ABSTRACT—In this paper, we describe a new species of a giant tortoise, Cheirogaster barcharidisi, sp. nov., from the Pliocene (Gonia Formation) of western Chalkidiki Peninsula, near Thessaloniki, Greece. The specimens constitute the most complete giant tortoise found to date in Greece, and provide materials for direct comparison with other described European forms. We assign it to the genus Cheirogaster, as opposed to Centrochelys, based upon the convex dorsal surface of the epipædial. Direct comparison with material from Europe shows that it differs from other giant tortoises attributed to Cheirogaster mainly in cranial and plastral morphology. Exceptional postcranial preservation allows the description of many skeletal elements, previously unknown or poorly described for Cheirogaster, as well as for a reappraisal of the previously published specimens from Greece.

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

INTRODUCTION

Until the end of the Pleistocene, giant tortoises were found on all continents except Australia and Antarctica (Auffenberg, 1974; Caccone et al., 1999). European fossil giant tortoises are known from many sites, occurring in Spain, France, Germany, Bulgaria, European Turkey, Switzerland, Greece, and few Mediterranean islands, ranging from the late Eocene of France to the early Pleistocene of Greece, Malta, and the Balearics (Lapparent de Broin, 2001, 2002). Our current understanding of the taxonomy and systematics of these fossil giant tortoises is rather poor, and most of them are now attributed to Cheirogaster, a genus erected by Bergouinioux (1935) for the late Eocene form Cheirogaster maiorini from France. The monophyly of this group has not been examined using modern phylogenetic approaches, and it is likely a polyphyletic group.

In Greece, giant tortoises have been known since the late 1920s, when Arambourg and Pivotet (1929) described several specimens collected from various sites in Axios Valley and Cape Megalo Emvolon, in northern Greece. These included a cranium and limb bones attributed to Testudo sp. (of giant size), which were later referred to Cheirogaster sp. (Lapparent de Broin, 2002). Later, Bachmayer et al. (1979) reported another unnamed giant tortoise from Megalo Emvolon. Apart from these specimens from the Thessaloniki area, other giant tortoises are known from the island of Samos (cf. Cheirogaster schafferi; Szalai, 1931), from Pikermi (cf. Cheirogaster cf. Ch. schafferi, late Miocene; Bachmayer, 1967), and Lesvos Island (cf. Cheirogaster aff. Ch. schafferi, early Pleistocene; Lapparent de Broin, 2002).

Recently, giant tortoises have been collected from three new localities (Epanomi, Nea Kallikratia, and Nea Michaniona) in the coastal area of the western Chalkidiki peninsula, near Thessaloniki (Fig. 1A). The Epanomi site is the most important of all, yielding two individuals (Fig. 1B) with good preservation. Two additional specimens from Nea Kallikratia and Nea Michaniona have also been collected. Finally, another giant tortoise has been collected from a site called Aggelochori (Fig. 1A), but it is not included in this study (G. Lazarides, pers. comm., 2010). To provide a basis for future studies of the relationships between the giant Greek tortoises and other related species, we herein describe the recently collected material from Thessaloniki and compare it with several relevant forms.

Institutional Abbreviations—AMPG, Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, Athens, Greece; BSPG, Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany; IPS, Institut Català de Paleontologia, Barcelona, Spain; LGPUT, Laboratory of Geology and Paleontology, University of Thessaloniki, Thessaloniki, Greece; MCNUS, Museum of Salamanca, Salamanca, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMW, Naturhistorisches Museum, Vienna, Austria; NWS, Naturmuseum Winterthur, Winterthur, Switzerland; PIMUZ, Paläontologische Institut und Museum, Universität Zürich, Zurich, Switzerland; SLQ, Salonsichecctions of Muséum National d'Histoire Naturelle, Paris, France; VM, Vriss Museum of Natural History, Lesvos, Greece.

Land Mammal Age Abbreviation—MN, European Mammal Neogene biozones.

GEOLOGIC SETTING

Western Chalkidiki Peninsula is composed of Neogene/Quaternary sediments (Fig. 2A) that were divided into six formations by Syrides (1990): Antonios Formation (middle–late Miocene), Triglia Formation (Vallesian–early Turolian, late Miocene), Trilophos Formation (latest Miocene = Pontian), Gonia Formation (early–middle Pleistocene), Moudania Formation (late Pleistocene–early Holocene), and Eleochoria Formation (late Pleistocene–Holocene) (Fig. 2B). Up to present, all of the giant tortoises have been found in the Gonia Formation, which is exposed on almost all the coastal slopes between Megalo Emvolon and Epanomi. This formation is complex in...
structure, with sands, clays, marls, sandstones, gravels in alternating lens-shaped beds, and massive marly limestones. Thus, as shown in Figure 2B, the Formation is divided into three members: the Silata, Rhodokipos, and Kallikratia members (Syrídes, 1990; Vassílieádou et al., 2003). The main characteristic of this formation is the presence of volcanic pebbles, which probably originated from the Almopia volcanoes (Syrídes, 1990). Samples of these pebbles were also collected from the fossil locality Epanomi, providing strong evidence that these deposits belong to the Gonia Formation. This is also confirmed by the sedimentologic context of the site (alternating sands, marls, and sandstones; see Fig. 2C), which is similar to the complex structure of this formation.

Fossil mammal remains are known from these deposits, allowing biostratigraphic inference of the geologic age of the Gonia Formation. Briefly, the presence of Dolichopithecus ruscínensis at Megalo Emvolon suggests a middle Pliocene (Ruscinian, MN15) age for this section (Koufos et al., 1991). South of Epanomi Village, materials of Mammuthus cf. meridionalis and Equus sp. suggest a latest Pliocene (MN16) age for this part of the formation (Athanassiou and Kostopoulos, 2010). Finally, analysis of the mammalian microfauna from the Nea Silata locality dates the lower part of the Gonia Formation to the Miocene/Pliocene boundary (MN13/14) (Vassílieádou et al., 2003). So far, the few fossil mammal localities clearly indicate that the Gonia Formation spans the entire Pliocene, because fossil tortoises are found throughout the entire formation. Further stratigraphical studies are required to provide a more accurate estimation of the geologic age of the different individual tortoises of the Thessaloniki area.

MATERIALS AND METHODS

In the text, for each different individual collected in the sites from Epanomi, Nea Kallikratia, and Nea Michaniona, we use an alias referring to the site by abbreviation and number of individual (e.g., individual EPN I). All the skeletal elements per individual have their own specimen number (e.g., cranium LGPUT EPN 102). Isolated elements are numbered from 1 to 99, EPN I skeletal elements from 100 to 199, EPN II from 200 to 287, MIC I from 300 to 303, and KLK I from 500 to 528. In the Supplemental Data, we provide a detailed inventory of the studied material, additional tables of measurements of the described elements with their graphical explanation, and a map with table summarizing the main Neogene localities of giant tortoises. We also provide additional photographic documentation of the studied and comparative materials. The detailed skeletal element representation per tortoise individual and site is given in Table 1. The description is based on the combined morphology of all the recovered individuals; in cases where some intraspecific differences are noted, we specify the skeletal element of the given individual.

We follow the systematics and taxonomy of Dubois and Bour (2010, and references therein). Cranial nomenclature follows Gaffney (1972). For the description of the cranium, we used...
several characters discussed in Joyce and Bell (2004). Shell nomenclature follows Zangerl (1969). Carpal and tarsal nomenclature follows Crumly (1984). For the purposes of this study, the new material was directly compared with that from other Greek localities such as Samos (NHMW), Thessaloniki (MNHN), Pikeremi (AMPG), as well as materials from France (MNHN), Germany (BSPG), and Switzerland (PIMUZ and NWS) (Table S1 in Supplemental Data). Comparisons based on the literature were made for giant tortoise material from Spain (Royo y Gómez, 1935), Cheirogaster maurini from France (Bergounioux, 1935), Lesvos material from Greece (Lapparent de Broin, 2002), and Tenevo material from Bulgaria (Stojanov, 2009).

SYSTEMATIC PALEONTOLOGY

Order CHELONII Latreille, 1800
Infraorder CRYPTODIRA Cope, 1868
Family TESTUDINIDAE Batsch, 1788
CHEIROGASTER Bergounioux, 1935
CHEIROGASTER BACHARIDISI, sp. nov.
(Figs. 3–7)

Holotype—EPN I, LGPUT EPN 100–199, female individual (Figs. 3, 4).

Referred Material—EPN II, LGPUT EPN 200–287, male individual (Figs. 5, 6); EPN 99 (Fig. 7A–C); KLK I, LGPUT KLK 501–528 (Fig. 7D–G); MIC I, LGPUT MIC 300–303.

Etymology—Named after Mr. Nikolaos Bacharidis, who discovered and excavated EPN I.

Locality and Age—Epanomi, western Chalkidiki Peninsula, Thessaloniki area, Greece: (x, y): (405485, 4474669) m, GPS datum EGSA ‘87, Hellenic Grid (Fig. 1B); Gonia Formation; Pliocene.

Diagnosis—A member of Cheirogaster (sensu de Broin, 1977) on the basis of the convex dorsal epiplastral lip. New species of Cheirogaster on the basis of the following combination of characters: fossa orbitalis in midway between the apertura narium externa and the posterior tip of the squamosal; elements of the zygomatic arch thick and short; squamosal processes converging posteriorly towards the midline; extended ventral emargination; posterior rim of carapace without indentations in supracaudal–11th marginal sulcus; rounded anterior lobe without gular projection anteriorly; short gulars contacting the anterior part of the entoplastron; entoplastron covered medially only by humeral scutes, and its posterior border coinciding with the humeropectoral sulcus; obtuse and reduced xiphiplastral notch. Differs from cf. Cheirogaster schafferi (Szalai, 1931) in the more...
posteriorly placed orbits, squamosals not parallel, and the more pronounced reduction of cheek area. Differs from ‘*Cheirogaster bolivari*’ (Hernández-Pacheco, 1917) from Alcala de Henares (carapace, figured in Royo y Gómez, 1935) in lacking an indented posterior carapace in the supracaudal–11th marginal sulcus. Differs from the Palencia specimen (figured in Royo y Gómez, 1935) in the presence of an anal notch, shorter anal s, and gulars not covering the anterior region of the entoplastron. Differs from *Cheirogaster perpiniana* (Depéret, 1885) in the more pronounced reduction of cheek area, posterior carapace lacking indentation on each side of the pygal, plastron with shorter epiplastral lip, humerals not covering posterior part of epiplastra medially, more developed anal notch, and squamosals not parallel. Differs from *Cheirogaster maurini* Bergounioux, 1935, among other characters not preserved in the new species, in that the gulars do not cover the anterior part of the entoplastron, larger entoplastron, shorter humerals, and much shorter pectorals.

### DESCRIPTION

#### Skull and Mandible

The skull is preserved only in EPN I (Fig. 3A, B), together with some parts of the mandible, which were found alongside the anterior region of the plastron. It is 210 mm in length. The dorsal region of skull is nearly complete, and lacks only the anterior-most region and a part of the right prootic-opisthotic. Much of the anterior palate is missing. The EPN I skull is slightly deformed in the areas of the left zygomatic arch and the condylus occipitalis. The sutures between the cranial bones are fused, indicating an adult individual. Anteriorly, where the sutures are visible, the maxillae are medially separated by the premaxillae (Fig. 3F, G). The fossa orbitalis is located approximately midway between the apertura narium externa and the midpoint of a line connecting the posterior tips of the squamosals. The prefrontals are wide, followed by narrower frontals. The well-developed processus trocholearis oticum is preserved only on the left side. The squamosals converge posteriorly towards the midline (Fig. 3A). The cristisupraoccipitalis is long and arched, covering the condylus occipitalis (Fig. 3C). The upper temporal emargination is extensive, with a large quadratojugal and no jugal contribution. The lower temporal emargination is also extensive, due to ventral reduction of the quadratojugal (Fig. 3C). Although the sutures between the bones are not visible, we are able to describe the upper and lower temporal emargination of the cranium. The upper temporal emargination is extensive, with a large quadratojugal and no jugal contribution. The lower temporal emargination is also extensive, due to ventral reduction of the quadratojugal (Fig. 3C). This is also observed on the left side. To our knowledge, this morphology has not been observed in any other cranium of *Cheirogaster* s. l., or any other tortoise. Normally, the quadratojugal develops a ventral process along the anterior rim of the cavum tympanii, which in some species even reaches the quadrate (see character 11 in Joyce and Bell, 2004). In *Cheirogaster bacharidisi*, this extended ventrolateral reduction of the bones in this area is an autopomorphy. Moreover, both sides exhibit no contact between the jugal and the pterygoid. The palate is incomplete anteriorly, but the large right foramen palatinum posteriori can be observed (Fig. 3B). Pterygoids are incompletely preserved. The condylus occipitalis is rounded, and the foramen magnum is dorsoventrally expanded. Additional photographs of the cranium are given in Figure S1 in the Supplemental Data.
FIGURE 3. *Cheirogaster bacharidisi*, sp. nov., EPN I, holotype, Pliocene. Cranium (LGPUT EPN 102) in A, dorsal, B, ventral, C, left lateral, and D, right lateral views. E, right squamosal, detail. F, anterior view. G, anterior-most part, drawing. **Abbreviations**: fpp, foramen palatinum posterius; ju, jugal; md, mandible; mx, maxilla; pm, premaxilla; po, postorbital; qj, quadratojugal; qu, quadrate; sq, squamosal. Both scale bars equal 50 mm.
Carapace
Carapacial elements are scarce among the Thessaloniki material. Only parts of the peripherals are preserved in the holotype (Fig. 4A, B), and the posterior part in EPN II (Fig. 5C–E). Additional indeterminable carapace fragments are preserved in KLK I. The carapace was probably low, as estimated by the preserved peripherals and the height of the scapula. In EPN II, the posterior carapace rim is continuous, without indentations in the supracaudal–11th marginal sulcus. The paired suprapygal plates are trapezoid in outline: the first is larger and embraces the second, which is lenticular in shape. The pygal plate is strongly convex and trapezoid in shape, with posteriorly converging lateral borders. The second suprapygal is overlapped by the vertebral-supracaudal sulcus (Fig. 5C–E). Thus, it preserves the ‘Geoche-lone’ type configuration (after Lapparent de Brion et al., 2006a), which can be hypothesized for the genus Cheirogaster. The 12th marginals are fused, both dorsally and ventrally.

Plastron
Both individuals from Epanomi (holotype and EPN II) preserve most of the plastron. Additional indeterminable plastral fragments are preserved in the individual KLK I. The holotype preserves a nearly complete plastron and only the anterior-most part of the epiplastron is missing. Because of the mounting strategy, only the visceral view is available for observation (Fig. 4A, B). Most of the postcranial skeleton is preserved on the visceral surface of the plastron, providing evidence for rapid burial of the individual. EPN II also preserves most of the plastron. It was found very close to the shoreline, and part of the specimen has been destroyed by exposure to seawater. EPN II is missing only the left anterior region and the ventral side is available for observation (Fig. 5A, B). The postcranial elements were disarticulated on the visceral surface of the plastron, indicating that some time had passed between death and final burial.

The holotype has short anterior and posterior lobes relative to the total length of the plastron (ca. 30 cm each). In contrast, the lobes of EPN II are longer (ca. 40 cm each). The holotype plastron has an approximate length of 115 cm, and that of EPN II is similar in length (112 cm). Dorsally, an epiplastral lip and deep excavation, characteristic of most terrestrial tortoises, is noted on the dorsovisceral surface of the anterior part of the lobe. The excavation forms either a weak gular pocket (holotype) or a step-like morphology (EPN II). The dorsal surface of the lip is slightly convex. The entoplastron is relatively small in visceral view (holotype). Ventrally, it is larger in size and width than long, with angular posterior borders. The hypo- and hypoplastra are long and wide, representing most of the surface of the plastron. The xiphiplastra are short and limited to the posterior part of the plastron, with angular posterior borders. The hyo- and hypoplastra are rather flat, almost of the same length (measured at midline) and width (measured across the hypo-hypoplastral suture), and has thin xiphiplastral extremities. These three characters, which were noted by Bourgat and Bour (1983) for the female Ch. perpiniana, allow us to infer that EPN I is a female individual. In EPN II, the plastron is rather longer than wide, shows a ventral depression in the posterior part, and preserves thick xiphiplastral extremities. All the above, as well as the incomplete ossification of bony sutures, indicate a subadult male individual.

The plastral formula (measured across the midline) is: hypoplastra ≈ epiplastra > xiphiplastra > entoplastron. Abdorminals > femorals > humerals > gulars > anals.

Vertebral Column
The few vertebral elements that are preserved are in EPN I. Only two cervical vertebrae are preserved in situ: the first one is below the crista supraoccipitalis of the cranium, whereas the second is below the right scapula. The caudal column is represented by 12 caudal vertebrae, each of which exhibits a simple procoelous morphology, with an anteriorly concave and posteriorly convex body, and a long dorsal arch with well-preserved anterior and posterior zygapophyses (Fig. 4R). Transverse processes decrease in length towards the end of the tail. The total length of the centrum varies from 10 to 30 mm.

Shoulder Girdle
Elements of the shoulder girdle are preserved in the holotype (with the left one in anatomical position) and in EPN II (disarticulated and fragmented). The scapulocoracoid preserves the triradiate shape that is typical of turtles (Fig. 5F). The scapula is situated vertically, preserving a long acromion process anteromedially, at an angle of 130°. The coracoid is short, with a narrow neck and expanded, fan-shaped end (Fig. 5G). The angle between the scapula and the coracoid is the same (130°), whereas the angle between the acromion and the coracoid is rather low (60°). Both the scapula and the coracoid are connected in a broad symphyseal area, forming an elongated, rounded glenoid cavity.

Pelvic Girdle
Elements of the pelvic girdle are preserved mainly in the holotype and in KLK I, whereas in EPN II only a few fragments were recovered. Most of the puboischiatic plate is preserved, together with the distal part of the right ilium (Fig. 4Q). These three elements contribute equally to form a deep spherical acetabulum. In EPN I, the end of a rounded pectineal process is preserved in situ.

Forelimb
Left and right humeri are both complete in the holotype, reaching 308 mm in length (Fig. 4C). In EPN II, the right humerus preserves the distal portion, whereas the left one preserves only the diaphysis. In KLK I, only the proximal part of the left humerus is preserved, showing the morphology of the trochanters. In the proximal region, the trochanters are well developed and almost parallel to the diaphysis. The latter has a considerable degree of curvature along its length, and is elliptical in cross-section. The humeral head is elliptical to rounded, with a weak neck. The ulnar and radial condyles form a wide trochlea. Dorsally, a strong, elongated eecyclindrical groove is present (Fig. 4C–E). The radius is preserved in both the holotype and in EPN II; in the
former, both left and right radii are preserved with associated carpal elements, whereas in the latter only the right radius is intact (Fig. 5H–J), with the left preserving only the diaphysis. The radius is straight, with a narrow diaphysis and broad epiphyses. The proximal end articulates with the entire width of the distal part of the humerus along an elongated surface, which is composed of two concave surfaces. The distal part has only a deep, elongate, and concave articular surface for the fused medial and lateral centrale. The ulna is preserved completely only in EPN II (Fig. 5K–M); in the holotype, only a fragment of the left ulna was recovered. The ulna has broad proximal and narrow distal parts, and the external face is curved in dorsal view. The proximal articular surface for the humerus is concave. The distal articular surface is convex with short transverse diameter. The lateral part of the bone has a triangular cross-section. The radius and the ulna articulate at two points: proximally with an almost triangular articulation surface, and distally with an elongated, narrow surface. The teardrop-shaped notch between them is longer than wide. Most carpal and tarsal elements are well preserved either in associations (EPN I; Fig. 4H) or isolated (EPN II). The main carpal element is the fused medial and lateral centrale, preserving the suture (Fig. 6A–E). The medial centrale articulates with the radius, whereas the lateral articulates with the intermediate. The intermediate articulates with both medial and lateral centrale, proximal to the suture (Fig. 6F). The intermediate also articulates with the distal parts of the radius and the ulna, and is triangular in cross-section. The intermediate has expanded articular surfaces both proximally and distally (Fig. 6G–J). The ulnare and the pisiform are not preserved. The second carpal row comprises five distinct distal carpals. Each one is composed of two main parts: a thick disc distally that is articulated with the metacarpals with a convex surface and a ventroproximal tubercle (Figs. 4M, N, 6P–Q). These two parts form a concave distal articular surface for the first row of carpals. There are five metacarpals, each exhibiting simple discoid morphology with convex proximal and distal articular surfaces (Fig. 6R, S). Each one is articulated with the first phalanx, which has a broad and concave proximal surface and a convex distal surface for the unguals (Fig. 6T, U). Anterior unguals are shorter, broader, and nearly straight in comparison with posterior unguals (Fig. 6V). All the carpal elements are close to astragalocalcaneum contact and articulates with the 5th proximal phalanx (Fig. 4I–L). Each proximal phalanx exhibits an elliptical concave proximal articular surface and a well-developed distal epiphysis bears convex articular surface for the astragalus. Parts of the fibula are preserved in the holotype, EPN II, and KLK I. The fibula is thin and elongate, with a small proximal part and a wider distal part. The distal epiphysis bears convex articular surface for the astragaloalcaneum, and articulates with the symphysial area. The fused astragaloalcaneum is preserved in the holotype (right side, in association with tarsal elements). EPN II (right, complete), and KLK I. This element preserves the suture (Fig. 6K–O). The astragalus forms the majority of the fused element, whereas the calcaneum is small. The ventral surface of the astragaloalcaneum is convex for the articulation of the distal tarsals. Well-preserved additional tarsal elements are found in the holotype and EPN II. Each distal tarsal exhibits a thin discoid shape, with a concave proximal and a convex distal surface. The metatarsals are wide proximally, with a concave articular surface and a convex distal end that exhibits a small concavity for articulation with the proximal phalanx (Fig. 4I–L). Each proximal phalanx exhibits an elliptical concave proximal articular surface and a well-developed convex distal surface for the ungual. Both the metatarsals and the proximal phalanges are asymmetrical with respect to the long axis of the element. Unguals exhibit a wide proximal articulation for the first phalanx and a pointed distal end.

In KLK I, almost all of the right hind limb bones are preserved in anatomical position, enabling a detailed description (Fig. 7F, G). Lacking are the caput femori, one distal tarsal (probably the 3rd), the 5th metatarsal along with the possible associated 5th phalanx, a claw (probably the 3rd), as well as the tips of the remaining unguals of the pes. The first four digits are preserved in parallel rows to each other, with the 5th (normally much reduced) separated from the rest. The 4th distal tarsal is positioned close to astragaloalcaneum contact and articulates with the 5th distal tarsal. There is a small overlap between the metatarsals. The large number of bony osteoderms is striking, and the pes appears to have been covered by them. The largest numbers of osteoderms are found on the posterior thigh, i.e., as crural bones. Immediately behind the femur, an enlarged, pointed bony structure is found, accompanied by a single more rounded osteoderm. These appear to be two bony crural spurs, similar to those found in the African spurred tortoise, Centrochelys sulcata Miller, 1779, and other terrestrial Testudinidae, such as Testudo graeca s.s. Additional medium-sized, rounded osteoderms have been found near the tubercles, as well as much smaller ones in the vicinity of the main bony tubercle.

Similar crural bones have been also preserved in EPN I. There is one isolated enlarged pointed tubercle, identical to the main tubercle of the KLK specimen (Fig. 4O, P), preserved with closely

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**Figure 4.** Chelodina brushed sp., sp. nov., EPN I, holotype, Pliocene. **A, B**, plastron (LGPUT EPN 101). **A**, plastron in situ cranium and postcranial bones in dorsal view; **B**, illustration of plastron in dorsal view. **C–R**, postcranial bones. Right humerus (LGPUT EPN 103) in **C**, posterior, **D**, ventral, and **E**, dorsal views. Left femur (LGPUT EPN 107) in **F**, posterior and **G**, ventral views. Right hind limb (LGPUT EPN 108–109) in **H**, dorsal view. Left metatarsal (LGPUT EPN 163) in **I**, dorsal and **J**, lateral views. **K**, left astragalocalcaneum; **L**, anterior views. Left distal carpal (LGPUT EPN 179) in **M**, lateral and **N**, distal views. Thigh vertebra (LGPUT EPN 184) in **O**, dorsal and **P**, ventral views. Pelvis (LGPUT EPN 115) in **Q**, dorsal view. Caudal vertebra (LGPUT EPN 185–193) in **R**, dorsal view. Abbreviations: **an**, anal; **as**+**cal**, astragaloalcaneum; **ect**, ectepicondylar groove; **en**, entoplastron; **ep**, epiplastron; **fe**, femoral; **fi**, fibula; **hymo**, hypostrastria; **hypo**, hypoplastron; **ti**, tibia; **xi**, xiphiplastron. Scale bars equal 200 mm (A, B), 100 mm (C–H), and 50 mm (I–R).
associated rounded osteoderms around it. Several pointed and half-pointed osteoderms have also been found in EPN I and EPN II, as well as few rounded crural osteoderms (Fig. 6W–Y).

DISCUSSION

The genus Cheirogaster s. l. was common in Europe from the Priabonian, with Cheirogaster maurini (Baby, France: type specimen for the genus) possibly originating from a common stem ‘Hadrianus’ ancestor from the Eocene of Laurasia. Work by Lapparent de Broin (2002) suggests that Cheirogaster is represented by at least 11 different species. Claude and Tong (2004) distinguish ‘Cheirogaster’ by a set of testudinid apomorphies, such as fusion of the 12th pair of marginals, epiplastral excavation, and the absence of a cervical scute. As might be expected, absence of clear autapomorphies in the diagnosis has raised questions about taxonomic assignments. In addition, the fragmentary record and many poor descriptions have cast further doubts on many of the published taxonomic assignments and ultimately the monophyly of Cheirogaster. A revision of the type species of Cheirogaster (Ch. maurini) will be required to answer the remaining questions about the taxonomy and phylogeny of the European giant tortoises.

The material from Thessaloniki preserves two out of three characters of the genus Cheirogaster s. l., because they are described in the emended diagnosis given by de Broin (1977). The first character (absence of cervical) is not preserved in any specimen of the Greek material. The remaining characters (Geochelone type configuration in posterior carapace, and epiplastral excavation) are found in the material described herein. The specimens also preserve some other characters, observed mainly in the almost complete Ch. perpiniana, such as convex raised epiplastral lip, a less-extended fusion of the humeral trochanters (Lapparent de Broin and van Dijk, 1999), and a moderate narrowing of the posterior xiphiplastron (Lapparent de Broin, 2003). Most of these character combinations are found in many other tortoises, and therefore are not diagnostic. In addition, the morphology of the humerals and pectorals of Ch. maurini is quite different from the typical configuration found in all Neogene forms attributed to Cheirogaster (very short pectorals with lateral expansions).

Despite the problems described above, there has been some effort toward placing the genus into an evolutionary framework. Specifically, Cheirogaster was hypothesized to be the sister taxon to the extant African genus Centrochelys based on morphological similarities (Lapparent de Broin, 2000, 2002). Lapparent de Broin (2008) describes several common characters between Cheirogaster and Centrochelys: both show a low shell, the absence of a cervical scute, and a similarly curved humerus. Differences between the two genera are found in the nuchal notch (which is always shallow in Centrochelys, but deep in some forms of Cheirogaster), the epiplastral lip (which is generally convex in Cheirogaster, but flat to concave in Centrochelys), the narrowed xiphiplastron in Centrochelys, and a decreased angle between the scapula and acromion in Centrochelys. Several characters identified in this work might suggest a close relationship between Ch. bacharidisi and Centrochelys sulcata, the African spurred tortoise. Centrochelys sulcata is characterized by the presence of two to three long conical tubercles on the posterior side of the thigh (Loveridge and Williams, 1957). Similar tubercles found on the posterior limbs of Ch. bacharidisi (found separated in EPN I, Fig. 4O, P; preserved in situ in KLK, Fig. 7F, G) could support a close relationship between Ch. bacharidisi and Centrochelys (note, however, that as with many tortoise characters, this one is homoplastic within Testudinidae; Lapparent de Broin et al., 2006b). Furthermore, the morphology of the posterior lobe of the plastron in EPN II is very similar to that of C. sulcata (MNHN collection; Lapparent de Broin, 2003:fig. 1a), in exhibiting moderate to strong narrowing and parallel lateral borders in the anal part of the xiphiplastron. Finally, the moderate narrowing of the xiphiplastron in the femoroanal sulcus of Ch. bacharidisi is intermediate between Centrochelys and Ch. perpiniana. Despite these apparent similarities, Ch. bacharidisi is attributed to Cheirogaster on the basis of the dorsally convex epiplastral lip.

Comparisons with Other Cheirogaster

As mentioned above, the fragmentary nature of the European material of Cheirogaster s. l. presents great difficulties with direct comparisons among the various species of the genus. For example, shell elements from the Greek cf. Cheirogaster schaferi are almost unknown, and only the cranium is available for comparison. Material of Cheirogaster from the Neogene of France is composed mainly of shell fragments (except for Cheirogaster perpiniana, which is nearly complete, and the complete shell of ‘Cheirogaster’ gigas [Bravard, 1844] from Bournoncle-Saint-Pierre; both in the MNHN exhibition). Most of the material from Spain was lost during the Spanish Civil War and the comparisons made herein were based mainly on older publications. Comparisons of the Greek material with several purported Cheirogaster forms follow. Photographs of comparative material are provided in Supplemental Data Figures S1–S8.

Comparison with the Late Miocene Samos Specimen—Cheirogaster bacharidisi differs from cf. Ch. schaferi (Szalai, 1931) from Samos (MN12–13; Lapparent de Broin, 2002) mainly in the morphology of the dorsal cranium (NHMW 2009z103/0001). The latter bears a straight cristae supraoccipitalis, high and thin zygomatic elements in a ‘T’-shaped configuration, and nearly parallel squamosals. In this specimen, the lower temporal area is less emarginated, in contrast with the EPN I cranium, where the ventral reduction of cranial bones is extensive. The most notable differences between EPN and Samos are seen in the position of the orbits, which are located more anteriorly, and the width of the posterior tips of squamosals (measurements 5 and 10, respectively, see Fig. S1 and Table S1 for measurements). It should be noted that the Samos cranium is partially restored; because the precise extent of the restoration is not known, the morphological comparisons with this specimen are incomplete. Another difference is seen in the distal femur from Samos (NHMW 1911/0005/0275), which is straight, unlike the curved distal femur of Ch. bacharidisi.

Comparisons with Other Material from Greece (Pikermi, Lesvos, and Thessaloniki)—Differences between Ch. bacharidisi and the Pikermi form (cf. Cheirogaster cf. schaferi, late Miocene, MN12–13, AMPG, Bachmayer, 1967; Lapparent de Broin, 2002) are seen mainly among the carpal bones. The Pikermi intermediate (AMPG 1874) is quite large, almost cubic, with an
angular articular surface for the medial and lateral centralia, whereas it is triangular with a rounded articular surface for the fused medial and lateral centralia in *Ch. bacharidisi*. The possible lateral centralia from Lesvos (in Lapparent de Broin, 2002:107, fig. 8) is most probably an ulnare, and this element is not known in *Ch. bacharidisi*. The Lesvos form is the youngest representative of this genus in continental Europe, as well as the largest one, and is represented by a few preserved skeletal elements and osteoderms (MN17, Greece, VM collection; Lapparent de Broin, 2002).

Regarding the cf. *Cheirogaster* sp. material from Thessaloniki (Arambourg and Piveteau, 1929), the incomplete cranium (MNHN 1921-5-SLQ-995) shows many similarities with cf. *Ch. schafferi* from Samos, in the position of the orbits and the morphology of the jugal. The cheek area is incomplete, but the preserved parts are different from *Ch. bacharidisi*, exhibiting less emargination. This material is considered late Miocene in age (Lapparent de Broin, 2001, 2002), probably because most of Arambourg and Piveteau’s (1929) material originates from various late Miocene localities in Axios Valley, Greece. Nevertheless, a portion of the material described in Arambourg and Piveteau (1929) was collected from Megalo Emvolon (French name for the site: Falaise de Karaburun, with discoveries of a giant Testudo sp.), which is of younger Ruscinian age (Pliocene, MN15; Koufos et al., 1991). Subsequently, this site yielded further elements of a giant tortoise (Bachmayer et al., 1979). Considering the interpretation of Arambourg and Piveteau’s (1929) work, and the labels associated with the tortoise fossils (MNHN 1921-5-SLQ collection), it seems likely that this tortoise was collected from Megalo Emvolon deposits and is, therefore, of Pliocene age. Personal observations showed that the postcranial material from Thessaloniki (MNHN 1921-5-SLQ collection: radius SLQ 998, 1003; ulna SLQ 999-1002; and osteoderms SLQ 1005-1030) are quite similar both morphologically and metrically with the material studied herein.

Preserved shell elements are found only in the Pikermi material (AMPG), most of which are parts of peripherals. One specimen with an eroded surface, originally identified as pleurals (costals) VII and VIII by Bachmayer (1967:pl. 87) (AMPG 1880), is actually a left epiplastron. It shows a shallow epiplastral excavation and a narrowing of the anterior lobe of the gularomoharalumeral sulcus, causing a projection of the epiplastral lip. The positions of the sulci show that the anterior part entoplastron would have been covered by the gulars. This morphology has not been observed in *Ch. bacharidisi*, but more shell material from cf. *Ch. schafferi* is required to make a clear comparison.

**Comparison with the Pliocene Perpignan Specimen—**

*Cheirogaster perpiniana* (Déperet, 1885) from Perpignan (MN15) is represented by a nearly complete skeleton of a female individual (MNHN 1887-26: Déperet and Donnezan, 1890; Bourgat and Bour, 1983). The skull is different from *Ch. bacharidisi* in the position of orbits, being placed more anteriorly (see measurement S in Fig. 8 and Table S1) and in the relative proportions of the cranium (Fig. 8). The preserved part of the crista supraoccipitalis is straight, whereas the posterior tips of the squamosals are slightly converging, but not to the degree seen in *Ch. bacharidisi*. They are also thick and rounded, as in cf. *Ch. schafferi* and the Thessaloniki form (MNHN 1921-5-SLQ-995), thus differing from the thin and pointed squamosals of *Ch. bacharidisi*. In *Ch. perpiniana*, the cheek area is less emarginated than in *Ch. bacharidisi*.

*Cheirogaster perpiniana* shows a posterior carapace with an indentation in the supracaudal–11th marginal sulcus on each side, unlike in *Ch. bacharidisi*. The plastron is similar in length to that of *Cheirogaster bacharidisi*, but the anterior and posterior lobes are relatively longer in *Ch. perpiniana* compared with those of the holotype of *Ch. bacharidisi*. The epiplastral lip projects anteriorly, with a shallow pocket, which exhibits the step-like morphology of EPN II but differs from the female EPN I, which exhibits a more pronounced gular pocket. The posterior lobe of the plastron is similar to that of EPN I, differing only in the anal notch, which is deeper and wider in *Ch. perpiniana*. In *Ch. perpiniana*, the humeral scales are expanded medially on the epiplastra, in contrast to *Ch. bacharidisi* where they medially cover only the entoplastron. Differences also occur in the postcranial elements, such as the coracoid being polygonal in the Perpignan form, whereas it is fan-shaped in *Ch. bacharidisi*. Finally, the femur is straighter in *Ch. perpiniana* than in *Ch. bacharidisi*.

**Comparison with the Lower–Middle Miocene Sandelzhausen Tortoise—**

The Miocene fossil lagerstätte Sandelzhausen (MNS) in southern Germany contains numerous mammalian, reptilian, and invertebrate remains, and is close to the boundary between the lower and middle Miocene (Moser et al., 2009). The Sandelzhausen tortoise (BSPG 1959 II 2033) was attributed to *Geochelone cf. perpiniana* by Schleich (1981), mainly because of the morphology of the postcranial elements. This Miocene giant tortoise differs from *Ch. bacharidisi* in the following characters: a significant gular projection of the epiplastral lip, (ca. 190 mm), the presence of a very deep epiplastral excavation, and an almost flat dorsal surface of the epiplastral lip. The posterior lobe has posteriorly converging borders and a very weak (almost nonexistent) anal notch. The preserved limbs are morphologically similar to *Ch. bacharidisi*, although proportionally smaller in size; the only significant difference is in the fused astragaloocalcaneum, which does not preserve the suture in the Sandelzhausen tortoise.

**Comparison with Spanish Material—**

Comparisons herein are based on published drawings of the various Spanish specimens. *Cheirogaster bacharidisi* differs from the carapace of the Alcala de Henares form (Royo y Gómez, 1935:467, fig. 1), which shows indentations on both sides the supracaudal–11th marginal sulcus. The plastron from Palencia (Royo y Gómez, 1935:470, fig. 4) has an entoplastron that is covered by gular scales in the anterior part, and which is located anteriorly to the humeropectoral sulcus. Also, the posterior lobe of the Palencia specimen has no anal notch and no narrowings in the femoroanal sulcus and exhibits medially expanded anal scutes. The posterior lobe of the taxon from Arévalo (Royo y Gómez, 1935:472, fig. 6) shows posteriorly converging borders and a deeper anal notch than *Ch. bacharidisi*. The cranium from Ciudad Universitaria, Madrid (Royo y Gómez, 1935:pl. 47), is significantly different in having a very wide skull roof, less extensive emargination, and orbits located more posteriorly, compared with *Ch. bacharidisi*. The plastron from Arévalo

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**FIGURE 6.** *Cheirogaster bacharidisi* sp. nov., Epanomi II individual, paratype, Pliocene. A–E, Right lateral and medial centrales (LGPUP EPN 280) in A, medial, B, ventral, C, lateral, D, dorsal views, and E, illustration of lateral and medial centrale, dorsal view. F, drawing of articulated intermediate, lateral and medial centrale, and distal carpals in dorsal view. G–J, right intermediate (LGPUP EPN 226) in G, dorsal, H, anterior, I, posterior, and J, medial views. K–O, right astragalo-calcaneum (LGPUP EPN 214) in K, anterior, L, ventral, M, dorsal, N, posterior views, and O, illustration of dorsal view. P–Q, right distal carpal (LGPUP EPN 229) in P, lateral, and Q, distal views. R–S, right metacarpal (LGPUP EPN 228) in R, dorsal, and S, medial views. T–U, plaxans (LGPUP EPN 220) in T, dorsal, and U, lateral views. V, ungual (LGPUP EPN 216), lateral view. W, pointed (LGPUP EPN 218), X, half -pointed (LGPUP EPN 241), and Y, crural osteoderms (LGPUP EPN 269), ventral views. Abbreviations: as, astragalus; cal, calcaneum; dc, distal carpal; int, intermediate; lat, lateral centrale; med, medial centrale. Scale bar equals 10 mm.
FIGURE 7. *Cheirolestes* *bacharidisi*, sp. nov., additional referred material, Pliocene. A–C, EPN (additional material). Left femur (LGPUT EPN 99) in A, anterior, B, ventral, and C, dorsal views. Kallikratia individual, left humerus (LGPUT KLK 503) in D, dorsal and E, ventral views. Articulated right posterior limb (LGPUT KLK 504–528) in F, posterior and G, ventral views. Abbreviations: as, astragalus; cal, calcaneum; dt, distal tarsal; fe, femur; fi, fibula; mt, metatarsal; os, osteoderm; ph, phalanx; ti, tibia; tu, tubercle; un, ungual. All scale bars equal 100 mm.
FIGURE 8. Crania of *Cheirogaster bacharidisi*, sp. nov., EPN I (LGPUT EPN 102); *Cheirogaster perpiniana* (MNHN 1887-26, late Pliocene, MN15, Perpignan, used as reference); cf. *Cheirogaster* sp. (MNHN 1921-5-SLQ-995, Pliocene, Thessaloniki); cf. *Cheirogaster schafferi* (NHMW 2009z0103/0001, late Miocene, MN12–13, Samos). See Table S2 and Figure S9 for measurement data. Measurements: 1, maximum length; 2, prosthion-squamosal length; 3, prosthion-opisthotic length; 4, prootic-opisthotic length; 5, prosthion-postorbital length; 6, width across frontals; 7, width ectorbital; 8, width across prefrontal; 9, width across jugal; 10, width across squamosal; 11, maximum width; 12, maximum height. Scale bar equals 100 mm.

(Jiménez Fuentes et al., 1986:320, fig. 3; MCNUS 5137) has an entoplastron covered by gulars in the anterior part and longer anterior and posterior lobes. Based on the preliminary descriptions of the crania from Can Mata (IPS 43809a; Luján et al., 2010), we suggest that they are closer in morphology with the Samos *Cheirogaster* form (NHMW 2009z0103/0001), because of the similarly shaped squamosals, and anteriorly positioned orbits.

**Comparisons with Other European Tortoises**—In Europe, there are several other identified forms of *Cheirogaster* s. l. that preserve comparable parts with *Cheirogaster bacharidisi*. *Cheirogaster vitodurana* (Biedermann, 1862) is represented by two specimens from Switzerland: the holotype, from Winterthur (NWS 13758, MN6) and a specimen from Veiltheim (Uitikon) (PIMUZ A/III 660, MN6; Peyer, 1946). This species differs from *Ch. bacharidisi* in having gulars that cover the entoplastron in the anterior part, and an almost flat dorsal epiplastral lip with a significant gular projection. *Cheirogaster eurysternum* (Gervais, 1859) from Saint-Gerand-le-Puy in France (MNHN SG 289–290, MN2; de Broin, 1977) has gulars that cover the entoplastron, a deep gular pocket, and an almost flat dorsal epiplastral lip. The plastron of *Cheirogaster ginsburgi* from Artenay, France (MN4; *Testudo ginsburgi* in de Broin, 1977:pl. 32, fig. 1), differs in having gulars that cover the anterior part of the entoplastron. The femur of *Ch. ginsburgi* (MNHN AR 538) differs in the development of the caput femori, which is not perpendicular to the diaphysis in dorsal view, unlike that seen in *Ch. bacharidisi*. In the southern Balkans, the only available material is from Tenevo, Bulgaria (MN15; Boev, 2008; Stojanov, 2009), which is identified as *Geochelone* sp. This material is fragmentary, but the remains of xiphiplastra (Stojanov, 2009:pl. III, figs. 3, 4), are quite similar to the plastron of EPN II (thickened anal region; plastral concavity suggesting male individual), and might be referable to *Ch. bacharidisi*.

**Intraspecific Variation and Sexual Dimorphism**

The diagnosis of the new species, *Cheirogaster bacharidisi* from Thessaloniki, is based on morphological characters from at least
four different individuals, which together have allowed the documentation of the entire postcranial skeleton and most of the shell. The morphologically similar postcranial elements allow us to attribute them to a single taxon. The morphological differences between the holotype and EPN II, which were found at the same stratigraphic level 20 m apart, can likely be attributed either to intraspecific variation or sexual dimorphism. These differences are the gular pocket is weakly developed in the holotype, and step-like in EPN II; the presence of a concavity in the posterior lobe of EPN II; the xiphiplastron, with converging borders in the holotype, but a pronounced narrowing of the femoroanal sulcus in EPN II; the presence of a concavity in the posterior limb. These tubercles are similar to those of the African spurred tortoise, Centrochelys, an extant species thought to be related to the European Cheirogaster. There is significant morphological variation between inferred male and female individuals, as well as intraspecific variation, especially in the plastron. Cheirogaster bacharidisi exceeded 1 m in shell length, and appears to have been a continental tortoise that was fully adapted to a terrestrial habitat, featuring several osteoderms covering its limbs. The new species increases our understanding of tortoise diversity in Greece. Finally, the new material described here will provide new insights for a much needed revision of Cheirogaster, which is in turn required to understand evolution of Old World giant tortoises through the Neogene and into the present.

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