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Original article

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

Georgios L. Georgalis [a], Benjamin P. Kear [b,*]

[a] School of Chemical Engineering, Aristotle University of Thessaloniki, Thessaloniki 54124 Greece
[b] Palaeobiology Programme, Department of Earth Sciences, Uppsala University, Villavägen 16, SE-75236 Uppsala, Sweden

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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 Eastern Mediterranean. This incorporates the presently oldest definitive representatives of 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 Lesvos. 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.

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). Paraskevaidis (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 Lesvos (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 testudinatans, 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.

☆ Corresponding editor: Gilles Escarguel.
* Corresponding author.
E-mail address: benjamin.kear@geo.uu.se (B.P. Kear).

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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 centrury 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 Vatiluk", 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 (Athanassiou 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,

Table 1
List of significant Greek fossil testudinatan occurrences.

Location, Unit	Geological Age	Taxon	References
Nostimo, Zeugostasion Formation	Early Miocene	*Nostimochelone lampra*	Georgalis et al. (2013)
Aliveri ("Aliveri-2 Site"), undifferentiated	Early Miocene	Emydidae (?) indet.	Boehme and Ilg (2003)
Karydia ("Karydia-2 Site"), undifferentiated	Early Miocene	Testudinata indet.	Boehme and Ilg (2003)
Thymiana, Keramaria Formation	Middle Miocene	*Testudo* sp. I	Paraskevaidis (1955); Chesi et al. (2009)
Thymiana, Keramaria Formation	Middle Miocene	*Testudo* sp. II	Paraskevaidis (1955); Chesi et al. (2009)
"Ravin de la Pluie", Nea Mesimvria Formation	Late Miocene	*Testudo* sp. nov.	Garcia et al. (2011)
"Vathylakkos-3", Vathylakkos Formation	Late Miocene	*Cheirogaster* cf. *schafferi*	Arambourg and Piveteau (1929); Lapparent de Broin (2001, 2002)
"Falaise de Karabouroun", Vathylakkos Formation	Late Miocene	*Testudo* cf. *marmorum*	Arambourg and Piveteau (1929); Gmira (1995); Lapparent de Broin (2001); Lapparent de Broin et al. (2006a)
Halmyropotamos, undifferentiated	Late Miocene	*Testudo marmorum*	Melentis (1970)
Megalo Rema, Pikermi Formation	Late Miocene	*Testudo marmorum*	Gaudry (1862, 1862–1867); Woodward (1901); Lapparent de Broin et al. (2006a)
Megalo Rema, Pikermi Formation	Late Miocene	*Cheirogaster* cf. *schafferi*	Woodward (1901); Bachmayer (1967); Lapparent de Broin (2001, 2002)
Samos, Mytilinii Formation	Late Miocene	*Cheirogaster schafferi*	Szalai (1931); Lapparent de Broin (2002)
Samos ("Mytilinii-4"), Mytilinii Formation	Late Miocene	*Testudo* sp.	Koufos et al. (2011)
Liossati ("Kiourka"), Pikermi Formation	Late Miocene or Early Pliocene	*Cheirogaster* cf. *schafferi*	Bachmayer and Symeonidis (1976)
Liossati ("Kiourka"), Pikermi Formation	Late Miocene or Early Pliocene	*Testudo* sp.	Bachmayer and Symeonidis (1976)
Maramena ("Maramena-1"), undifferentiated	Latest Miocene	*Mauremys* sp.	Gad (1990)
Maramena, undifferentiated	Latest Miocene	Testudinidae indet.	Mueller-Töwe et al. (2011)
Makrygialos, Makrygialos Formation	Latest Miocene–earliest Pliocene	Testudinidae indet.	Sylvestrou and Kostopoulos (2006)
Allatini, Trilophos Formation	Latest Miocene–earliest Pliocene	*Testudo amiatae*	Campana (1917)
Silata, Gonia Formation	Latest Miocene–Early Pliocene	*Testudo* sp.	Syrides (1990)
Megalo Emvolon, Gonia Formation	Latest Miocene–Early Pliocene	*Testudo* cf. *graeca*	Bachmayer et al. (1980); Koufos (2006)
Megalo Emvolon, Gonia Formation	Latest Miocene–Early Pliocene	*Testudo* sp.	Boehme and Ilg (2003); Koufos (2006)
Epanomi, Gonia Formation	Latest Miocene–Early Pliocene	*Cheirogaster* cf. *schafferi*	Vlachos (2011)
Nea Michaniona, Gonia Formation	Latest Miocene–Early Pliocene	*Cheirogaster* cf. *schafferi*	Vlachos (2011)
Aggelochori, Gonia Formation	Latest Miocene–Early Pliocene	*Cheirogaster* cf. *schafferi*	Vlachos (2011)
Nea Kallikrateia, Gonia Formation	Latest Miocene–Early Pliocene	*Cheirogaster* cf. *schafferi*	Vlachos (2011)
Vevi, Vevi Formation	Early Pliocene	Testudinata indet.	Boehme and Ilg (2003)
Dimitra, undifferentiated	Early Pliocene	Testudinata indet.	Syrides (1995)
Vorio ("Vorio-1"), Ptolemais Formation	Early Pliocene	Emydidae indet.	Boehme and Ilg (2003)
Vorio ("Notio-1"), Ptolemais Formation	Early Pliocene	*Testudo* sp.	Boehme and Ilg (2003)
Vorio ("Notio-1"), Ptolemais Formation	Early Pliocene	Testudinidae indet.	Boehme and Ilg (2003)
Apolakkia, Apolakkia Formation	Early Pliocene	Testudinata indet.	Mueller-Töwe et al. (2011)
Apolakkia, Apolakkia Formation	Early Pliocene	Testudoolithidae	Mueller-Töwe et al. (2011)
Vatera ("V-site"), Vatera Formation	Late Pliocene–Early Pleistocene	*Testudo* cf. *graeca ibera*	Lapparent de Broin (2002); Lyras and Van der Geer, 2007
Vatera ("V-site"), Vatera Formation	Late Pliocene–Early Pleistocene	cf. *Cheirogaster* aff. *schafferi*	Lapparent de Broin (2002)
Psychiko, undifferentiated	Early Pleistocene	*Testudo* sp.	Bachmayer and Symeonidis (1970)
Lakonia, undifferentiated	Early Pleistocene	*Testudo marginata*	Schleich (1982)
Megalopolis, Choremi Formation	Early Pleistocene	*Mauremys rivulata* or *Mauremys sensu lato*	Melentis (1966); Chesi et al. (2007)
Megalopolis, Choremi Formation	Early Pleistocene	*Emys orbicularis*	Van Vugt et al., 2000
Petralona Cave, undifferentiated	Middle Pleistocene	Testudinidae indet.	Kretzoi (1977); Kretzoi and Poulianos (1981)
Petralona Cave, undifferentiated	Middle Pleistocene	*Testudo graeca*	Kretzoi (1977); Kretzoi and Poulianos (1981)
Xerias, undifferentiated	Late Pleistocene	*Testudo* sp.	Tsoukala et al. (2011)

Table 1 (*Continued*)

Location, Unit	Geological Age	Taxon	References
Kandilia Cave, undifferentiated	Middle–Late Pleistocene	*Testudo graeca ibera*	Kuss (1975)
Gerani Cave, undifferentiated	Late Pleistocene	*Testudo marginata cretensis*	Bachmayer et al. (1975)
Zourida Cave, undifferentiated	Late Pleistocene	*Testudo marginata cretensis*	Bachmayer et al. (1975)
Bate Cave, undifferentiated	Late Pleistocene	*Testudo marginata cretensis*	Kotsakis (1977)
Simonelli Cave, undifferentiated	Late Pleistocene	*Testudo marginata cretensis*	Kotsakis (1977)
Simonelli Cave, undifferentiated	Late Pleistocene	*Mauremys rivulata* or *Mauremys sensu lato*	Kotsakis (1977); Chesi et al. (2007)
Kalo Chorafi Cave, undifferentiated	Late Pleistocene	Testudinata indet.	Dermitzakis (1977)
Bali Cave, undifferentiated	Late Pleistocene	Testudinata indet.	Dermitzakis (1977)
Mavromouri Cave, undifferentiated	Late Pleistocene	Testudinata indet.	Dermitzakis (1977)
Charkadio Cave, undifferentiated	Late Pleistocene	*Testudo marginata*	Bachmayer and Symeonidis (1975); Theodorou et al. (2007)
Vraona Cave, undifferentiated	Late Pleistocene–Holocene	*Mauremys rivulata* or *Mauremys sensu lato*	Rauscher (1995); Chesi et al. (2007)
Vraona Cave, undifferentiated	Late Pleistocene–Holocene	*Emys orbicularis*	Symeonidis et al. (1979); Fritz (1995); Rauscher (1995)

MN 14–15; Hordijk and de Bruijn, 2009) lignite and interbedded marl deposits in the Ptolemais Formation (western Macedonia) have generated testudinid material, together with an aquatic emydid (Boehme and Ilg, 2003).

Mueller-Töwe et al. (2011) described a clutch of five turtle eggs and numerous turtle eggshell fragments from the Early Pliocene (Zanclean; Ruscinian ELMMZ, MN 15) Apolakkia Formation, near Apolakkia in southwestern Rhodes. The Apolakkia Formation comprises alternating marls and clay-silts through to conglomerate horizons that contain freshwater gastropods and carapace fragments of small turtles (Willmann, 1981; Mueller-Töwe et al., 2011). Mueller-Töwe et al. (2011) attributed the eggs to a large-bodied tortoise because of their estimated maximum diameters of 40–50 mm.

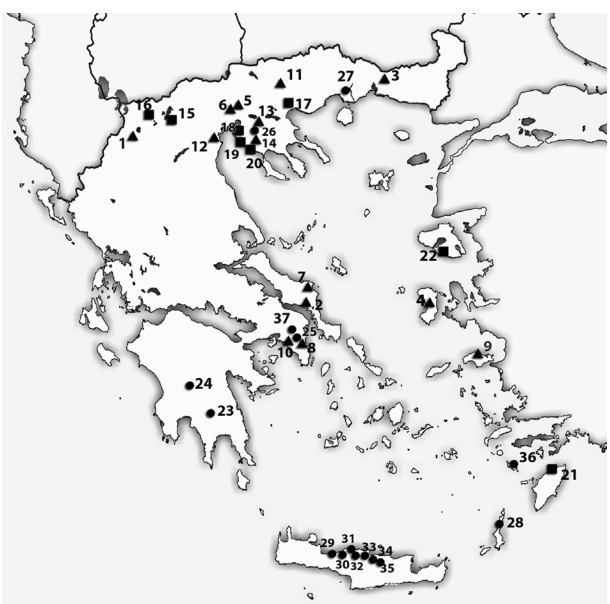

Fig. 1. Principal Miocene (▲), Pliocene (■) and Pleistocene-Holocene (●) fossil turtle localities in Greece. **1**, Nostimo; **2**, Aliveri; **3**, Karydia; **4**, Thymiana; **5**, "Ravin de la Pluie"; **6**, Vathylakkos Formation localities; **7**, Halmyropotamos; **8**, Pikermi (Megalo Rema); **9**, Samos; **10**, Liossati; **11**, Maramena; **12**, Makrygialos; **13**, Allatini; **14**, Silata; **15**, Vorio; **16**, Vevi; **17**, Dimitra; **18**, Megalo Emvolon; **19**, Nea Michaniona, Aggelochori and Epanomi; **20**, Nea Kallikrateia; **21**, Apolakkia; **22**, Vatera; **23**, Lakonia; **24**, Megalopolis; **25**, Psychiko; **26**, Petralona Cave; **27**, Xerias; **28**, Kandilia Cave; **29**, Gerani Cave; **30**, Zourida Cave; **31**, Bate Cave; **32**, Simonelli Cave; **33**, Kalo Chorafi Cave; **34**, Bali Cave; **35**, Mavromouri Cave; **36**, Charkadio Cave; **37**, Vraona Cave.

2.3. Late Pliocene to Middle Pleistocene

The Late Pliocene-Early Pleistocene Vatera Formation (Piacenzian; Villanyian or early-middle Villafranchian *sensu* Rook and Martínez-Navarro, 2010 ELMMZ, MN 16-17 incorporating the stratigraphical revision of Gibbard et al., 2010) on the island of Lesvos is renowned for its association with the Miocene "petrified forest", listed as a UNESCO Global Geopark in 1998, as well as clay pits that preserve a diverse array of fossil plants (Lyras and Van der Geer, 2007). Vertebrate remains occur within the upper part of the sequence, which incorporates fluvial breccia-conglomerates, sandy clays, and sandy conglomerates (Drinia et al., 2002). Mammals (e.g., bovids, giraffids; Van der Geer and Sondaar, 2002; Koufos, 2009) and turtles including possible representatives of the extant *Testudo graeca ibera* Pallas, 1914, as well as collossal cf. *Cheirogaster* aff. *schafferi* remains have been recovered (Lapparent de Broin, 2002; Lyras and Van der Geer, 2007).

Turtle assemblages from the Pleistocene of Greece contain exemplars of extant lineages. The Megalopolis Basin in the northern Peloponnese is arguably the most well-known locality, with lacustrine silts and clay interspersed with lignite seams that range through six fossiliferous horizons of Early to Late Pleistocene age (Löhnert and Nowak, 1965; Melentis, 1966; Van Vugt et al., 2000). The most productive is the Middle Pleistocene Marathousa Member (Choremi Formation), which is well exposed in open cut lignite mines, and has yielded a diversity of vertebrates including turtles referrable to the living emydid *Emys orbicularis* (Linnaeus, 1758) (Van Vugt et al., 2000), and geoemydids either conspecific with *Mauremys rivulata* (Valenciennes, 1833) or more broadly attributable to *Mauremys sensu lato* (Melentis, 1966; Chesi et al., 2007).

2.4. Late Pleistocene to Holocene

Late Pleistocene turtle bones have been documented from the famous Simonelli, Bate, and other caves on Crete (Table 1; Fig. 1), where testudinids, emydids and geoemydids have been found (Kotsakis, 1977). The Zourida and Gerani caves are especially important for specimens of the endemic Cretan tortoise *Testudo*

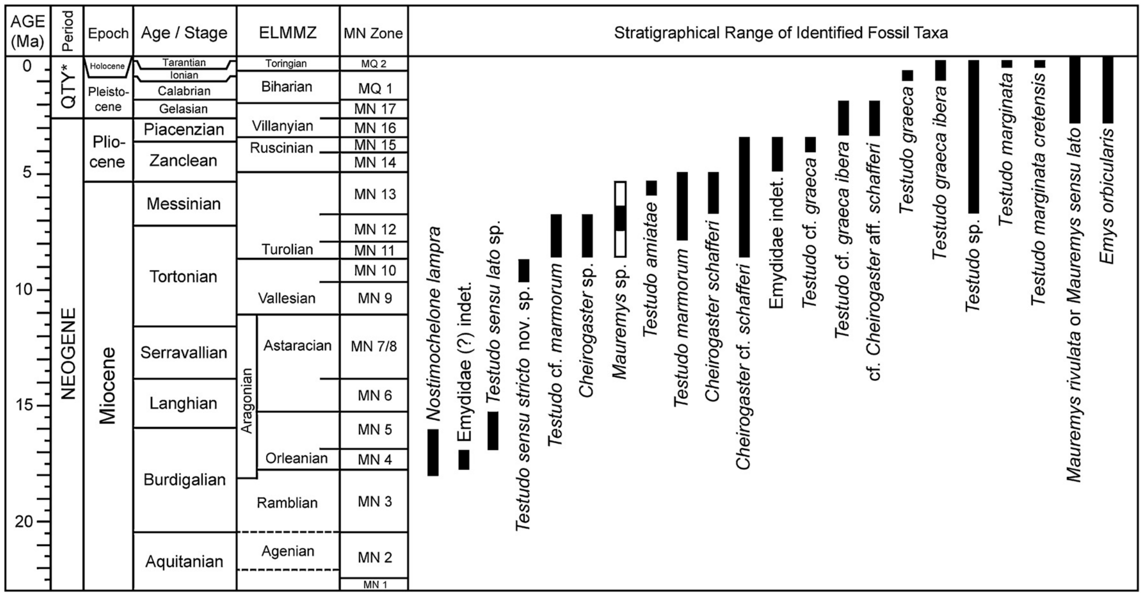

Fig. 2. Stratigraphical chart showing the documented range of presently identified Greek fossil turtle taxa. Stage and zonation parameters derived from Steininger (1999), Gibbard et al. (2010), and Gradstein et al. (2012). Black fill indicates recorded distribution; white fill represents possible age range; QTY*, Quaternary.

marginata cretensis Bachmayer, Brinkerink and Symeonidis, 1975. Indeterminate probable testudinid material has been discovered in Kandilia Cave on Karpathos island in the southern Aegean (Kuss, 1975), and in Charkadio Cave on the Dodecanese island of Tilos, the latter dating from between 4500–3500 years before present (Theodorou et al., 2007). On mainland Greece, Pleistocene fossils attributed to *Testudo* sp., *Testudo marginata* Schoepff, 1793, and *Testudo graeca* have been reported from Psychiko near Athens (Bachmayer and Symeonidis, 1970), Lakonia in the Peloponnese (Schleich, 1982), Xerias in eastern Macedonia (Tsoukala et al., 2011), and Petralona Cave in Chalikidiki (Table 1); Petralona additionally manifests a large-bodied tortoise of uncertain affinities (Kretzoi and Poulianos, 1981). The Late Pleistocene to Holocene strata of Vraona Cave in Attica near Athens, has produced fossils of the aquatic terrapins *Mauremys* and *Emys* Duméril, 1805 (Symeonidis et al., 1979; Fritz, 1995; Rauscher, 1995; Chesi et al., 2007).

3. Systematic palaeontology

Dubois and Bour (2010) argued that the crown turtle (*sensu* Joyce et al., 2004) ordinal name, "Testudines Batsch, 1788", is invalid beyond the family-series, and thus can only be applied to Tesudinidae *sensu stricto*. These authors also critiqued the apomorphy-based nominal "Testudinata Klein [in Behn], 1760", which was defined by Joyce et al. (2004: 996) on the presence of a "complete turtle shell", because it referenced a German translation (Klein, 1760) of an older document in Latin (Klein, 1751), published prior to Linnaeus (1758). Unfortunately, Dubois and Bour (2010) failed to propose any alternative terminology. Rather, they concluded that prior to formal action by the International Commission on Zoological Nomenclature (ICZN), the higher taxonomy of turtles "will remain a matter of personal or collective tastes, opinions and arbitrary decisions of zootaxonomists" (Dubois and Bour, 2010: 156). Because of this ambiguity, we have provisionally retained the clade-based scheme of Joyce et al. (2004) as a phylogenetic framework for discussing fossil turtles; our only exception is "Geoemydidae Theobald, 1868", which we include here because of chronological priority (see David, 1994).

Institutional abbreviations: AMPG, Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Athens; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMW, Naturhistorisches Museum, Vienna; NMP, Nostimo Museum of Palaeontology, Nostimo Kastorias; AUTH, Aristotle University of Thessaloniki, Thessaloniki.

TESTUDINATA Klein [*in* Behn], 1760

Remarks: Taxon authorship following Joyce et al. (2004), but see Dubois and Bour (2010) for comments.

PLEURODIRA Cope, 1864

PODOCNEMIDOIDEA Cope, 1868 (Gaffney et al., 2011)

Nostimochelone Georgalis, Velitzelos, Velitzelos and Kear, 2012 (Georgalis et al., 2013)

Nostimochelone lampra Georgalis, Velitzelos, Velitzelos and Kear, 2012 (Georgalis et al., 2013)

Remarks: The printed version of Georgalis et al. (2013), and its contained nominal *N. lampra*, was postdated from 2012 to 2013. However, under article 21.4 of the ICZN (www.iczn.org), the earliest demonstrated date of this published work's existence (21st August 2012) should be adopted for the formal nomenclatural act. The authors have therefore posted a correction on *ZooBank* (www.zoobank.org) under the registration: urn:lsid:zoobank.org:pub:106421D1-ABEF-4368-BB45-464C929FF83E.

Thus far known only from the holotype (NMP V1), the partial carapace and plastron of *N. lampra* (Fig. 3A, B) represent the oldest currently described turtle fossil from Greece. Georgalis et al. (2013) identified classic pleurodiran synapomorphies including a sutural articulation of the pelvis to the shell, together with the presence of laterally positioned "equidimensional" mesoplastra, and extensive overlap of the pectoral scutes on the entoplastron. These features are diagnostic for podocnemiderans, and more specifically podocnemidoids (Gaffney et al., 2006), although Gaffney et al. (2011) listed overlap of the pectoral scutes on the entioplastron amongst the defining features of Podocnemididae. *N. lampra* is also uniquely characterised by a mosaic of other traits, in particular, the presence of six elongate and remarkably transversely-compressed neurals, and a broad nuchal embayment that extends onto the first peripherals (Georgalis et al., 2013). The latter character state was used to differentiate *N. lampra* from Afro-Eurasian podocnemidids,

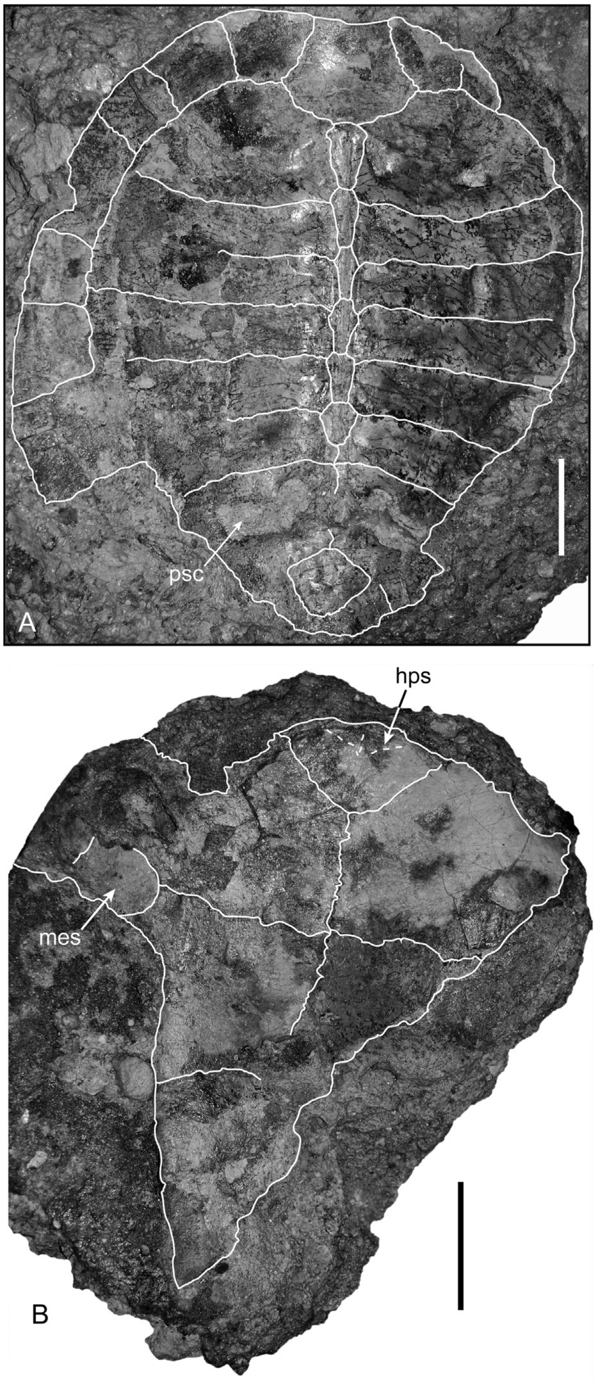

Fig. 3. *Nostimochelone lampra*: holotype (NMP V1) carapace (**A**, in visceral view) and incomplete plastron (**B**). *N. lampra* is Greece's currently oldest described turtle taxon from the Early Miocene Zeugostation Formation of Nostimo, northwestern Macedonia. hps, humero-pectoral sulcus; mes, mesoplastron; psc, pelvis sutural contact. Scale bars: 50 mm.

especially *Cordichelys antiqua* (Andrews, 1903). However, Gaffney et al. (2011) have subsequently demonstrated that *C. antiqua* does exhibit an embayed nuchal; but *N. lampra* remains distinguishable because of its demonstrably narrower nuchal shape and neural series proportions (Gaffney et al., 2011: 50; Georgalis et al., 2013).

Mueller-Töwe et al. (2011) listed an anomalous fossil turtle occurrence: "*Lambrochelone nostimiensis* gen. and sp. nov." from "Nostimo (Kastoria)", with an erroneous citation: "Georgalis, G.L., Velitzelos, E., Velitzelos, D.E. and Kear, B.P. (in press): *Lamprochelone nostimiensis* gen. and sp. nov., an enigmatic new testudinoid turtle from the Miocene of Northern Greece. Journal of Vertebrate Paleontology." As clarified by two of the collaborating authors of this article (G. Theodorou and S.J. Roussiakis, pers. comm. 2011), Mueller-Töwe et al. (2011) intended to mention *N. lampra* and cite Georgalis et al. (2013) but did not verify the nomenclatural condition of the fossil or its publication status. Both "*Lambrochelone nostimiensis*" and its *lapsus calami* "*Lamprochelone nostimiensis*", are therefore *nomina nuda* under article 72.3 of the ICZN (www.iczn.org), because neither a name-bearing type nor a diagnosis were fixed in the Mueller-Töwe et al. (2011) article.

CRYPTODIRA Cope, 1868
TESTUDINOIDEA Batsch, 1788 (Fide ICZN) [or TESTUDINOIDEA Fitzinger, 1826 (Converted Clade Name *sensu* Joyce et al., 2004)]
TESTUDINIDAE Batsch, 1788
Testudo Linnaeus, 1758
Testudo marmorum Gaudry, 1862

Remarks: The earliest appearance of *Testudo sensu lato* in Greece is in the Middle Miocene (Langhian) Keramaria Formation (Paraskevaidis, 1955; Chesi et al., 2009), with species attributable to *Testudo sensu stricto* (defined by a hypo-xiphiplastral hinge) also noted from both the Late Miocene (Tortonian) Nea Mesimvria Formation (Garcia et al., 2011), and Upper Miocene (Messinian) or Lower Pliocene Liossati locality of the Pikermi Formation (Bachmayer and Symeonidis, 1976). The only formally-named taxon, however, is *T. marmorum* from the Messinian Pikermi Formation at Megalo Rema (holotype MNHN PIK 3683), which is currently the stratigraphically oldest confirmed species within the *Testudo sensu stricto* lineage (Lapparent de Broin, 2000; Lapparent de Broin et al., 2006a, b, c).

T. marmorum is characterised by a transversely compressed carapace that flares posteriorly (as in *T. marginata*), a narrow nuchal, eight neurals, and an abdomino-femoral sulcus that transects the hinge; the presence of mobile xiphiplastra complies with *Testudo sensu stricto* (Auffenberg, 1974; Lapparent de Broin et al., 2006b; Fig. 4A–C). Lapparent de Broin et al. (2006c) considered the taxon to be a member of the "*Testudo marginata* group", and a possible sister of *T. marginata*. *T. marmorum* is best represented by shell material from the Pikermi Formation, but as yet there are no cranial elements (Woodward, 1901; Bachmayer and Symeonidis, 1970). Other possible occurences include the Tortonian-Messinian Vathylakkos Formation near Thessaloniki (Arambourg and Piveteau, 1929; Gmira, 1995; Lapparent de Broin, 2001; Lapparent de Broin et al., 2006a, b, c), the Tortonian-Messinian deposits of Halyropotamos on Euboea (Melentis, 1970), and undifferentiated Tortonian (Turolian ELMMZ, MN 11) strata at Küçükçekmece, near Istanbul, Turkey (Malik and Nafiz, 1933; Lapparent de Broin, 2002).

Testudo amiatae Pantanelli, 1893

Remarks: In addition to *T. marmorum*, the only other extinct small-bodied testudinid species documented from Greece is *T. amiatae* from the latest Miocene (Messinian-Zanclean) Trilophos Formation of Allatini, near Thessaloniki (Campana, 1917). This taxon was first described from Tuscany (Pantanelli, 1893; Chesi et al., 2009), with the only known Greek specimen (Fig. 4D, E) consisting of a poorly-preserved shell (AMPG(y) 1917/1970/2) referred solely on the basis of its immobile xiphiplastra, a distinguishing feature of *Testudo sensu lato* (Lapparent de Broin et al., 2006b, c). However, our inspection of AMPG(y) 1917/1970/2 found the posterior plastron to be missing, thus its taxonomic assignment is impossible to substantiate. Auffenberg (1974) considered *T. amiatae* to be a junior synonym of *T. antiqua* Bronn, 1831, and the species is otherwise placed outside of *Testudo sensu stricto* (Chesi et al., 2009).

Testudo graeca Linnaeus, 1758 *sensu lato*

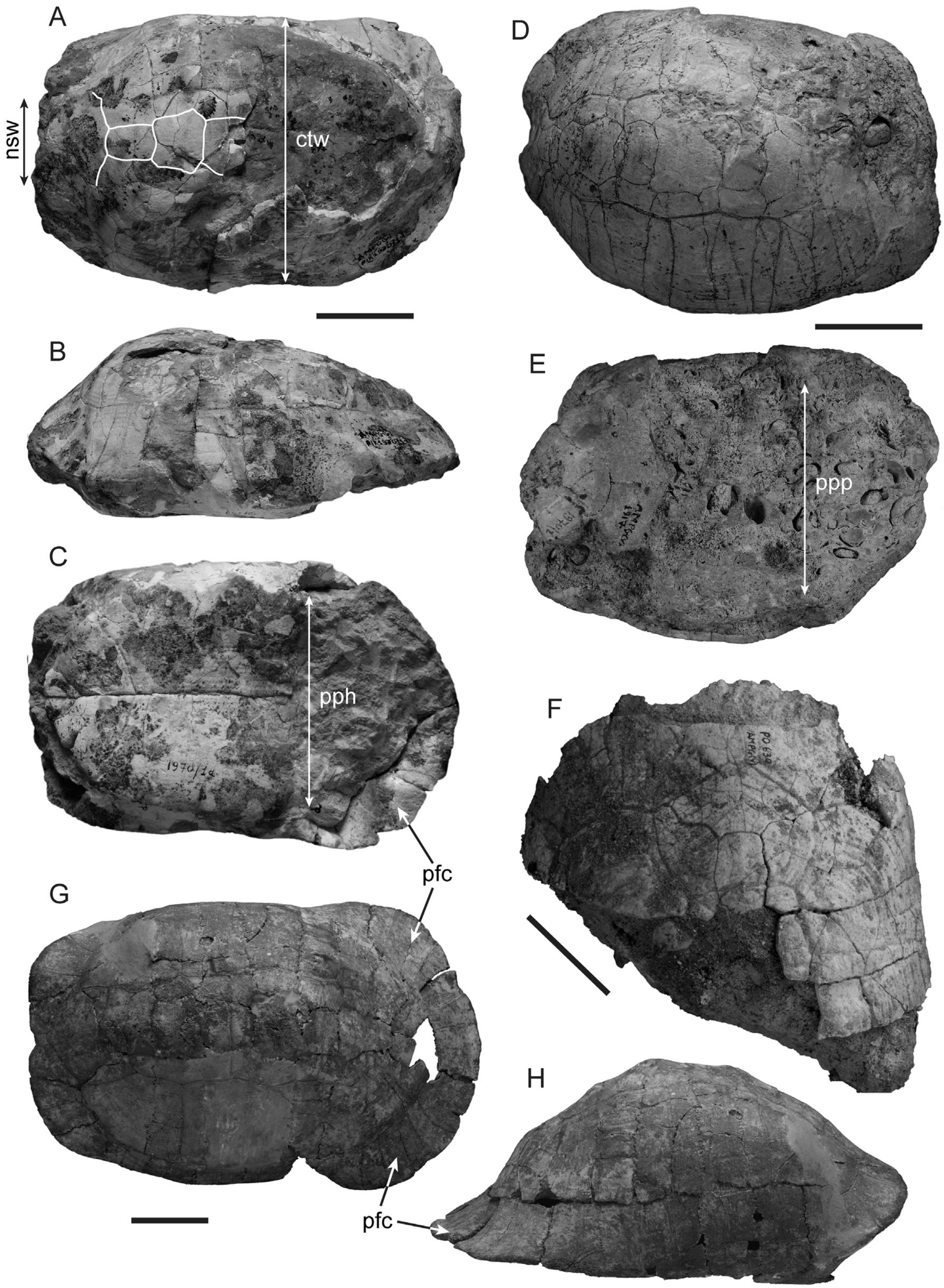

Fig. 4. Examples of testudinid fossils from the Late Miocene-Late Pleistocene of Greece. **A–C**. *Testudo marmorum*: carapace and plastron (AMPG(y) PIR 1970/1d) in dorsal (A), lateral (B) and ventral (C) views; Late Miocene, Pikermi Formation of Megalo Rema, Athens. **D**, **E**. *Testudo amiatae*: carapace and plastron (AMPG(y) 1917/1970/2) in dorsal (D) and ventral (E) views; latest Miocene, Trilophos Formation, Allatini near Thessaloniki. **F**. *Testudo* cf. *graeca*: partial carapace (AMPG(y) PO 630) in dorsal view; Late Pliocene Formation, Lesvos. **G**, **H**. *Testudo marginata cretensis*: carapace and plastron (AMPG, unregistered) in dorsal (G) and lateral (H) views; Late Pleistocene, Zourida Cave, Crete. ctw, carapace transverse width; pfc, posterior flange of carapace; pph, posterior plastral hinge; ppp, position of posterior plastron; nsw, nuchal suture width. Scale bars: 50 mm.

Remarks: The extant *T. graeca sensu lato* today occurs throughout southern Greece and the Aegean-Ionian islands (Valakos et al., 2010). Its subspecies differentiations are controversial, being variously regarded as regional morphotypes (Parham et al., 2006a; Fritz and Havaš, 2007) or closely related, but specifically distinct sister taxa (Perälä, 2002; Guyot, 2004). Fossil examples from Greece have been found in the Late Pliocene-Early Pleistocene (Piacenzian-Gelasian) Vatera Formation of Lesvos

(Fig. 4F). These were attributed to *Testudo* cf. *graeca ibera* based on the hypo-xiphiplastral hinge, narrow extension of the femoral scutes onto the hypoplastra, and a rounded carapace (Lapparent de Broin, 2002); this taxon is presently distributed throughout the south-eastern Balkan Peninsula, Asia Minor and the Caucasus (Fritz and Havaš, 2007). Lyras and Van der Geer (2007) reported additional *T. graeca* remains from the Vatera Formation, and Pleistocene occurrences virtually identical to modern forms are known from cave deposits at Petralona in Chalkidiki (Kretzoi, 1977; Kretzoi and Poulianos, 1981) and Kandilia on Karpathos (Kuss, 1975).

Testudo marginata Schoepff, 1795

Remarks: *Testudo marginata* is the largest modern representative of the genus *Testudo*, reaching a maximum carapace length of ~400 mm (Fritz et al., 2005). The species is presently found in mainland Greece (apart from Thrace) and the Aegean-Ionian islands (Valakos et al., 2008). It additionally occurs in Albania and Sardinia, the latter possibly facilitated via human transportation (Bringsøe et al., 2001; Fritz et al., 2005; Fritz and Havaš, 2007). Bour (1995) erected *T. weissingeri* Baur, 1995 to distinguish small-bodied *T. marginata* populations endemic to the Peloponnese. However, this proposal has not been widely accepted, and Fritz et al. (2005) and Fritz and Havaš (2007) considered *T. weissingeri* to be either a subspecies or a junior synonym of *T. marginata* (*contra* Bour, 2004a, b).

The earliest fossil occurrences of *T. marginata* are from the Early Pleistocene of Lakonia (Schleich, 1982) with the extinct subspecies *Testudo marginata cretensis* (Bachmayer et al., 1975), also recovered from Late Pleistocene sediments in the Zourida (Fig. 3G, H), Gerani, Bate, and Simonelli caves on Crete (Bachmayer et al., 1975; Kotsakis, 1977; Brinkerink, 1996). Interestingly, the current Cretan *Testudo* population is thought to have been introduced by humans, perhaps for food (Lymberakis and Poulakakis, 2010). Indeed, butchering might explain the unusual taphonomic accumulations of tortoise limb bones in other latest Pleistocene-Holocene cave assemblages around the Aegean (e.g., Charkadio on Tilos; Theodorou et al., 2007); note that isolated turtle limb elements similarly dominate Pleistocene-Holocene middens in other island settings (e.g., Vanuatu; White et al., 2010).

Cheirogaster Bergounioux, 1935

Cheirogaster schafferi (Szalai, 1931)

1931. *Testudo schafferi* nov. sp. – Szalai, p. 1, pls IV, V, figs 1, 2.

Remarks: The remains of gigantic tortoises represent some of the most spectacular vertebrate fossils found in the Greek region. Paradoxically, however, they have received little research attention despite being known for nearly 85 years (Arambourg and Piveteau, 1929; Szalai, 1931). Lapparent de Broin (2002) provided the most recent comprehensive review of the documented specimens, provisionally assigning all of the diagnostic material to the widespread European giant tortoise genus, *Cheirogaster*. Certainly, the enormous holotype skull (NHMW 2009z0103/0001; 231 mm-long between the tip of the premaxilla and the occipital condyle; Fig. 5A, B) of the presumed endemic Greek species, *C. schafferi* from the Late Miocene (Messinian) Mytilinii Formation of Samos, conforms to the generic character definition proposed by Luján et al. (2010). Key features including the presence of a foramen praepalatinum, and three prominent paired ridges on the maxillary triturating surfaces that delineate a "posterior maxillary pit" (similar to that described in *Cheirogaster* cranial remains from the Tortonian of Catalonia; Luján et al., 2010: 166) are also observable in a second partial cranium (MNHN 1921-5, SIQ 995; Fig. 5C, D) recovered from the Tortonian-Messinian Vathylakkos Formation near Thessaloniki (Arambourg and Piveteau, 1929; Lapparent de Broin, 2002).

Numerous isolated limb elements, shell fragments, and especially osteoderms attributable to *Cheirogaster* have also been recovered from both the Mytilinii (Szalai, 1931; Lapparent de Broin, 2002) and Vathylakkos formations (Arambourg and Piveteau, 1929), as well as the Late Miocene-earliest Pliocene Pikermi Formation at Megalo Rema (Woodward, 1901; Bachmayer, 1967) and Liossati (Bachmayer and Symeonidis, 1976), various localities within the Early Pliocene (Zanclean) Gonia Formation including Epanomi, Nea Michaniona, and Aggelochori (Athanassiou and Kostopoulos, 2010; Vlachos, 2011, 2012), and the Late Pliocene-early Pleistocene (Piacenzian-Gelasian) Vatera Formation on Lesvos (Lapparent de Broin, 2002). These bones seem to be morphologically indistinguishable (although being proportionately larger) from more complete specimens such as the articulated skeleton of *C. perpiniana* Depéret, 1885 (MNHN 1887-26) from the Early Pliocene of southern France (Depéret, 1890; Depéret and Donnezan, 1890; Bourgat and Bour, 1983). This famous specimen has a carapace length of 114 cm, and has been used as a basis for estimating comparative size of the largest Vatera Formation individual at *ca.* 186 cm (measurements from Lapparent de Broin, 2002). Recently, a thesis by Vlachos (2011) reported a new species of *Cheirogaster* represented by a virtually complete skeleton (AUTH EPN100-198) of 150 cm carapace length. This specimen derived from the Gonia Formation at Epanomi. Large eggs with aragonitic shells have also been found in the Early Pliocene (Zanclean) Apolakkia Formation on Rhodes (Mueller-Töwe et al., 2011). Indeterminate large tortoise bones were recorded from the Middle Pleistocene Petralona Cave in Chalkidiki (Kretzoi and Poulianos, 1981), but these postdate the latest known stratigraphical occurrences of *Cheirogaster* (Upper Pliocene; Lapparent de Broin, 2002) and cannot yet be confidently attributed to this taxon.

GEOEMYDIDAE Theobald, 1868

Remarks: Taxon authorship following David (1994), but see Joyce et al. (2004) for comments.

Mauremys Gray, 1869

Remarks: Only one species of *Mauremys*, *M. rivulata* (Valenciennes, 1833), is today distributed throughout Greece (Valakos et al., 2008), and is regarded by some (e.g., Fritz and Havaš, 2006) to be the senior synonym for regional variants of the Balkan pond turtle: *M. caspica cretica* (Mertens, 1946), and *M. caspica orientalis* (Bedriaga, 1881). Gad (1990) noted the occurrence of fragmentary *Mauremys* fossils in the Upper Miocene at Maramena, near Serres in Macedonia. All other documented remains are similarly incomplete, but are Quaternary in age and have been considered conspecific with either *M. rivulata* or *M. caspica sensu lato* – e.g., Middle Pleistocene Marathousa Member of Megalopolis Basin in the Peloponnese (Melentis, 1966), Late Pleistocene Simonelli Cave on Crete (Kotsakis, 1977), and Late Pleistocene-Holocene Vraona Cave near Athens (Rauscher, 1995; Chesi et al., 2007). Interestingly, the relatively "young" stratigraphical range of this material could comply with the hypothesized recent influx of *M. rivulata* into the Balkan Peninsula, which has been inferred on the basis of molecular divergence data (Fritz et al., 2008).

EMYDIDAE Rafinesque, 1815

Remarks: The extant *Emys orbicularis* is presently widespread in Greece (Valakos et al., 2008). Conversely, the Greek fossil record of emydids is fragmentary and/or incompletely described, with only a few occurrences of *Emys orbicularis* from the Middle Pleistocene Megalopolis Basin (Van Vugt et al., 2000), and Late Pleistocene-Holocene Vraona Cave in Attica (Symeonidis et al., 1979; Fritz, 1995; Sommer et al., 2007). Much older supposed emydid-like remains have been mentioned from Early Miocene (Burdigalian) deposits near Aliveri on Euboea, and the Early Pliocene (Zanclean) Ptolemais Formation at Vorio in Macedonia (Boehme and Ilg, 2003). These specimens are currently housed in

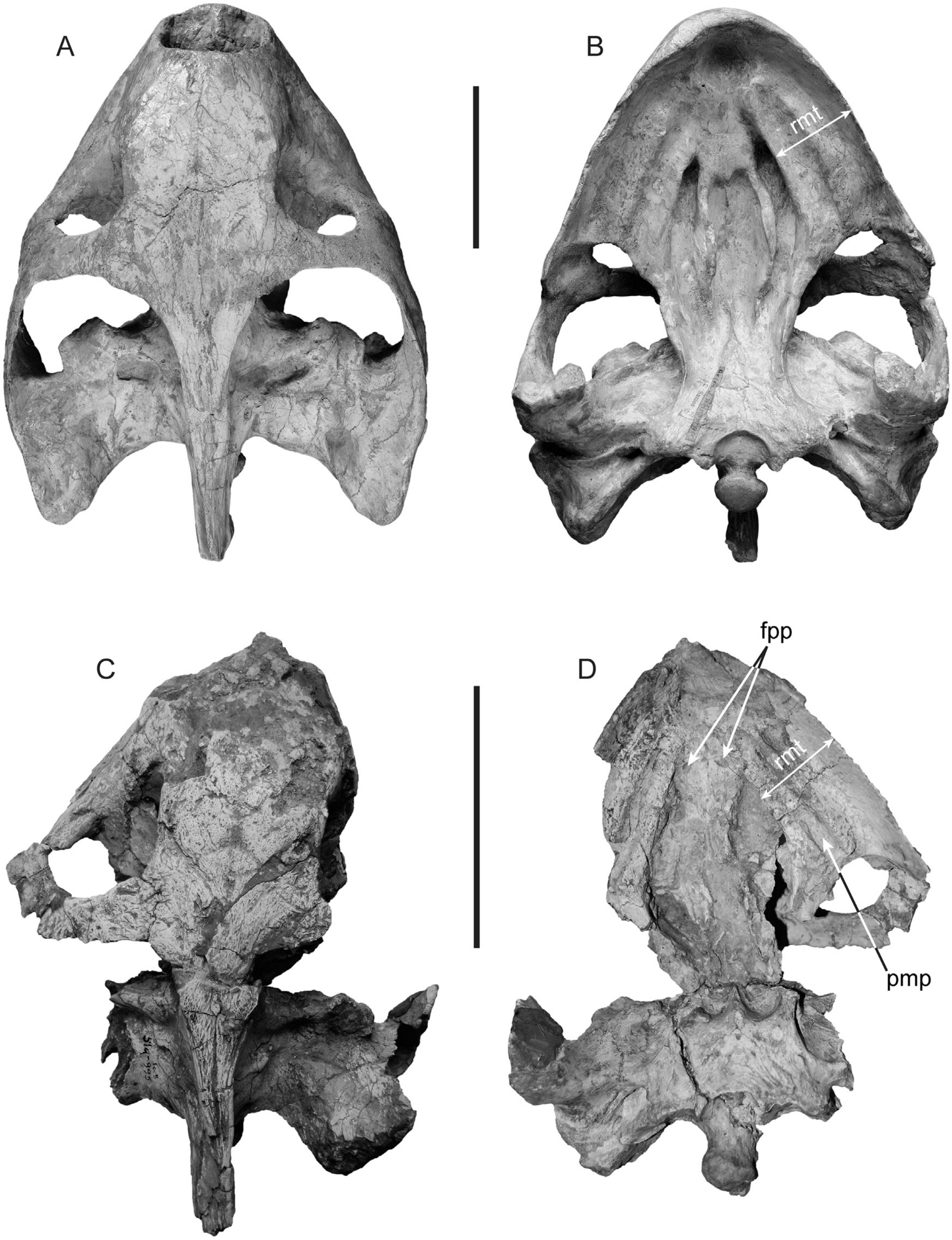

Fig. 5. Skulls attributed to the gigantic tortoise *Cheirogaster*. **A**, **B**. *Cheirogaster schafferi*: holotype (NHMW 2009z0103/0001) in dorsal (A) and palatal (B) views; Late Miocene, Mytilinii Formation, Samos. **C**, **D**. *Cheirogaster* sp. (MNHN 1921-5, SIQ 995) in dorsal (C) and palatal (D) views; Late Miocene, Vathylakkos Formation, near Thessaloniki. fpp, foramen praepalatinum; pmp, "posterior maxillary pit"; rmt, ridges of the maxillary triturating surfaces. Scale bars: 100 mm.

the geological collection at the University of Utrecht in Holland, where they remain unstudied.

4. Discussion: palaeobiogeography, palaeoecology, and divergence times

Fossil turtle remains have been known from Greece for over 150 years (e.g., Gaudry, 1862), and yet the history of published research has been comparatively sparse. Nonetheless, those finds that have been documented serve to highlight the Aegean region as an important source of information on the diversity and distribution of post-Paleogene Afro-European testudinatans.

4.1. Miocene podocnemidoids

Greece's stratigraphically oldest documented turtle and first pleurodiran taxon, *Nostimochelone lampra*, constitutes one of the youngest constrained (late Burdigalian) podocnemidoidean occurrences within Europe (Georgalis et al., 2013). The only other example is a partial carapace (now lost) from undifferentiated Miocene strata in Malta (Lapparent de Broin and Werner, 1998; Lapparent de Broin, 2000, 2001). This specimen was described as "*Podocnemis*" *lata* Ristori, 1895, but considered a *nomen dubium* by Gaffney et al. (2006). The association of *N. lampra* with a tidal estuarine setting also implies a marine-adapted lifestyle similar to that envisaged for some contemporaneous podocnemidids (e.g., *Bairdemys* Gaffney and Wood, 2002 from the Oligocene-Miocene of the U.S.A., Puerto Rico, and Venezuela; Weems and Knight, 2013) and Cretaceous-Eocene bothremydids (Gaffney et al., 2006). Furthermore, the prevalence of such littoral marine habitats throughout the eastern Mediterranean during the Early and Middle Miocene (Kovar-Eder et al., 2008) advocates a possible Tethyan dispersal route for podocnemidoidean turtles from Africa into Europe and Asia during the earliest part of the Neogene (Meylan et al., 2009).

4.2. Miocene-Holocene testudinids

The recognition of *Testudo sensu lato* fossils from the Middle Miocene of Chios (Paraskevaidis, 1955; Chesi et al., 2009), together with the Late Miocene *T. marmorum* from Pikermi and *Testudo* sp. nov. from "Ravin de la Pluie" (Garcia et al., 2011), accords with a Neogene divergence of *Testudo sensu stricto*, which might have occurred as recently as 5–15 Ma (Parham et al., 2006b; Lourenço et al., 2012). Coincidence of these taxa with formation of the Arabian-Anatolian landbridge in the Early Miocene (Rögl, 1999) also complies with proposed timing of European-African migration events: either extending from a Palearctic centre as traditionally envisaged from fossils (Lapparent de Broin, 2000); or alternatively, from Africa as derived from DNA sequence tree topologies (Le et al., 2006). Note that an African origin requires multiple instances of dispersal to explain the distribution of *Testudo sensu lato* in Northern and Western Europe (Lapparent de Broin, 2001).

Radiation of the presently extant *T. graeca* and *T. marginata* appears to have commenced in the Miocene (Lourenço et al., 2012), with stratigraphically early fossils derived from the Late Pliocene-Early Pleistocene of Levos (Lapparent de Broin, 2002; Lyras and Van der Geer, 2007), and the Early Pleistocene of Lakonia (Schleich, 1982), respectively. The mode of their subsequent dispersal thoughout the Aegean islands is intriguing, since long-distance floating (e.g., tortoises are known to survive long periods adrift at sea; Meylan and Sterrer, 2000) could have been augmented by human transportation in more recent prehistory (Bringsøe et al., 2001; Lymberakis and Poulakakis, 2010). Indeed, human interaction and/or post-glacial environmental perturbations might have played a role in the extinction of the Cretan endemic tortoise, *Testudo marginata cretensis*, which is not confidently known beyond the Pleistocene (Brinkerink, 1996).

The terminal stratigraphical occurrence of *C. schafferi*-like postcranial remains in the Late Pliocene-Early Pleistocene Vatera Formation of Lesvos has been mooted as evidence for "a North-South [latitudinal] gradient of disappearance" of gigantic tortoises following the onset of climatic cooling in the latter part of the Neogene (Lapparent de Broin, 2002: 120). Certainly, their Miocene speciation maximum occurs in Mediterranean Europe, with *C. schafferi* from Samos and seven other recognised taxa found in France and Spain (for a full species list, see Lapparent de Broin, 2002: 127–128). Origin of the *Cheirogaster* lineage, however, is much older, with *C. maurini* Bergounioux, 1935 appearing in the Late Eocene (late Priabonian) of Baby in southern France (Broin, 1977). Such antiquity would imply a Palearctic/Asian origin for the radiation as a whole. Conversely, the hypothesised sister placement with the African large-bodied taxon *Centrochelys* Gray, 1872 (Lapparent de Broin, 2002), whose extant form *Geochelone* (*Centrochelys*) *sulcata* (Miller, 1799) was referred to *Geochelone sensu stricto* by Le et al. (2006), would suggest an emergence in Africa prior to the establishment of an effective land connection with Europe. The minimum divergence estimate for *Geochelone sensu stricto* is the Late Eocene (Lourenço et al., 2012), but as yet there are no identifiable African-Arabian *Centrochelys*-like fossils older than the Early-Middle Miocene (post Burdigalian; Lapparent de Broin and Van Dijik, 1999; Lapparent de Broin, 2000). Moreover, the earliest African large-bodied tortoises from the Late Eocene-Early Miocene are referable to other endemic lineages (e.g., *Gigantochersina* Chkhikvadze, 1989, and *Namibchersus* Lapparent de Broin, 2003; Lapparent de Broin, 2000, 2003; Holroyd and Parham, 2003).

Unfortunately, evaluation of these contrasting scenarios is difficult because neither the generic affinities of the gigantic *Centrochelys*-like remains, nor the monophyly of *Cheirogaster* have been rigorously scrutinized. Nevertheless, Luján et al. (2010) recently inferred a close relationship between at least those Miocene *Cheirogaster* spp. represented by adequate cranial remains. In addition, re-examination of the Greek material is currently underway (Vlachos, 2012; Georgalis and Kear, ongoing work) and will hopefully provide robust character frameworks with which to assess homology.

Selection for gigantism in tortoises is often attributed to "island-effects" including absence of predators/competing herbivores, simple eco-community structure, and seasonally intermittent food supplies (Arnold, 1979). Contrastingly, however, the occurrence of collosal *Cheirogaster* remains in the Mytilinii and Vatera formations indicates that peak body sizes were historically more pronounced in mainland taxa. The simultaneous appearance of the most massive Greek *Cheirogaster* specimens (inferred carapace length of ~2 m) with other equally gigantic tortoises in Africa and Asia (Lapparent de Broin, 2002) could therefore have been prompted by other factors such as the onset of widespread climatic cooling/drying during the Late Miocene-Late Pliocene; the increased body-size conferring an advantage for maintaining higher metabolic activity (through inertial homeothermy) and/or reflecting a dietary shift towards greater consumption of C_4 vegetation (necessitating a voluminous fermentative gut), which dominated concomitantly spreading savannah grasslands throughout Mediterranean Europe (Suc et al., 1999).

4.3. Miocene-Holocene geoemydids and emydids

The occurrence of *Mauremys* in the Late Miocene (Gad, 1990) and *M. rivulata*/*M. caspica sensu lato* in the Pleistocene-Holocene of Greece (Melentis, 1966; Kotsakis, 1977; Rauscher, 1995), evidences both the Neogene presence of geoemydids in south-eastern Europe and the subsequent distributional segregation of extant Eastern Mediterranean *Mauremys* spp. after the Pleistocene, perhaps in response to climate change (Lapparent de Broin and Van Dijik, 1999; Lapparent de Broin, 2001; Chesi et al., 2009). Indeed, temperature sensitivity is also thought to have controlled the dispersal history of *Emys* (Chesi et al., 2007), whose pre-Pleistocene European record is sparse (Lapparent de Broin, 2001) but syntopic with *Mauremys* in at least the Megalopolis Basin of the Peloponnese (Melentis, 1966; Van Vugt et al., 2000). Additional enigmatic reports of emydid-like remains from the Early Miocene and Pliocene of Euboea and Macedonia (Boehme and Ilg, 2003) require confirmation, but could potentially ellucidate the pre-Miocene absence of Emydidae *sensu stricto* as either a product of missing data, or evidence for moderate climatic conditions permitting an influx across the Bering Strait (Lapparent de Broin, 2001).

5. Conclusions

The documented evolutionary and palaeobiogeographical chronicle of turtles from Greece and the Aegean rim of western Turkey is incompletely known (see Lapparent de Broin, 2001). The stratigraphically oldest remains have been tentatively attributed to primitive aquatic testudinoids (cf. *Palaeochelys* Meyer, 1847) and recovered from undifferentiated middle Oligocene to Middle Miocene sediments near the Sea of Marmara in Turkey (Schleich, 1994). Current research has additionally revealed Early Miocene podocnemidoids (Georgalis et al., 2013), and is exploring the radiation of both extant (Garcia et al., 2011) and gigantic extinct testudinids (Kear and Georgalis, 2009; Georgalis and Kear, 2010; Vlachos and Tsoukala, 2011; Vlachos, 2012). In contrast, the complete absence of trionychid and chelonioid fossils from Greece is puzzling, especially given the extant occurrence of these clades within the region (Taskavak et al., 1999; Fritz and Havaš, 2007; Corsini-Foka and Massetti, 2008; Valakos et al., 2008). Nonetheless, discovery of these and other groups (e.g., chelydrids; Paicheler et al., 1978) in geographically proximal areas (e.g., Romania, Bulgaria, Turkey; Khosatzky et al., 1983; Pamouktchiev et al., 1998; Lapparent de Broin, 2002; Stojanov, 2009) suggests that this phenomenon might result from limited sampling as well as depositional biases, emphasising the need for further research on what is arguably the richest testudinatan fossil record from the Balkan Peninsula.

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References

Arambourg, C., Piveteau, J., 1929. Les vertébrés du Pontien de Salonique. Annales de Paléontologie 18, 59–138.
Arnold, E.N., 1979. Indian Ocean giant tortoises: their systematics and island adaptations. Philosophical Transactions of the Royal Society of London, Series B 286, 127–145.
Athanassiou, A., Kostopoulos, D.S., 2010. On Pliocene mammal remains in the area of Epanomi (Macedonia, Greece). Scientific Annals, School of Geology, Aristotle University of Thessaloniki 99, 63–68.
Auffenberg, W., 1974. Checklist of fossil land tortoises (Testudinidae). Bulletin of Florida State Museum of Biological Science 18, 121–251.
Bachmayer, F., 1967. Eine Riesenschildkrote aus den altpliozane Schichten von Pikermi (Griechenland). Annales Géologiques des Pays Helléniques 19, 512–526.
Bachmayer, F., Symeonidis, N., 1970. Die fossilen Schildkrotenreste des Geologisch-Palaontologischen Institutes der Universitat von Athen. Annales Géologiques des Pays Helléniques 22, 227–246.
Bachmayer, F., Symeonidis, N., 1975. Schildkrotenreste (*Testudo marginata* SCHOEPFF) aus der Hohle « Charkadio », auf der Insel Tilos (Dodekanes, Griechenland). Annales Géologiques des Pays Helléniques 26, 324–327.
Bachmayer, F., Symeonidis, N., 1976. Eine neue "Pikermi" Fundstelle im Gebiet von Liossati (Kiourka), nordlich von Athen (Griechenland) (Beschreibung einer Riesenschildkrote). Annales Géologiques des Pays Helléniques 28, 8–16.
Bachmayer, F., Brinkerink, J., Symeonidis, N., 1975. Pleistozane Schildkroten aus Hohlen der Insel Kreta. Annales Géologiques des Pays Helléniques 27, 110–121.
Bachmayer, F., Mlynarski, M., Symeonidis, N., 1980. Fossile Schildkroten aus dem Pliozan von Megalo Emvolo (Karaburun) bei Saloniki (Griechenland) A. Eine fossile Maurische Landschildkrote (*Testudo* cf. *graeca* LINNE) B. Fossile reste von Riesenschilkroten. Annales Géologiques des Pays Helléniques 31, 267–276.
Boehme, M.A., Ilg, A., 2003. fosFARbase. www.wahre-staerke.com (accessed September, 2012).
de Bonis, L., Bouvrain, G., Koufos, G.D., 1988. Late Miocene Mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphic significance. Modern Geology 13, 141–147.
de Bonis, L., Bouvrain, G., Geraads, D., Koufos, G.D., 1992. Diversity and paleoecology of Greek Late Miocene mammalian faunas. Palaeogeography, Palaeoclimatology, Palaeoecology 91, 99–121.
de Bonis, L., Bouvrain, G., Sen, S., 1997. A giraffid from the Middle Miocene of the island of Chios, Greece. Palaeontology 40, 121–133.
de Bonis, L., Bouvrain, G., Koufos, G.D., 1999. Palaeoenvironments of the hominoid primate *Ouranopithecus* in the Late Miocene deposits of Macedonia, Greece. In: Agustí, L., Rook, L., Andrews, P. (Eds.), Hominoid Evolution and Climatic Change in Europe. Cambridge University Press, London, pp. 205–237.
Bour, R., 1995. Une nouvelle espèce de tortue terrestre dans le Péloponnèse (Grèce). Dumerillia 2, 23–54.
Bour, R., 2004a. *Testudo marginata*. Manouria 7, 27–29.
Bour, R., 2004b. *Testudo weissingeri*. Manouria 7, 42–43.
Bourgat, R., Bour, R., 1983. La Tortue géante de Perpignan : *Cheirogaster perpiniana* (Depéret, 1885). Bulletin de la Société Agricole, Scientifique et Littéraire des Pyrénées-Orientales 91, 167–177.
Bringsøe, H., Buskirk, J.R., Willemsen, R.E., 2001. *Testudo marginata* Schoepff, 1792–Breitrandschildkröte. In: Fritz, U. (Ed.), Handbuch der Reptilien und Amphibien Europas. Band 3/IIIA: Schildkröten I. Aula-Verlag, Wiebelsheim, pp. 291–334.
Brinkerink, H.P., 1996. Tortoises and Turtles from the Pleistocene of Crete. In: Reese, D.S. (Ed.), Pleistocene and Holocene Fauna of Crete and it's First Settlers. Monographs in World Archaeology, Prehistory Press 28, pp. 207–210.
de Broin, F., 1977. Contribution à l'étude des chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum national d'Histoire naturelle, Paris 38, 1–366.
Campana, D., 1917. *Testudo* del Mioceno superiore di Capoudgilar (Salonik). Bollettino della Società Geologica Italiana e del Servizio Geologico d'Italia 36, 69.
Chesi, F., Delfino, M., Abbazzi, L., Carboni, S., Lecca, L., Rook, L., 2007. New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the central Mediterranean. Rivista Italiana di Paleontologia e Stratigrafia 113, 287–297.
Chesi, F., Delfino, M., Rook, L., 2009. Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. Journal of Paleontology 83, 379–388.
Corsini-Foka, M., Massetti, M., 2008. On the oldest record of the Nile Soft-shelled turtle, *Trionyx triunguis* (Forskal, 1775), in the Eastern Aegean islands (Greece). Zoology in the Middle East 43, 108–110.
David, P., 1994. Liste des reptiles actuels du monde. I. Chelonii. Dumerilia 1, 7–127.
Delfino, M., 2004. Tassonomia, biogeografia e biocronologia delle erpetofaune greche del Neogene e del Quaternario. Unpublished report for Consiglio Nazionale delle Ricerche, Rome, 139.
Delfino, M., Kotsakis, T., Arca, M., Tuveri, C., Pitruzella, G., Rook, L., 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas 30, 641–656.
Depéret, C., 1890. Sur la découverte d'une tortue de terre géante au mont Léberon. Comptes Rendus de l'Académie des Sciences, Paris 60, 915–917.
Depéret, C., Donnezan, A., 1890. Classe des Reptiles. O. des Chéloniens. Mémoire de la Société Géologique de France, Paléontologie 3, 194.
Dermitzakis, M., 1977. [The Quaternary fossil mammals in the caves and karstic holes of Crete and their significance]. Bulletin de la Société Spéléologique de la Grèce 14, 152–190 (in Greek).
Drinia, H., Dermitzakis, M.D., Kouli, K., Tsourou, T., 2002. Sedimentary facies analysis and paleoenvironmental interpretation of Vatera Formation, Lesvos Island, Greece. Annales Géologiques des Pays Helléniques 39, 15–35.
Dubois, A., Bour, R., 2010. The distinction between family-series and class-series nomina in zoological nomenclature, with emphasis on the nomina created by Batsch (1788, 1789) and on the higher nomenclature of turtles. Bonn Zoological Bulletin 57, 149–171.
Fritz, U., 1995. Kritische Übersicht der Fossilgeschichte der Sumpfschildkröten-Gattung *Emys* A. Duméril, 1806 (Reptilia: Testudines: Emydidae). Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 48, 243–264.
Fritz, U., Havaš, P., 2007. Checklist of the chelonians of the world. Vertebrate Zoology 57, 149–368.
Fritz, U., Siroki, P., Kami, H., Wink, M., 2005. Environmentally caused dwarfism or a valid species – is *Testudo weissingeri* Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. Molecular Phylogenetics and Evolution 37, 389–401.
Fritz, U., Ayaz, D., Buschbom, J., Kami, H.G., Mazanaeva, L.F., Aloufi, A.A., Auer, M., Rifai, L., Silic, T., Hunsdorfer, A.K., 2008. Go east: phylogeographies of *Mauremys caspica* and *M. rivulata* – discordance of morphology, mitochondrial and nuclear genomic markers and rare hybridization. Journal of Evolutionary Biology 21, 527–540.
Gad, J., 1990. Nachweis einer Schildkröte des *Mauremys-Ocadia*-Komplexes aus dem Obermiozän von Nordgriechenland. Salamandra 26, 311–313.
Gaffney, E.S., Tong, H., Meylan, P.A., 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. Bulletin of the American Museum of Natural History 300, 1–698.

Gaffney, E.S., Meylan, P.A., Wood, R.C., Simons, E., Campos, D., de, A., 2011. Evolution of the side-necked turtles: the family Podocnemididae. Bulletin of the American Museum of Natural History 350, 1–238.

Garcia, G., de Lapparent de Broin, F., de Bonis, L., Koufos, G.D., Valentin, X., Kostopoulos, D., Merceron, G., 2011. A new terrestrial Testudinidae from the Late Miocene hominoid locality ‘‘Ravin de la Pluie’’ (Axios Valley, Macedonia, Greece). In: Van der Geer, A., Athanassiou, A. (Eds.), 9th Annual Meeting of the European Association of Vertebrate Palaeontologists, Program and Abstracts. Natural History Museum of Crete, Heraklion, pp. 26–27.

Gaudry, A., 1862. Note sur les débris d’Oiseaux et de Reptiles trouvés à Pikermi, Grèce, suivie de quelques remarques de paléontologie générale. Bulletin de la Société Géologique de France 19, 629–640.

Gaudry, A., 1862–1867. Animaux fossiles et géologie de l’Attique. Savy, Paris.

Georgalis, G.L., Kear, B.P., 2010. New records of fossil turtles from Greece. Journal of Vertebrate Paleontology 30, 95A.

Georgalis, G.L., Velitzelos, E., Velitzelos, D.E., Kear, B.P., 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the Lower Miocene of northern Greece. In: Brinkman, D.B., Holroyd, P.A., Gardner, J.D. (Eds.), Morphology and Evolution of Turtles. Springer, Dordrecht, pp. 277–287.

Georgiades-Dikeoulia, E., Velitzelos, E., Koskeridou, E., 2000. The *Crassostrea gryphoides* Schlot. Miocene banks of Greece as palaeoenvironmental indicators. Geological Society of Greece, Special Publications 9, 101–108.

Gibbard, P.L., Head, M.J., Walkers, M.J.C., The Subcommission on Quaternary Stratigraphy, 2010. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. Journal of Quaternary Science 25, 96–102.

Gmira, S., 1995. Étude des Chéloniens fossiles du Maroc. Anatomie. Systématique. Phylogénie. Cahiers de Paléontologie, CNRS, Paris.

Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G., 2012. The Geologic Time Scale 2012, vol. 2. Elsevier, Amsterdam.

Guyot, G.E., 2004. Numéro spécial *Testudo*. Manouria 22, 1–152.

Holroyd, P.A., Parham, J.F., 2003. The antiquity of African tortoises. Journal of Vertebrate Paleontology 23, 688–690.

Hordijk, K., de Bruijn, H., 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). Annales Géologiques des Pays Helléniques 44, 21–103.

Joyce, W.G., Parham, J.F., Gauthier, J.A., 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78, 989–1013.

Kear, B.P., Georgalis, G.L., 2009. Evolution of gigantic tortoises from the Neogene of Europe. Journal of Vertebrate Paleontology 29, 124A–125A.

Khosatzky, L.J., Christov, L., Nankinov, D., 1983. An Eocene soft-shelled turtle from Bulgaria. Schriftenreihe Geologische Wissenschaften 19/20, 271–280.

Klein, I.T., 1751. Quadrupedum Dispoitio Brevisque Historia Naturalis. Ionas Schmidt, Lipsia.

Klein, I.T., 1760. Klassification und kurze Geschichte der Vierfüßigen Thiere (translation by F.D. Behn) Jonas Schmidt, Lübeck.

Kostopoulos, D.S., Koufos, G.D., Sylvestrou, I.A., Syrides, G.E., Tsombachidou, E., 2009. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 2. Lithostratigraphy and Fossiliferous Sites. Beiträge zur Paläontologie 31, 13–26.

Kotsakis, T., 1977. I resti di anfibi e rettili pleistocenici della grotta ‘‘Bate’’ (Rethymnon, Creta). Atti della Accademia Nazionale dei Lincei 63, 571–582.

Koufos, G.D., 2006. The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. Annales Géologiques des Pays Helléniques 4, 183–214.

Koufos, G.D., 2009. The Late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: new collection. 1. History of the Samos fossil mammals. Beiträge zur Paläontologie 31, 1–12.

Koufos, G.D., Syrides, G., Koliadimou, K., 1991. A Pliocene primate from Macedonia. Journal of Human Evolution 21, 283–294.

Koufos, G.D., de Bonis, L., Sen, S., 1995. *Lophocyon paraskevaidisi*, a new viverrid (Carnivora, Mammalia) from the Middle Miocene of Chios Island, Greece. Geobios 28, 511–523.

Koufos, G.D., Kostopoulos, S., Vlachou, T., Konidaris, G., 2011. A synopsis of the Late Miocene mammal fauna of Samos Island, Aegean Sea, Greece. Geobios 44, 237–251.

Kovar-Eder, J.H., Jechorek, H., Kvaček, Z., Parashiv, V., 2008. The integrated plant record: an essential tool for reconstructing Neogene zonal vegetation in Europe. Palaios 23, 97–111.

Kretzoi, M., 1977. The fauna of small vertebrates of the middle Pleistocene at Petralona. Anthropos 4, 131–143.

Kretzoi, M., Poulianos, N., 1981. Remarks on the middle and lower Pleistocene vertebrate fauna in the Petralona Cave. Anthropos 8, 57–72.

Kuss, S.E., 1975. Die pleistozänen Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpathos und Rhodos (Griechenland). Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 65, 25–79.

de Lapparent de Broin, F., 2000. African chelonians from the Jurassic to present: phases of development and preliminary catalogue of the fossil record. Palaeontologia Africana 36, 43–82.

de Lapparent de Broin, F., 2001. The European turtle fauna from the Triassic to the Present. Dumerilia 4, 155–216.

de Lapparent de Broin, F., 2002. A giant tortoise from the Late Pliocene of Lesvos Island (Greece) and its possible relationships. Annales Géologiques des Pays Helléniques 39, 99–130.

de Lapparent de Broin, F., 2003. Miocene chelonians from southern Namibia. Memoir of the Geological Survey of Namibia 19, 67–102.

de Lapparent de Broin, F., Van Dijk, P.P., 1999. Chelonia from the Late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates: palaeogeographical implications. In: Whybrow, P.J., Hill, A. (Eds.), Fossil Vertebrates of Arabia. Yale University Press, New Haven, pp. 136–162.

de Lapparent de Broin, F., Werner, C., 1998. New Late Cretaceous turtles from the Western Desert, Egypt. Annales de Paléontologie 84, 131–214.

de Lapparent de Broin, F., Bour, R., Parham, J.F., Perälä, J., 2006a. *Eurotestudo*, a new genus for the species Testudo hermanni Gmelin, 1789 (Chelonii, Testudinidae). Comptes Rendus Palevol 5, 803–811.

de Lapparent de Broin, F., Bour, R., Perälä, J., 2006b. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): first part. Annales de Paléontologie 92, 255–304.

de Lapparent de Broin, F., Bour, R., Perälä, J., 2006c. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): second part. Annales de Paléontologie 92, 325–357.

Le, M., Raxworthy, C.J., McCord, W.P., Mertz, L., 2006. A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 40, 517–531.

Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Laurenti Salvii, Holmiae 1, 1–823.

Löhnert, E., Nowak, H., 1965. Die Braunkohlenlagerstaette van Khoremi im Becken von Megalopolis/Peloponnes. Geologisches Jahrbuch 82, 847–867.

Lourenço, J.M., Claude, J., Galtier, N., Chiari, Y., 2012. Dating cryptodiran nodes: origin and diversification of the turtle family Testudinoidea. Systematic Biology 62, 496–507.

Luján, A., Alba, D., Fortuny, J., Carmona, R., Delfino, M., 2010. Cranial remains of *Cheirogaster* Bergounioux, 1935 (Testudines: Testudinidae) from the Late Miocene of EcoPark de Can Mata (Vallès-Penedès Basin, Catalonia, Spain). Cidaris 30, 163–168.

Lymberakis, N., Poulakakis, N., 2010. Three continents claiming an archipelago: the evolution of Aegean’s Herpetofaunal Diversity. Diversity 2, 233–255.

Lyras, G.A., Van der Geer, A.A.E., 2007. The Late Pliocene vertebrate fauna of Vatera (Lesvos Island, Greece). Cranium 24, 11–24.

Malik, A., Nafiz, H., 1933. Vertébrés fossiles de Küçükçekmece. Bulletin de la Faculté des Sciences d’Istanbul 3-4, 1–119.

Marinos, G., Symeonidis, N., 1974. Neue Funde aus Pikermi, Attika und eine allgemeine geologische bersicht dieses paläontologischen Raumes. Annales Géologiques des Pays Helléniques 26, 1–27.

Melentis, J.K., 1966. Studien über fossile Vertebraten Griechenlands: 10. *Clemmys caspica* aus dem Pleistozän des Beckens von Megalopolis im Peloponnes (Griechenland). Annales Géologiques des Pays Helléniques 17, 169–181.

Melentis, J.K., 1970. Studien über fossile Vertebraten Griechenlands: 19. Die Pikermifauna von Halmyropotamos (Euböa–Griechenland). Annales Géologiques des Pays Helléniques 19, 285–411.

Meylan, P.A., Sterrer, W., 2000. *Hesperotestudo* (Testudines: Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. Zoological Journal of the Linnean Society 128, 51–76.

Meylan, P.A., Gaffney, E.S., de Almeida Campos, D., 2009. *Caninemys*, a new side-necked turtle (Pelomedusoides: Podocnemididae) from the Miocene of Brazil. American Museum Novitates 3639, 1–26.

Mueller-Töwe, I.J., Kjeldahl, T.A.K., Milàn, J., Vallon, L., Theodorou, G., Lindgren, J., Roussiakis, J.S., Bromley, R.G., 2011. First chelonian eggs and carapace fragments from the Pliocene of Rhodes, Greece. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 262/3, 309–322.

Paicheler, J.-C., de Lapparent de Broin, F., Gaudant, J., Mourer-Chauvire, C., Rage, J.-C., Vergnaud-Grazzini, C., 1978. Le Bassin lacustre miocène de Bes Konak (Anatolie, Turquie). Géologie et introduction à la paléontologie des Vertébrés. Geobios 11, 43–65.

Pamouktchiev, A., de Lapparent de Broin, F., Anguelov, A., 1998. Nouvelle trouvaille de tortue fossile en Bulgarie. Annuaire de l’Université de Sofia ‘‘St. Kliment Ohridski’’ Faculté de Géologie et Géographie, Livre 1 Géologie 90, 5–8.

Pantanelli, D., 1893. *Testudo amiatae* n. sp. Atti della Società Toscana di Scienze Naturali 12, 11.

Paraskevaidis, I., 1955. Zwei Schildkroten Reste aus dem Obermiozan von Chios. Annales Géologiques des Pays Helléniques 6, 133–141.

Parham, J.F., Türkozan, O., Stuart, B.L., Arakelyan, M., Shafei, S., Macey, J.R., Papenfuss, T.J., 2006a. Genetic evidence for premature taxonomic inflation in Middle Eastern tortoises. Proceedings of California Academy of Sciences 57, 955–964.

Parham, J.F., Macey, J.R., Papenfuss, T.J., Feldman, C.R., Türkozan, O., Polymeni, R., Boore, J., 2006b. The phylogeny of Mediterranean tortoises and their close relatives based on complete mitochondrial genome sequences from museum specimens. Molecular Phylogenetics and Evolution 38, 50–64.

Perälä, J., 2002. Morphological variation among Middle Eastern *Testudo graeca* L., 1758 (sensu lato) with a focus on taxonomy. Chelonii 3, 78–108.

Pianka, R.E., King, D., King, R.A., 2004. Varanoid Lizards of the World. Indiana University Press, Bloomington.

Rauscher, K.L., 1995. Die herpetofauna der Vraona-Holhe (Attika) in Griechenland. Annales Géologiques des Pays Helléniques 36, 39–41.

Richter, A., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). Münchner Geowissenschaften Abhandlungen 28, 35–38.

Roemer, F., 1870. Über *Python euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. Zeitschrift der Deutschen Geologischen Gesellschaft 22, 582–590.

Rögl, F., 1999. Mediterranean and Paratethys palaeogeography during the Oligocene and Miocene. In: Agustí, J., Rook, L., Andrews, P. (Eds.), The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge University Press, Cambridge, pp. 8–22.
Rook, L., Martínez-Navarro, B., 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. Quaternary International 219, 134–144.
Roussiakis, S., 2002. Musteloids and feloids (Mammalia, Carnivora) from the Late Miocene locality of Pikermi (Attica, Greece). Geobios 35, 699–719.
Savoyat, E., Monopolis, D., Bizon, G., Yannetakis, C.P., 1971. Geological Map of Greece. Nestorion Sheet. Scale 1:50,000. Institute of Geology and Mineral Exploration, Athens (formerly Institute for Geology and Subsurface Research, Athens).
Schleich, H.H., 1982. *Testudo marginata* Schoepff aus plio/pleistozänen Ablagerungen SE-Lakoniens (Peloponnes, Griechenland). Paläontologische Zeitschrift 56, 259–264.
Schleich, H.H., 1994. Fossil schildkröten und krokodilreste aus dem tertiar Thrakiens (W-Turkei). Courier Forschungsinstitut Senckenberg 173, 137–151.
Sommer, R.S., Persson, A., Wieseke, N., Fritz, U., 2007. Holocene recolonization and extinction of the pond turtle, *Emys orbicularis* (L., 1758), in Europe. Quaternary Science Reviews 26, 3099–3107.
Steininger, E., 1999. Chronostratigraphy, geochronology, and biochronology of the Miocene "European Land Mammal Megazones". In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr Friedrich Pfiel, München, pp. 9–24.
Stojanov, A., 2009. Erster Nachweis einer Riesenlandschildkröte (*Geochelone s.l.* Gray, 1872) aus Bulgarien. Revue de Paléobiologie 28, 457–470.
Suc, J.-P., Fauquette, S., Bessedik, M., Bertini, A., Zheng, Z., Clauzon, G., Suballyova, D., Diniz, F., Quézel, P., Feddi, N., Clet, M., Bessais, E., Taoufiq, N.B., Meon, H., Combourieu-Nebout, N., 1999. Neogene vegetation changes in West European and West circum-Mediterranean areas. In: Agustí, J., Rook, L., Andrews, P. (Eds.), The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge University Press, Cambridge, pp. 378–388.
Sylvestrou, A.I., Kostopoulos, S.D., 2006. *Pseudomeriones megistos* nov. sp. (Gerbillinae, Mammalia) from the Latest Miocene of Northern Greece and its phylogenetic relationships. Geobios 40, 833–848.
Symeonidis, N., Bachmayer, F., Zapfe, H., 1979. Ergebnisse weiterer Grabungen in der Höhle von Vraona (Attika, Griechenland). Annales Géologiques des Pays Helléniques 30, 291–299.
Syrides, G.E., 1990. [Lithostratigraphical, Biostratigraphical and Palaeogeographical Study of the Neogene/Quaternary Sedimentary Formations of Chalkidiki Peninsula.] Ph.D. dissertation, (unpubl.). [in Greek]Aristotle University of Thessaloniki
Syrides, G.E., 1995. Neogene mollusk faunas from Strymon basin/Macedonia, Greece. First results for biochronology and palaeoenvironment. Geobios 28, 381–388.
Szalai, T., 1931. Schildkrotenstudien: I. *Testudo schafferi* nov. sp. Eine riesenschildkrote ausdem Pliozan von Samos. Annalen des Naturhistorischen Museums in Wien 46, 153–157.
Szyndlar, Z., 1991. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estudios Geológicos 47, 237–266.
Szyndlar, Z., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). Münchner Geowissenschaften Abhandlungen 28, 35–39.
Szyndlar, Z., Rage, J.-C., 2003. Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Warsaw.
Szyndlar, Z., Zerova, G., 1990. Neogene cobras of the genus *Naja* (Serpentes: Elapidae) of East Europe. Annalen des Naturhistorischen Museums in Wien 91A, 53–61.
Taskavak, E., Reimann, M.J., Polder, W.N., 1999. First record of the Nile Soft-Shelled Turtle, *Trionyx triunguis*, from Kos Island, Greece, with comments on its occurrence in the eastern Mediterranean. Chelonian Conservation and Biology 3, 510–512.
Theodorou, G.E., Roussiakis, S.J., Athanassiou, A., Filippidi, A., 2010. Mammalian remains from a new site near the classical locality of Pikermi (Attica, Greece). Scientific Annals, School of Geology, Aristotle University of Thessaloniki 99, 109–119.
Theodorou, G.E., Symeonidis, N., Stathopoulou, E., 2007. *Elephas tiliensis* n. sp. from Tilos island (Dodecanese, Greece). Annales Géologiques des Pays Helléniques 42, 19–32.
Tsoukala, E., Mol, D., Pappa, S., Vlachos, E., Longhem, W., Vaxevanopoulos, M., Reumer, J., 2011. *Elephas antiquus* in Greece: new finds and a reappraisal of older material (Mammalia, Proboscidea, Elephantidae). Quaternary International 245, 339–349.
Valakos, E.D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., Foufopoulos, J., 2008. Amphibians and Reptiles of Greece. Edition Chimera/Serpents Tale, Frankfurt.
Van der Geer, A.A.E., Sondaar, P.Y., 2002. The postcranial elements of *Paradolichopithecus arvernensis* (Primates, Cercopithecidae, Papionini) from Lesvos, Greece. Annales Géologiques des Pays Helléniques 39A, 71–86.
Van Vugt, N., de Bruijn, H., van Kolfschoten, M., Langereis, C.G., Okuda, M., 2000. Magneto- and cyclostratigraphy and mammal-faunas of the Pleistocene lacustrine Megalopolis Basin, Peloponnesos, Greece. Geologica Ultraiectina 189, 1–167.
Vasileiadou, K.V., Koufos, G.D., Syrides, G.E., 2003. Silata, a new locality with micromammals from the Miocene/Pliocene boundary of the Chalkidiki Peninsula, Macedonia, Greece. Deinsea 10, 549–562.
Vlachos, E., 2011. [Contribution to the Study of the Gigantic Tortoises from the Pliocene of Epanomi (Thessaloniki)]. Master thesis [in Greek] Aristotle University of Thessaloniki (unpubl.).
Vlachos, E., 2012. Special remarks on the posterior limb morphology of the giant continental tortoises from the Pliocene of Thessaloniki area (Macedonia, Greece). In: Joyce, W.E. (Ed.), Symposium on Turtle Evolution, 2–4 June 2012, Program and Abstracts. University of Tübingen, Germany, p. 46.
Vlachos, E., Tsoukala, E., 2011. New finds of giant tortoises from Thessaloniki area: the most complete *Cheirogaster* Bergounioux, 1935 skeleton in Greece. In: Van der Geer, A., Athanassiou, A. (Eds.), 9th Annual Meeting of the European Association of Vertebrate Palaeontologists, Program and Abstracts. Natural History Museum of Crete, Heraklion, p. 59.
Weems, R.E., Knight, J.L., 2013. A new species of *Bairdemys* (Pelomedusoides: Podocnemididae) from the Oligocene (early Chattian) Chandler Bridge Formation of South Carolina, USA, and its palaeobiogeographic implications for the genus. In: Brinkman, D.B., Holroyd, P.A., Gardner, J.D. (Eds.), Morphology and Evolution of Turtles. Springer, Dordrecht, pp. 289–303.
White, W.A., Worthy, T.H., Hawkins, S., Bedford, S., Sprigg, M., 2010. Megafaunal meiolaniid horned turtles survived until early human settlement in Vanuatu, Southwest Pacific. Proceedings of the National Academy of Sciences, USA 107, 15512–15516.
Wielandt-Schuster, U., Schuster, F., Harzhauser, M., Mandic, O., Kroh, A., Röge, F., Reisinger, J., Liebetrau, V., Steininger, F.F., Piller, W.E., 2004. Stratigraphy and paleoecology of Oligocene and early Miocene sedimentary sequences of the Mesohellenic Basin (NW Greece). Courier Forschungsinstitut Senckenberg 248, 1–55.
Willmann, R., 1981. Evolution, systematik und stratigraphische bedeutung der Neogenen süsswassergastropoden von Rhodos, Kos, Ägäis. Palaeontographica 174, 10–235.
Woodward, A.S., 1901. On the bone beds of Pikermi, Attica and on similar deposits in Northern Euboea. Geological Magazine 8, 481–486.