Morales & Pickford, 2005; Pickford, 2007). Cause of the lack of post-cranial remains of miocenic lutrines, humerus PU128525 and epistropheus RGM179156 were compared with the extant lutrine *Lutra lutra* and the sea otter *Enhydra lutris*, mostly for morphofunctional than taxonomical features.

SYSTEMATIC PALEONTOLOGY

Family MUSTELIDAE Swainson, 1835
Subfamily LUTRINAE Bonaparte, 1838
Tribe LUTRINI Sokolov, 1973

Genus *Paralutra* Roman & Viret, 1934

Paralutra garganensis Willemsen, 1983
(Figs 1, 2a-c, 4a-b)

1983 *Paralutra garganensis* WILLEMSEN, p. 2, Pl. 1, figs 2-3.

Holotype - RGM 261151, Fragment of a left maxillary bone with P⁴ and M¹ in situ (Figs 1, 2a).

Paratype - RGM 261152, Right calcaneus (Fig. 4a).

List of referred material - Fragment of a left maxillary bone with P⁴ in situ and alveoli of P³ and M¹ (TRF001F9; Fig. 2b); left upper canine (RGM 178193; Fig. 2c); epistropheus (RGM 179156; Fig. 4b).

Description and comparisons - TRF001F9 - fragment of a left maxillary bone with P⁴ in situ and alveoli of P³ and M¹ (Fig. 2b). Measurements are given in Tab. 1. Material from a fissure labelled “Fina 9” (F9; De Giuli et al., 1987, 1990). Size and morphological features of the TRF001F9 P⁴ match those of the type specimen described and illustrated by Willemsen (1983). The only minor differences in the morphology of our F9 specimen, in respect to the holotype, are: 1) the P⁴ mesial cingulum ends in the bucco-mesial corner of the tooth; 2) the P⁴ hypocone, at a less advanced wear stage, has its cusp showing two small tips.

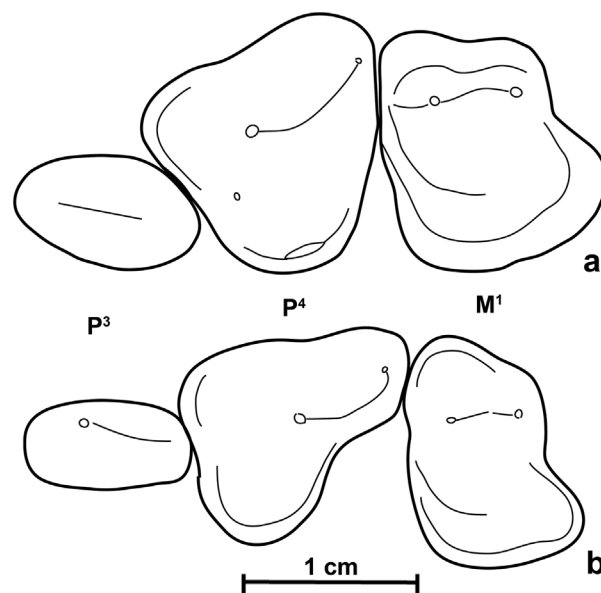


Fig. 3 - Composite outlines of tooth-rows P³-M¹ from two *Paralutra* species: a) *Paralutra garganensis*, M¹ and P⁴ (holotype RGM 261151), with estimated shape and position of P³ based on roots sockets of TRF001F9. b) *Paralutra jaegeri*, P³ and P⁴ (FSL 214195; Stuttgart 4082 in Helbing, 1936), M¹ (FSL 214181; Darmstadt 936 in Helbing, 1936).

In addition to features observable in the holotype RGM 261151, the specimen from F9 shows that the distal root socket of the P³ is about twice as wide as the mesial one and is at the same level as the lingual root of P⁴. Judging from the root sockets, P³ was probably oriented in line with the P⁴ talon. The maxillary portion P³ - M¹ was shorter and stouter than in *Paralutra jaegeri* (see Fig. 3).

The talon of *Paludolutra campanii* is very characteristic and does not fit with the morphology of TRF001F9. We eventually note more morphological similarities with *Paludolutra maremmana*: 1) hypocone with ephemerally splitted cusp; 2) the absence of cutting edge. The protocone of the holotype of *P. maremmana* is damaged however we can hypotesize that it is an isolated cusp, as in *P. campanii* and TRF001F9, while in *Paralutra jaegeri* the protocone is part of the mesial ridge of the talon. In TRF001F9 the talon is more extended distally than in *P.*

	Buccal length	Talon max. length	Width	Paracone height
RGM 261151	12.6	(10.8)	12.0	8.3
TRF001F9	12.1	10.9	11.4	8.0
<i>Paludolutra campanii</i>	16.1	13.8	15.0	-
<i>Paludolutra maremmana</i>	(14.0)	12.8	12.8	-
<i>Tyrrhenolutra helbingi</i>	12.5	7.5	13.1	-
<i>Enhydriodon lluecai</i>	12.1	8.9	12.4	-

Tab. 1 - Miocenic Lutrinae P⁴. Measurements in mm, in parenthesis approximate value. Holotype RGM 261151 measurements from Willemsen (1983); *Paludolutra* and *Tyrrhenolutra* measurements from Hürzeler (1987); *Enhydriodon lluecai* measurements from Crusafont-Pairó & Golpe (1962b).

	Total Height	Width at base of the crown	Length at base of the crown
RGM 178193	41.7	9.0	10.2
<i>Paludolutra campanii</i>	-	12.6	13.8
<i>Paludolutra maremmana</i>	-	8.6	9.6

Tab. 2 - Miocenic Lutrinae upper canine. Measurements in mm. *Paludolutra* measurements from Hürzeler (1987).

maremmana and has amore circular outline. In *P. campanii* parastyle extends mesially to the base of the paracone. This extension is unobservable on *P. maremmana* P⁴ (due to damaged type specimen) while is absent in *Tyrrhenolutra helbingi* and TRF001F9. The general morphology of M¹ in the holotype RGM 261151 recalls the one seen in *Tyrrhenolutra helbingi*, although the hypocone is more distally extended in RGM 261151. Finally, TRF001F9 is slightly smaller than in both *Paludolutra* species, and as large as in *Tyrrhenolutra* (affinities of the latter genus are much unclear, being considered of uncertain status and included by different authors either in Aonichyni, or Enhydrini; Pickford, 2007).

In comparison with the P⁴ of *Paludolutra lluecai* (Morales & Pickford, 2005; Pickford, 2007), our specimen has 1) almost the same proportion, 2) the protocone much smaller and more deported labially close to the paracone, 3) the hypocone split to a less extent, 4) the talon more extended distally.

As a matter of fact, the structure of the P⁴ in *Paludolutra campanii* and *Paludolutra maremmana* (the latter extraordinarily close to *P. lluecai*) possesses a protocone which is close to the paracone, resembling the structure of the P⁴ of more usual mustelids (*Mustela*, *Martes*, etc.), consequently there is no development of an anterior valley near the junction of the protocone and paracone, and only a cingulum united to the parastyle (Morales & Pickford, 2005).

RGM 178193 - left upper canine (Fig. 2c). Measurements are given in Tab. 2. The tooth comes from a fissure labelled "Fina H" (FH; Freudenthal, 1976). Compared to the lower canines of *Paralutra jaegeri* (LGR 4186 and LGR 4187), RGM 178193 is really large. This upper canine belongs to a large specimen well corresponding to the morphotype of *Paralutra garganensis*. In addition some morphological features of the tooth match with *P. jaegeri*: the enamel is crumpled and wrinkled, and the high denticulated cingulum decreases on the buccal side. The same features are also observed in *Paludolutra* remains.

RGM 179156 - epistropheus (Fig. 4b). Measurements are given in Tab. 3. Specimen from fissure labelled "Gervasio 1" (G1; Freudenthal, 1976). RGM 179156 is high, with short centrum. The dens (odontoid process) is cylindrical, and as long as one third of the total length of the centrum. The cranial articular surfaces for the atlas are almost as high as wide. The transversal foramen is large and open behind the cranial articular surface. The ventral surface of the centre shows two fossae for the insertions of the *musculus longuscapitis*, separated by

	Centrum length	Centrum height	Centrum width	Total height
RGM 179156	31.6	12.3	29.7	51.1

Tab. 3 - *Paralutra garganensis* epistropheus. Measurements in mm.

an acute crest, and delimited laterally by two diverging crests ending by the lateral processes (unfortunately broken). The post-zygapophyses are inclined at about 20° from the longitudinal axis of the centre. The spinous process is elongated caudally with an angle of about 30° in respect to the longitudinal axis of the centre. The caudal extension of the spinous process is about half its total length (36.9 mm) and twice the length of the cranial extension. Comparing with extant lutrine, RGM 179156 is definitely shorter than the epistropheus of *Lutra lutra* but longer than *Enhydra lutris*.

Lutrinae indet. (Fig. 4c)

List of referred material - Left humerus (PU 128525; Fig. 4c).

Description and comparisons - PU 128525 - left humerus (Fig. 4c). Measurements are given in Tab. 4. Specimen from a fissure labelled Cava Dell'Erba, F4/A (uncorrelated fissure). The proximal epiphysis is highly damaged, and cannot be described; the great tuberosity and a part of the head are broken. The lesser tuberosity, in part preserved, seems to be separated from the greater tuberosity by a large bicapital groove. These damages make it difficult to determine the age of the specimen; however some part of the partially preserved proximal part suggests that the proximal epiphysis was not yet fused. The proximal part of diaphysis exhibits trapezoid outline. The deltoid crest is prominent and fused with the pectoral crest at mid-diaphysis level (32.0 mm from the head). On the medial face of the humerus there is a proximodistally elongated groove for *musculus teres major*. This insertion is quite short (8.0 mm). The pectoral crest is present almost throughout the length of the diaphysis; it is weak on the proximal diaphysis and forms a small tuberosity, while on the distal one it become stronger. The epicondylar crest is strong; its outer rim is irregular (probably slightly damaged); the cranial face is concave and the caudal face is convex. On the distal epiphysis the lateral epicondylar process, as well as a part of the *capitatum* and of the

	Length from head	Smallest width of diaphysis	Width of the trochlea	Width of distal epiphysis
PU 128525	59.4	5.0	10.5	16.4
LGR 3782	-	5.8	13.1	18.8
LGR 3769	-	5.2	12.9	18.1

Tab. 4 - Lutrinae humeri from Gargano (left humerus PU 128525) and CCC comparative sample (LGR 3782, proximal right humerus; LGR 3769 proximal left humerus). Measurements in mm.

trochlea are broken. It is thus difficult to appreciate the relative proportions between these elements. There is a shallow groove on the *capitatum* for the coronoid process of the radius. The oleocranon fossa is deep, oval and is perforated by a small round foramen. The median epicondylar process is medially extended, has a triangular outline and has, cranially, a deep groove for insertion for

the *musculus pronator teres*. The entepicondylar foramen is elongated proximodistally, and is proximally closed by a weak bar. Among the indeterminate material within the LGR collection (kept at CCC), two distal humeri (LGR 3782 and LGR 3769) fit well with the morphology of our specimen from Gargano. Both are slightly larger than PU 128525, which is small-sized and represents a young

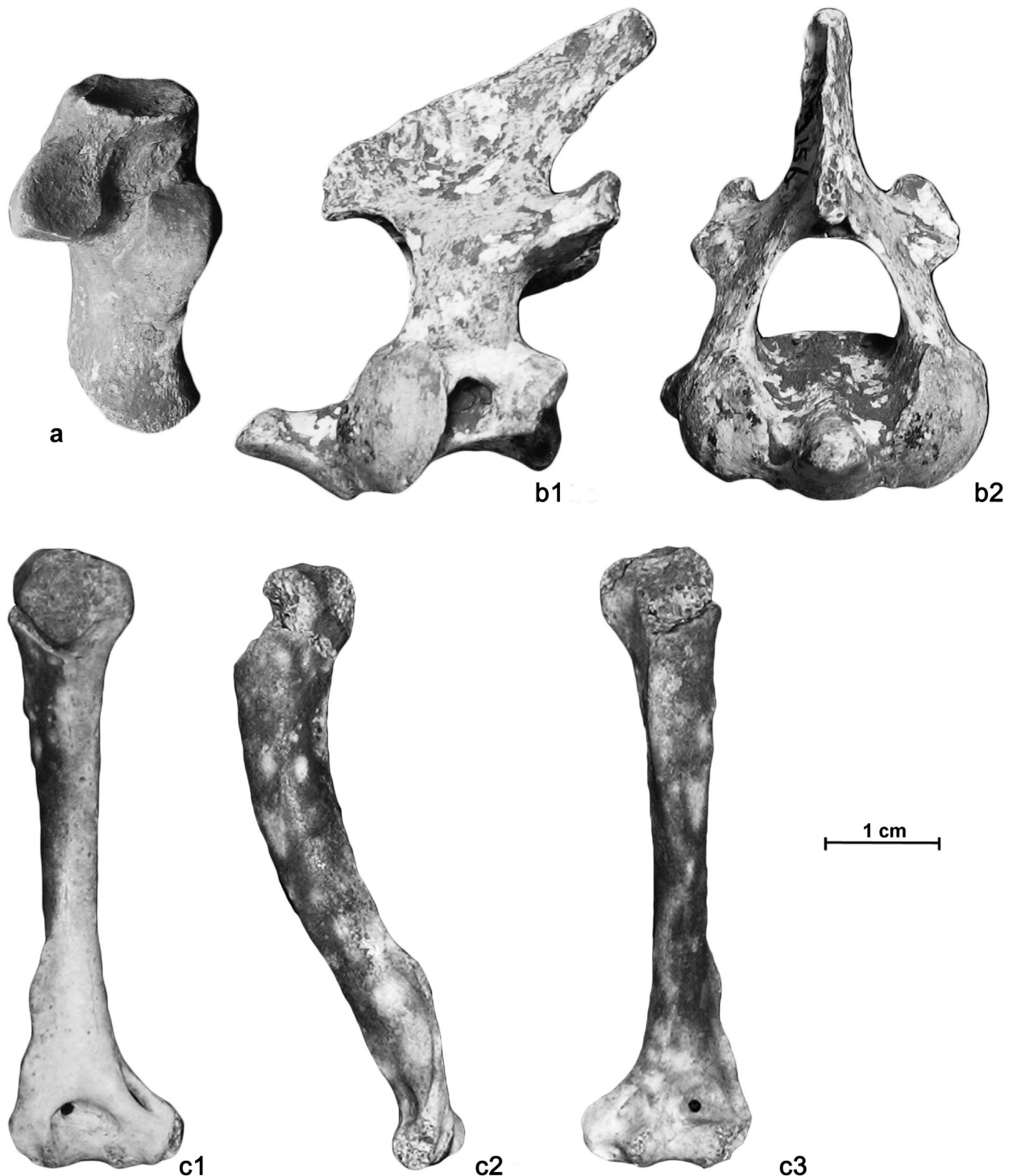


Fig. 4. a-b) *Paraluutra garganensis* postcranial elements: a) Paratype right calcaneum RGM 261152, dorsal view. b) *Epistropheus* RGM 179156, in lateral (b1) and cranial (b2) views. Lutrinae postcranial element: c) *Lutrinae* indet., Left humerus PU 128525, in caudal (c1), lateral (c2) and cranial (c3) views.

individual. One right humerus of *Paralutra jaegeri* from La Grive Saint-Alban in France is mentioned (Viret, 1951, Pl. IV, fig. 12). The direct examination of the CCC remains revealed that, although of comparable size, the morphology of specimen LGR 3787 does not fit with PU 128525, due to a number of morphological traits, such as 1) the stronger pectoral crest which delimitates a deep *sulcus spiralis*, 2) the weaker deltoid crest, 3) the deep trough for the attachment of the olecranon ligament, and 4) the lateral epicondylar crest laterally more developed and proximally less expanded. The humerus PU 128525 shares the same morphological feature with *Lutra lutra*, although slightly less curved. PU 128525 is also definitely less curved than the *Enhydra lutris* humerus, differing from it also by 1) the pectoral crest much developed, 2) the V deltoid much prominent, 3) the deep trough for the attachment of the olecranon ligament.

DISCUSSION

The occurrence of a very diverse number of bunodont lutrine species in the fossil record of the Old World is reported by many authors since the second half of nineteenth century, and their taxonomy has been the subject of much debate, principally because of the fragmentary nature of their fossil record (Meneghini, 1863; Falconer, 1868; Lydekker, 1884a, b, 1885, 1890; Pilgrim, 1931, 1932; Hürzeler, 1987; Willemsen, 1999; Morales & Pickford, 2005; Pickford, 2007). The Late Miocene-Early Pliocene geographical range of these taxa is enormous, being recorded from North America (Repenning, 1976; Berta & Morgan, 1985), Europe (Meneghini, 1863; Pilgrim, 1931; Villalta & Crusafont-Pairó, 1945; Crusafont-Pairó & Golpe, 1962a, b; Hürzeler, 1987; Willemsen, 1992, 1999; Alcalá, 1994), Asia (Falconer, 1868; Lydekker, 1884a; Pilgrim, 1931, 1932; Pickford, 2007) and Africa (Stromer, 1931; Hendey, 1974; Petter et al., 1991; Werdelin, 2003a, b; Morales & Pickford, 2005; Morales et al., 2005; Werdelin & Peigné, 2010).

As recently pointed out (Pickford, 2007), uncertainty in taxonomy are consequence that no one type specimen, among these many described taxa, possesses associated upper and lower dentitions, and that the generally reduced samples size, makes the inter-specific variability hardly recognizable. The recent availability of larger samples from Africa and India allowed Morales & Pickford (2005) and Pickford (2007) to revise and discuss taxonomy of the Old World fossil record of some Lutrinae. At least four subfamilies are differentiated in the Late Neogene of the Old World (and North America as well): Lutrini, Aonychini, Enhydrini, Enhydriodontini (cfr. fig. 23 in Pickford, 2007). The degree of uncertainty in the interpretation of the relationships between and within the groups is however still high, because the numerous lacunae in the fossil record and mostly because of the occurrences of convergences in dentognathic adaptations. Teeth and mandibles features tend in fact to acquire similar morphologies in relation to independent dietary shifts, from predominant piscivory to a diet dominated by shellfish (crustaceans and molluscs) producing the related development towards bunodont dentitions and robust mandibles (Morales & Pickford, 2005).

Willemsen (1992) found out that the diagnosis of *Paludolutra maremmana* and *Enhydriodon lluecai* (Crusafont-Pairó & Golpe, 1962b) are almost identical and suggested that *Paludolutra* lineage derived from *E. lluecai*. In this scheme *Tyrrhenolutra helbingi* has a somewhat isolated position, and it could represent an early branch of the *Enhydriodon* group or possibly a relative of *Paralutra* (the uncertain affinities of *Tyrrhenolutra* are discussed also by Pickford, 2007). In Willemsen (1992) scheme, from the ancestral form *Vishnuonyx chinjiensis* began a radiation giving rise to three lines: one in the Indian subcontinent (*Sivaonyx bathygnathus*, *Enhydriodon falconeri*, *Enhydriodon sivalensis*), one in Europe (*Enhydriodon lluecai*, *Enhydriodon maremmana*, *Enhydriodon campanii*) and a third in North America (*Enhydriodon cf. lluecai* and *Enhydriodon* sp. nov. from California, and *Enhydra lutris*). Such an interpretation needs to be cautiously considered until the question whether the bunodont dentitions of the North American otters evolved as result of convergent adaptation with those of the Old World or whether the similarities in morphology and dimensions represent shared derived characters.

According to Pickford (2007), the genus *Paralutra* (to which is attributed our Gargano otter) is included within the Tribe Lutrini. A relationship between Lutrini and Enhydriodontini seems unlikely because *P. jaegeri*, the oldest known member of the genus (Helbing, 1936), is too young, geologically, to fulfil the role of *Vishnuonyx* ancestor (Pickford, 2007). Furthermore, details in dentition of *Paralutra* species (such as *Paralutra garganensis*) are substantially different from that of any enhydriodontine.

Considering the hypothesis of grouping and relationships among Neogene otter-like carnivores provided by Pickford (2007), the endemic Italian lutrine record differs according the paleogeographic history of the different paleobiogeographic domains where they occurs (the Tusco-Sardinian Paleobioprovince on the Tyrrhenian side and the Abruzzi-Apulia paleobioprovince on the Adriatic one).

On the Tyrrhenian side, the Enhydrini genus *Paludolutra* differentiated (most probably from the genus *Potamotherium*) in western Europe (Spain) during the Late Miocene (Tortonian), and expanded its geographic range into the endemic OZF (“*Oreopithecus* Faunal Zone”, Bernor et al., 2001) in the Tusco-Sardinian paleobioprovince.

The Adriatic emerged lands (the Abruzzi-Apulia paleobioprovince) were instead reached by the Lutrini genus *Paralutra*. The origin of the Lutrine genus *Paralutra* is not clear. According to some authors (Ginsburg et al., 1983; Willemsen, 1992) it would have originated from *Mionyctis* (an Early Miocene, MN 4-5, piscivorous genus described by Ginsburg, 1968) but the latter genus has been moved into the Melinae by Ginsburg & Morales (1996).

The arrival of *Paralutra garganensis* in Gargano could be estimated to have occurred, from the European mainland, during Late Miocene pre-Messinian times, well in agreement with the age proposed for the “*Mikrotia* fauna” (Freudenthal & Martín-Suárez, 2010).

According De Giulio et al. (1987, 1990) the faunal assemblage from fissure F9 (where our left maxillary came from) represents a relatively advanced local biochron

in the “*Mikrotia* fauna” evolutionary history scheme characterised by the occurrence of a large sized *Mikrotia* species and but one species of *Prolagus*. On the other hand, according to Freudenthal (1976), the fissure filling that yielded the *Paralutra garganensis* type specimens (Fina H, coded as FH), also documents a discontinuity within the micro-mammals record and is one of the first fissures with the largest species of *Mikrotia* (*M. magna*; Freudenthal, 1976).

The new remains here described thus further attest the sporadic occurrence of *Paralutra garganensis* during advanced local *Mikrotia* biochrons, and until the very late stage “San Giovannino” of the biochronological subdivision established for the “*Mikrotia* fauna” (Freudenthal, 1976; De Giuli et al., 1990; Masini et al., 2010). As a matter of fact, the humerus PU 128525 is not correlated in the biochronological schemes of the “*Mikrotia* fauna” assemblages. It is close in morphology and size with the actual lutrine *Lutra lutra* and some indeterminate remains from La Grive Saint Alban but different in morphology from the presumed continental ancestor *P. jaegeri*. We cannot rule out that this element (due to its small size and the uncertainty of its biochronological attribution) may be a coeval different species of *Paralutra garganensis*.

The position of the P³ (as revealed by the relative position of its alveole) and the stout structure of the maxillary bones in specimen TRF0019F9 is providing further evidence, in addition to the wide talon of the P⁴ as already stressed by Willemsen (1983), for the interpretation of a feeding adaptation of *Paralutra garganensis* towards a diet characterised by a high amount of hard food (shellfish) (Willemsen, 1980, 1983).

Usually the length of the vertebral axis portion in semi-aquatic mammals is correlated with the diet, the proportion of the head and the locomotion (Howell, 1930). In the case of *Paralutra garganensis* we assume that the epistropheus, shorter than in *Lutra lutra*, could be related to a more benthic-based diet (Howell, 1930; Bisailon et al., 1976), probably feeding on shellfish, corroborating the conclusion on P⁴ morphology of the analysis by Willemsen (1983). As a matter of fact, since epistropheus is longer than in *Enhydra lutris* (an almost aquatic mammal), *Paralutra garganensis* has a less degree of aquatic behaviour than *Enhydra lutris*. Willemsen (1982) on the basis of calcaneum morphology also concluded that *P. garganensis* behaviour was probably less aquatic than *Lutra lutra*.

Further study of the functional morphology of the available postcranial elements of *Paralutra garganensis* is needed for a better understanding of the locomotion and feeding behaviour of this endemic lutrine carnivore.

CONCLUSIONS

The identification of new material attributable to *Paralutra garganensis* in the “Terre Rosse” fossil record allows us to improve the description of this taxon, for the first time since the discovery and description of the type specimens (Willemsen, 1983). The new remains enable us to describe new morphological features for *P. garganensis* and to confirm the occurrence, and the ecological stability,

of a lutrine carnivore (the only top predator in addition to *Crododylus* sp., Delfino et al., 2007 and bird of prey as *Tyto gigantea* and *Garganoaetus freudenthali*; Ballman, 1973, 1976) in the insular ecosystem of the “*Mikrotia* fauna”.

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