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Research Article

New *Hoplitomeryx* Leinders, 1984 remains from the Late Miocene of Gargano (Apulia, Italy)

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Abstract

Natural selection in isolated environments led to the positive selection of species bearing an extraordinary array of morphological traits and a very high grade of endemism. The unbalanced mammal assemblage found in the Upper Miocene karst infillings of the Gargano Peninsula (southern Italy), and especially the intriguing ruminant *Hoplitomeryx*, is one of the best examples of fast, isolated evolution. *Hoplitomeryx* exhibits a peculiar combination of craniodental and postcranial characters, some of which are unique among the other ruminant families. For this reason, its phylogenetic position is still puzzling and far from being clarified. Thus, every contribution to a more comprehensive knowledge of the genus is crucial to better understand the evolutionary process that led to such an advanced and peculiarly adapted ruminant. Here we report newly discovered dentognathic remains from the Gargano Peninsula, which are attributed to six different species of *Hoplitomeryx* on the basis of morphological and metrical evidence. Overall, our results show that the different species of *Hoplitomeryx* are clearly distinguished from each other on the basis of the dental morphology, which accounts for the high intraspecific and interspecific variability of the genus. In addition, we describe for the first time a new type of “Muntiacus-like” upper canine, with no-spiralization, more robust shaped and with more rounded anterior margin than the upper canines previously reported for *Hoplitomeryx*.

Introduction

Isolated populations of terrestrial mammals have always raised a strong interest and received a great deal of attention in a broad range of scientific disciplines (Foster, 1964; van Valen, 1973; Sondaar, 1977; Heaney, 1978; Lomolino, 1985, 2005; McNab, 2002; Meiri et al., 2006; Raia and Meiri, 2006; van der Geer, 2014a). So far, however, all the processes that lead to the origin, development and extinction of insular mammals are still poorly understood, as they follow a different evolutionary pathway than that of their mainland relatives (Sondaar, 1977). Restricted (both geographically and ecologically) environments are well-known to act as evolutionary laboratories, probably favoured by low interspecific competition and predation release (especially regarding large mammals) (Lomolino, 1985; Heaney, 1978; Millien, 2006; Meiri et al., 2011), but also induced by limited food resources, thereby causing rapid and extensive adaptive radiations (McNab, 2002). Even if body size changes are the best-known adaptation in insular environments, which can be easily observed in many (extant and extinct) insular taxa (van Valen, 1973; Heaney, 1978; Lomolino, 1985, 2005; Raia et al., 2003; Lomolino et al., 2012; van der Geer, 2013, 2014a), there are remarkable modifications in the craniodental and postcranial anatomy of the insular species if compared to their mainland counterparts (Sondaar, 1977). In some cases, the morphological changes are so ex-

tensive and peculiar that is not easy to trace back their closest mainland ancestor (e.g., *Myotragus*, *Maremmia*, *Tyrrhenotragus*, etc).

This is the case of the Hoplitomerycidae (Mammalia, Ruminantia) (Fig. 1A), first described along with its type genus *Hoplitomeryx* Leinders, 1984, and type species *Hoplitomeryx matthei* Leinders, 1984, based on the fossil material recovered in the late 1960s from the Late Miocene karst infillings of the limestone quarries between Apricina and Poggio Imperiale (Foggia, southern Italy). Hoplitomerycidae possess a unique combination of cranial and postcranial morphological traits, thus showing five unbranched, non-deciduous, cranial appendages (two orbital pairs and one nasal), two lacrimal orifices, non-pneumatized skull roof, hollow large auditory bullae, sabre-like upper canines, short premolar series lacking of p1 and p2, non-molarized p4, large and bicuspid third lobe of m3, and closed metatarsal gullies (Leinders, 1984). Concerning the dentition, Hoplitomerycidae presents low- to medium-crowned teeth, the absence of *Dorcatherium* and *Palaomeryx* folds, the mesostyle often emerging labially and overlying on the postparacrista, the absence of the cingula in the upper cheek teeth, and the upper molars often wider than longer (Mazza and Rustioni, 2011). Importantly, the authors erected and described five new species of *Hoplitomeryx* (*H. apruthiensis*, *H. apulicus*, *H. falcidens*, *H. magnus*, and *H. minutus*) based on dental specimens from the fossil sites of Gargano and Scontrone (southern Italy). More recently, the characters used for this classification have been questioned, based on the fact that there are no significant differences in the dental mor-

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phology of the different species of *Hoplitomeryx* (Hennekam, 2014; van der Geer, 2014b). Accordingly, five of the species described by Mazza and Rustioni (2011), retaining all the dental characters given in the description of the former species, have been moved to the new genus *Scontromeryx* van der Geer, 2014, which also includes the new species *Scontromeryx mazzai* van der Geer, 2014, and three more new species of *Hoplitomeryx* (*H. devosi*, *H. kriegsmanni*, and *H. macpheeii*, van der Geer, 2014) have been proposed mainly on the basis of differences in body size. Mazza et al. (in press) invalidates the new genus *Scontromeryx* and the species defined by van der Geer (2014b).

The systematics (which is treated separately in the discussion section) and the phylogeny of Hoplitomerycidae are still unsettled, while great controversy concerns its taxonomical position within Ruminantia. By showing two lacrimal orifices and closed metatarsal gulleys, Leinders (1984) originally accommodated the family in Cervioidea. However, the presence of keratin-covered horns in the genus *Hoplitomeryx* led some authors to consider it closer to Bovidae (Hasanin and Douzery, 2003), while others suggested that it could be a holdover of a primitive stock with a basal position in Ruminantia in because of the morphology of the astragalus (Mazza and Rustioni, 1996, 2008, 2011; Mazza, 2013a,b; Mazza et al., in press). In a similar way, the mainland ancestors of the fauna (Mazza and Rustioni, 2008; van den Hoek Ostende et al., 2009; Freudenthal et al., 2013; Mazza, 2013a,b), the processes of colonization of the paleo-island (Butler, 1980; De Giuli et al., 1987b; Abbazzi et al., 1996; Masini et al., 2002; Angelone, 2005; Mazza and Rustioni, 2008; van den Hoek Ostende et al., 2009; Freudenthal and Martín Suárez, 2010; Freudenthal et al., 2013), and the age of the faunal assemblage (Valleri, 1984; Freudenthal, 1985; De Giuli et al., 1987a; Abbazzi et al., 1996; Freudenthal and Martín Suárez, 2010; Pavia et al., 2010; Freudenthal et al., 2013) have raised a strong (and still unresolved) debate.

In all this controversy, any new contribution to an improved knowledge of this intriguing genus is crucial to better understand the evolutionary process that led to such an advanced and adapted taxon. Therefore, here we describe new Late Miocene *Hoplitomeryx* remains from the Terre Rosse faunal assemblage of the Gargano Peninsula, collected during extensive field work in the 1980s by the Department of Earth Sciences of the University of Florence. The majority of the specimens are identified at the species level, others exhibit yet unknown morphologies, which further increases the already elevated variability that has been already found in Hoplitomerycidae.

Materials and methods

Abbreviations

Anatomical Abbreviations — AL, Antero-posterior length (in mm); LW, Labio-lingual width (in mm); pp, premolar row (in mm); mm, molar row (in mm); H, crown Height (in mm); and HI, Hypsodonty Index (H/AL).

Institutional and Fossil Collection Abbreviations — NBC, Naturalis Biodiversity Center (Leiden, Netherlands); DST, Dipartimento di Scienze della Terra, Università degli Studi di Firenze (Florence, Italy); RGM, specimens coming from the Gargano karst infillings and housed at the NBC; SCT, specimens coming from the Tortonian fossiliferous *Lithothamnium* Limestone member of Scontrone, National Park of Abruzzi (L'Aquila, southern Italy); TRF, “Terre Rosse” collection of the DST (collections of 1980s field work by the team directed by Claudio De Giuli).

Studied Material and Comparative Sample

The *Hoplitomeryx* material studied in this work has been recovered from the “Terre Rosse” deposits, which are peculiar residual clays locally found as karst infillings in the area between Apricena and Poggio Imperiale (southern Italy; Fig. 1B). The fissures are locally capped by Tortonian and Lower Messinian marine transgressions (Ricchetti et al., 1992). *Hoplitomeryx* is one of the components of the *Mikrotia* faunal assemblage (see Freudenthal, 1971; De Giuli and Torre, 1984; De Giuli et al., 1985, 1987a,b; Abbazzi et al., 1996; Masini et al.,

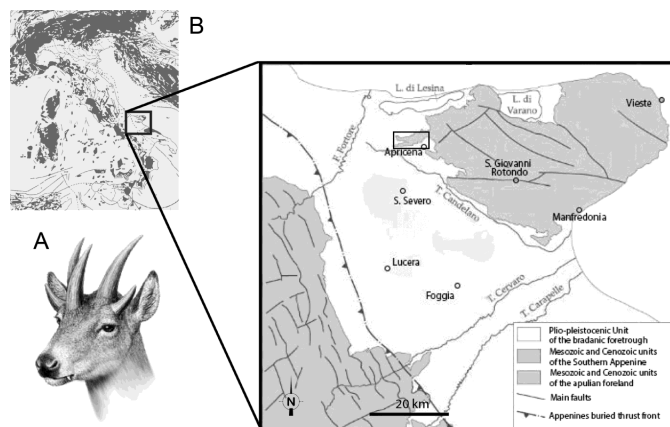


Figure 1 – A, Life reconstruction of *Hoplitomeryx* (artwork by Mauricio Antón); B, Geographical and geological setting of the Gargano Peninsula (southern Italy). The karst morphologies filled with fossiliferous deposits affect the limestones of the geological unit mapped dark grey (black square). Geological sketch from Carta Geologica d'Italia scale 1:50,000, foglio 396. SAN SEVERO.

2010; Savorelli, 2013 for further faunal description). Based on stratigraphical, faunistic and biochronological analyses, a Late Miocene age has been assigned to the so-called *Mikrotia* fauna (Freudenthal, 1976; D'Alessandro et al., 1979; Valleri, 1984; Ricchetti et al., 1992). The fossil remains here described are housed at the DST. The comparative sample includes dentognathic specimens of *Hoplitomeryx* spp. from the Terre Rosse faunal assemblage (i.e., Gargano) and from Scontrone.

Dental Nomenclature

Since a variety of nomenclatures are proposed for describing dental features in Ruminantia, in this work we followed that of Bärmann and Rössner (2011) in order to avoid unclear homologies between molar and premolar structures (e.g. protocone, preparacrista). However, for the upper dentition, we use “metaconule” in place of “hypocone” for the posterior lingual cusp of the upper molars (Gentry et al., 1999), because the former is prevalent in the literature. According to Heintz (1970), the postprotocrista is sometimes divided into two portions. Gentry et al. (1999) recognized that this feature is typical of the upper molars of cervids, and called it “neocrista”. Following Bärmann and Rössner (2011), we distinguish between “internal postprotocrista” and “external postprotocrista” to prevent any ambiguity between the paired crests of Heintz (1970) and Gentry et al. (1999). For the lower dentition, we use “mesostylid” (Hamilton, 1973) instead of “parastylid” since the prefix meso- is more consistent for a stylid located anteriorly to the metaconid. Also, we prefer the use of “external postprotocristid” and “external postmetacristid” terms rather than “*Palaemeryx*” (Janis and Scott, 1987) and “*Dorcattherium*” folds (Geraads et al., 1987), respectively, to indicate the pair of crests that several ruminants possess instead of a single crest on the posterior portion of the protoconid and metaconid, to avoid issues of homology or non-homology between these structures. Capital letters indicate upper dentition, while lower case letters are used for lower teeth.

Methods

Measurements (Tab. 1) were taken with a digital calliper, and morphometric analysis were performed using SPSS v. 19 statistical software. Relative width and length (i.e., labio-lingual width and antero-posterior length) of the different teeth were considered and measurements included in a dataset for known species of *Hoplitomeryx* from Gargano and Scontrone. The classification proposed by Fortelius et al. (2002), which is based on the ratio of height to length of the crown of the molars, has been adopted to evaluate differences in crown height. Thus, the values of the height to length ratio of the upper and lower molars were determined with the acronym HI (Hypsodonty Index), and teeth classified as brachydont (with a ratio of less than 0.8), mesodont (ratio of 0.8–1.2) and hypsodont (a ratio > 1.2) (Fortelius et al., 2002). Given that

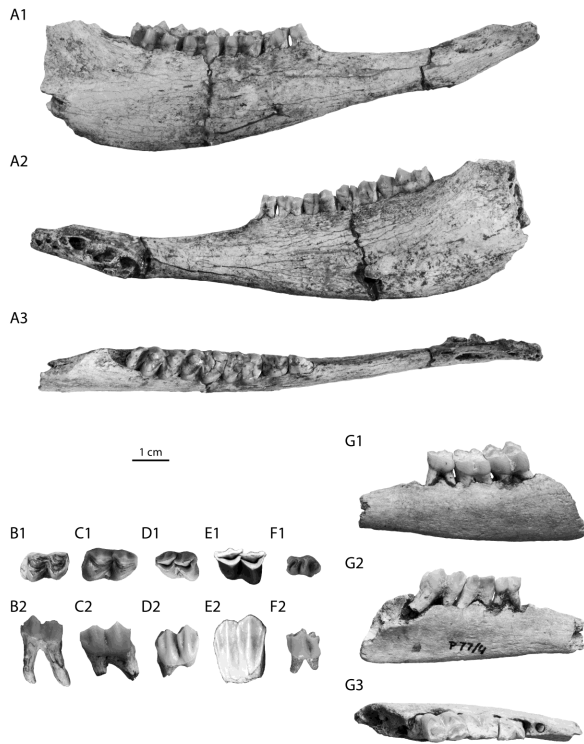


Figure 2 – Lower dentognathic remains of *Hoplitomeryx* spp. from Gargano. A, *H. falcidens*, TRF-U011, right hemimandible, in lateral (A1), medial (A2), and dorsal (A3) views; B, *H. apulicus*, TRF-U006-F1, isolated m2 in occlusal (B1) and lingual (B2) views; C, *H. matthei*, TRF-U002-P77/4, isolated m2, in occlusal (C1) and lingual (C2) views; D, *H. minutus*, TRF-U004-F1, isolated m1, in occlusal (D1) and lingual (D2) views; E, *H. apruthiensis*, TRF-U007-F1, isolated unerupted m2, in occlusal (E1) and lingual (E2) views; F, *H. apulicus*, TRF-U012, isolated p4, in occlusal (F1) and lingual (F2) views; G, *H. apulicus*, TRF-U001-P77/4, mandibular fragment, in labial (G1), lingual (G2), and occlusal (G3) views.

the present analysis is based on the dental remains of hoplitomerycids and there are no postcranial elements among the sample, here we use the classification proposed by Mazza and Rustioni (2011) instead that by van der Geer (2014b).

Results and Discussion

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
 Order ARTIODACTYLA Owen, 1848
 Suborder RUMINANTIA Scopoli, 1777
 Infraorder PECORA Linnaeus, 1758
 Family HOPLITOMERYCIDAE Leinders, 1984
 Genus *HOPLITOMERYX* Leinders, 1984

Hoplitomeryx Leinders, 1984 — Rustioni et al., 1992: pp. 229, 235, figs. 3–5; Mazza and Rustioni, 1996: pp. 93–95, 300, 305, fig. 1; Mazza and Rustioni, 2008 (partim): p. 208, 212, 214; Mazza and Rustioni, 2011: p. 1304–1308, 1310, 1312–1316, 1318, 1322, 1324, 1330, figs. 1–5; Patacca et al., 2013: p. 5; van der Geer, 2014b: pp. 21–27, fig. 4–7; Mazza et al., in press.

cf. *Amphimoschus* Gray, 1852 — Rustioni et al., 1992: p. 230, 236, figs. 4–5; Mazza and Rustioni, 1996: p. 94, 96; Mazza and Rustioni, 1999: p. 300, 304, fig. 1.

large-sized artiodactyl (present-day fallow deer sized) — Mazza and Rustioni, 1996: p. 94, fig. 1.

Taxon A — Mazza and Rustioni, 1999: p. 306, figs. 1–2.

Taxon B — Mazza and Rustioni, 1999: p. 307, fig. 2.

Taxon C — Mazza and Rustioni, 1999: p. 307.

Scontromeryx van der Geer, 2014b: pp. 14–21.

Type Species — *Hoplitomeryx matthei* Leinders, 1984.

HOPLITOMERYX FALCIDENS Mazza and Rustioni, 2011

(Fig. 2A1–A3)

Taxon A — Mazza and Rustioni, 1999 (partim): p. 306.

Hoplitomeryx falcidens Mazza and Rustioni, 2011 — Mazza and Rustioni, 2011: p. 1304, 1312, 1330, fig. 1, 2, 5, tables 1, 2.

Hoplitomeryx matthei Leinders, 1984 — van der Geer, 2014b (partim): p. 22, 27.

Scontromeryx falcidens van der Geer, 2014 — van der Geer, 2014b: pp. 15–17, Table 2.

Holotype — Left hemimandible SCT 177.

Paratypes — Maxillae SCT 70, RGM 260941, RGM 261447, RGM 425201; mandibles SCT 103, SCT 82, RGM 261133, RGM 178568, RGM 178630, RGM 215000, RGM 261132.

Type Locality — Tortonian Scontrone Member of the *Lithothamnium* Limestone (Patacca et al., 2008; 41°45′15.54″ N, 14°2′13.14″ E).

Referred Material — TRF-U011: mandibular ramus (p3–m3), fissure unknown.

Description

Lower Dentition — The lower premolars are elongated with a shallow posterior valley. The p3 is narrower than p4. The cristids of the mesolingual conid are absent. The anterior lobe of the lower molars are wider than posterior ones. In occlusal view, the labial conids appear triangular and bent posteriorly. Blunt ectostylids occur in all the molars; being smaller from m1 to m3. The lingual wall is smooth, and the cuspid shows rounded edges. The entoconulid and hypoconulid are well spaced, with a teardrop shape in occlusal view. The cingulids are absent, although the high degree of dental wear might have erased the posterior ones. The m3 has no external postprotocristid and posterior ectostylid. HI could not be measured because of the very high degree of wear.

Mandible — TRF-U011 is a slender right hemimandible, with sharp ventral border. The vertical ramus and the incisors are not preserved. The horizontal ramus is very high dorso-ventrally, especially under the molars. The diastema and the mandibular symphysis are long, suggesting the existence of a significantly long rostrum.

HOPLITOMERYX APULICUS Mazza and Rustioni, 2011

(Fig. 2B1–B2, F1–F2, G1–G3)

Taxon A (partim) — Mazza and Rustioni, 1999 (partim): p. 306, fig. 1.

Hoplitomeryx apulicus Mazza and Rustioni, 2011 — Mazza and Rustioni, 2011: p. 1304, 1318, 1330, figs 2, 3, 5, tables 1, 2.

Scontromeryx apulicus van der Geer, 2014 — van der Geer, 2014b: p. 17, Table 2.

Holotype — Right hemimandible SCT 88.

Paratypes — Mandibles SCT 76, SCT 88, RGM 260966; RGM 178446, RGM 178445, RGM 178656, RGM 260940, RGM 261150, RGM 425091, RGM 425234.

Type Locality — Tortonian Scontrone Member of the *Lithothamnium* Limestone (Patacca et al., 2008; 41°45′15.54″ N, 14°2′13.14″ E).

Referred Material — TRF-U001-P77/4: mandibular fragment (p4–m2), fissure P77/4; TRF-U006-F1: isolated m2, fissure F1; TRF-U012: isolated p4, fissure unknown.

Description

Lower Dentition — The p4 TRF-U012 is quite elongated and has a deep anterior valley (even in worn teeth like in the p4 of TRF-U001-P77/4), which lacks of anterolingual and posterolingual cristids. The anterior conid is rudimentary. The molars are tightly in contact, with lobules that are slightly verging backwards. The internal postprotocristid of m2 is fused with the preentocristid. The ectostylids lack or are rudimentary. There are no visible cingulids, although the intense wear might have obliterated the posterior ones. Because of the intense degree of wear, HI was impossible to measure in specimen TRF-U001-P77/4 and TRF-U006-F1.

Mandible — Fig. 2G1–G3 show the mandible of a small- or medium-sized ruminant. It preserves the rostral part of the horizontal ramus, from the diastema to the m2. The specimen is slender, with almost parallel ventral and dorsal borders and drop-like cross section.

***HOPLITOMERYX MATTHEI* Leinders, 1984**

(Fig. 2C1–C2)

Hoplitomeryx Leinders, 1984, ear region type I, horn core type I (= *Hoplitomeryx matthei*) — Leinders, 1984: p. 15, 35, pl. 1, 2.

Taxon C — Mazza and Rustioni, 1999 (partim): p. 307.

Hoplitomeryx Leinders, 1984 — Mazza and Rustioni, 1999 (partim): p. 305.

Hoplitomeryx matthei Leinders, 1984 — Mazza and Rustioni, 2011: p. 1320, 1321, 1330, fig. 6, tables 1, 2.

Scontromeryx mazzai van der Geer, 2014 — van der Geer, 2014b (partim): p. 18, Table 2.

Holotype — Skull RGM 260965.

Paratypes — Skull fragments RGM 260944, RGM 260.945, RGM 261092, RGM 261093, RGM 260933, RGM 261100, RGM 261096, RGM 261102; nasal horncores: RGM 260902, RGM 260898, RGM 260922, RGM 260923, RGM 261098; orbital horncores: RGM 261097, RGM 261099, RGM 178286, RGM 260926.

Type Locality — Holotype from the Messinian karstic fissure filling of Pirro 11 A in the limestone quarry Pirro between Apricena and Poggio Imperiale, Foggia, southeastern Italy (41°48'12" N, 15°23'4" E).

Referred Material — TRF-U002-P77/4, isolated m2, fissure P77/4.

Description

Lower Dentition — The labial conids of the tooth are triangular in occlusal view, with the hypoconid larger than the protoconid, separated by a low ectostylid. The anterior cingulid is weak. There are no cingulids on other sides of the tooth. Smooth enamel, with low ribs, on the lingual wall, while is somewhat more corrugated on the labial one. There are traces of residual cementum visible just over the ectostylid.

***HOPLITOMERYX MINUTUS* Mazza and Rustioni, 2011**

(Fig. 2D1–D2)

Taxon A — Mazza and Rustioni, 1999 (partim): p. 306, fig. 1, 2.

Hoplitomeryx minutus Mazza and Rustioni, 2011 — Mazza and Rustioni, 2011: p. 1304, 1306, 1330, fig. 1, 5, tables 1, 2.

Scontromeryx minutus van der Geer, 2014 — van der Geer, 2014b: p. 15, Table 2.

Holotype — Right hemimandible SCT 77.

Paratypes — Mandibles SCT 60, SCT 73, SCT 78, SCT 155, RGM 261147, RGM 261136.

Type locality — Tortonian Scontrone Member of the *Lithothamnium* Limestone (Patacca et al., 2008; 41°45'15.54" N, 14°2'13.14" E).

Referred material — TRF-U004-F1, isolated m1, fissure F1.

Description

Lower dentition — The labial conids have a marked triangular shape and are inclined backwards. The tooth has slender trapezoidal outline in occlusal view. The blunt ectostylid reaches 1/4 of the paraconid height. The metastylid is well developed. The lingual wall of the lobules present a well-developed rib. The anterior cingulid is weak. The enamel is smooth and there are visible residual traces of cementum on lingual and labial walls.

***HOPLITOMERYX APRUTHIENSIS* Mazza and Rustioni, 2011**

(Fig. 2E1–E2)

Hoplitomeryx Leinders, 1984 — Mazza and Rustioni, 1996: p. 95.

Hoplitomeryx sp. Leinders, 1984 — Mazza and Rustioni, 1999: p. 305, fig. 1.

Taxon B — Mazza and Rustioni, 1999: p. 307, fig. 2.

Hoplitomeryx apruthiensis Mazza and Rustioni, 2011 — Mazza and

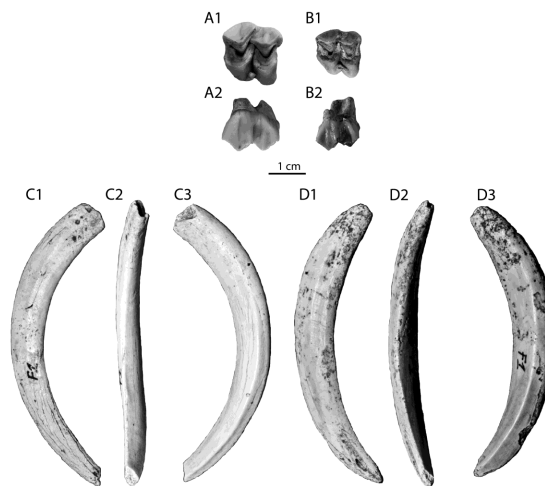


Figure 3 — Upperdentognathic remains of *Hoplitomeryx* spp. from Gargano. A, *H. magnus*, TRF-U003-F1, isolated M2, in occlusal (A1) and labial (A2) views; B, *Hoplitomeryx* sp., TRF-U005-F1, isolated M1, in occlusal (B1) and labial (B2) views; C, *Hoplitomeryx* sp., TRF-U009-F1, isolated upper canine, in lingual (C1), posterior (C2), and labial (C3) views; D, *Hoplitomeryx* sp., TRF-U010-F1, isolated upper canine, in lingual (D1), posterior (D2), and labial (D3) views.

Rustioni, 2011: p. 1304, 1322, 1330, fig. 4, 5, tables 1, 2.

Scontromeryx apruthiensis van der Geer, 2014 — van der Geer, 2014b: pp. 18–20, Table 2.

Holotype — Right hemimandible SCT 29.

Paratypes — Maxillae SCT 59, SCT 125; mandibles SCT 16, SCT 50, SCT 51, SCT 58 + SCT 67, SCT 79, SCT 71, SCT 81, SCT 89, SCT 102, SCT 195, RGM 261134, RGM 425473, RGM 178547.

Type Locality — Tortonian Scontrone Member of the *Lithothamnium* Limestone (Patacca et al., 2008; 41°45'15.54" N, 14°2'13.14" E).

Referred Material — TRF-U007-F1: Isolated m2, fissure F1.

Description

Lower Dentition — High-crowned (HI=1.23) m2, compressed labio-lingually and elongated antero-posteriorly, giving the tooth a trapezoidal shape in occlusal view. It has no cingulids nor ectostylid. The conids are well spaced from one another. The lingual wall is quite corrugated. The mesostylid is well developed and protrudes postero-lingually. There are marked ribs on both metaconid and entoconid. The tooth does not show wear and presents open roots, probably suggesting that is an unerupted germ.

***HOPLITOMERYX MAGNUS* Mazza and Rustioni, 2011**

(Fig. 3A1–A2)

cf. *Amphimoschus* Gray, 1852 — Mazza and Rustioni, 1996: p. 96, fig. 6.

large-sized artiodactyl (present-day fallow deer sized) — Mazza and Rustioni, 1996: p. 94, fig. 1.

Hoplitomeryx magnus Mazza and Rustioni, 2011 — Mazza and Rustioni, 2011: p. 1304, 1324, 1325, 1328, 1330, figs 4, 5, tables 1, 2.

Scontromeryx magnus van der Geer, 2014 — van der Geer, 2014b: p. 20, Table 2.

Holotype — Left hemimandible SCT 20.

Paratypes — Maxillae SCT 18, SCT 86, RGM 260951; mandibles RGM 260951, RGM 261135, RGM 261144.

Type Locality — Tortonian Scontrone Member of the *Lithothamnium* Limestone (Patacca et al., 2008; 41°45'15.54" N, 14°2'13.14" E).

Referred Material — TRF-U003-F1: isolated M2, fissure F1.

Description

Upper Dentition — The tooth has a squared occlusal shape. It presents a very robust mesostyle, elongated anterior-labially and overlapping the postparacrista in lingual view. Marked rib on the labial wall of the para-

Table 1 – List of the specimens and dental measurements of new *Hoplitomeryx* specimens from Gargano. Abbreviations: C, canine; M/m, molar; p, premolar; AL, antero-posterior length; LW, labio-lingual width; H, crown height; and HI, Hypsodonty Index.

Tooth position	Side	Catalogue number	Fissure	AL (mm)	LW (mm)	H (mm)	HI
C	Right	TRF-U009-F1	F1	10	5.8	70.4	
C	Right	TRF-U010-F1	F1	11.6	7.7	68.4	
M1	Right	TRF-U005-F1	F1	11.8	12.3	9.8	
M2	Right	TRF-U003-F1	F1	15.4	16.9	7.2	0.47
p3	Right	TRF-U011	-	-	5	-	
p4	Left	TRF-U001-P77/4	P77/4	7.2	5.7	-	
p4	Right	TRF-U011	-	7.2	6.1	-	
p4	Left	TRF-U012	-	9	5.2	6.7	
m1	Left	TRF-U001-P77/4	P77/4	7.6	7.2	-	
m1	Left	TRF-U004-F1	F1	11.2	7.8	9.4	
m1	Right	TRF-U011	-	8.5	8.2	-	
m2	Left	TRF-U001-P77/4	P77/4	10.4	7.5	-	-
m2	Right	TRF-U002-P77/4	P77/4	13.7	9.1	8.9	0.65
m2	Right	TRF-U006-F1	F1	10.8	7.7	-	-
m2	Left	TRF-U007-F1	F1	13.1	8	16.1	1.22
m2	Right	TRF-U011	-	11.2	8.5	-	-
m3	Right	TRF-U011	-	16	8.5	-	-

cone. Stout entostyle emerging from the metaconule, showing traces of dental wear. The anterior lobe is wider than the posterior one and displaced lingually.

HOPLITOMERYX ssp.

(Fig. 3B1–B2, C1–C3, D1–D3)

Hoplitomeryx Leinders, 1984, size 2 — van der Geer, 2005: p. 330, 331, 333; van der Geer, 2008 (partim): p. 153, 154, fig. 4, 5, 6.

Hoplitomeryx Leinders, 1984, size 1 — van der Geer, 2008 (partim): p. 153, fig. 4, 6.

Hoplitomeryx sp. Leinders, 1984 — Mazza and Rustioni, 2011: p. 1326.

Scontromeryx sp. van der Geer, 2014 — van der Geer, 2014b: p. 21.

Hoplitomeryx devosi van der Geer, 2014 — van der Geer, 2014b (partim): p. 23, fig. 4, 5, 7, Appendix III.

Hoplitomeryx macpheeii van der Geer, 2014 — van der Geer, 2014b (partim): p. 25 fig 4, 7, Appendix III.

Hoplitomeryx matthei Leinders, 1984 — van der Geer, 2014b (partim): p. 22, fig. 4, 5, 6, Appendix III.

Hoplitomeryx kriegsmanni van der Geer, 2014 — van der Geer, 2014b (partim): p. 26, fig. 6, 7, Appendix III.

Hoplitomeryx sp. Leinders, 1984 — van der Geer, 2014b (partim): p. 27.

Referred material — TRF-U005-P77/4 isolated upper M1, fissure P77/4; TRF-U009-F1 isolated upper canine, fissure F1; TRF-U010-F1 isolated upper canine, fissure F1.

Description

Upper dentition — TRF-U005-P77/4 presents a barely visible anterior and posterior cingula. Almost as wide as long, it has fairly rectangular shape in occlusal view. The mesostyle is well developed, but less than in TRF-U003-F1. Premetacrista, postprotocrista, postparacrista and premetaconulecrista remain unfused regardless the wear state. The postparacrista reaches and touches the premetaconulecrista, but without fusing together. There are two strong and flattened entostyles, one that emerges from the protocone and the other from the metaconule. Both entostyles are worn. The tooth generally has smooth enamel with residual cementum on the labial wall.

Upper canines — There are two different types of canine, both massive, with a sharpened posterior margin, and smooth enamel, sometimes showing ripples probably connected with growth of the tooth. The first (TRF-U009-F1) is slender, triangular in cross-section, flat anteriorly, and spiralized (i.e., with an evident torsion along the axis), and with the crown forming almost 3/4 of the entire tusk length. The second

one (TRF-U010-F1) is more robust, with a drop-like section, rounded anteriorly, untwisted, and with the crown that is half the length of the tusk, or even less.

The classification of Hoplitomerycidae

Over the years, different taxonomical arrangements have been proposed for Hoplitomerycidae. Initially, the family comprised only the genus *Hoplitomeryx* and the type species *H. matthei* (Leinders, 1984). Mazza and Rustioni (2011), following the discovery of the Scontrone fossil site, erected and described five new species (*H. apruthiensis*, *H. apulicus*, *H. falcidens*, *H. magnus*, and *H. minutus*) based on the dental characters of the specimens from both Scontrone and Gargano. Recently, a revision of the family has been proposed (van der Geer, 2014b), in which five of the species described by Mazza and Rustioni (2011) were moved to the new genus *Scontromeryx* van der Geer, 2014 (retaining all the dental characters given in the description of the former species) and that also includes the new species *Scontromeryx mazzai* van der Geer, 2014. The author also proposed three new species belonging to the genus *Hoplitomeryx* (*H. devosi*, *H. kriegsmanni*, and *H. macpheeii*, van der Geer, 2014) mainly on the basis of differences in body size. The author justified the necessity of the new genus *Scontromeryx* on three main differences, which are the presence or absence of the p2 and P2, of the sabre-like upper canines, and of the nasal horn core. However, the latest review proposed by Mazza et al. (in press) demonstrated that these three hypothesis do not subsist and invalidated the genus *Scontromeryx*, with its type species *Scontromeryx mazzai*, and the three species *H. devosi*, *H. kriegsmanni*, and *H. macpheeii*. Following this review and the latest evidences concerning the systematic of *Hoplitomeryx*, we used the classification from Mazza and Rustioni (2011) for the present analysis.

New material from Gargano

Dimensionally, the Gargano teeth analysed in this study (Tab. 1) group into three different size classes: a small one (TRF-U001-P77/4, TRF-U004-F1, TRF-U006-F1, TRF-U011 and TRF-U012), an intermediate one (TRF-U002-P77/4, TRF-U005-F1 and TRF-U007-F1), and a large one (TRF-U003-F1). The three classes can be associated with the known species of *Hoplitomeryx* (Fig. 4); with *H. minutus*, *H. apulicus*, and *H. falcidens* falling in the first group of small species, *H. apruthiensis* and *H. matthei* showing an intermediate size, and *H. magnus* being a very large, well separated species (Fig. 4).

The lower cheek teeth are more numerous and better-preserved than the upper cheek teeth. The latter are mostly isolated specimens, only a few of them are still preserved in their maxillary bones and none is in a good state of preservation. In addition, the upper molars of most of the

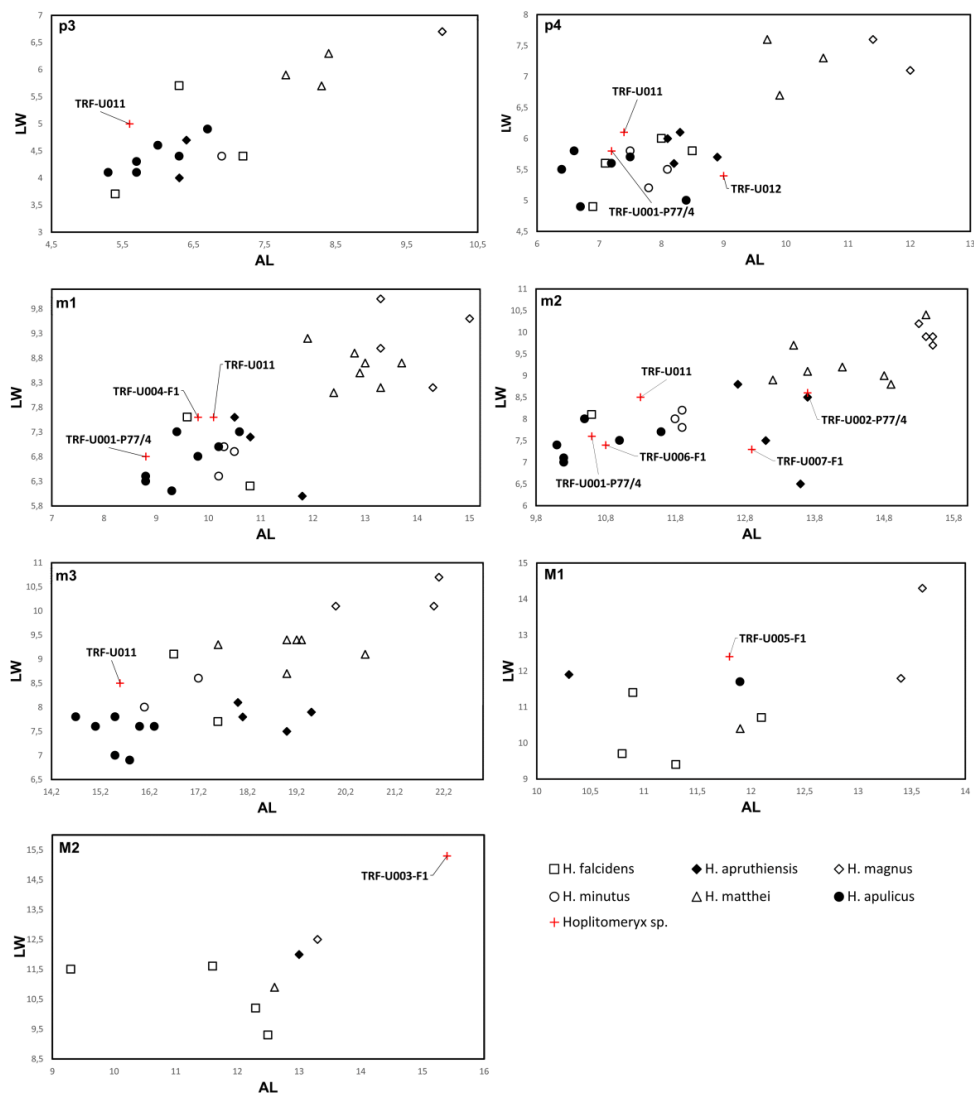


Figure 4 – Proportions (antero-posterior length vs labio-lingual width) of the teeth of *Hoplitomeryx* of the studied collection, and comparison with species from Gargano and Scontrone.

species of *Hoplitomeryx* have been poorly described or not described at all. This does not allow a reliable assignment of the M1 TRF-U005-P77/4 to any of the known species. However, its morphological traits clearly fall into variability of the genus *Hoplitomeryx*, to which it is here ascribed.

The size of the isolated M2 TRF-U003-F1 falls outside the known range of variability for *Hoplitomeryx*, being bigger than any upper molar measured until now. However, the smooth enamel on both lingual and labial walls, the very strong mesostyle and well developed parastyle, the presence of a robust rib on the wall of the paracone, and the absence of a rib on the wall of the metacone are characters found in the species *H. magnus*. TRF-U003-F1 is therefore the first well preserved upper molar to be ascribed to this species.

With regard to the lower dentition (Fig. 2), the p4 TRF-U012 and that preserved on the hemimandible TRF-U001-P77/4 share the same morphology. Similarly, in TRF-U006-F1, and in the m2 of TRF-U001-P77/4, the mesolingual conid is slightly larger than the mesolabial one. They have a well developed anterior stylid, robust posterolingual and posterolabial conids, and a rudimentary anterior conid. The mandibular fragment TRF-U001-P77/4 presents a straight ventral profile of the horizontal ramus. All these specimens show close morphological similarities to *H. apulicus*, and are therefore ascribed to this species. In contrast to the description given in the diagnosis of this species, teeth show a uniform dental wear (like in paratypes RGM 178656, RGM 425234; Fig. 5B1–B3, Fig. 6D1–D3).

The teeth of the mandible TRF-U011 are deeply worn, and most of their occlusal features are obliterated. Only the m3, which erupted later than the other cheek teeth, and the labial walls of the premolars and of the two first molars, maintain some visible traits, such as a low and blunt ectostylid in the m1, becoming progressively lower in m2 and m3, a hypoconulid and entoconulid separated by a narrow back fossa. However, the peculiar convex ventral profile and sharp ventral margin of the mandible ramus, is one of the most distinctive features of *H. falcidens* (like in RGM 215000, RGM 178630; Fig. 5C1–C3, Fig. 6D1–D3).

The isolated m2 TRF-U002-F1 has corrugated labial enamel, small traces of residual cementum, tightly connected anterior and posterior lobes, preentocristid almost fused with the internal postprotocristid, well developed metastylid protruded posteriorly, and a blunt, low ectostylid. All these features are typical of *H. matthei* (as shown by RGM 260943 and RGM 261110; Fig. 6A1–A3, C1–C3).

In occlusal view the isolated m1 TRF-U004-F1 presents triangular lingual conids, marked ribs on the lingual walls, strong metastylid, weak anterior cingulid, and well developed ectostylid. For all these features the specimens has the typical morphological traits of an m1 of *H. minutus* (RGM 261147; Fig. 6B1–B3). The tooth presents also a uniformly smooth enamel and residual traces of cementum, in contrast to the description given in the diagnosis.

The isolated m2 germ TRF-U007-F1, like the m1 of the hemimandible RGM 178547 (Fig. 5A1–A3), shows no ectostylid, has almost vertical and very low mesostylid and entostylid in lingual view, is com-

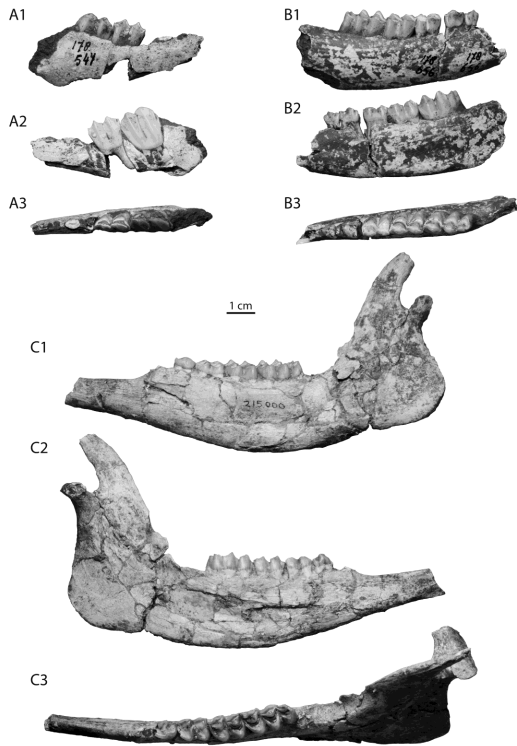


Figure 5 – Dentognathic remains of *Hoplitomeryx* spp. from the NBC collection. A, *H. apruthiensis*, RGM 178547, right hemimandible fragment, in lateral (A1), medial (A2), and dorsal (A3) views; B, *H. apulicus*, RGM 178656, right hemimandible, in lateral (B1), medial (B2), and dorsal (B3) views; C, *H. falcidens*, RGM 215000, left hemimandible, in lateral (C1), medial (C2), and dorsal (C3) views.

pressed labio-lingually and elongated antero-posteriorly, and has the internal postprotocristid that is tightly in contact with preentocristid. According to Mazza and Rustioni (2011), the presented specimen shows close morphological affinities to *H. apruthiensis*.

Because most of the specimens in the collection are intensely worn, the HI (which is only measurable in TRF-U003-F1, TRF-U002-P77/4, and TRF-U007-F1) based on the m2 does not seem to be most appropriate to discriminate among species. Nonetheless, the crown height that was measured for specimen TRF-U007-F1 (Tab. 1) is noteworthy, because this is the first time that a high crowned tooth (according to the definition provided by Fortelius et al., 2002) is found in *Hoplitomeryx*. This indicates that the genus had a higher dimensional and morphological variability than known until now. It must be stressed, however, that TRF-U007-F1 is a tooth germ, thus implying that its morphology might have been slightly different when erupted.

Hoplitomeryx was known to be equipped with extremely elongated upper canines, with very sharpened posterior border and a counter clock-wise torsion along the axis, as observed in the extant *Moschus* (Leinders, 1984; Sánchez et al., 2010). The right upper tusk TRF-U009-F1 (Fig. 3C1–C3) shows this typical traits, and can therefore be classified as standard type of upper canine of *Hoplitomeryx*. However, the only complete maxilla that still preserves the upper canine is RGM 260941 which was ascribed to *H. falcidens* by Mazza and Rustioni (2011: fig. 2A–C). RGM 260951 is a fragmentary specimen, which was ascribed to *H. magnus*. It presents an upper canine similar to that of RGM 260941, but the morphology of this tooth is still uncertain due the bad state of preservation of the fossil. Therefore, it is still unknown if all the species of *Hoplitomeryx* possessed these peculiar teeth. Another difficulty is attributing these upper canines to either *H. falcidens* or *H. magnus*. The other canine (TRF-U010-F1) reported here is morphologically very different. It is more robust, with rounded anterior margin, not spiralized, and with the crown height to total length ratio quite different than that of the other upper tusks (0.4 in TRF-U010-F1, 0.75 in TRF-U009-F1). This upper fang is very similar to those of the barking deer *Muntiacus*. Despite that they have never been described

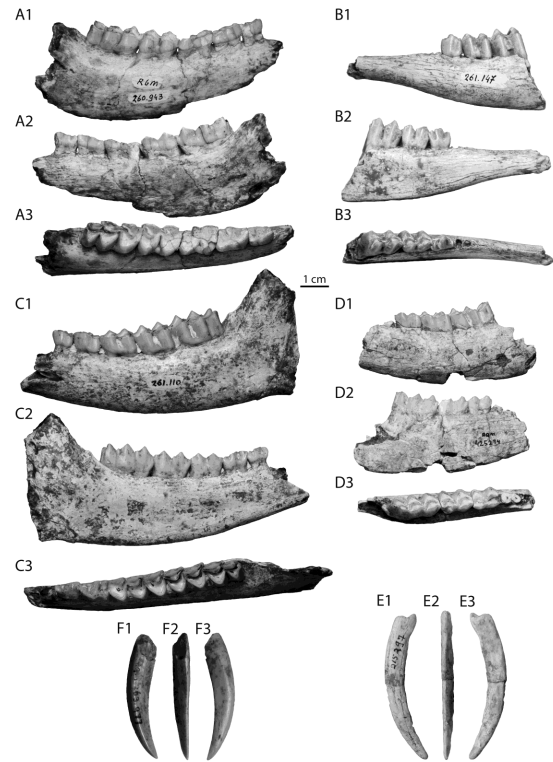


Figure 6 – Dentognathic remains of *Hoplitomeryx* spp. from the NBC collection. A, *H. matthei*, RGM 260943, right hemimandible, in lateral (A1), medial (A2), and dorsal (A3) views; B, *H. minutus*, RGM 261147, left hemimandible fragment, in lateral (B1), medial (B2), and dorsal (B3) views; C, *H. matthei*, RGM 261110, left hemimandible, in lateral (C1), medial (C2), and dorsal (C3) views; D, *H. apulicus*, RGM 425234, left hemimandible fragment, in lateral (D1), medial (D2), and dorsal (D3) views; E, *Hoplitomeryx* sp., RGM 215297, upper canine, in labial (E1), lingual (E2), and posterior (E3) views; F, *Hoplitomeryx* sp., RGM 263977, upper canine, in labial (F1), lingual (F2), and posterior (F3) views.

(or even reported) for *Hoplitomeryx*, upper canines of this type are frequent among the Gargano sample collection (e.g., RGM 261525 and RGM 263977; Fig. 6E1–E3, F1–F3). Nonetheless, and because none of these upper fangs have been found preserved in the maxilla, they cannot be reliably ascribed to any of the known species of *Hoplitomeryx*. These “*Muntiacus*-like” and “*Moschus*-like” upper canines could not be possessed by the same species. Nor could the large upper fang TRF-U010-F1 belong to *H. falcidens*, whereas it may be possessed by the larger-sized *H. magnus*. The fact that *Hoplitomeryx* is the only large mammal known to date in the palaeo-island of Gargano, as well as the only ruminant among the mammal assemblage (Leinders, 1984), provides strong support for assuming that this dental element (never figured or described before) belongs to some species of the genus. Moreover, and because one of the main findings of our study is that *Hoplitomeryx* species exhibit a higher than expected morphology variability (as already pointed by Mazza and Rustioni, 2011 in their cheek teeth, a similar degree of natural variability could be expected to be found in the upper canines of the genus. This new finding concerning the variable upper canines in *Hoplitomeryx* could be not so surprising than expected *a priori* if the very intriguing nature of this enigmatic ruminant is taken into account. Despite that the most feasible option is to attribute this new type of canine shape to *Hoplitomeryx*, more material (especially concerning upper canines) is needed in order to confirm our proposal and discard the (possible) existence of any other new and still unknown ruminant among the material of Gargano.

Conclusions

Here we describe and figure new fossil remains of the ruminant *Hoplitomeryx* from the Upper Miocene deposits of Gargano (Apulia, southern Italy). The reported specimens are metrically and morphologically attributed to the following six species: *H. apruthiensis* (TRF-U007-F1); *H. apulicus* (TRF-U001-P77/4, TRF-U012 and

TRF-U006-F1); *H. falcidens* (TRF-U011); *H. magnus* (TRF-U003-F1); *H. matthei* (TRF-U002-P77/4); and *H. minutus* (TRF-U004-F1). Thus, our sample contributes substantially to the present knowledge of the intraspecific and interspecific morphological variability of *Hoplitomeryx*. Results seem to indicate that the classification adopted by Mazza and Rustioni (2011) to discriminate species of *Hoplitomeryx* based on morphological differences of teeth (a classification strengthened by Mazza et al., in press) is preferable to that proposed by van der Geer (2014b) based almost exclusively on dental size.

Several robust, mesially-rounded, non-spiralized *Muntiacus*-like upper canines are reported for the first time in *Hoplitomeryx*, which add crucial information to both the family and the genus. The presence of such a different type of morphology of upper canines in *Hoplitomeryx*, as those exhibited by (among others) the extant *Moschus* and *Muntiacus*, reveals a greater variability in dental morphology than expected from the cheek teeth alone.

Finally, our study reveals that archaic and advanced species of *Hoplitomeryx* may have occurred both in Abruzzo and Apulia, which confirms the strong faunal connection that existed between the Tortonian site of Scontrone and the Messinian one of Apricena, as already proposed by Mazza and co-authors (Mazza and Rustioni, 2011; Mazza et al., in press). ☞

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