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Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)

Testudines☆

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ABSTRACT

A new specimen of *Testudo sensu stricto* from the late Miocene locality Nikiti 2 (NIK; Macedonia, Greece) is described. It is a small-bodied testudinid very close to the species *Testudo marmorum*, but it can be differentiated from it by some minor features not observed on the holotype specimen of *T. marmorum*. It belongs to the group of extant and extinct testudinids that have a hypo-xiphiplastral hinge, which is a character of the *Testudo sensu stricto* lineage. It is characterized by a dome-shell shape that flares posteriorly with slightly posterior upturned peripherals, a large and flat dorsal epiplastral lip, xiphiplastra with straight and parallel lateral margins, and a quadrangular, long and very thick pygal.

1. Introduction

During the last century, several testudinid fossils have been reported from the Miocene of Greece (e.g., Gaudry, 1862, 1862–1867; Woodward, 1901; Arambourg and Piveteau, 1929; Paraskevaidis, 1955; Bachmayer, 1967). This well-diversified family – the Testudinidae – is currently represented in the Mediterranean area by small land tortoises belonging to the monophyletic *Testudo* clade (Le et al., 2006; Parham et al., 2006a, b; Corsini et al., 2014), consisting of six currently recognized species (Kuyl et al., 2002), of which two are found in Greece: *Testudo marginata* Schoepff, 1792, and *T. graeca* Linnaeus, 1758 (Parham et al., 2006b).

The use of the name *Testudo* Linnaeus, 1758 and its taxonomic definition is still debated, and several authors have erected three distinct genera for some species of *Testudo .sensu lato* (*sensu* Lapparent de Broin, 2000, 2001): *Agrionemys* for the *T. horsfieldi* lineage (Khozatsky and Mlynarsky, 1966), *Eurotestudo* for the *T. hermanni* lineage (Lapparent de Broin et al., 2006a), and *Chersus* containing *T. marginata* and *T. kleinmanni* (*fide* Gmira, 1993 and Kuyl et al., 2002). Nevertheless, recent works based on molecular data (Parham et al., 2006b; Lourenço et al., 2012) generally agree that the genus *T. sensu stricto* is restricted to three species (from the Mediterranean, Caucasus and Iran areas) that are diagnosed by a hinge between the xiphi- and hypoplastron: *T. graeca* Linnaeus, 1758 (type species), *T. marginata* Schoepff, 1792, and *T. kleinmanni* Lortet, 1883.

Concerning the testudinid fossil record, numerous and important discoveries across Greece have led to a better understanding of tortoise diversity and distribution during the Miocene–Pliocene period, which have been recently summarized in Georgalis and Kear (2013). However, only a few specimens of tortoises were described and formally identified as representatives of *Testudo sensu lato* (Table 1), and even fewer have been attributed to the *Testudo sensu stricto* lineage.

A single testudinid specimen is studied in the present article; it was collected during excavations at the locality of Nikiti 2 (NIK). This locality is located in the Chalkidiki Peninsula (Macedonia, Greece), near the village of Nikiti and about 120 km southwest to Thessaloniki. The Nikiti 2 fossiliferous horizon belongs to the Nikiti Formation, consisting of pebbles, gravels, sands at the base, and of sands, clay-sands and gravels alternated with red-brown clay-sands near the top. The site has provided a rich early Turolian (MN 11) mammal fauna, which is studied in the present volume. More details about the stratigraphy and age of NIK are given in Koufos (2016) and Koufos et al. (2016). The studied material is housed and catalogued in the collections of the Laboratory of Geology and Palaeontology of the Aristotle University of Thessaloniki (LGPUT). The new material was directly compared with extant and fossil specimens of *T. graeca*, *T. kleinmanni*, *T. marginata*, and *T. marmorum* from the collections of the MNHN (Paris, France).

2. Systematic palaeontology

Reptilia Laurenti, 1768
Testudines Batsch, 1788

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Cryptodira Cope, 1868
Testudinoidea Fitzinger, 1826
Testudinidae Batsch, 1788
Genus ***Testudo*** Linnaeus, 1758
Testudo cf. marmorum
Fig. 1

Material: NIK-1946, a complete carapace.

Locality: Nikiti 2 (NIK), Chalkidiki, Macedonia, Greece.

Age: Early Turolian, MN 11, late Miocene.

Description: The specimen corresponds to an unusually well preserved complete shell (dimensions: 189 mm long × 130 mm wide); the bony surface both of the shell and the plastron displays all anatomical details. The carapace is domed (Fig. 1(c)). The posterior carapacial border spreads out posteriorly [as in *T. marginata* and *T. marmorum* (MNHN PIK 3683)] with an elongated and curved pygal. The anterior border of the carapace is almost straight with a modest nuchal notch. The cervical scale is very narrow. The nuchal bone is hexagonal with long anterior sides and short posterior sides. The neural series is formed by eight plates with the following formulae: an elongated and sub-rectangular neural 1, two large octagonal neural 2, neural 4 and a slightly compressed hexagonal neural 6, between two squarish neural 3 and neural 5. The posterior neurals consist of an irregular hexagonal neural 7 subdivided into two parts (Fig. 1(a)), and a smaller neural 8. The pleural 1, that overlaps the nuchal, contacts marginal scutes 1–4. The vertebral scutes show the characteristic pattern with a lyre-shaped vertebral 1 and vertebrals 1, 2 and 3 as broad as long. The vertebral 5 is fan-shaped and narrower anteriorly than posteriorly. At the posterior carapacial border with elevated peripherals, the suprapygals are differentiated into one trapeze embracing sp1 and a very reduced sp2, a condition already observed in *T. graeca* from Morocco (N° REP 21 and 23 in Lapparent de Broin et al., 2006a). The curved long (40 mm) and thick pygal plate (an asymmetric rectangle with a width of 30 mm and 10 mm for the anterior and posterior parts, respectively; Fig. 1(d)) without medial sulcus indicates that the specimen represents a male individual (Bour, 1983).

The plastron (Fig. 1(b)) shows a strong longitudinal medial concavity, another sexually dimorphic character seen in male specimens. The short anterior lobe is almost triangular (25 mm long) whereas the posterior is longer (45 mm) with straight lateral borders and a large anal notch forming a 25–30° angle. The bridge of the plastron is 75 mm long. The dorsal epiplastral lip is well developed, medially elongated, with a uniform height along its entire width. It appears rounded anteriorly and less flat compared to *T. graeca*. The gular pocket is not visible due to the sediments. The gulars are triangular and their surface is concave comparing to the humerals that are convex antero-posteriorly. The humero-pectoral sulcus does not contact the entoplastron; it is located far posteriorly from the border of the entoplastron (Fig. 1(b)). The abdomino-femoral sulcus is very close to the hypo-xiphiplastral suture, indicating the presence of a plastral hinge (Fig. 1(b)). The posterior lobe is formed nearly exclusively by the xiphiplastra. Most of the lateral margins of the xiphiplastra are straight and paralleled to each other, as in *T. marmorum*. The femoroanal sulci join in the midline at an approximately 70° angle.

3. Discussion

The specimen from Nikiti 2 (NIK) is a small-bodied testudinid characterized by a combination of characters that slightly differentiates it from other Greek taxa. This testudinid species shows all the characteristics of the genus *Testudo sensu lato*, including the plate and scute proportions and configurations, the triangular-shaped gulars, the dorsal epiplastral lip curved onto the entoplastron, as well as a hypo-xiphiplastral hinge, which is a typical feature of *T. sensu stricto* (Lapparent de Broin et al., 2006a). This morphology, manifested by the complete medial and lateral fusion of the hypo-xiphiplastral suture and the abdomino-femoral sulcus, is observed in the relatively advanced *Testudo* species (Lapparent de Broin et al., 2006a). It is present in the *marginata* and *graeca* groups, as well as in *T. kleinmanni*. The testudinid from NIK shares with *T. marmorum* (MNHN PIK 3683) from Pikermi (MN 12, Greece) a similar carapace size with 8 neurals, a shell that flares posteriorly with slightly elevated posterior peripherals (apomorphic character of the *T. marginata* group), and also straight xiphiplastral borders. The general shape of its carapace, well rounded and not elongated, differentiates the NIK specimen from *T. marginata* and *T. marmorum* (holotype specimen). The testudinid from Nikiti differs also from *T. marmorum* by its prominent quadrangular pygal, which is very curved and remarkably elongated. Furthermore, it is close to the species *T. graeca* by its suprapygal-pygal configuration made of a second semi-lenticular suprapygal, anteriorly embraced by the first.

The knowledge of the small testudinid fossil record from Greece is still incomplete, resulting in part from limited sampling, as well as depositional biases in the Neogene deposits, and especially for the early and middle Miocene continental formations (Koufos, 2006). Besides, it is very difficult to correctly determine a fossil *Testudo* taxon at the species level due to the intraspecific morphological variations observed in some morphological characters. Some authors have already discussed this polymorphic variations observed for extant and fossil populations of *Testudo* sp. (Lapparent de Broin et al., 2006b, c; Delfino et al., 2009; Corsini et al., 2014). For example, the position of the humero-pectoral sulcus with respect to the entoplastron varies in *T. graeca* and *T. hermanni*. Similarly, the variability in the neural series and the shapes of the suprapygals has been recognized for individuals and populations of *T. graeca* (our observations on extant Moroccan specimens housed in the MNHN Paris), *T. horsfieldi* and *T. antiqua* (Corsini et al., 2014). On the basis of the observed features and known morphological variations, we assign the specimen NIK-1946 to *T.* cf. *marmorum*. It is a small-bodied testudinid very close to the species *T. marmorum*, but it can be distinguished from it by some minor features (in particular its suprapygal-pygal configuration and its prominent quadrangular and elongated pygal), not observed on the holotype specimen. However, an in-depth revision of *T. marmorum* at the population level will be probably necessary when additional material will be discovered.

The Neogene testudinid fauna from Greece is still incompletely known (Georgalis and Kear, 2013). Concerning the Testudinidae, especially for the genus *Testudo*, numerous fossil specimens have been reported from different stratigraphical formations of the Greek Miocene (Table 1). Nevertheless, formally described taxa include only two late Miocene species: *T. marmorum* from Pikermi (uppermost middle Turolian, 7 Ma; Lapparent de Broin, 2000; Koufos, 2006), and *T. amiatae* from Allatini (Late Turolian/Early Ruscinian; Bachmayer and Symeonidis, 1970), a small testudinid which has been recently reviewed (Vlachos et al., 2014). Based on molecular data (Parham et al., 2006b; Lourenço et al., 2012), the divergence of derived *Testudo* with a kinetic hinge in the plastron, ranges from 23 Ma to 10 Ma or from 15 Ma to 5 Ma. Although the molecular divergence dates suggest this age for *T. graeca* and *T. marginata*, the oldest known fossils are stratigraphically younger than 5 Ma (Lapparent de Broin, 2002; Koufos, 2006; Lyras and Van der Geer, 2007; Georgalis and Kear, 2013). The new specimen of *Testudo* from NIK (early Turolian, 8.7 Ma) is older than *T. marmorum* from Pikermi and provides additional data that allow a better understanding of the phylogenetic history of the *T. sensu stricto* lineage.