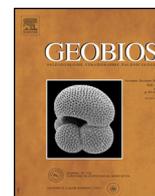




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Original article

The fossil turtles of Greece: An overview of taxonomy and distribution[☆]

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ABSTRACT

Turtle remains are common in the Miocene–Holocene deposits of Greece, and are a key focus of the growing research interest in Neogene herpetofaunas from the Aegean region. Some of the most important finds include one of Europe's stratigraphically youngest pleurodiran taxa, *Nostimochelone lampra*, from the Early Miocene of Macedonia, together with arguably the richest record of fossil tortoises from the quintessential genus *Testudo sensu stricto* from the Late Miocene of Attica and Macedonia, and numerous specimens of the colossal (carapace ~2 m-length) testudinid *Cheirogaster* from Late Miocene–Late Pliocene sediments in southern and northern Greece, as well as on the eastern Aegean islands of Samos and Lesbos. Tantalising, but as yet unconfirmed Miocene accounts of the geoemydid *Mauremys* in Macedonia, and indeterminate emydid-like remains from Euboea, also provide potentially significant range extensions. Although hampered by a historically sparse documentation, the fossil turtles of Greece are a significant resource that record both assemblage changes and the origin of modern lineages.

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1. Introduction

Although reports exist on the fragmentary remains of crocodylians (Boehme and Ilg, 2003), lizards (varanids, agamids, lacertids, anguids, and scincids; Richter, 1995; Boehme and Ilg, 2003; Pianka et al., 2004; Delfino, 2004; Delfino et al., 2008), and snakes (pythonids, boids, colubrids *sensu lato*, elapids, viperids, and typhlopids; Roemer, 1870; Szyndlar and Zerova, 1990; Szyndlar, 1991, 1995; Szyndlar and Rage, 2003; Boehme and Ilg, 2003), turtles are by far the most ubiquitous fossil “reptiles” known from mainland Greece and its surrounding island territories. The first recorded finds date from the mid-nineteenth century, when excavations commenced at the world-renowned Late Miocene (Messinian) fossil locality of Pikermi, near Athens. Gaudry (1862, 1862–1867) eventually described this material, which included the extinct tortoise *Testudo marmorum* Gaudry, 1862 – the oldest attested species of the iconic *Testudo* Linnaeus, 1758 *sensu stricto* lineage (Lapparent de Broin, 2000; Lapparent de Broin et al., 2006a, b, c).

Since then, a number of important discoveries have followed. Examples include Greece's most ancient named turtle taxon, *Nostimochelone lampra* Georgalis, Velitzelos, Velitzelos and Kear, 2012 (see corrected publication date below) from the Early

Miocene (Burdigalian) Zeugostasion Formation, at the village of Nostimo near Kastoria in northwestern Macedonia, which simultaneously represents the first pleurodiran turtle from Greece and one of the last occurrences of the predominantly Gondwanan podocnemidoidean clade from Europe (Georgalis et al., 2013). Paraskevaïdis (1955) published on two fossil tortoises from the Middle Miocene (Langhian) Keramaria Formation of Thymiana on Chios, which are considered amongst the oldest representatives of *Testudo sensu lato* (Chesi et al., 2009). Also less well-known, but certainly more spectacular, are the gigantic tortoises from Mio-Pliocene sediments around Thessaloniki (Tortonian; Arambourg and Piveteau, 1929; Lapparent de Broin, 2002), at Pikermi (Woodward, 1901; Bachmayer, 1967), and on the eastern Aegean islands of Samos (Tortonian–Messinian; Szalai, 1931) and Lesbos (Zanclean; Lapparent de Broin, 2002). These fossils have been placed within the genus *Cheirogaster* Bergounioux, 1935, and include the endemic species *C. schafferi* (Szalai, 1931) from the Mytilinii Formation of Samos, possibly one of the world's largest-bodied land-living turtles (carapace ~2 m-length; Lapparent de Broin, 2002).

Because of the dearth of detailed published information about Greek fossil testudinians, this paper aims to provide a comprehensive synopsis of the most notable occurrences, together with background information on their source localities and geological settings. This is intended as a foundation for future research on new finds, and the re-evaluation of previously described taxa.

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2. Geographical and stratigraphical framework

2.1. Early to Middle Miocene

Turtle fossils have been documented from many localities throughout Greece, and in sediments ranging in age from the Early Miocene through to Holocene (Table 1; Figs. 1 and 2). The stratigraphically-oldest known source unit is the Zeugostasion Formation, a series of sandy marls, clastic sandstones and laminated conglomerates that are rich in marine molluscs (Georgiades-Dikeoulia et al., 2000); it has yielded the isolated shell of a pleurodiran turtle, *N. lampra* (Georgalis et al., 2013). The Zeugostasion Formation forms part of a marine transgressive succession that crops out within the Mesohellenic Basin of northwestern Macedonia, and is considered to be late Burdigalian (Early Miocene) in age based on foraminiferal assemblages (Savoyat et al., 1971) and an Sr-isotope age range of ~16–18 Ma from equivalent sections (Wielandt-Schuster et al., 2004). Other undifferentiated Early Miocene (Burdigalian; possibly middle Orleanian European Land Mammal Mega-Zone [ELMMZ], MN 4) fluviatile sediments at Aliveri on the island of Euboea, and Karydia near Komotini in Thrace, have also yielded emydid and indeterminate testudinatan remains (Boehme and Ilg, 2003).

Middle Miocene turtle material is known from the Keramaria Formation of Thymiana on the island of Chios. These fine sandstone and siltstone strata have produced a distinctive array of terrestrial mammals (Koufos et al., 1995; Bonis et al., 1997), which infer a Langhian age (late Orleanian ELMMZ, MN 5 *sensu* Koufos, 2006, 2009). Paraskevaidis (1955) reported on tortoise shell components from this deposit but more specific stratigraphical information is not yet available.

2.2. Late Miocene to Early Pliocene

Late Miocene-Pliocene turtle fossils are prolific in Greece, and are exclusively represented by testudinoids. The stratigraphically oldest finds are Tortonian (late Vallesian ELMMZ, MN 10 *sensu* Koufos, 2006) and derive from the Nea Mesimvria Formation. This unit comprises a series of indurated sand and gravel beds that crop out in the Axios river valley near Thessaloniki. Vertebrate fossils have been recovered from three excavation sites in the upper part of Nea Mesimvria Formation: “Xirochori-1”, “Ravin des Zouaves-1”, and “Ravin de la Pluie”. “Ravin de la Pluie” has yielded hominoid remains (Koufos, 2006), together with an articulated shell apparently representing a new species of *Testudo sensu stricto* (Garcia et al., 2011).

The famous Pikermi Formation, which underlies suburban areas of Athens, consists of red marl and lenticular masses of pebbly conglomerate with occasional sandy layers (Woodward, 1901). Its exceptionally rich terrestrial mammal fauna was recently summarised by Roussiakis (2002). Gaudry (1862) described the first turtle specimens from a complex series of quarries situated along the Megalo Rema stream, east of Athens. These included *T. marmorum*, which has also been recovered from coeval strata on Euboea (Melentis, 1970). The various fossiliferous horizons at Megalo Rema (two according to Gaudry, 1862–1867, or up to three according to Woodward, 1901) are considered to be chronologically homogeneous, with a predominantly Messinian age (Turolian ELMMZ, MN 12–13; Theodorou et al., 2010). Subsequent excavations at the geographically proximal “Chomateres” locality (also called “Kisdari”, which is situated ~1 km along the ravine from Megalo Rema), and “Pikermi Valley-1” (approximately 500 m east-southeast of Megalo Rema, and ~1.7 km southwest of “Chomateres”) have yielded similar mammal taxa (Marinos and Symeonidis, 1974; Koufos, 2006; Theodorou et al., 2010). However, a fourth site at Liossati (also called “Kiourka”), just north of Athens, is

possibly younger, being latest Miocene-earliest Pliocene in age. Liossati has produced shell fragments of giant tortoises as well as other smaller testudinids (Bachmayer and Symeonidis, 1976; Lapparent de Broin, 2000; Lapparent de Broin et al., 2006a, b).

The Mytilinii Formation of Samos Island in the eastern Aegean is another historically well-known Messinian unit (Turolian ELMMZ, MN 13) comprising fluviolacustrine volcanoclastic tuffaceous silts and massive tuffs (Kostopoulos et al., 2009; Koufos et al., 2011). Fossils excavated in the early twentieth century were often commercially traded with museums. Unfortunately, this method of collecting has led to poor stratigraphical control. Thus, only limited site information exists for many important finds such as the skull of the gigantic testudinid *Cheirogaster schafferi* (Szalai, 1931), and several other small tortoise specimens, some of which incorporate cranial material (Lapparent de Broin, 2002; Koufos, 2006, 2009).

Outcrops of the Vathylakkos Formation are situated near the villages of Vathylakkos, Prochoma, and Nea Mesimvria, close to Thessaloniki (Bonis et al., 1988). The Vathylakkos Formation consists of light-colored marls, sands, and gravels, and includes a very rich assemblage of Tortonian-Messinian (latest Vallesian to early Turolian ELMMZs, MN 11–12) bovids, equids, giraffids, and rare cervids (Bonis et al., 1988, 1992, 1999; Koufos, 2006). Arambourg and Piveteau (1929) reported the remains of a gigantic tortoise, *Cheirogaster* sp., found in 1916 at “Ravin de Vatilik”, which probably equates to the “Vathylakkos-3” locality of Koufos (2006). A second smaller specimen was also attributed to *Testudo* cf. *marmorum*, and derived from “Falaise de Karabouroun”, a site that might incorporate part of the predominantly Pliocene Gonia Formation at Megalo Emvolon near Thessaloniki (Arambourg and Piveteau, 1929).

The Gonia Formation itself (uppermost Miocene-lowermost Pliocene) is one of the younger units within the predominantly fluvio-lacustrine sediments of western Chalkidiki in Macedonia. Sequentially this stratum intercalates between the Antonios Formation (Lower-Middle Miocene and Upper Miocene), Triglia Formation (Upper Miocene), Trilophos Formation (uppermost Miocene), and the uppermost Moudania Formation (Lower Pliocene; Syrides, 1990). The Gonia Formation is by far the most fossiliferous of these deposits, and consists of both lenticular and massively bedded clays, sandstones, marls, and marly limestones (Syrides, 1990). Koufos et al. (1991) summarised the vertebrate assemblage from Megalo Emvolon as characteristic of an arid savannah, with tortoise species assigned to either *Testudo* cf. *graeca* Linnaeus, 1758, *Testudo* sp., or *Cheirogaster* cf. *schafferi* (Bachmayer and Symeonidis, 1970; Bachmayer et al., 1980; Koufos et al., 1991; Koufos, 2006). There is not a single clear fossiliferous horizon at Megalo Emvolon. Instead, several small fossil concentrations; probably Early Pliocene (Zanclean; Ruscinian ELMMZ, MN 15) in age, are dispersed throughout the sequence (Koufos et al., 1991; Koufos, 2006).

Other Macedonian Late Miocene-Early Pliocene localities with sporadic testudinid records include the Gonia Formation at Silata, which has yielded *Testudo* sp. (Syrides, 1990; Vasileiadou et al., 2003; Koufos, 2006), together with Epanomi, Nea Kallikrateia, Nea Michaniona, and Aggelochori, all of which manifest remains of *Cheirogaster*, most notably a virtually complete skeleton that is currently under study (Athanasidou and Kostopoulos, 2010; Vlachos, 2011). The Trilophos Formation at Allatini is known for *Testudo amiatae* Pantanelli, 1893, a species originally reported from Italy (Koufos et al., 1991). Unidentified testudinids (Mueller-Töwe et al., 2011), as well as the geoemydid *Mauremys* Gray, 1869 (Gad, 1990) have been documented from undifferentiated Upper Miocene strata at Maramena, near Serres. Syrides (1995), Sylvestrou and Kostopoulos (2006), and Boehme and Ilg (2003) reported additional sites with testudinid fossils (Table 1; Fig. 1). Commercially mined Lower Pliocene (Zanclean; Ruscinian ELMMZ,

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