Late Miocene tortoises from Samos, Greece: implications for European Neogene testudinid systematics and distributions

Evangelos Vlachos, Adán Pérez-García, Socrates Roussiakis, Georgios L. Georgalis & Benjamin P. Kear

To cite this article: Evangelos Vlachos, Adán Pérez-García, Socrates Roussiakis, Georgios L. Georgalis & Benjamin P. Kear (2019) Late Miocene tortoises from Samos, Greece: implications for European Neogene testudinid systematics and distributions, Journal of Vertebrate Paleontology, 39:6, e1722950, DOI: 10.1080/02724634.2019.1722950

To link to this article: https://doi.org/10.1080/02724634.2019.1722950
LATE MIOCENE TORTOISES FROM SAMOS, GREECE: IMPLICATIONS FOR EUROPEAN NEOGENE TESTUDINID SYSTEMATICS AND DISTRIBUTIONS

EVANGELOS VLACHOS,* 1,2 ADÁN PÉREZ-GARCÍA, 3 SOCRATES ROUSSIAKIS, 4 GEORGIOS L. GEORGALIS, 5,6 and BENJAMIN P. KEAR 7

1 CONICET and Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100, Trelew, Chubut, Argentina, evlacho@mef.org.ar; 2 School of Geology, Faculty of Sciences, Aristotle University of Thessaloniki, Thessaloniki, Greece; 3 Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, Paseo de la Senda del Rey, 9, 28040 Madrid, Spain, paleontolo@gmail.com; 4 Department of Historical Geology and Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Panepistimiopolis 15784, Athens, Greece, srousiak@geol.uoa.gr; 5 Department of Earth Sciences, University of Turin, Via Valperga Caluso 35, 10125 Turin, Italy; 6 Laboratory of Evolutionary Biology, Department of Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 84215 Bratislava, Slovakia, dimetrodon82@gmail.com; 7 Museum of Evolution, Uppsala University, Norbyvägen 16, SE-752 36 Uppsala, Sweden, benjamin.kear@em.uu.se

ABSTRACT—The world-famous upper Miocene fossil localities on the Aegean island of Samos in Greece have produced a rich fossil record that sheds light on the evolution of eastern Mediterranean terrestrial faunas over a one-million-year interval of the late Neogene. Fossils have been discovered on Samos since antiquity, although a succession of paleontological and commercial collecting expeditions over the last 130 years has resulted in specimens now being distributed throughout museums all over the world. Here, we survey the fossil tortoise remains from Samos, which are significant because they include early antecedents of the modern Testudo lineage, together with spectacular examples of the European Neogene gigantic testudinid †Titanochelon, which represents one of the largest-bodied terrestrial turtle taxa documented to date. All of the Samos fossils derive from the Mytilini Formation, which spans the late MN11–early MN13 Neogene land mammal zones. The small-bodied tortoise remains include two incomplete shells that are morphologically consistent with basal testudonans and phylogenetically distinct from the coeval species Testudo marmorata found on mainland Greece. The Samos gigantic tortoise †Testudo schafferi was based on a spectacularly large skull and femur. However, we describe new plastron fragments, limb elements, and osteoderms that are compatible with †Titanochelon specimens from southern Greece and Anatolia. This could imply faunal links with the distinctive ‘Pikermian’ local assemblages from Asia Minor and concurs with the proposed late Miocene–Pliocene biogeographic segregation of large mammals from the eastern Aegean margin and Turkey relative to those occurring in northwestern Greece and the Balkan Peninsula.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP


INTRODUCTION

The late Miocene mammal localities on Samos Island (Fig. 1), and Pikermi on the Greek mainland near Athens, constitute some of the most important fossil sites in the circum-Mediterranean region (Koufos, 2006). Indeed, the discovery of fossils on Samos was first recorded in antiquity (see Solounias, 1981, and references therein), and through the work of extensive excavations conducted in the 19th and 20th centuries, the fossils are today known to span deposits of late MN11–early MN13 in age (Koufos et al., 2009). The many thousands of specimens recovered to date were historically dispersed throughout museums and other research institutes all over the world. Unfortunately, however, these ‘old collections’ are rarely associated with adequate locality information (Koufos, 2006; Koufos et al., 2009). In contrast, new systematic exploration has brought to light many significant fossils (recently summarized by Koufos and Nagel, 2009) that document the evolution of mammalian assemblages on Samos throughout a continuous stratigraphic interval of the late Miocene (Koufos et al., 2009, 2011). This updated biosuccession has also provided a context for correlating some of the ‘old collections’ with new age-constrained localities (Kostopoulos et al., 2009). Furthermore, comparative studies of the late Miocene eastern Mediterranean mammal assemblages have demonstrated that those found on Samos are more closely related to the ‘Eastern Block’ local faunas from Asia Minor, as opposed to those from the Balkan Peninsula of western Greece and Bulgaria (Kostopoulos, 2009a). Such distinctions have yet to be demonstrated for the coeval herpetofauna but have been suggested for at least the spectacular European gigantic tortoises (Vlachos et al., 2014), whose published records were variously summarized by Lapparent de Broin (2001, 2002), Georgalis and Kear (2013), and Vlachos (2015). Other Greek fossil testudinid occurrences have been documented elsewhere by Tsoukala et al. (2011), Vlachos and Tsoukala (2014, 2016), and Vlachos et al. (2014, 2015).

Charles Immanuel Forsyth Major was the first to mention the presence of tortoise fossils from Samos, which he listed under the generic designation of Testudo (Forsyth Major, 1888 1891,
Forsyth Major’s expeditions were funded by the Barbey-Boissier family (see Solounias, 1981, and references therein), with most of the recovered material eventually being deposited in the MGL. In 1899–1900, the fossil dealer Bernhard Sturtz also collected Miocene vertebrate remains from Samos, with some of his specimens being purchased by the NHMW (others were sent to Stuttgart, Frankfurt, and London; Koufos, 2009) and probably including the famous giant tortoise skull later described by Tibor Szalai in 1931 (Szalai, 1931). Theodore Skoufos, professor of geology and paleontology at Athens University, undertook further excavations on Samos during the summer of 1903, documenting his findings in the proceedings of the rectorate of Athens University, as well as in a subsequent newspaper interview (Koufos, 2009; S.R., unpubl. data). This report mentioned the discovery of three fossil tortoises that may correspond to specimens now in the AMPG. In 1924, the renowned American fossil collector Barnum Brown visited Samos and shipped large amounts of fossil material, including tortoise remains, to the AMNH. However, it was not until Szalai (1931) that any of the late Miocene tortoises found on Samos were formally described, with the species †Testudo schafferi Szalai, 1931, being erected for a cranium and femur in the NHMW. Although the validity of this species has never been questioned, its generic combination has undergone several revisions over the years, with various references to Testudo Linnaeus, 1758 (original combination), to the historical ‘wastebasket’ genera Geocheleon Fitzinger, 1836, and †Cheirogaster Bergounioux, 1935, and finally to †Titanochelon Pérez-García and Vlachos, 2014 (see Lapparent de Broin, 2002; Georgalis and Kear, 2013; Vlachos et al., 2014; Vlachos, 2015, and references therein). In addition, Chkhikvadze (2001, 2006, 2007, 2010) assigned some Samos giant tortoise remains from the AMNH to †Centrochelys natadzei Chkhikvadze, 1989 (elsewhere classified with †Colossochelys or †Megalochelys), a taxon described from the upper Miocene of Georgia. Solounias (1981) otherwise listed three distinct species in the Samos quarries: a giant Testudo sp. from the quarry named ‘Q1,’ ‘Te. schafferi’ from quarry ‘S3,’ and the small-sized Testudo cf. marmorum from quarry ‘QA.’ Koufos (2009:9) also recorded tortoise remains from recent excavations, including one shell now stored in the Samos Museum of Natural History (G. D. Koufos, pers. comm. to G.L.G.) that has yet to be examined.

In this paper, we revise the published type material of ‘Te. schafferi’ and assess previously undocumented tortoise remains from the NHMW, AMPG, and MGL. These incorporate the large testudinid fossils from Charles Forsyth Major’s excavations in 1887 and 1889, and the 1924 AMNH collection recovered by Barnum Brown. Moreover, we describe a testudinid carapace and plastron pair from the AMPG that was found by Theodore Skoufos in 1903, together with another in the GNHM that was acquired via a private donation. Our objectives are to (1) determine whether the late Miocene small-bodied tortoises from Samos are compatible at the species level with their coeval mainland equivalent, *Te. marmorum* (Pérez-García and Vlachos, 2014; Pérez-García et al., 2016; Vlachos and Rabi, 2018); (2) determine whether the giant testudinids from Samos are taxonomically distinct from those found in the southern Balkans; and (3) evaluate the affinities of the Samos tortoise assemblages to the broader context of late Miocene ‘Pikenman’ faunas (sensu Kostopoulos, 2009a) from Asia Minor.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York, New York, U.S.A.; AMPG, Museum of Paleontology and Geology of the National and Kapodistrian University of Athens, Athens, Greece; FFSM, Fürstlich Fürstenbergisches Sammlung Donaueschingen, Donaueschingen, Germany; GNHM, Goulandris Natural History Museum, Athens, Greece; MGL, Geological Museum of Lausanne, Lausanne, Switzerland; MGSB, Museu de Geologia del Seminari de Barcelona, Barcelona, Spain; NHMW, Natural History Museum of Vienna, Vienna, Austria.

**PROVENANCE AND BIOSTRATIGRAPHIC CORRELATION OF THE ‘OLD COLLECTIONS’**

The stratigraphic provenance of the ‘old collections’ of testudinid fossils recovered from Samos is problematic (Koufos, 2009), and with the exception of those from the AMNH, all are representative of compositionally mixed assemblages from different localities (Koufos, 2009). For example, the collection labels...
from MGL record Adrianos ravine as the source of their material, yet Koufos (2009) reported that these same specimens derived from multiple sites. Likewise, the AMPG remains are listed as having been excavated from Adrianos, Katakoumena, Bartzikos, and Bainsianti based on historical archives held at the National and Kapodistrian University of Athens, as well as newspaper interviews provided by Theodore Skoufos (see Koufos, 2009; S.R., unpubl. data).

Based on the accompanying information, most of the AMNH testudinids were apparently recovered from quarry ‘Q1.’ This locality was relocated and systematically investigated by researchers from the Aristotle University of Thessaloniki, including Ioannis Melentis from 1963 to 1985 and George Koufos and Dimitris Kostopoulos from 1993 to present (Koufos, 2009; Kostopoulos et al., 2009, and references therein). Although some other sites were undoubtedly sampled (Koufos, 2009), the AMNH quarry ‘Q1’ collection represents the upper section of the Mytilinii Formation (upper Miocene; see Kostopoulos et al., 2009), which can be correlated with the MTLA–C sites and the Samos Dominant Mammal Assemblage of 7.2–6.9 Ma (late MN12; Koufos et al., 2009). Only one testudinid element, AMNH 1878 (an isolated humerus), was seemingly recovered from quarry ‘Q5,’ which is equivalent to the uppermost Mytilinii Formation and has an age estimate of 6.9–6.7 Ma (Koufos et al., 2009; Kostopoulos et al., 2009). However, the accompanying accession information states that this bone was found in association with ‘mammal 229599;’ which has been identified as the giraffid Samotherium boissieri. Solounias (1981) considered this to be a biostratigraphic index taxon for quarry ‘Q5,’ although Kostopoulos (2009b) has since recognized †Cypriotem保守 {parah, 2006 (unranked clade) as the giraffid Samotherium boissieri. Solounias (1981) otherwise correlated †S. boissieri with the Samos Primary Mammal Assemblage, which is 7.8–7.4 Ma.

The partial plastron AMNH 1772 has no locality information; however, Solounias (1981:40) described a ‘very large’ Testudo sp. from quarry ‘Q1,’ which most likely represents the majority of the AMNH specimens; notably, though, Solounias (1981) failed to mention any testudinid fossils from quarry ‘Q5’ despite these being present in the AMNH. Solounias (1981) also documented †Testudo* schafferi from the ‘S3’ locality on Samos, together with the small-bodied Testudo cf. marmoratum from ‘QA (= ‘Q1’); these are both dated to 6.9–6.7 Ma (Koufos et al., 2009). The †Te. cf. marmoratum occurrence probably corresponds to the MGL material, which is accompanied by handwritten labels made by Solounias in 1978. As such, we restrict our age assignment of these remains to late MN11–early MN13, which spans the entire chronostratigraphic distribution of the Samos vertebrate assemblages (Koufos et al., 2009).

**SYSTEMATIC PALEONTOLOGY**

**TESTUDINES** Batsch, 1788, sensu Joyce, Parham, and Gauthier, 2004

**CRYPTODIRA** Cope, 1868, sensu Joyce, Parham, and Gauthier, 2004

**TESTUDINOIDEA** Fitzinger, 1826, sensu Joyce, Parham, and Gauthier, 2004

**TESTUDINIDAE** Gray, 1825, sensu Joyce, Parham, and Gauthier, 2004

**TESTUDONA** sensu Parham in Parham et al., 2006 (unranked clade)

†TESTUDO* ANTIQUA* Bronn, 1831

‘TESTUDO* aff. ANTIQUA’ (Fig. 2)

**Referred Material**—AMPG 1999, an almost complete carapace (Fig. 2A–F); GNHM 22, the anterior half of a carapace and a plastron (Fig. 2G–L).

**Locality, Unit, and Age**—Samos Island, Mytilinii Formation, late MN11–early MN13. There is no precise quarry information available for either of these referred specimens.

**Description**

AMPG 1999 lacks only the pygal–peripheral 11 area (Fig. 2A–F). The shell is elongate and domed (Fig. 2A, B, E, F). The nuchal is as wide as long, and roughly hexagonal in shape with a shallowly concave anterior edge. The posterolateral edges are sinuous, with the posterior margin being narrow and projecting (Fig. 2C). Eight neuars are present (Fig. 2B), with rounded dorsal protuberances present on the vertebral sulci of neural 1, neural 3, neural 5, and neural 8 (Fig. 2E, F). Neural 1 is longer than wide and rectangular with rounded edges. The anterior margin is much narrower than the posterior. Neural 2 is octagonal, and likewise narrower anteriorly than posteriorly. Neural 3 is quadrangular and as wide as long. Neural 4 is octagonal, as wide as long, and has anterior and posterior sides of equal width. Neural 5 is rectangular and wider than long. Neural 6 is hexagonal with short anterolateral sides. Neural 7 is also hexagonal and smaller than neural 6 but again possesses short anterolateral edges. Neural 8 is the smallest in the sequence and almost quadrangular in shape, with shallowly convex margins. Two supraprygal is present and together form a trapezoidal plate (Fig. 2D). The first suprapygal is much larger than the second and more elongate. The second suprapygal is lenticular and wider than long.

Like the neuars, the costals are differentiated such that costal 1 is conspicuously elongate and contacts the nuchal, neuars 1 and 2, and peripherals 1–3. Costal 2 and costal 4 are mediolaterally shortened and project laterally to create an alternating sequence with costal 3 and costal 5 (these are sequentially mediolaterally and laterally short). Costal 6 and costal 7 have similar shapes but bear an extended median edge for contact with the hexagonal neuars. Costal 8 is the smallest and has a rounded medial side that contacts both costal 7 and suprapygal 1 but does not extend to contact the neuars; the posteromedial margin of costal 7 thus contacts not only costal 8 but also suprapygal 1 (Fig. 2D). The peripherals are all long and narrow, with the edge from the bridge being anteroposteriorly shorter and taller.

The scute sulci are clearly traceable on the carapace of AMPG 1999 (Fig. 2B). The elongate cervical scute outline has a narrower anterior versus posterior edge and covers almost half of the medial length of the nuchal. Vertebral 1 would have been shorter and narrower than the succeeding scutes. Vertebrals 2–4 appear to have been wider than the pleural scutes in dorsal view; they extended transversely across neural 1, neural 3, neural 5, and neural 8. The pleural scute is rectangular and wider than long. Marginal 6 lacks any obvious contact with pleural 3 (Fig. 2E). The pleuromarginal sulci otherwise closely follow the costoperipheral sutures (Fig. 2E, F).

GNHM 22 preserves the anterior and middle sections of the shell. It is permanently fixed to a display mount (Fig. 2G–L), which obscures parts of the plastron from view (Fig. 2J, K). Most of the left side of the carapace and the posterior lobe of the plastron are also missing. The remaining carapace is elongate and domed. The nuchal is as wide as long and approximately hexagonal, with a shallowly concave anterior edge. The shape of neural 1 is not discernible; however, neural 2 is octagonal, and neural 3 is quadrangular and as wide as long. Remnants of the neural-costal contact suggest that neural 4 is octagonal. The medial contacts of costal 1 are not preserved. Costal 2 and
FIGURE 2. †Testudo aff. antiqua from the upper Miocene of Samos Island. A–F, AMPG 1999, almost complete carapace: A, dorsal view; B, drawing of the dorsal view; C, detail of the nuchal; D, detail of the posterior view; E, left lateral view; F, right lateral view. G–L, GNHM 22, partial shell: G, dorsal view; H, drawing of the dorsal view; I, anterior view; J, ventral view; K, drawing of the ventral view; L, right lateral view. Some important characters are indicated in red. Bony plate and scute abbreviations in lower- and uppercase, respectively. Abbreviations: ABD, abdominal; CE, cervical; cos, costal; en, entoplastron; ep, epiplastron; GU, gular; HU, humeral; hyo, hyoplastron; hypo, hypoplastron; MA, marginal; ne, neural; nu, nuchal; PEC, pectoral; per, peripheral; PLE, pleural; sp, suprapygal; VE, vertebral. Scale bars equal 5 cm.
costal 4 are mediolaterally short and laterally elongate; they alternate with costal 3, which is otherwise mediolaterally extended and laterally short.

The cervical scute outline of GNHM 22 is transversely narrow and anteroposteriorly elongate. The first vertebral scute appears to have been unusually short, with vertebrals 2–3 being wider than the pleural scutes. The vertebrals extended transversely across neural 1 and neural 3. The pleurals were seemingly rectangular and wider than long. The pleuromarginal sulci trace the costoperipheral sutures (Fig. 2L). The plastron of GNHM 22 (Fig. 2J, K) has a broadly rounded anterior lobe. Its anterior margin comprises the narrow epiplastral lip. The epiplastral slab is well developed and convex in profile, at least based on our inspection of its observable components (Fig. 2I). The entoplastron is nearly as wide as long, and hexagonal in outline with straight anterolateral margins. The posterior edges of the entoplastron are rounded. The hyoplastra and the hypoplastra are long and broad; their central sections are both flat, which together with the broad carapace indicates that GNHM 22 was probably a female.

The gular scutes are similarly broad and would have covered the medial section of the epiplastron, as well as the anterior part of the entoplastron. The gularhumeral sulcus is convex and forms an acute angle relative to the longitudinal midline. The humerals otherwise covered the remaining part of the entoplastron. The humeropectoral sulcus is mediolaterally straight and laterally convex; medially it also transsects the posterior end of the entoplastron. The pectorals are equal in length to the humerals and cover the anterior half of the hyoplastra; they are unusually elongate, with their medial length equal to just over half that of the medial hyoplastral suture (the maximum extent is partly obscured by the display mount). Most of the abdinal scute outline is preserved and appears to have extended across both the posterior extremity of the hyoplastra and the anterior half of the hypoplastra.

**Character-State Comparisons**

Both AMPG 1999 and GNHM 22 are morphologically consistent with members of the Testudona clade. Unfortunately, however, the diagnostic presence/absence of a hypo-xiphiplastral hinge (see Lapparent de Broin et al., 2006; Luján et al., 2016; Vlachos and Tsoukala, 2016; Vlachos and Rabí, 2018) cannot be confirmed in either specimen. Nevertheless, AMPG 1999 exhibits a characteristically symmetrical suture between costal 7 and suprapygal 1; this encloses costal 8 and excludes it from contact with neural 8 (Fig. 2D). A similar condition has been identified on at least the right side of a †Testudo antiqua specimen (FFSM 3446) from the middle Miocene of Germany (see Corsini et al., 2014; Fig. 2.1). Such an atypical costal-suprapygal configuration distinguishes AMPG 1999 from the various species of Testudo sensu lato (Testudo graeca, Testudo marginata, Testudo kleinmanni, and †Chersine hermanni), as well as from †Testudo marmorum (Vlachos, 2015). Another similar case of abnormal morphology was illustrated by Pérez-García (2017; Fig. 5) and included anomalous supernumerary costals in the posterior section of the carapace of a †Te. antiqua individual from the middle Miocene of Spain (MGSB25324a). In addition, GNHM 22 possesses unusually long medial sulci for the pectoral scutes (Fig. 2J, K), a character state that is also found in Indotesudo Lindholm, 1929 (see Vlachos and Rabí, 2018), and might be plesiomorphic amongst testudinids, and other extinct small testudinids specifically. Finally, the dorsal width of vertebral scutes 2–4 exceed that of the pleurals in GNHM 22 (Fig. 2A, B); this is distinct from other testudinids, including †Te. antiqua, in which the vertebral scutes are conspicuously narrower (see Corsini et al., 2014), as well as from Te. marmorum, in which pleural 1 extends over the nuchal (Vlachos, 2015).

Notably, AMPG 1999 and GNHM 22 are closely comparable to middle Miocene (upper Serravalian) testudinid remains recovered from near Thymiana on Chios, which were described by Paraskevaidis (1955). These specimens comprise two internal shell steinkerns that Paraskevaidis (1955) identified as Testudo sp. Paraskevaidis (1955) deposited his fossils in the Bayerische Staatsammlung für Paläontologie und Geologie in 1940, but they were later lost during World War II (footnote in Paraskevaidis [1955]; M. Moser, pers. comm., 2011, 2017). Nonetheless, illustrations by Paraskevaidis (1955) clearly show that the neurals and suprapygal scutes were similarly shaped to those of AMPG 1999 and GNHM 22, as well as an apparent contact between suprapygal 1 and costal 7 (see Fig. 3). Although this morphological compatibility is marked, we cannot confirm our observations without first-hand inspection of the material and therefore refrain from formally proposing any taxonomic relationship at present.

**Taxonomic Implications**

Traditionally, all of the small-bodied fossil testudinids from Europe were classified within the genus Testudo sensu lato. Numerous species have since been described dating back to the Oligocene (see Lapparent de Broin, 2001, for summary). DNA sequence phylogenies have placed Testudo within the derived testudinid clade, Testudona (Parham et al., 2006), which also contains the extant genera Indotestudo and Malacochersus. A robust taxonomic framework based on molecular data has therefore been established for interpreting the fossils (Le et al., 2006; Fritz and Bininda-Emonds, 2007; Guillou et al., 2012; Pereira et al., 2017). Yet, the fundamental distinction between the hypo-xiphiplastral ‘hinged’ Testudo sensu stricto species Testudo graeca, Testudo marginata, and Testudo kleinmanni and the ‘non-hinged’ Testudo sensu lato taxa ‘Testudo’ hermanni and ‘Testudo’ horsfieldii is still being debated. As a result, the generic assignment of various small testudinids taxa is changeable, with ‘Te.’ hermanni being attributed to Chersine (= Eurotestudo; see Lapparent de Broin et al., 2006; Fritz and Bininda-Emonds, 2007) and ‘Te.’ horsfieldii to Agrionemys (Khosatzky and Młynarski, 1966; Lapparent de Broin et al., 2006, and others). Similarly, some non-hinged fossil taxa, such as ‘Te.’ antiqua, have been transferred to †Paleotestudo (see Pérez-García, 2017, and references therein).

The small-bodied fossil testudinids from Greece are almost entirely represented by ‘hinged’ species, including Te. graeca, Te. marginata, and Te. marmorum (Vlachos, 2015, and references therein). On the other hand, the non-hinged †Chersine hermanni has been identified from Pleistocene deposits in northern mainland Greece (Vlachos, 2015), as well as the latest Pleistocene–Holocene deposits of the Franchthi Cave in the Peloponnesse (Vlachos and Delfino, 2016). Therefore, although the ‘hinged’ species of Testudo are most prevalent in Greece, character-state compatibility between the Samos remains and other species, such as ‘Te.’ antiqua, together with the occurrence of this stemward radiation elsewhere in the Greek record, prompts our rejection of their historically advocated affinity to Te. marmorum (Solounias, 1981).

The small testudinid from Samos shows some characteristics that could allow its distinction as a new species, but as explained above, the unknown stratigraphic position and the uncertain association of the two referred specimens do not allow us to propose this with confidence. As a nomenclatural solution, we therefore follow the recommended protocols of Bengtson (1988) in utilizing the testudonan traditional generic epithet ‘Testudo,’ but with the specific prefix ‘aff.’ to denote taxonomic
novelty, and reference to ‘antiqua’ in recognition of character-state compatibility without assumption of phylogenetically definitive homology.

GEOCHELONA sensu Vlachos and Rabi, 2018 (unranked clade)
TITANOCHELON Pérez-García and Vlachos, 2014
TITANOCHELON SCHAFFERI (Szalai, 1931) (Figs. 4–8)

Testudo schafferi Szalai, 1931.
†Geochelone schafferi Auffenberg, 1974.
††Cheirogaster schafferi Lapparent de Broin, 2001.
†Centrochelys natadzei = Testudo (†Colossochelys) cf. atlas Chkhikvadze, 2001, partim (based on AMNH material only).
†Colossochelys natadzei Chkhikvadze, 2006, partim (based on AMNH material only).
†Cheirogaster schafferi Georgalis and Kear, 2013.
†Titanochelon schafferi Pérez-García and Vlachos, 2014.

**Lectotype**—NHMW 2009z0103/0001, cranium. Szalai (1931) did not designate a holotype in his original publication (Art. 73.1, International Code of Zoological Nomenclature; International Commission on Zoological Nomenclature [ICZN], 1999). Therefore, the cranium (NHMW 2009z0103/0001) and attributed femur (NHMW 1911/0005/0275) may be considered syntypes under Article 73.2 of the International Code of Zoological Nomenclature. Neither of these specimens was demonstrably recovered from the same individual (see explanation below). Szalai (1931) and Lapparent de Broin (2002) both treated these elements as associated, but they are actually cataloged under separate batch numbers. The cranium was originally assigned a batch number (NHMW 1913-2) corresponding to a bulk shipment of specimens purchased from the fossil dealer Bernhard Sturtz during 1913 (U. Gohlich [NHMW], pers. comm. to B.P.K., 2009). The femur was alternatively inventoried two years earlier in 1911 (batch NHMW 1911-V275) and is thus unlikely to have been found in association with the skull. There is no other information available to convince us that the NHMW material belongs to the same individual. Consequently, we hereby formally designate the cranium NHMW 2009z0103/0001 as the lectotype of Testudo schafferi Szalai, 1931.

**Referred Material**—NHMW 1911/0005/0275, a left femur (paralectotype); NHMW 1911/1, a distal carpal; NHMW 1911/2, a phalanx; NHMW 1911/3, an osteoderms; MGL 101613 to MGL 101622 (formerly S.1222–1231; mentioned in Forsyth Major, 1891, 1894), 10 isolated osteoderms; MGL 101623 (formerly S.1266; mentioned in Forsyth Major, 1891, 1894), an osteoderm series preserved in anatomical position; MGL 101624 (formerly S.1267; mentioned in Forsyth Major, 1891, 1894), a complete right epiplastron; MGL 101624a (formerly S.1267a; mentioned in Forsyth Major, 1891, 1894), an indeterminate plastral fragment (probably associated with MGL 101624), AMNH ‘Q1’ specimens: AMNH 1752, a distal phalanx; AMNH specimen with uncertain source locality: AMNH 1772, the middle and posterior sections of a plastron.

**Emended Diagnosis**—†Titanochelon schafferi is classified within Testudinidae based on an expansive upper temporal emargination in the skull; an extensive plastral scute area covering the visceral side of the plastron; a well-developed epiplastron; fused trochanters on the femur; and the limbs bearing well-developed osteoderms. †Titanochelon schafferi can be referred to the genus †Titanochelon with the following character states: the frontals are narrower than the prefrontals; the crista supraoccipitalis is elongate; a circular pit indents on the ventral surfaces of the premaxillae; both the gularohumeral sulcus and sagittal axis are...
angled at >45°; the humeropectoral sulcus is oriented perpendicular to the longitudinal axis and has a well-developed lateral alteration in curvature; the pectoral scutes are anteroposteriorly short; and the humerus has a curved diaphysis. †Titanochelon schafferi differs from other species of †Titanochelon in its proportionately short preorbital cranium relative to †Titanochelon bacharidisi; a reduced lower temporal emargination in comparison with †Ti. bacharidisi; straight crista supraoccipitalis, which is otherwise weakly downcurved in both †Titanochelon bolivari and †Ti. bacharidisi; gular scutes not covering the entoplastron as in †Ti. bolivari and †Titanochelon vitodurana, or contacting the anterior border of the entoplastron as in †Ti. bacharidisi; the humeropectoral sulcus is situated posterior to the entoplastron, as opposed to contacting its medial edge as in †Ti. bolivari; expansion of the humeral scutes onto the posterior sections of the epiplastra resembles †Titanochelon perpiniana but is not evident in other †Titanochelon species; and the distal end of the humerus is asymmetrical as in †Ti. bolivari but differs from other †Titanochelon species. Finally, †Ti. schafferi manifests an autapomorphic broad fusion of the medial and lateral centralia, with the lateral centrale constituting about a third of the maximum element width; this is substantially greater than in other species of †Titanochelon (the centrale is not fused in †Ti. bolivari).

**Locality, Unit, and Age**—Various specimens from different localities in the Mytilinii Formation on Samos Island. These range in age from the upper Miocene late MN11 to early MN13.

**Description**

**Lectotype**—The lectotype cranium NHMW 2009z0103/0001 is virtually complete (Fig. 4) but has been accentuated by plaster reconstruction, particularly along the right premaxillary-maxillary margin, as well as part of the right and all of the left postorbital bar, and across large sections of the palate. A thick covering of consolidants and plaster has also been applied to the bone surfaces, probably in preparation for display. This has obscured

---

**Abbreviations**

- **ane**: apertura narium externa
- **ap**: apertura postotica
- **bo**: basioccipital
- **bs**: basisphenoid
- **cm**: condylus mandibularis
- **co**: condylus occipitalis
- **cs**: crista supraoccipitalis
- **fjp**: foramen jugulare posterius
- **fm**: foramen magnum
- **fnh**: foramen nervi hypoglossi
- **fo**: fossa orbitalis
- **fr**: frontal
- **fst**: foramen stapedio-temporale
- **fti**: fossa temporalis inferior
- **fts**: fossa temporalis superior
- **ica**: insicura columella auris
- **ju**: jugal
- **LAR**: labial ridge
- **LIR**: lingual ridge
- **LTE**: lower temporal emargination
- **MMR**: median maxillary ridge
- **mx**: maxilla
- **op**: opisthotic
- **pa**: parietal
- **prf**: prefrontal
- **pmp**: premaxillary pit
- **po**: postorbital
- **pr**: prootic
- **pt**: pterygoid
- **pto**: processus trochlearis oticus
- **qj**: quadratojugal
- **qu**: quadrangle
- **soc**: supraoccipital
- **sq**: squamosal
- **UTE**: upper temporal emargination
- **vo**: vomer
many of the cranial sutures except for those on the skull roof, which are intersected by fine cracks.

The cranium of NHMW 2009z0103/0001 is compact (Fig. 4A), with a broad and rounded apertura narium externa (Fig. 4G); this projects above the level of the prefrontals medially. The visible cranial sutures (Fig. 4A, B) include those of the prefrontals, which form the anteromedial rim of the fossa orbitalis (see Table 1 for measurements). The frontals measure 56 mm along the median interfrontal suture and 32.7 mm along the better-preerved right frontal-parietal suture; they contribute to the medial rim of the fossa orbitalis. The fossa orbitalis itself is rounded and situated within the anterior third of the anteroposterior length of the skull. The posterior margin of the fossa orbitalis is bordered by the postorbital bars, which are imperfectly preserved, although their dorsal contacts with the frontal (anteriorly) and the parietal (posteriorly) are clearly evident on the skull roof. The ventral contribution of the postorbital bar, and its articulation with the jugal, is only visible on the right-hand side of the skull (the left has been reconstructed in plaster). This entire region (including the extensively fragmented jugal and squamosal) is also reinforced by a layer of glue, making contacts between individual elements difficult to identify. Nevertheless, the postorbital bars have been restored as being straight in lateral view and obliquely sloped in anterior view. This (together with the laterally flaring posterior extremity of the maxilla) imparts a distinctly anterolateral orientation to the fossa orbitalis.

The frontals are anteriorly constricted, making the prefrontals appear wider than the frontals in dorsal view. The parietals have a maximum midline length of 64.3 mm and a maximum anterior suture width of 36.0 mm along their anterior sutures. The posterior supraoccipital suture cannot be observed. The parietal contacts the postorbital laterally. The supraoccipital forms an elongate and straight crista supraoccipitalis that extends beyond the level of squamosals. The fossa temporalis superior extends approximately two-thirds along the entire length of the skull and contributes to the upper temporal emargination. It is bordered medially by the postorbital, the parietal, and the supraoccipital, and laterally by the postorbital, the quadratojugal, and the squamosal.
The squamosal has near-parallel sides and is rounded posteriorly. The quadratojugal contacts the squamosal along its dorsal margin and the quadrate along its ventral margin. In addition, the quadratojugal sutures to the jugal on the left side of the skull; the antrum postoticum also has a robust incisura columellae auris (Fig. 4E, F).

The individual bones of the braincase are exposed on the right side of the skull. The prootic is elongate and contributes to the medial face of the processus trochlearis oticum, although the full extent of this contact is unclear. The prootic sutures anteriorly to the parietal and posteromedially to the supraoccipital. The prootic-opisthotic contact is broad in dorsal view, and the quadrate is involved in the processus trochlearis oticum. The quadrate also sutures to the quadratojugal and the squamosal. The quadrate and the prootic further delimit the foramen stapedio-temporale.


Vlachos et al.—Late Miocene tortoises of Samos (e1722950-9)
The foramen magnum is expansive (Fig. 4H) and bordered ventrally by the hemispherical condylus occipitalis. The processus paraoccipitalis contacts the squamosal. The foramen nervi hypo- glossi and foramen jugalare posteriori are situated adjacent to the condylus occipitalis.

The palatal surface of the braincase exposes the ‘V’-shaped basisphenoid and a deep depression, which is situated immediately anterior to the condylus occipitalis on the basioccipital (this also contacts the pterygoids). Further anteriorly, the expansive lower temporal emargination is bordered by the quadrate, the quadratojugal, and the jugal, although the sutures between these elements are difficult to trace (Fig. 4C, D). The palatal surface of the premaxillae is indented by a conspicuous deep pit; however, a mixture of adhering plaster, glue, and matrix makes it difficult to determine whether this has been accentuated by damage during collection and/or preparation.

The triturating surface of the premaxillae forms the anteriormost section of the labial ridge. Three parallel ridges are otherwise present on the maxillae, with the labial ridge being preserved only on the right-hand side of the skull. A pair of median maxillary ridges extend between the labial and lingual ridges, but they do not contact the premaxillae. In contrast, the lingual maxillary ridges reach the pterygoids and project anteriorly beyond the tip of the medial ridges and onto the premaxillae.
triturating ridges preserve any trace of tubercles, and the lingual and medial maxillary ridges are connected by a low transverse ridge and adjacent shallow concavity.

Finally, the vomers intersect between the pterygoids, but the paired foramina praepalatinum are not identifiable; this could be a result of preservation or coverage by lingual extensions of the maxillary ridges (see Gerlach, 2001). The foramen palatinum posterius is likewise not visible, but the fossa temporalis interior was clearly expansive.

**Referred Specimens**—Attributable plastral components include a broken anterior lobe (AMNH 1905; Fig. 5A–D), a right epiplastron (MGL 101624; Fig. 5E–H), middle and posterior sections of a plastron (AMNH 1772; Fig. 5I–K), and another indeterminate plastral fragment (MGL 101624a). These incomplete bones are proportionately incompatible with each other, suggesting that they derive from multiple individuals; however, we estimate that a reassembled plastron would have been over 700 mm in maximum length. This is considerably smaller than expected from the corresponding cranium NHMW 2009z0103/0001, for which Lapparent de Broin (2002) calculated a maximum shell length of 1,850 mm extrapolated from the complete skeleton of *T. perpiniana*.
The obvious lack of a plastral concavity, coupled with weak xiphiplastral extremities, on AMNH 1772 also indicates that this individual was a female.

AMNH 1905 preserves a rounded anterior plastral lobe with a straight anterior-most border. The epiplastral lip is well developed but has a weak posterior extension and shallow gular pocket (Fig. 5A, B). The gular surface is convex (Fig. 5B). There is no obvious constriction along the gularohumeral sulcus (Fig. 5C, D), and the gular scute outlines terminate before the anterior side of the entoplastron (Fig. 5B, D); the humeral scutes would thus have extended onto the epiplastra. The gularohumeral sulci form an angle of >45° relative to the sagittal axis. The anterior edge of the entoplastron on AMNH 1772 (Fig. 7C) is slightly wider than tall, with a concave proximal end. Both of the femoral trochanters are massive proximal end. Both of the femoral trochanters are fused, and the head is longer than wide, with an almost perpendicular orientation relative to the longitudinal axis of the diaphysis. A broad fossa extends between the femoral head and the trochanters. The diaphysis thins distally and has an elliptical cross-section. The distal end of the femur expands into the subequal sized tubular and fibular condyles. Posteriorly, these are joined by a thin ridge, which encloses a deep concavity.

Other than an unidentifiable coracoid or a pelvic fragment (AMNH 1897; Fig. 7A), the additional recovered appendicular bones belong to the distal limb. A fused right medial-lateral centrale (AMNH 1887; Fig. 7B) is conspicuously broad, with the lateral centrale constituting over one-third of its total width. The proximal articular surfaces are flattened, as opposed to the distal articular surfaces, which are shallowly concave for insertion of the distal carpal. The associated intermediate (AMNH 1887; Fig. 7C) is slightly wider than tall, with a concave proximal surface and paired distal articulations for the fused medial and lateral centralia. The ulnare (AMNH 1887; Fig. 7D) is likewise broad and compact. Conversely, the distal carpal is transversely compressed (AMNH 1887; Fig. 7E) and bears a proximal protuberance, together with a flattened ventral metacarpal contact. The various metacarpals (AMNH 1887; Fig. 7F–G) are either spherical or flattened with shallowly concave articular surfaces. The forelimb phalanges (AMNH 1887; Fig. 7H–I) have a concave proximal articular surface and a distal convexity that supported the ungual. The distal phalanges are comparable but are usually more rounded and marginally longer than wide (AMNH 1887; Fig. 7J). Several additional phalanges that are much longer than wide possibly could belong to the hind limb (AMNH 1887; Fig. 7K).

Lastly, a large number of osteoderms are preserved in the MGL and AMNH collections (Fig. 8). Especially those from MGL 101623 (Fig. 8A–C) were found in articulation and associated with a mammal jaw and other tortoise shell fragments; Fig. 8A, B). These are all overlapping and suggest an extensive coverage over the limbs in life. The other isolated osteoderms include sharply pointed (MGL 101622, Fig. 8D; AMNH 1897, Fig. 8E); bluntly pointed (e.g., MGL 101619; Fig. 8F), and rounded (AMNH 1897; Fig. 8U, V) examples, although none of these are morphologically consistent with thigh tubercles.

Character-State Comparisons

The remains assigned to †Titanochelon schafferi are closely comparable to those of both †Titanochelon bacharidisi from the Pio-
cene of northern Greece (see Vlachos et al., 2014) and †Titanochelon bolivari from the middle Miocene central Spain (see Pérez-García and Vlachos, 2014). †Titanochelon bacharidisi, in particular, shares proportionately elongate frontals that are medially longer than the prefrontals and contribute to the orbital rim (Vlachos et al., 2014:fig. 3a; Vlachos, 2015:fig.3.7a, b), as well as a distinct median maxillary ridge (Vlachos et al., 2014:fig. 3b; Vlachos, 2015:fig. 3c, d) and a deeply inset ventral surface on the basioccipital anterior to the condylus occipitalis (Vlachos et al., 2014:fig. 3b). Despite this, the orbits of T. schafferi differ in being positioned further anteriorly, and both the upper and lower temporal emarginations are visibly less expansive (Vlachos et al., 2014:fig. 3c, d). †Titanochelon schafferi also possesses a diagnostically straight crista supraoccipitalis and rounded squamosals; the crista supraoccipitalis of †T. bacharidisi is otherwise curved, and the squamosals are tapering and extend beyond the level of condylus occipitalis (Vlachos et al., 2014:fig. 3).

The anterior plastral fragment (AMNH 1905) attributed to T. schafferi can be distinguished from those of other Miocene species, such as †T. bolivari from Spain (Pérez-García and Vlachos, 2014:fig. 3, and other figures therein) and †Titanochelon viotudurana from the middle Miocene of Switzerland (Peyer, 1942: Table 1. Measurements (in mm) of †Titanochelon schafferi, lectotype (NHMW 2009Z0103/0001).

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skirt length (premaxilla to occipital condyle)</td>
<td>231</td>
</tr>
<tr>
<td>Skirt length (prefrontals to surraquoapical crest)</td>
<td>228.3</td>
</tr>
<tr>
<td>Maximum skirt width (external edge of quadrates)</td>
<td>194</td>
</tr>
<tr>
<td>Skirt length/width ratio</td>
<td>0.84</td>
</tr>
<tr>
<td>Depth of skirt at postorbital bar</td>
<td>66.3</td>
</tr>
<tr>
<td>Depth of skirt at quadrate</td>
<td>68.4</td>
</tr>
<tr>
<td>Maximum length of orbit</td>
<td>47.8</td>
</tr>
<tr>
<td>Maximum depth of orbit</td>
<td>34.2</td>
</tr>
<tr>
<td>Width between orbits</td>
<td>66.6</td>
</tr>
<tr>
<td>Width of external nare</td>
<td>43.9</td>
</tr>
<tr>
<td>Height of external nare</td>
<td>29</td>
</tr>
<tr>
<td>Width between posteroventral maxilla</td>
<td>177.6</td>
</tr>
<tr>
<td>Width between external edge of pterygoids</td>
<td>67.5</td>
</tr>
<tr>
<td>Width fossa temporalis inferior (palatal fossa)</td>
<td>57.3</td>
</tr>
<tr>
<td>Width of occipital condyle</td>
<td>25.1</td>
</tr>
<tr>
<td>Width of foramen magnum</td>
<td>21.6</td>
</tr>
</tbody>
</table>

Vlachos et al.—Late Miocene tortoises of Samos (e1722950-12)
pl. 2), in its gular scute area not covering the entoplastron (this contrasts with †Ti. bacharidisi and Ti. perpiniana). Conversely, the humeral scute outline in AMNH 1772 expands anteriorly onto the epiplastra like that of Ti. perpiniana (personal observations of the authors); the humeropectoral sulcus is also situated behind the entoplastron, whereas it contacts the entoplastron posteromedially in †Ti. bacharidisi (Vlachos et al., 2014:fig. 5b). Furthermore, the entoplastron of Ti. schafferi (based on AMNH 1905 and AMNH 1772) was seemingly pentagonal in outline, with a rounded posterior edge unlike the clearly kite-shaped entoplastron of †Ti. bacharidisi (Vlachos et al., 2014:fig. 5b).

Of the appendicular elements referred to †Titanochelon schafferi, the humerus (AMNH 1878) has asymmetrical distal condyles similar to those of †Ti. bolivari (Pérez-García and Vlachos, 2014: fig. 4e, f); however, it contrasts with the humerus of †Ti. bacharidisi, in which the condyles are of equal length (Vlachos et al., 2014:fig. 3c–e). The femoral diaphysis of the paralelotype NHMW 1911/0005/0275 is also almost straight, unlike the curved femoral shaft in †Ti. bacharidisi (Vlachos et al., 2014:fig. 3c). On the other hand, the fused medial and lateral centralia of AMNH 1887, although unusually broad, resemble those of †Ti. bacharidisi (Vlachos et al., 2014:fig. 6a–e) and are taller and anteroposteriorly shorter than the centralia of †Ti. bolivari (Pérez-García and Vlachos, 2014:fig. 4i–k); the medial and lateral centralia are not fused in †Ti. bolivari, bolivari, except for a single example from the upper Miocene of Cerro del Otero in northeastern Spain (Pérez-García and Vlachos, 2014:fig. 19).

Although Chkhikvadze (2001, 2006, 2007, 2010) assigned the AMNH collection of Ti. schafferi fossils to †Centrochelys natadzei, both Chkhikvadze (1989:fig. 15) and Danilov et al. (2017: fig. 108) illustrated short and wide gular scutes, a medially straight gularhualomeral sulcus, and an elongate flattened epiplastral lip that collectively serve to distinguish the Georgian material from the Ti. schafferi plastral described herein. We also posit that C. natadzei is possibly not referable to †Titanochelon because of its conflicting plastral character states.

In contrast, Pérez-García and Vlachos (2014) discussed indeterminate †Titanochelon specimens from upper Miocene (MN11) strata at Kayadibi in the Konya Province of central Anatolia, Turkey (see Pérez-García and Vlachos, 2014). These fossils were originally identified as †Cheirogaster cf. bolivari by Staesche et al. (2007) but share the absence of a gular scute extension onto the entoplastron and positioning of the humeropectoral sulcus behind the entoplastron with both the AMNH 1905 and AMNH 1772 examples of Ti. schafferi. Nevertheless, the Kayadibi remains exhibit a narrower entoplastron profile and more elongate epiplastral lip differences that could be intraspecifically variable based on comparisons with †Ti. bolivari (Pérez-García and Vlachos, 2014).

The maximum carapace length of around 1.85 m proposed for Ti. schafferi by Lapparent de Broin (2002) was calculated from the lectotype cranium (NHMW 2009b0103/0001) and the paralelotype femur (NHMW 1911/0005/0275). Although the additional appendicular elements that we herein describe from NHMW and MGL are consistent with such proportions, the plastral fragments suggest much smaller individuals, likely not exceeding 1 m in maximum carapace length. This apparent variation in dimensions might be due to either ontogeny and/or sexual dimorphism. Indeed, Vlachos et al. (2014) recorded similarly contrasting male and female plastral lengths in individuals of †Ti. bacharidisi, but these exhibited an almost 20% difference in the length of their limb bones.

**Taxonomic Implications**

The giant tortoise fossils from Samos were historically assigned to the extant genera Testudo and Geocheleon (see Auffenberg, 1974, for summary), although these are now taxonomically restricted based on analyses of both DNA (e.g., Le et al., 2006; Fritz and Bininda-Emonds, 2007; Guillou et al., 2012; Pereira et al., 2017) and fossil (Vlachos, 2018; Vlachos and Rabi, 2018) evidence. The extinct genus †Cheirogaster has also been widely applied to European giant tortoises, including the Samos material (de Bron, 1977; Lapparent de Broin, 2001, 2002); however, Pérez-García and Vlachos (2014) argued that this name should be limited to the type species, †Cheirogaster maurini Bergougnoux, 1935, from the uppermost Eocene (Priaobian) of France. †Titanochelon has thus been established to encompass all of the Neogene and Pleistocene remains that are phylogenetically placed within the ‘Geocheleon complex,’ or as a derived lineage within Geocheolina (sensu Vlachos and Rabi, 2018). Currently, only two named Greek species of †Titanochelon are considered valid—†Titanochelon bacharidisi (Vlachos et al., 2014) and †Titanochelon schafferi, the latter being formally transferred to the genus †Titanochelon herein. Georgalis and Kear (2013), Vlachos (2015), and Vlachos and Tsoukalas (2016) also reviewed other indeterminate †Titanochelon-like remains found elsewhere in Greece.

**DISCUSSION**

**Phylogenetic Implications of the Samos Testudinids**

We assessed the phylogenetic relationships of the Mytilini Formation tortoise fossils from Samos using a total-evidence data set (Supplemental Data 1) integrating morphological scores from Vlachos and Rabi (2018) and DNA sequence information from Guillou et al. (2012). We first deleted some of the more distant outgroups from the matrix, together with several incompletely scored ingroup testudinids that are known to create topological uncertainty (see Vlachos and Rabi, 2018, for discussion). Finally, we changed a number of scores for some ambiguous characters (see Appendix 1).

We conducted a parsimony analysis using TNT (Goloboff et al., 2008), with bootstrap and Jackknife supports (GC [group present/contradicted]; Goloboff et al., 2003) calculated using the Resampling command. Bremer supports were compiled with the bremer.run script. We also computed a reduced consensus tree using the IterPCR script from Pol and Escapa (2009).

Our initial tree bisection reconnection (TBR) yielded 100 most parsimonious trees (MPTs) of 12,441 steps (best score hit 724 times out of 1,000), whereas the final TBR round with trees from RAM failed to add any new trees (consistency index = 0.32; retention index = 0.572). The strict consensus tree (Fig. 9A) unanonymously placed †Titanochelon schafferi within the †Titanochelon genus-level clade based on the shared presence of a ‘V’-shaped basiphenoid, together with anterior and posterior buttsonts contacting the costals, a lack of contact between the inguinal and femoral scutes, and a reduced anal notch (see Supplemental Data 2 for a full list of synapomorphies). Nevertheless, like Vlachos and Rabi (2018), the species-level relationships within †Titanochelon remained unresolved, with a polytomy driven by conflicting characters and missing data (Fig. 9B and Supplemental Data 3). The topologically disruptive character states occurred primarily within the cranium and the plastron and include (character numbers follow those listed in the nexus file) the form of the labial ridge at the premaxillary contact (24), relative extent of the squamosals (54), shape of the crista supraocipitalis (56), contact between the gular scutes (122), and relative overlap of the humeropectoral sulcus onto the entoplastron (126). Notably, plastral characters are especially pertinent for differentiating the various species of †Titanochelon. Missing entries for several key characters were also identified by our iterPCR and are potentially important for resolving the †Titanochelon polytomy: 15, 26, 40, 44, 52 (cranium); 82, 104,
FIGURE 9. Total-evidence phylogenetic analysis of tortoise taxa from the upper Miocene of Samos. A, strict consensus of 100 most parsimonious trees. Bremer support and Bootstrap/Jackknife GC frequencies are indicated at each node. Arrows indicate the alternative recovery positions of the small testudinid taxon from Samos. B, †Titanochelon species-level polytomy driven by conflicting character states in the cranium and the plastron.
Recent studies have treated them as conspecific within the middle Miocene †Paleotestudo canetotiana were both retained within an unresolved Pan-Testudo radiation; although retained as separate taxa herein (sensu Vlachos and Rabi, 2018), other recent studies have treated them as conspecifics under Paleotestudo antiqua (see Pérez-García, 2016).

The early Eocene stem testudinid †Fontainechelon cassouleti (Claude and Tong, 2004) from France was placed as sister to the North American †Hadramus corsoni Leidy, 1871, and nestled amongst a more inclusive clade comprising the North American †Oligophoros latunicus (Cope, 1873) and the middle Eocene European †Pelorochelon soriana Pérez-García et al., 2016, and †Testudo eocaenica Hummel, 1935. †Testudo sharunensis Yeh, 1965, from the late Eocene of Asia, was positioned outside of the Testudinidae clade, suggesting that although constrained as a monophyletic lineage, the precise interrelationships and taxonomy of stem testudinids still remains uncertain.

The small testudinid taxon from Samos displays a unique score set relative to both †Testudo antiqua and †Paleotestudo canetotiana (see Appendix 1). Our inclusion of the Samos material (first round of TBR producing 132 trees with best score hit 519 times out of 1,000; second round yielding 160 trees of 12,444 steps) accordingly returned multiple possible placements within Testudonida: (1) as a basally branching relative of the Indotestudo + Testudo clade; (2) as the basal-most member of the Indotestudo species radiation; (3) as an immediate sister to Indotestudo kaiseni (Gilmore, 1931); or (4) as the most basal taxon in the clade leading to the extant Testudo (gray dashed lines in Fig. 9). Curiously, all of these hypotheses were driven by the same single character state—the development of elongate pectoral scutes. Experimentation with artificially scoring the hypaploplastral hinge as present (a change of ‘?’ to ‘2’; which yielded a first round of TBR with 159 trees, best score hit 539 times out of 1,000, and a second round of 160 trees of 12,445 steps) had no effect on these results. Another experimental analysis rescoring the contact between costal 7 and suprapygal 1 as enclosing costal 8 (treated as present in the Samos testudinid and ambiguous in †Te. antiqua) likewise produced identical results (first round of TBR with 160 trees, best score hit 521 times out of 1,000, and a second round of 160 trees of 12,445 steps). Consequently, we conclude that whereas the Samos taxon may eventually prove to be more basally positioned than both †Testudo’ antiqua and †Paleotestudo canetotiana, we refrain from overinterpretation herein until more informative fossils come to light.

Implications for Late Neogene Tortoise Mediterranean Biogeography

Although extremely rare in comparison with coeval mammal remains (e.g., Koufos, 2009), the Mytilinii formation testudinid fossils found on Samos contribute a potentially important biogeographic correlation linking late Miocene terrestrial vertebrate communities across the Greco-Iranian faunal province. Indeed, large-bodied tortoises are especially dispersive, because unlike terrestrial mammals that typically require continental connectivity for migration, they can readily transit across substantial bodies of water by Boating (Gerlach et al., 2006). On the other hand, small-bodied testudinids tend to utilize land bridges but can still distribute across considerable geographic areas over sufficient periods of time. As an example, extant species such as Testudo graeca are estimated to have achieved a circum-Mediterranean distribution in only a few million years after their initial radiation during the Pliocene–Pleistocene (Fritz et al., 2009).

Given these considerations, the late Miocene testudinids from Samos may support arguments for a regionalized ‘Eastern Block’ ‘Pikermian’ vertebrate fauna (sensu Kostopoulos, 2009a), which integrated assemblages from the southern Balkans (e.g., Pikermi in southeastern Greece), together with those from the eastern Aegean, including Samos, and Asia Minor. Of particular note are the demonstrably different small-bodied tortoises from Samos, which appear to have represented a unique basal testudonan lineage (but with similar anatomy to other basally branching small testudinids, such as †Testudo’ antiqua) taxonomically distinct from †Testudo marmorum and Te. graeca, both found on mainland Greece (Georgalis and Kear, 2013; Vlachos, 2015, and references therein).

Likewise, plastral remains attributed to the gigantic geochelonian †Titanochelon schafferi resemble specimens recovered in Anatolia (see Pérez-García and Vlachos, 2014), and the lectotype (NHMW 2009/0103/0001) can be morphologically contrasted with that of †Titanochelon bachardiisi, which is the species most frequently excavated from deposits in northern Greece (Vlachos, 2015, and references therein). Although admittedly inconclusive, these observations support the hypothesis that some degree of biogeographic segregation was evident between the Samos tortoises and their Balkan counterparts during the late Miocene. Future discoveries should therefore add to this emerging evidence for faunal provinciality and contribute to unraveling the broader patterns of late Neogene biogeography in the eastern Mediterranean.

CONCLUSIONS

The eastern Aegean island of Samos is famous for late Miocene vertebrate fossils that span the late MN11–early MN13 interval. Although rare, tortoise remains are some of the most spectacular and have been recorded for nearly 130 years, with collections today distributed throughout museums and other research institutions across Greece (AMPG, GNHM), Austria (NHMW), Switzerland (MGL), and the U.S.A. (AMNH).

Here, we describe examples of at least two distinct testudinid taxa: a small-bodied basal testudonan that is morphologically similar to specimens previously documented from the eastern Aegean island of Chios (Paraskevaidis, 1955), as well as the basally branching †Testudo antiqua, which is otherwise distributed throughout Germany and Spain (Corsini et al., 2014; Pérez-García, 2017), and the colossal †Titanochelon schafferi, which represents a widely dispersed lineage of European gigantic geochelonians incorporating some of the world’s largest tortoise fossils documented to date (Lapparent de Broin, 2002; Georgalis and Kear, 2013; Pérez-García and Vlachos, 2014).

The distinctive late Miocene tortoise assemblage from Samos reveals important taxonomic distinctions relative to coeval equivalents from mainland Greece. In particular, the crown-Testudo species †Testudo marmorum (previously identified from Samos by Solounias, 1981) and †Titanochelon bachardiisi from the Pliocene of northern Greece (see Vlachos et al., 2014) manifest contrasting character states that infer faunal segregation. Indeed, the identification of giant tortoise plastral fragments from Anatolia (Pérez-García and Vlachos, 2014) that resemble those attributed to †Titanochelon schafferi herein hints at potential biogeographic links with Asia Minor and supports proposals for a discrete ‘Pikermian’ terrestrial vertebrate bioprovince (Kostopoulos, 2009a) that was differentiated from that found in the southern Balkans during the late Miocene. Relatively large-sized †Titanochelon material from the late Miocene (MN12) of northern Greece exists (Vathyllakos locality); however, this is represented exclusively by fragmentary postcranal material (an osteoderm and a pelvis; Arambourg and Piveteau, 1929:pl. 1) and cannot thus afford any reliable comparison with the almost coeval †Titanochelon schafferi.
ACKNOWLEDGMENTS

We thank C. Mehling (AMNH), G. Theodorou, G. Lyras (AMPG), E. Vardala-Theodorou (GNHM), M. Harzhauser, U. Göhlich, and R. Gemel (NHHW), R. Marchant (MGL), and M. Moser ( Bayerische Staatssammlung für Paläontologie und Geologie, Munich) for access to specimens and information. Photographs were also generously provided by U. Göhlich (NHHW) and R. Marchant (MGL). We are deeply appreciative to G. Bever, I. Danilov, and I. Claude for their valuable comments on the manuscript. The Willi Hennig Society sponsors the use of TNT software. A.P. acknowledges funding from the Spanish Ministerio de Ciencia, Innovación y Universidades (IJCI-2016-30427).

LITERATURE CITED


Submitted April 25, 2019; revisions received September 16, 2019; accepted October 13, 2019.

Handling editor: Gabriel Bever.


*Testudo castrensis*—Removed, based on Pérez-García et al. (2016), which showed that the reconstruction of de Broin (1977) contains anatomical information that cannot be seen in the type specimen.

*Paleotestudo canetotiana*—Based on Pérez-García (2017) and personal observations.

Modified scorings: 88 (2 → 0, 1, 2); 99 (1 → 0, 1); 104 (1, 2); 110 (1). New scorings: 132 (1); 133 (1); 134 (1); 135 (1)

*†Testudo antiqua*—Based on Corsini et al. (2014).

Modified scorings: 99 (0 → 1); 102 (0 → 1); 121 (1 → 1, 2); 124 (0 → 0, 1)

*†Pelorochelon soriana*—Based on Pérez-García et al. (2017) and personal observations. Here the intraspecific variation is taken into account.

Modified scorings: 78 (0 → 1); 82 (0 → 1); 86 (2 → 0, 2); 111 (0 → 2); 119 (0 → 0, 1); 123 (0 → 0, 1); 136 (1 → 0, 1)

*Testudo eocaenica*—Based on Hummel (1935). The scorings are based only on the first specimen figured by Hummel (1935):
fig. 3), pending revisions of the other specimens that will allow a full account of the intraspecific variability.

Modified scorings: 80 (1 → 0); 118 (0 → 1); 126 (2 → 1, 2)
New scorings: 121 (0)

Scoring of the small testudinid from Samos:

???????????????????????????????????????????????????????-

???????????????????????????????????????????????????????????????????????????????????????-

???????????????????????????????????????????????????????????????????????????????????????-

??????