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Original article

Hoplitomerycidae (Ruminantia; Late Miocene, Central-Southeastern Italy): Whom and where from?☆

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ABSTRACT

The endemic monogeneric fossil family Hoplitomerycidae currently includes six known species, the remains of which are found in Lower Tortonian coastal tidal-flat layered calcarenites at Scontrone, in Abruzzo (central Italy), as well as in karstic fissure fillings, supposedly of Messinian age, in the Gargano Promontory, Apulia (southeastern Italy). Their remains are found associated with bones of many other vertebrates which indicate the existence of a vast territory, the so-called Abruzzo-Apulia Platform, which was isolated from the nearest mainland at least from the Early Oligocene up to the latest Miocene. A recent cladistic analysis showed that the classification of the hoplitomerycids in Cervoidea, which currently enjoys vast popularity, is not justified. The family is characterized by a set of cranial and postcranial primitive traits, above all their non-parallel-sided astragalus, that suggest that the family probably stemmed from a primitive ruminant stock somewhere before the emergence of Pecora, consistent with geological evidence showing that about 29 Ma a land-bridge connected the Abruzzo-Apulia Platform with the Balkans across the Adriatic Sea, approximately where the Tremiti islands are today. The present study intended to reconnect to the results of the cladistic analysis and to extend them in the attempt to track down the possible ancestors of Hoplitomerycidae. The family expectedly radiated developing autapomorphic features that make the search quite arduous. Nonetheless, its primitive, leftover characters relate it to Oligocene basal ruminants with asymmetric astragalus. Following the distribution of the non-parallel astragalus through space and time leads to speculate a possible origin of the family from primitive Tragulina representatives that dispersed in Anatolia in the course of the Oligocene. Current reconstructions of the Early Oligocene paleogeography of the eastern Mediterranean show that the Apulian Platform was connected via a cross-Adriatic land-bridge to the Balkans, Anatolia and by that way also to middle and central Asia and central-eastern Europe.

1. Introduction

Hoplitomeryx Leinders, 1983 is a genus comprising six endemic species of ruminants in the monogeneric family Hoplitomerycidae. Fossil remains of the hoplitomerycids are retrieved from layered coastal tidal-flat calcarenites of Lower Tortonian age that crop out at Scontrone, in Abruzzo (central Italy), but also from karstic fissure fillings, supposedly of Messinian age, in limestone quarries in the Gargano Promontory, Apulia (southeastern Italy). In both localities, hoplitomerycids are accompanied by other vertebrates, crocodiles, chelonians, giant birds, giant insectivores and, only in Gargano, a full range of small mammals. Most of these taxa are endemic. This proves, confirmed by extensive geological evidence, that these animals populated a vast land, the so-called Apulian Platform (Patacca et al., 2008a, 2008b), which was isolated from the nearest mainland areas for most of its existence.

1.1. Paleontological background

Mazza (2013) performed a cladistic analysis based on a character-taxon matrix of 121 features (48 cranial, 51 dental and 22 postcranial characters) and 18 past and living ruminant taxa (see this paper for details). A crucial feature is the shape of the astragalus, which is non-parallel-sided in all hoplitomerycids. Mazza (2013) carried out the analyses both including and excluding this trait to test how central this bone is to establishing the relationships of hoplitomerycids with the other ruminants included in the investigation. The inclusion of the astragalus placed Hoplitomerycidae as sister group of two other clades: one formed by Bovidae, Cervidae, Moschidae, and Palaeomerycidae; the other including Antilocapridae, Giraffidae, and Climacoceridae. In other words, the non-symmetrical astragalus excludes hoplitomerycids from Pecora. Many astragali of *Hoplitomeryx* were found at both Scontrone and Gargano. They are of a rather large range of size and could not be confidently attributed to any of the known species. Nonetheless, they are all morphologically similar, double-pulleyed and with non-parallel trochleae. An asymmetric astragalus is

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typical of basalmost artiodactyls (Diacodexidae, Leptictidae, Archaeomerycidae, Hypertragulidae, Praetragulidae), tragulids (*Tragulus*, *Hyemoschus*), but also of Protoceratidae, *Palaeohypsodontus*, *Myotragus*, and Suidae (Janis and Scott, 1987; Blondel, 1997; Vislobokova, 2001; Vislobokova and Trofimov, 2002; Métais et al., 2003). Whereas the exclusive non-parallel-sided astragalus is a shared primitive character state in earlier ruminants, it may likely result from convergence, and therefore be an apomorphic acquisition in later taxa. Because the astragali of the hoplitomerycids are all similar regardless the size, they are most probably an ancestral reminiscence. The six known species of the family are the end products of adaptations to different niches, and likely also to different habitats. Actually, the species differ markedly dentally (they range from brachyodont to mesodont dentition), but also in size and proportions (Mazza and Rustioni, 2011). In spite of this, they all possess the same kind of astragalus (see below for further discussion).

1.2. Paleogeographical background

The conclusions of Mazza's (2013) cladistic analysis are congruent not only with the paleontological information hitherto disclosed from Scontrone and Gargano, but also with the geological and geostructural evidence that comes from the Adriatic offshore and the central-southern part of the Apennine and eastern Italy. In the course of its existence, the Apulian Platform connected twice, during the Early Oligocene, around 29 Ma, and then again during the latest Miocene, to the nearby Balkans mainland by trans-Adriatic land-bridge, approximately where the Tremiti islands are today (Patacca et al., 2008b). The Apulian Platform was finally involved, at the very end of the Miocene or in the earliest Pliocene, in the Apennine build-up and included in Italy's mainland.

The connection with the Balkans provides crucial chronological and geographical constraints in the search for the origin of Hoplitomerycidae. The family possesses an array of characters recalling those of many higher ruminants: e.g., bovid-like horns; cervid-like double lacrimal orifices and closed metatarsal gulleys; giraffid-like prominent occiput, horns laterally compressed and fairly bent backwards, teeth with well-developed styles(-ids), humeri with rather deep trochlear troughs, metacarpal bones with the relief between the two components of the proximal articular surface placed laterally to the medium trough. Hoplitomerycids show no trace of ethmoidal vacuities, unlike cervids and giraffids, and have cannon bones with flat volar surfaces like bovids and giraffids. The list could be extended to moschids and antilocaprids as well. This shows that Hoplitomerycidae originated earlier than the radiation of Pecora and then likely evolved convergently to the latter. Because the different lineages of higher ruminants started appearing between the Late Oligocene and the Early Miocene, the ancestors of Hoplitomerycidae must have reached the Apulian Platform at the time of its earliest connection with the Balkans, and therefore during the late Early Oligocene.

In paleogeographical reconstructions of the Oligocene of the central Mediterranean (Rögl, 1999; Rasser et al., 2008), Anatolia was a key crossroads that connected middle and central Asia and central-eastern Europe to the Balkans and to the Apulian Platform, via the trans-Adriatic istmus (Fig. 1). During the latest Early Oligocene, the way towards the Apulian Platform was therefore open to faunas from any of these regions. These were the areas where the research was targeted, lighted by the headlights of hoplitomerycid's ancestral reminiscences.

1.3. Aims

This study reconnects to Mazza's (2013) cladistic analysis and tracks down the possible ancestors and area of provenance of Hoplitomerycidae. To reach this goal the research was more particularly directed to the family's ancestral leftover traits, taking a direction opposite to that followed by cladistic analysis, which typically focuses on apomorphic characters. Because Hoplitomerycidae are highly endemized ruminants, most of their archaic traits have been obliterated by endemic overprint. Comparative morphological analysis, however, turned out to be the most appropriate means to detect remainders of the family's far past.

2. Material and methods

This work is based on the morphological analysis of cranial, dental and postcranial remains of Hoplitomericydae found at Scontrone and Gargano. Scontrone provided 510 specimens until

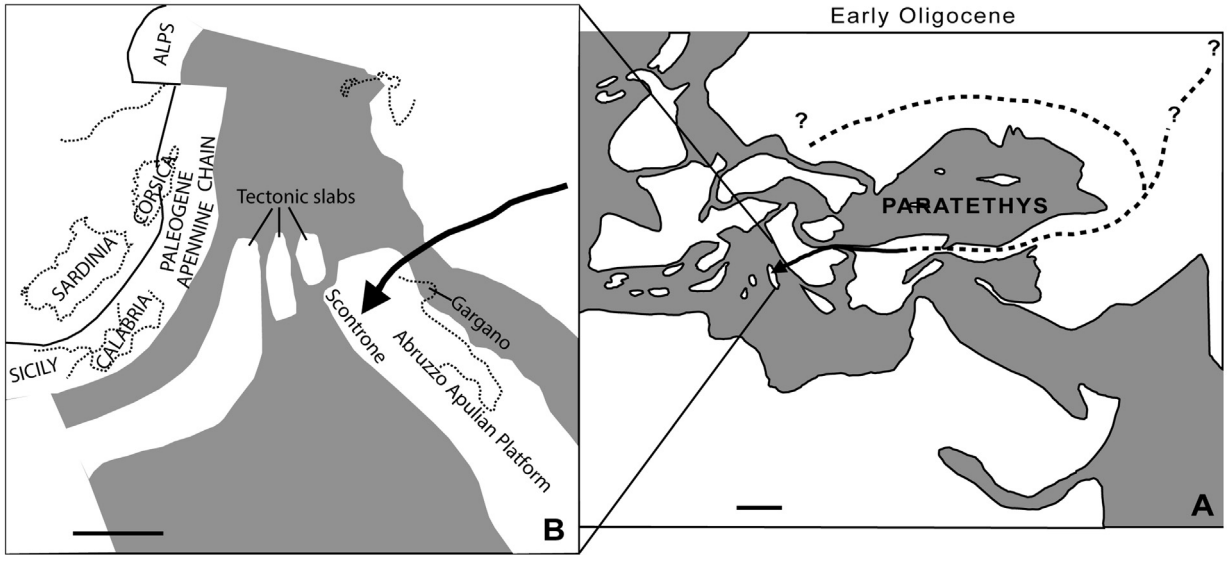

Fig. 1. Paleogeography of the Mediterranean and Paratethys basins during the Early Oligocene. **A**. Reconstruction of the paleogeography of the peri-Mediterranean and peri-Paratethyan areas (from Popov et al., 2004, modified). The arrow shows the possible pathways followed by the ancestors of Hoplitomerycidae to reach the Apulian Platform. **B**. Magnified view of the Central Mediterranean (from Patacca et al., 2008a, modified). The arrow indicates the location of the trans-Adriatic istmus through which the ancestors of Hoplitomerycidae colonized the Apulian Platform. Scale bars: 500 km (A), 200 km (B).