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REAPPRAISAL OF *TESTUDO ANTIQUA* (TESTUDINES, TESTUDINIDAE) FROM THE MIOCENE OF HOHENHÖWEN, GERMANY

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ABSTRACT—*Testudo antiqua* is one of the few fossil turtle names to have survived the past 200 years of taxonomic reshuffling with its original genus and specific epithet intact. The nine currently known specimens were collected from the middle Miocene Hohenhöwen locality in southern Germany. Because the available Hohenhöwen material was never fully described, we here completely document all known specimens. It is unclear which of these specimens formed the original *T. antiqua* type series, so we herein selected the best preserved representative as the neotype. A phylogenetic analysis places *T. antiqua* in a basal polytomy within the clade *Testudo*, indicating that *T. antiqua* may represent the ancestral morphology of *Testudo*. As with a number of other published studies, ours was unable to resolve relationships between the three extant *Testudo* lineages (the *hermanni*-group, the *graeca*/*kleinmanni*/*marginata* group, and the *horsfieldii*-group). Finally, with a view toward locating more turtles and in order to better understand the geological and ecological context of these tortoises, we visited Hohenhöwen several times to search for the original collection sites, but we were unable to locate the original fossil quarries described in the literature.

INTRODUCTION

IN THE 250 years since Linnaeus placed all known turtles into *Testudo*, the genus has been reduced to only five extant species (e.g., Joyce et al., 2004; Fritz and Havas, 2007; Rhodin et al., 2008) and a handful of closely related fossil forms (e.g., Lapparent de Broin et al., 2006a, 2006b, 2006c). Perhaps the best preserved among these fossil forms is *Testudo antiqua* Bronn, 1831, one of the first fossil turtles ever described (Kuhn, 1964). Through coincidence of its close relationship with the type species of *Testudo*, *T. graeca* Linnaeus, 1758, it is also one of the few fossil turtles named in the early nineteenth century that has not been referred to a new genus during the past two centuries of splitting and renaming. The original specimens of *T. antiqua* were collected from the Hohenhöwen site in southwestern Germany, a vertebrate locality which is now considered to be of middle Miocene age (ca. 13 Ma, see below). *Testudo antiqua* was initially described by Bronn in 1831, who compared it to extant *T. graeca* and *Chelonoidis denticulata* Linnaeus 1766 (then *T. tabulata*). The illustrations in that original description are highly idealized, so the actual features of the originally described specimens are impossible to determine. *Testudo antiqua* was re-described by von Meyer in 1865, who produced more accurate illustrations that were also idealized in some aspects. More recently, Schleich (1981) included *T. antiqua* in a large morphometric study of fossil turtles from Germany, partially illustrating four specimens, photographing others, and finally designating a lectotype from the alleged syntype series. Eight specimens of *T. antiqua* are currently held in German collections (FFSM, SMNS, UFGC). A ninth specimen from Hohenhöwen is housed in a French collection (MT), and was partially photographed, though not illustrated, by Broin (1977). It is apparent from the historical descriptions that other specimens were at one point available but their whereabouts are now unknown.

Testudo antiqua belongs to a widespread group of closely related tortoises than have inhabited Europe, Asia, and North Africa since the Miocene. This group has undergone major taxonomic revision in the past four decades, and considerable controversy has been associated with the nomenclature of these turtles (e.g., Khozatsky and Mlynarski, 1966; van der Kuyl et al., 2002; Perälä, 2002; Bour, 2004: Parham et al., 2006a, 2006b; Lapparent de Broin et al., 2006a, 2006b, 2006c; Fritz et al., 2007; Fritz and Bininda-Emonds, 2007). It is clear from both molecular and morphological studies that all of the close relatives of *T. graeca* (i.e., *T. marginata* Schoepff, 1792, *T. hermanni* Gmelin, 1789, *T. horsfieldii* Gray, 1844, and *T. kleinmanni* Lortet, 1883) form a monophyletic clade, and some molecular studies have provided support for inclusion of *Indotestudo* and *Malacochersus* in this clade (see phylogenetic analysis below). It is our opinion that taxonomic endeavors should aim at stabilization of names within well-defined monophyletic clades (e.g., Parham 2006a, Joyce et al., 2004), so in this work we follow Fritz and Bininda-Emonds (2007) in retaining the original taxonomic designation for all of these tortoises within *Testudo*. This includes *T. horsfieldii*, which was placed into the genus *Agrionemys* by Khozatsky and Mlynarski (1966), *T. hermanni*, which was placed in the genus *Eurotestudo* by Lapparent de Broin et al. (2006a), and *T. marginata* and *T. kleinmanni*, which were placed in the genus *Chersus* by Gmira (1993).

Determination of the exact phylogenetic position of *T. antiqua* has been hampered by the lack of a complete illustration and description of all the known material, so it is not known whether *T. antiqua* is ancestral to or part of the modern *Testudo* clade. *Testudo antiqua* was included in a large study (Lapparent de Broin et al., 2006b, 2006c) that elucidated the relationships between fossil and extant *Testudo,* and the authors concluded that *T. antiqua* lies along the *T. hermanni* lineage. However, they did not have direct access to any of the specimens held in German collection or complete illustrations of the entire syntype series, and the scoring of *T. antiqua* was therefore inaccurate for several characters. Because of the aforementioned questions and phylogenetic ambiguities, we herein fully illustrate and describe all of known *T. antiqua* material from Hohenhöwen. With well-

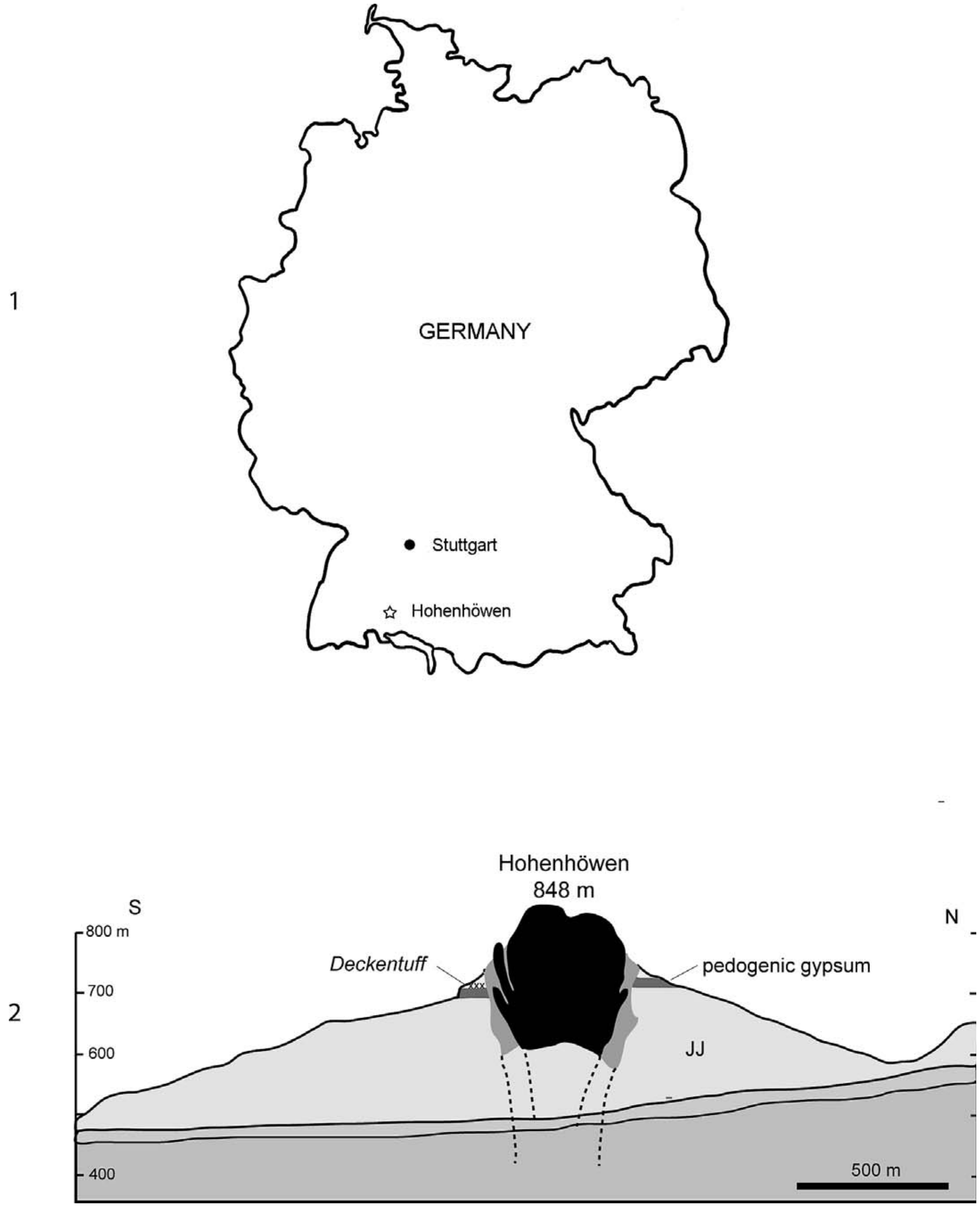

FIGURE *1*—*1*, the Hohenhöwen site is located in Baden-Württemberg, near the south-western German village of Engen; *2*, measured section of Hohenhöwen outcrop. The Deckentuff, which overlays the fossiliferous gypsum, has been dated at 12.5–13 Ma.

described material, we then cladistically explore the phylogenetic relationships of *T. antiqua* using a modified version of the character matrix reported by Lapparent de Broin et al. (2006b, 2006c). The resulting tree is then compared to recent molecular trees, and the possibility that *T. antiqua* displays the ancestral morphology of modern *Testudo* is raised.

GEOLOGICAL AND TAPHONOMIC SETTING

Institutional abbreviations.—FFSM, Fürstlich Fürstenbergisches Sammlung Donaueschingen, Donaueschingen, Germany; MT, Museum de Toulouse, Toulouse, France; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UFGC, University of Freiburg, Geological Collections, Freiburg, Germany.

Geology.—The Hohenhöwen (or Hohenheven) locality in southwestern Germany (Fig. 1.1) was first described as a freshwater gypsum (*Süsswasser-Gips*) in the early 1800s (Bronn, 1831). The site is located on the northeast flank of the Hohenhöwen promontory near the village of Engen in the Hegau region of southwestern Baden-Württemberg, Germany (Schreiner, 1983, 1992; Fig. 1.1). The fossiliferous layers were apparently first collected at the beginning of the early 1800s, perhaps exposed by a massive landslide involving the entire eastern flank of the massif in 1817. The Hohenhöwen hill is the second highest elevation (846 mm above sea-level) of the Hegau. The top of this hill is comprised of a basalt chimney, which penetrates the 250 m thick *Jüngerer Juranagelfluh* (JJ) unit (Fig. 1.2; Schreiner, 1992). The JJ unit is a clayey to silty marl containing pebbles of Mesozoic limestones, sandstones, and the

Variscan basement. It is part of the Upper Freshwater Molasse along the northern margin of the western North Alpine Foreland Basin and is interpreted as the erosional detritus deposited into alluvial fans by the rising Black Forest Mountains (Schreiner, 1992). Toward the top of the JJ at Hohenhöwen, beds of massive pedogenic gypsum have yielded pockets of fossil vertebrates (according to Walchner, 1851, p. 983, shells of 10 to 12 *Testudo antiqua* individuals were found in close proximity). The gypsum beds are overlain on the southwest flank of Hohenhöwen at 730 m by 10 m volcanic tuffs (Fig. 1.2), which, according to Schreiner (1992), can be correlated with the *Deckentuff* (700 m) at the nearby Hohenstoffeln locality. The latter tuff has been dated by K-Ar method to 12.5 Ma (sanidine; Lippoldt et al., 1963) and to 12.8–13.0 Ma (hornblende; Schreiner, 1966, 1983). These ages compare well with biochronological data retrieved from mammalian fossils found together with *T. antiqua* at the Hohenhöwen site. According to Stehlin (1926) and Tobien (1957) the following mammalian species are recorded: *Lagospis verus*, *Gomphotherium* sp., *Anchitherium aurelianense, Euprox furcatus*, and ?*Micromeryx flourensianus*. This association resembles the well-known JJ locality Anwil (Switzerland, 75 km southwest of Hohenhöwen), which contains all of the aforementioned animals except *Gomphotherium* sp. (Engesser, 1972). Anwil is biostratigraphically dated to about 13.3 Ma (Kälin and Kempf, 2009). Thus, both radiometric dating and mammalian biochronology support an absolute age of the Hohenhöwen fossils of about 13 Ma (MN8, middle Miocene). It is worth noting that we revisited Hohenhöwen several times and were unable to relocate the original quarry, which appears to have been covered by more recent landslides and is now overgrown by forest. This is a poignant reminder that fossil localities do not necessarily last forever.

Taphonomy and faunal associations.—*Testudo antiqua* appears to have been part of a vibrant ecosystem evidenced by diverse terrestrial gastropods (Seemann, 1930) and fragmentary postcranial remains of carnivorans, elephants, horses, deer, and pikas (Stehlin, 1926, Tobien, 1957). All of these fossils are housed at FFSM and are in need of revision. The host sediment is a massive pedogenic gypsum bed (i.e., Süwassergips) that contains red and yellow-mottled clays and marls (Rote Letten of von Althaus, 1832). This type of rock indicates seasonal arid climate conditions during deposition with mean annual precipitation below 300 mm (Retallack, 1994). An old description of the site by Walchner (1851) suggests that all of the fossils were recovered in close proximity to each other, although the original locality and collection descriptions are not clearly described. Interestingly, in contrast to the mammals, nearly all of the turtles are in relatively high state of articulation, suggesting that burial was rapid. Controlled studies by Brand et al. (2003), as well as observations by Dodd (1995) and Corsini and Chamberlain (2008), suggest that turtles completely submerged in water disarticulate within two years, while in semiarid to arid conditions freshwater turtle shells exposed on the surface completely disarticulate within three to four years (Dodd, 1995; Brand et al., 2003). So it is likely that the Hohenhöwen tortoises were buried quickly, within months of death. Interestingly, no non-shell bones were recovered with any of the turtles, and we observed only one possible non-shell bone fragment among all of the steinkerns. Our experience with other tortoise assemblages (Corsini et al., 2006) suggests that non-shell elements are observable in one-half to three-quarters of the turtles observed in the field, so with nine specimens there is a high probability that if non-shell elements are present they should be observable in at least several cases. This suggests that many of the non-shell bones were removed from the carcass by scavengers. Apart from the missing non-shell bones, there is no overt evidence of scavenging or other post-mortem alteration (bite or gnaw marks). This is surprising, because in other locations where high concentrations of tortoises are recovered, calcium scavenging by rodents (via gnawing) or larger animals that leave tooth marks on the shell bone is often observed on many specimens (for example the White River tortoises [Corsini et al., 2006] or the late middle Miocene fauna from Gratkorn [Gross et al., 2011, fig. 6a]). Together, the absence of non-shell bones and absence of gnaw marks suggests an ecosystem devoid of small mammals able to scavenge calcium but containing scavengers, perhaps birds, able to remove the non-shell bones.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus, 1758
CRYPTODIRA Cope, 1868
TESTUDINIDAE Gray, 1825
TESTUDO Linnaeus, 1758

Type species.—*Testudo graeca* Linnaeus, 1758.

TESTUDO ANTIQUA Bronn, 1831

Neotype.—Given that we were not able to identify a single individual from Bronn's (1831) original syntype series, we herein designate the best-preserved specimen, MT PAL 2012.0.10, as the neotype, and abandon the lectotype designation by Schleich (1981) (see Remarks below).

Diagnosis.—*Testudo antiqua* is diagnosed as a member of Testudinidae by the presence of a thickened epiplastral lip, coincidence of the costal/peripheral suture with the pleural/marginal sulcus, wedged-shaped costals, and high peripherals. *Testudo antiqua* can be placed within *Testudo* by the presence of an elongate cervical scute, a narrow nuchal notch defined by the first marginals, a quadrangular pygal that is wide anteriorly and narrow posteriorly, a humeral-pectoral sulcus that does not cross entoplastron, an epiplastral excavation that penetrates nearly half of the thickness of the anterior portion of the epiplastron, two suprapygals, and a suprapygal 1 that embraces the half-moon shaped suprapygal 2. *Testudo antiqua* differs from *T. graeca*, *T. marginata*, and *T. kleinmanni* and their fossil relatives in lacking a posterior plastral hinge, and from *T. horsfieldii* and its relatives by being high-domed. The vertebral series differs from *T. graeca* in being somewhat narrower than the vertebral series of *T. graeca* but not as narrow as that observed in *T. hermanni*.

Type locality.—Hohenhöwen, Engen, Baden-Württemberg, Germany. Pedogenic gypsum, middle Miocene, MN8 (~13 Ma, also see Geological Setting).

Referred material.—FFSM 3446.1, FFSM 3446.2, FFSM 3446.3, FFSM 3446.4, SMNS 4450*,* SMNS 51467, SMNS 51469, UFGC 9.

Remarks.—The original description of *T. antiqua* is based on shell material from three to four specimens collected at Hohenhöwen, but Bronn's (1831) descriptions and illustrations are insufficient for identification of the individuals in that original syntype series within the available material. Von Meyer (1865) clearly illustrated FFSM 3446.1, perhaps also UFGC 9, and stated that Bronn examined those two in his original work, but we were unable to independently verify this assertion. Schleich (1981) felt compelled to designate SMNS 4450, a poorly prepared and extremely deformed individual, as the lectotype, probably because it was readily available at the Stuttgart Museum (SMNS). However, given that we found no evidence that SMNS 4450 was indeed part of the syntype series, the designation of a lectotype is dubious to us, and we also question the assignment of type status to a specimen with so many missing characters. Karl (2013) more recently argued that the specimen housed at the University of Freiburg Geological Museum (UFGC 9) should be the lectotype, based mainly upon the fact that von Meyer (1865) was thought to have viewed that specimen. However, he makes no clear connection between that specimen and the specimens viewed by Bronn in 1806. The designation of a lectotype is therefore not valid, as lectotypes must demonstrably be part of the original syntype series. We therefore conclude that a neotype designation is appropriate, and designate MT PAL.2012.0.10 as the neotype because: 1) it originates from the type locality; 2) it is the best-preserved specimen; and 3) it is easily accessible in a large public collection. We finally note that one specimen at FFSM is also quite well preserved, but we omitted this specimen from consideration, because it is not housed at a regular, public museum.

DESCRIPTION

FFSM 3446.1.—Specimen FFSM 3446.1 is an approximately 95 percent complete shell with some dorsal and lateral deformation toward the left (Fig. 2). No cranial or post-cranial elements are present. The characteristic (for Hohenhöwen) red-orange mottling of the bone surface is present. Missing from the carapace is the outer right portion of peripheral 1, a small piece of the border of peripheral 2, the posterior half of peripheral 11, a small piece from the central portion of the distal end of peripheral 10, the pygal bone, parts of costals 7 and 8, and a small piece of costal 6. The suture between neural 7 and 8 is not visible, and the junctions of left costals 7 and 8 with neurals 7 and 8 are asymmetric relative to the right side. This asymmetry is the result of an anomalous contact between right costal 7, neural 8, and suprapygal 1. This irregular arrangement was also noted in a specimen of *Testudo hermanni boettgeri* figured by Lapparent de Broin (2006b, fig. 10). The alignment of neural 7 with neural 8 is also skewed, but whether this occurred during life or is the result of preservation cannot be determined. The plastron is nearly complete, missing only the right lobe of the anal notch, a small portion of the left lobe of the anal notch, and the anterior-most regions of the epiplastra.

FFSM 3446.2.—Specimen FFSM 3446.2 is a well-preserved steinkern with attached plastron (Fig. 3). No cranial or post-cranial elements are present. The locations of most visceral sutures of the carapace are well preserved in the dorsal view. The exceptions are the pygal sutures, which are not apparent. Two small pieces of the carapace are present but detached from the main steinkern (not figured). In ventral view approximately 80 percent of the plastron is present, and the epiplastron is removable from the main steinkern. Missing are anterior and lateral portions of the right hyoplastron, lateral and posterior portions of the right hypoplastron, and most of the right xiphiplastron including the anal notch region. The left lateral portions of the hyoplastron and hypoplastron are missing, as is most of the right xiphiplastron including the anal notch region.

FFSM 3446.3.—This specimen is a shell that is approximately 90 percent intact but exhibits overall poor preservation of the sulci and sutures (Fig. 4). Most of the neural bones are not discernible, including their contacts with the costals. The characteristic red-orange mottling of the Hohenhöwen site is present on the bones. No cranial or post-cranial elements are present. Missing from the carapace are the distal portions of right peripheral 10, all of right peripheral 11, all of the pygal, the posterior half of left peripheral 10, all of left peripheral 11, the posterior quarter of the suprapygal, and the lower third of the left costal 8. The carapace is also missing a small portion of the anterior margin of the nuchal bone and a piece from the margin of peripheral 1. The plastron is intact but the surface is covered with chips and divots, likely the result of poor preparation, which disrupt most of its surface. A particularly large divot occurs on the left hypoplastron just anterior of the center; it occupies nearly 20 percent of the surface area of this bone.

FFSM 3446.4.—This specimen was held in a box labeled 3446.5 but had 3446.4 written on the steinkern. It is an approximately 65 percent complete shell (Fig. 5). No cranial or post-cranial elements are present. The characteristic (for Hohenhöwen) red-orange mottling of the bone surface is present. The dorsal view shows the carapace missing all of the left peripherals, the pygal, and right peripherals 8, 9, 10, and 11. The distal portions of right peripherals 4, 5, 6, and 7 are missing as well. Also missing are the lower sections of all of the left costals, the left edge of the pygal, and the lower left terminus of suprapygal 2. On the right a large section containing the distal half to two-thirds of costals 2, 3, and 4 is absent, and the lower half of costal 5 shows damage. Approximately 75 percent of the plastron is present, although the epiplastron, part of the entoplastron, and the anterior portions of the right hyoplastron are still encased in matrix. Missing from ventral view are large portions of the left and right hyo- and hypoplastra, and the entire xiphiplastra. However, the xiphiplastra and the right portion of the right hypoplastron are present as a large detached fragment (not figured), but can only be viewed from the visceral side because the ventral surface is encased in matrix.

SMNS 4450.—This specimen (proposed lectotype of Schleich 1981) is an approximately 85 percent complete shell that has been significantly deformed, primarily through dorsal-ventral compression (Fig. 6). No cranial or post-cranial elements are present. The shell bones have the red-orange mottling that is characteristic of Hohenhöwen specimens. The anterior one third of the nuchal is absent and the lateral edge of the left and right peripherals 1 and 2 are also damaged. Also missing from the left side is the distal half of peripheral 6 and all of peripherals 7–11. Missing from posterior right is the distal half of peripheral 8, most of peripheral 9, and all of peripherals 10 and 11. The pygal bone, suprapygal 2, and the lower two thirds of suprapygal 1 are also absent. The rear of the turtle has been slightly overthrust onto the fore at the junction between vertebral scute 3 and 4. The plastron is intact but severely deformed and poorly prepared. It was deformed through folding into the visceral space, whereas the xiphiplastron was slightly twisted to the left such that the prominent anal notch no longer aligns with the midline.

SMNS 51467.—This fragmentary specimen consists of approximately 50 percent of a plastron (Fig. 7). Ventral and visceral views are available and the epiplastral excavation is apparent. The typical red-orange mottling is present on both the visceral and the ventral surfaces. Missing are the anterior third of the left epiplastron and a small piece of the anterior right epiplastron. The lateral and posterior portions of the left and right hyoplastra are missing, as is most of the right hyoplastron. The left hypoplastron is approximately 75 percent intact with the anterior and lateral portions missing. Also absent are the posterior two thirds of the xiphiplastron. The left inguinal notch is intact and exhibits a small inguinal scute (not figured).

SMNS 51469.—This is an approximately 70 percent complete shell with some lateral and anteroposterior deformation (Fig. 8). No cranial or post-cranial elements are present. As with most of the other specimens, the shell bones are marked by mottled red-orange coloration on both carapace and plastron. The anterior region of the shell has been polished, whether by geological processes or during preparation is unknown. Missing from the carapace on the left are the distal portions of peripherals 9 and 10, as well as all of peripheral 11. The pygal and much of the suprapygal are absent, as are right peripheral 9–11. The distal third of right peripherals 1 and 2 are gone, as are the termini of left peripherals 1 and 2. A large indentation is present at the anterior border of the nuchal region and the left anterior sulcus of vertebral 1 extends all the way to the margin of the shell with no evidence of a cervical scute. The right terminus of vertebral 1 is missing, and an unusual sulcus traverses the nuchal bone near the terminus. An unusual arrangement of anterior sutures and what appear to be malformed and/or supernumerary bones in the nuchal region suggests that one or more of the ossification centers were damaged, perhaps during early development. The posterior 20 percent of the plastron is missing, as is a very small region of the anterior epiplastron.

UFGC 9.—This is an approximately 70 percent complete

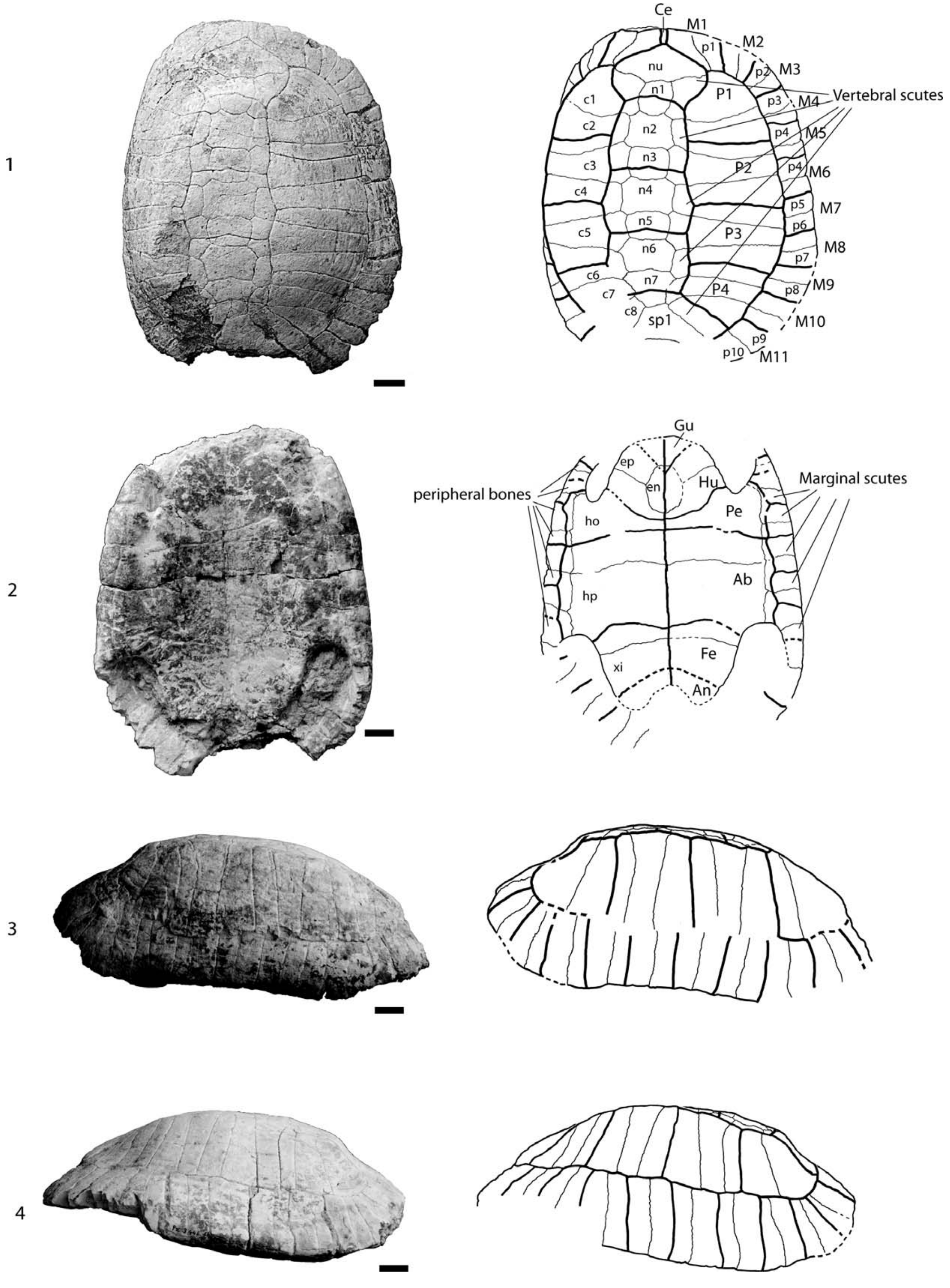

FIGURE 2—FFSM 3446.1, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–4*, photographs and illustrations of shell in dorsal, ventral, left lateral, and right lateral views, respectively. Note that while the suprapygal region is damaged, the suture between suprapygal 1 and 2 is readily apparent in the sub-surface bone that remains. Heavy lines represent sulci, light lines bone sutures. Bones: ep=epiplastron, en=entoplastron, ho=hyoplastron, hp=hypoplastron, xi=xiphiplastron, nu=nuchal, n1-7=neural bones, c1-8=costal bones, sp=suprapygal; scutes: Gu=gular, Hu=humeral, Pe=pectoral, Ab=abdominal, Fe=femoral, and An=anal, Ce=cervical, P1-4=pleural scutes, M1-11=marginal scutes. Scale bar=2 cm.

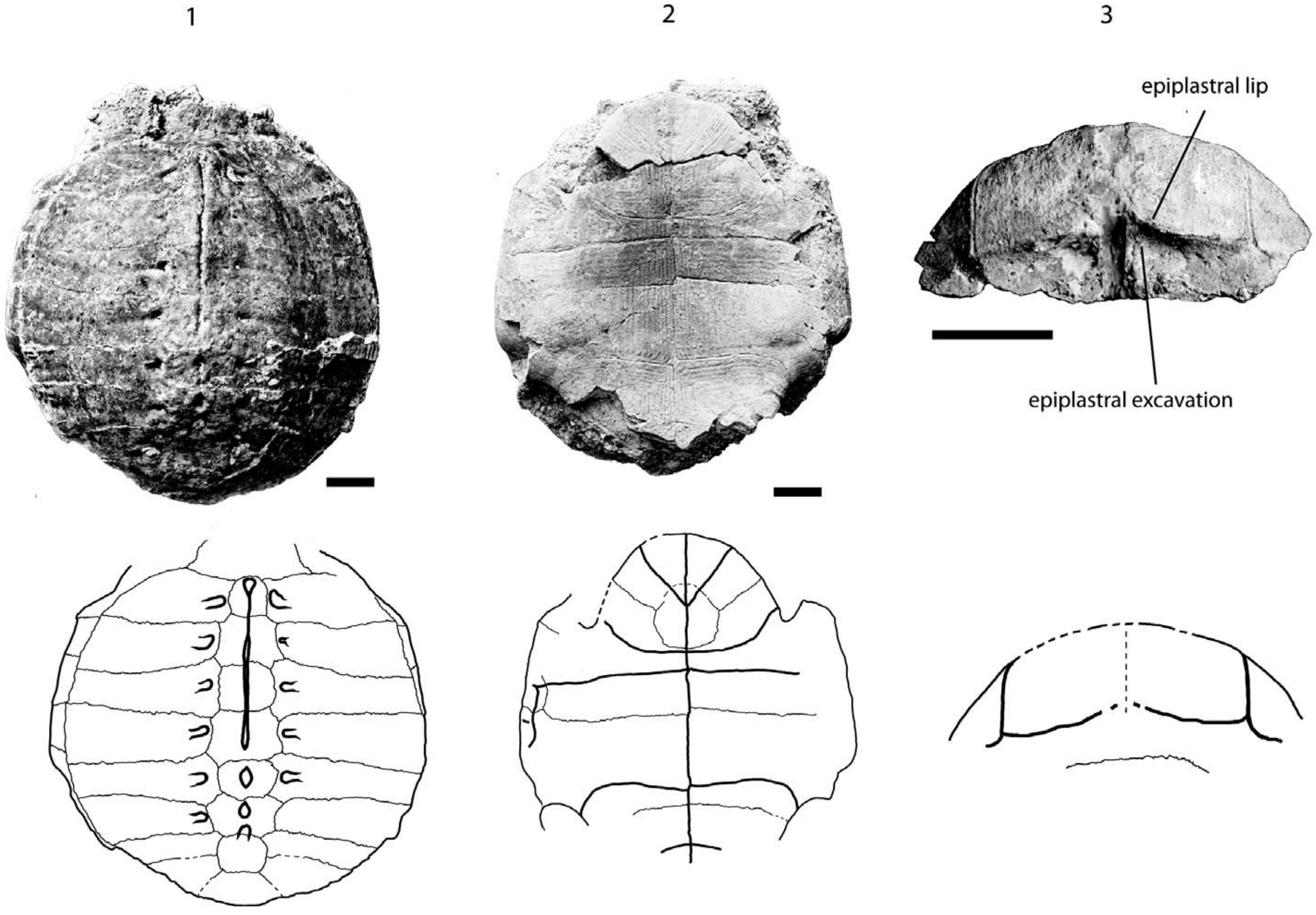

FIGURE *3*—FFSM 3446.2, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1*, *2*, photographs and illustrations of steinkern and partial plastron in dorsal and ventral views, respectively; *3*, epiplastron in visceral view. Heavy lines represent sulci, light lines bone sutures. See Figure *2* for labeled bones and scutes. Scale bar=2 cm.

specimen consisting of a shell with no cranial or post cranial elements (Fig. 9). Some deformation is evident in ventral view, primarily an inward folding of the plastron at the midline and slight rightward deformation of the carapace. The characteristic red-orange mottling is not immediately evident because a dark epoxy coating covers most of the bone; however, in places devoid of the epoxy, the characteristic red-orange mottling of the Hohenhöwen turtles is apparent. Missing from the carapace are the nuchal, all of the right peripherals excerpt part of peripheral 8, the right half of the pygal, and right peripherals 1, 2, 8, and 9. Most of the distal portions of left costal 1 and right costals 1–7 are missing, as are the anterior two thirds of neural 1 and the anterior portions of peripheral 3. A fragment containing the left half of the pygal, peripheral 11, and peripheral 10 is detached from the main carapace but held in place by the matrix (not figured). The plastron is missing nearly all of both epiplastra except a small posterior piece of the left bone. Anterior and lateral sections of the right hyoplastron are gone, as are lateral portions of the right hypoplastron. During preservation, the xiphiplastron and part of the left posterior hypoplastron detached and migrated inward and posteriorly while remaining fixed within the matrix.

MT PAL.2012.0.10.—The neotype, this well-preserved specimen is represented by a nearly intact shell (Fig. 10). The carapace is deformed laterally toward the right, and is missing on the left peripherals 9, 10, most of 11, and the distal third of peripheral 8. The central parts of the suprapygal region are cracked and chipped. The pygal is present, but significantly deformed. The anterior margins of the nuchal, and lower portions of right peripheral 1 and peripheral 2 are partially degraded. The right lateral edges of neural 7 and 8 are deformed, and most of right costal 8 and the upper half of right costal 7 are damaged. The plastron is intact except for the anterior margins of the epiplastron, which have been slightly degraded. The anterior half of the left epiplastron has also been deformed, being bent toward the carapace. The xiphiplastral lobes are largely intact but have suffered some minor degradation at the margins. The wide space between the terminus of the pygal and the posterior margin of the xiphiplastron (i.e., the relatively short posterior lobe of the plastron) suggests that this turtle is a female.

Overall description.—*Testudo antiqua* is a medium sized turtle. We were unable to identify any unambiguous autapomorphies that characterize the species. Those specimens sufficiently complete for measuring range between 18–21 cm in length and 14–17 cm in width. Six specimens (FFSM 3446.1, FFSM 3446.3, FFSM 3446.4, MT PAL.2012.0.10, UFGC 9, and SMNS 51469) are sufficiently preserved to show that *T. antiqua* had a high-domed aspect with height to width ratios of between 0.59 and 0.74. Sex is difficult to determine for most specimens, because of damage and deformation, but at least two of them (UFGC 9 and MT PAL.2012.0.10) appear to be female based upon the relatively long distance between the pygal and the posterior margin of the plastron.

Carapace.—In those specimens without extensive deformation or degradation (FFSM 3446.1, FFSM 3446.3, SMNS 51469, MT

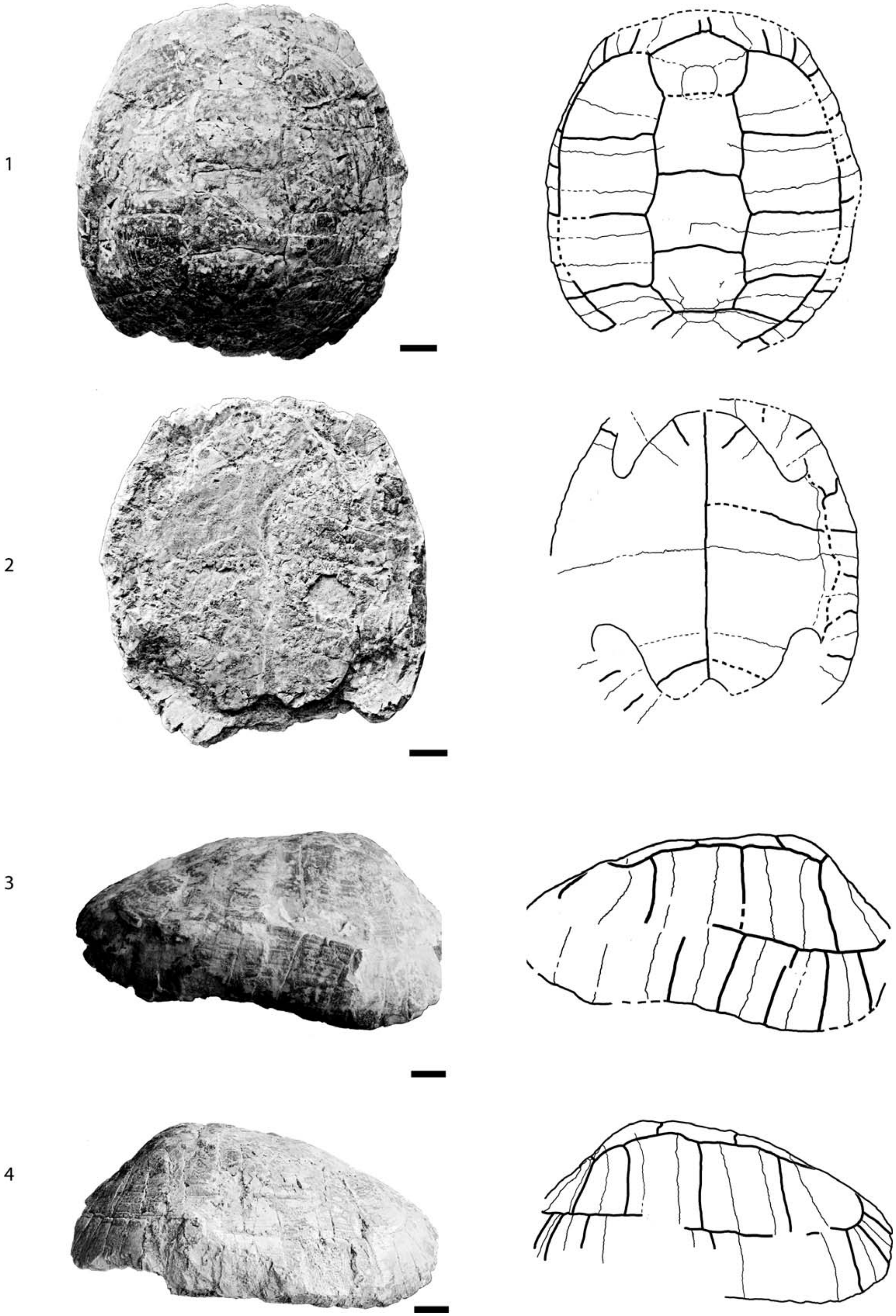

FIGURE 4—FFSM 3446.3, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–4*, photographs and illustrations of shell in dorsal, ventral, right lateral, and left lateral views, respectively. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

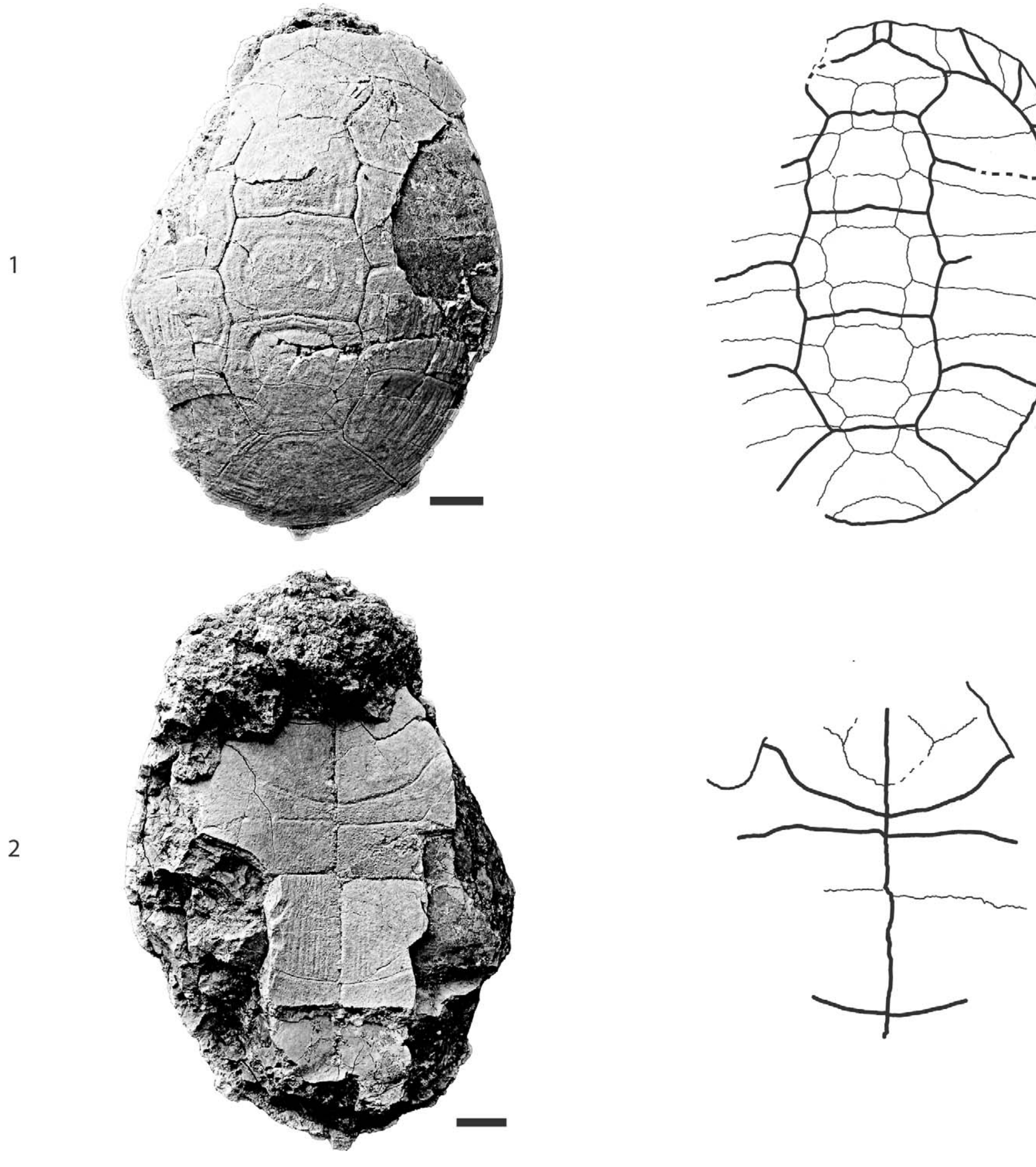

FIGURE *5*—FFSM 3446.4, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1*, *2*, photographs and illustrations of shell in dorsal and ventral views, respectively. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

PAL.2012.0.10) it is apparent that the carapace broadens posteriorly with the widest point occurring at the apices of inguinal notches. In two of these specimens, FFSM 3446.1 and FFSM 3446.4, the anterior border of the carapace is virtually undamaged, showing it to be slightly incut beginning at a small protrusion where the posterior sulcus of marginal 1 intersects the border of the shell. The cervical scute is well developed, longer than wide (intact in FFSM 3446.1, FFSM 3446.3, FFSM 3446.4, MT PAL.2012.0.10), and the lateral sulci are parallel to each other such that the anterior and posterior borders of the cervical are nearly the same width. The cervical scutes of the series range between 25–35 percent length of the nuchal bone. The neural count can be determined in eight of the nine specimens; it varies, with six of the specimens exhibiting eight neurals (FFSM 3446.1, FFSM 3446.4, SMNS 4450, MT PAL 2012.0.10, UFGC 9) and two of them exhibiting seven neurals (FFSM 3446.2, SMNS 51469). Neural 1 is always tetragonal and lozenge-shaped (roughly square or rectangular) with anterior and posterior

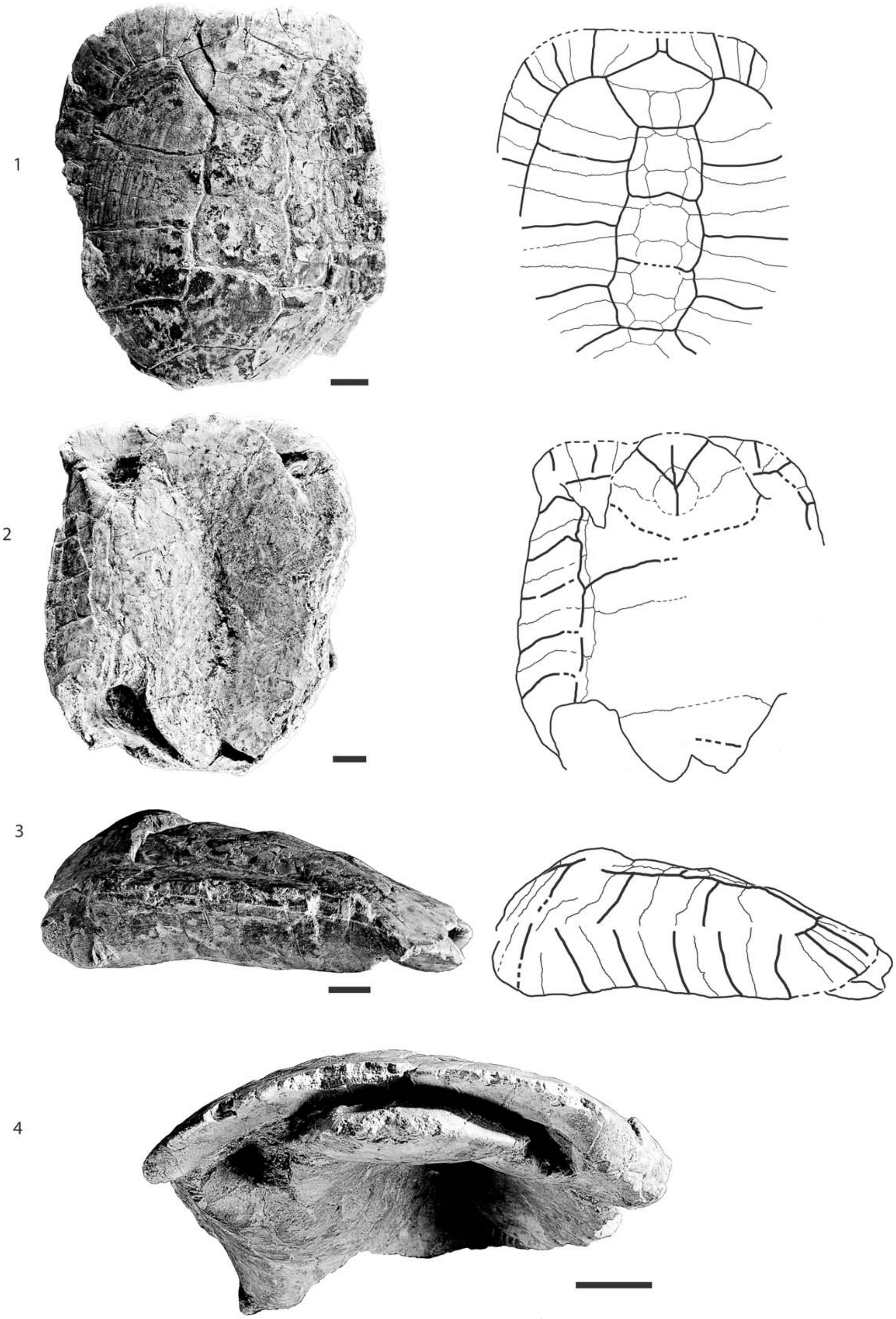

FIGURE 6—SMNS 4450, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–4*, photographs and illustrations of shell in dorsal, ventral, right lateral, and anterior views, respectively. The anterior view shows the thickness of the epiplastral lip. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

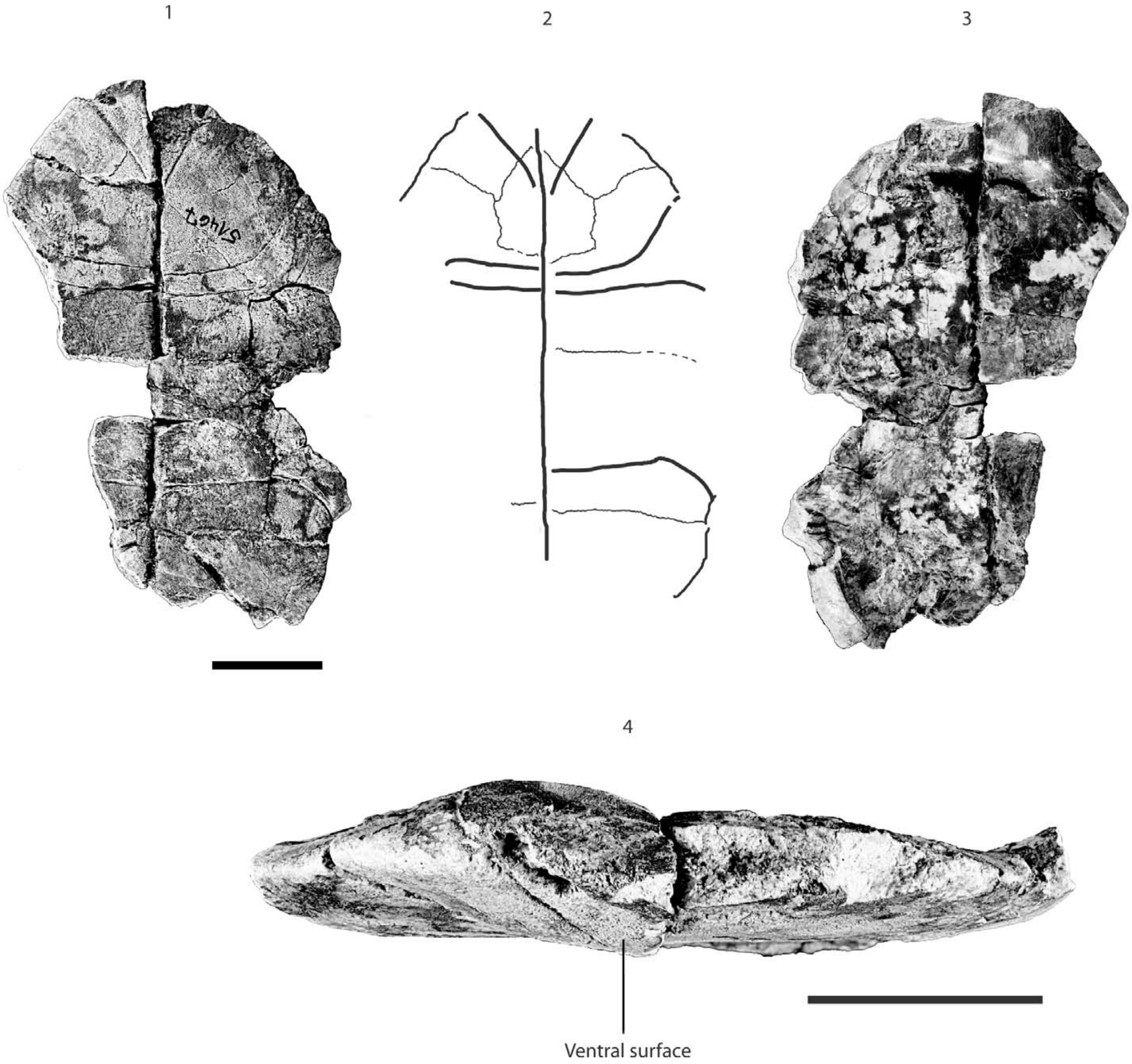

FIGURE 7—SMNS 51467, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–4*, a partial plastron in ventral view, ventral illustration, visceral view, and anterior view, respectively. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

borders of equal, or nearly equal width. Neural 2 is always octagonal, whereas neural 3 is always tetragonal. The subsequent neurals vary greatly in shape amongst the population, being usually tetragonal, hexagonal, or octagonal. The posterior neurals of two of the specimens (FFSM 3446.3, SMNS 51467) cannot be distinguished. The neural formulae are as follows: FFSM 3446.1 (4/8/4/8/4/6/?/?), FFSM 3446.2 (4/8/4/8/4/8/4/?), FFSM 3446.3 (4/?/?/?/?/?/?/6), FFSM 3446.4 (4/8/4/8/4/6/6/6), SMNS 4450 (4/8/4/8/4/6/6/6), SMNS 51467 (?/?/?/?/?/?/?/?), SMNS 51469 (4/8/4/8/4/8/6/-), UFGC 9 (?/8/4/6/6/6/6/6), MT PAL.2012.0.10 (4/8/4/8/4/6/6/6). Vertebral scute 1 is present in five of the specimens, and in all cases shows the characteristic ‘onion dome’ shape that occurs in all *Testudo* sp. and *Indotestudo* sp. and does not contact marginal scute 2. In some cases this scute is longer than wide, and in others it is as long as it is wide. Vertebral scute 2 is in all specimens slightly narrower anteriorly. This scute is roughly hexagonal, though in some cases scute is narrowed laterally and deviates from a symmetrical hexagon. Vertebral scute 3 is hexagonal with equal anterior and posterior spans. Vertebral scute 4 is narrower posteriorly than anteriorly (intact in all except FFSM 3446.2), although the degree of narrowing varies from 61–80 percent (posterior to anterior border ratio). Vertebral scute 5 is much narrower anteriorly than posteriorly, and the lateral sulci descend through the eighth costal to contact the pleural marginal sulcus in all cases except FFSM 3446.3 where the right sulcus crosses into costal 7 prior to contact with the pleural marginal sulcus. Pleural 1 always contacts marginal scutes 1–5, and slightly overlaps the nuchal. There are eight costals and costals 2–6 are moderately wedged (alternating converging and diverging from the midline to the pleural marginal sulcus). Four of the nine

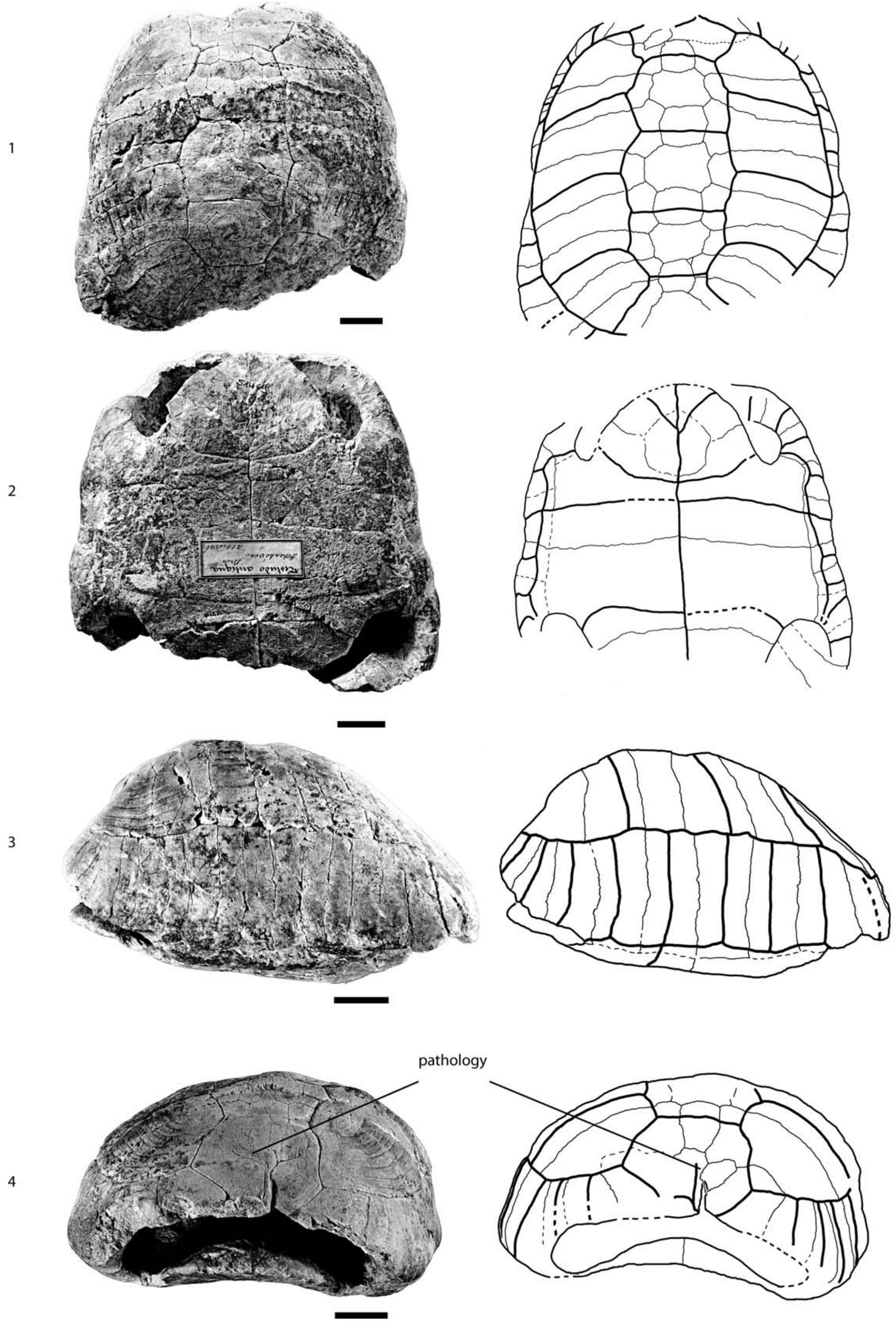

FIGURE 8—SMNS 4450, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–4*, photographs and illustrations of shell in dorsal, ventral, left lateral, and anterior views, respectively. The anterior view shows the thickness of the epiplastral lip and the pathological suture and scute patterns in the nuchal region. This turtle has unusual scute and suture patterns in the anterior portion of the plastron, which indicate a pathology suffered during life. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

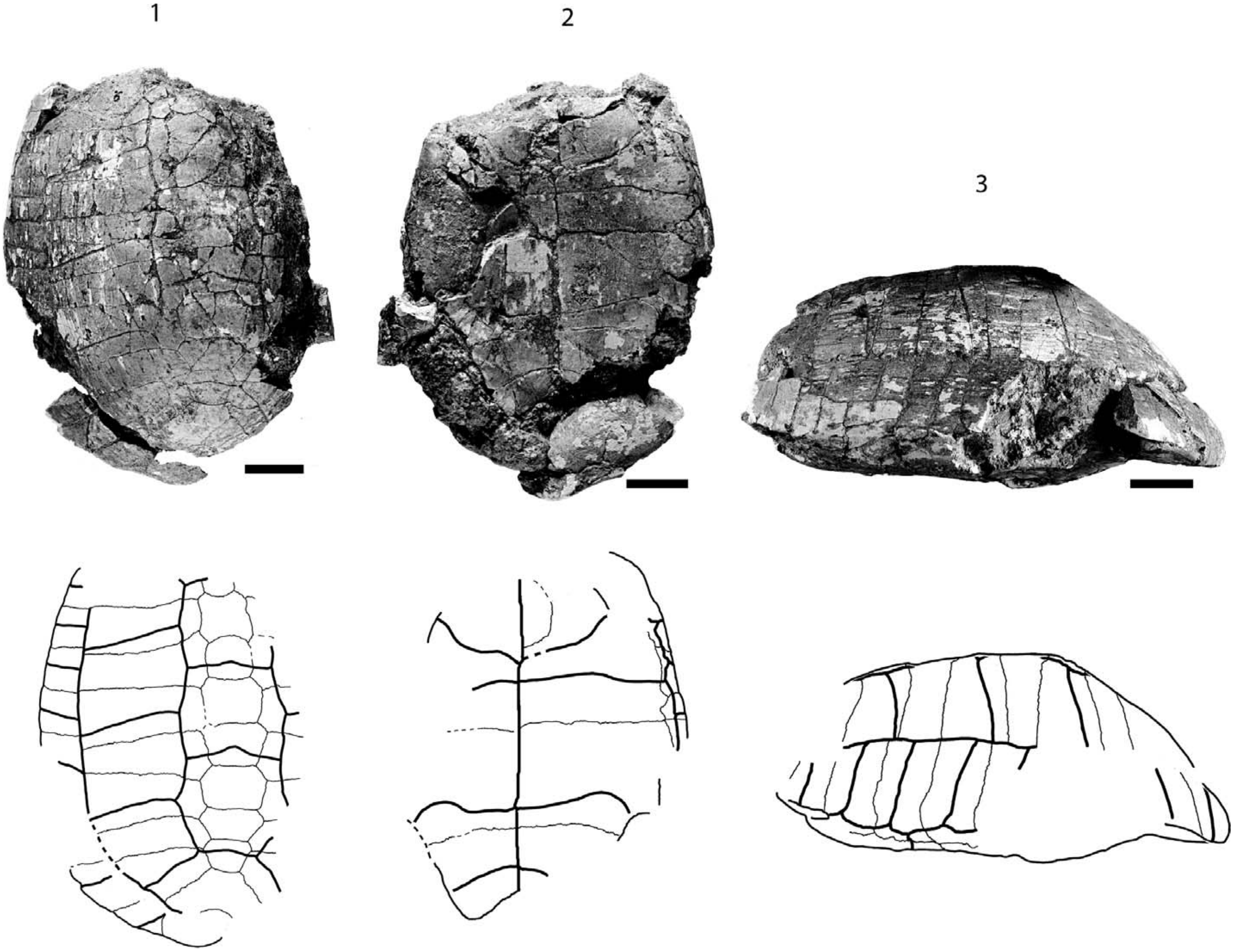

FIGURE *9*—UFGC 9, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–3*, photographs and illustrations of shell in dorsal, ventral, and left lateral views, respectively. Most of the right side of this specimen is missing, so only the left lateral view is shown. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

specimens (FFSM 3446.1, FFSM 3446.4, UFGC 9, MT PAL.2012.0.10) have sufficient preservation to assess the morphology of the suprapygals; in these there are two suprapygals, with suprapygals 1 embracing suprapygals 2 in such a way that it assumes the shape of a boomerang whose lateral processes contact the peripherals. In addition, another fragmentary specimen consisting of only a suprapygal and a few other fragments (from the FFSM collection, FFSM 3446.12, not illustrated herein) has a well-preserved suprapygal region that also clearly exhibits the boomerang embrasure. Since this condition occurs in North American species of *Gopherus* as well as in the extinct *Stylemys* and *Hesperotestudo* species (Hutchison, 1996), we consider it to be the ancestral condition for *Testudo*. The pygal, preserved only in MT PAL.2012.0.10, in a slightly deformed state, is slightly hooked toward the interior of the shell, a condition observed in *T. hermanni* and to a lesser degree in *T. graeca*. In this specimen, the twelfth marginal scutes appear to be completely fused.

Plastron.—The plastron is nearly as wide as it is long. The epiplastron does not project beyond the anterior border of the carapace (i.e., no gular horn). A visceral view of the epiplastron is possible in two of the specimens (SMNS 51467, FFSM 3446.2), and a distinct excavation is evident. This excavation penetrates nearly half way through the thickest part of the anterior epiplastron. The lip is pronounced but does not extend to the anterior suture of the entoplastron. A ventral view of the plastron shows that the gular sulci meet in the upper half of the entoplastron (FFSM 3446.1, FFSM 3446.2, SMNS 4450, SMNS 51469, SMNS 51467, MT PAL.2012.0.10). In the specimens that preserve most or all of the entoplastron (SMNS 51467, UFGC 9, MT PAL.2012.0.10, FFSM 3446.2), it is intersected in the posterior half by the imaginary line between the axillary notches. The humeral-pectoral sulcus does not contact the entoplastron except for MT PAL.2012.0.10, where the humeral-pectoral sulcus coincides with the posterior suture of the entoplastron. In that specimen, the humeral-pectoral sulcus displays the double-hump sinuosity seen in *T. hermanni* and some *T. graeca*. The abdominal-femoral sulcus does not contact the hypo-xiphiplastral suture in any of the specimens, indicating absence of a plastral hinge. The same sulcus originates at the midline near a line between the apices of the inguinal notch, proceeds anterior to that line, and then returns posterior to contact the inguinal notch just below the apex. The xiphiplastral suture is closer to the abdominal-femoral sulcus than to the anal-femoral sulcus (seen in FFSM 3446.1, FFSM 3446.2, SMNS 51467, UFGC 9, MT PAL.2012.0.10). There is a prominent anal notch, and the anal-

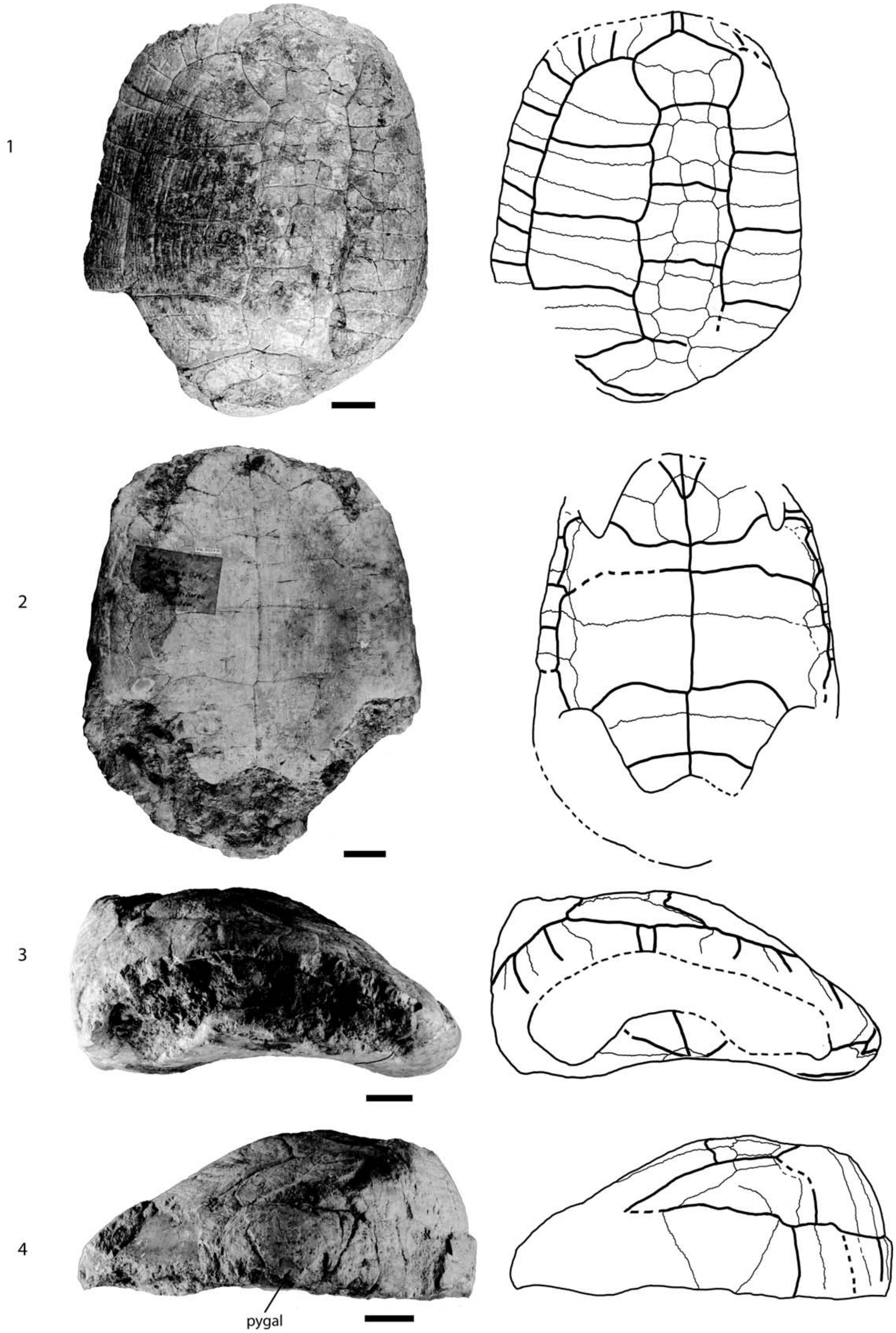

FIGURE *10*—MT PAL.2012.0.10, *Testudo antiqua*, middle Miocene of Hohenhöwen, Germany. *1–4*, photographs and illustrations of shell in dorsal, ventral, anterior, and posterior views, respectively. This is the only specimen that preserves an intact pygal bone. Heavy lines represent sulci, light lines bone sutures. See Figure 2 for labeled bones and scutes. Scale bar=2 cm.

femoral sulcus contacts the midline well above the apex of the anal notch (seen in FFSM 3446.1, FFSM 3446.3, UFGC 9, MT PAL.2012.0.10). In all specimens except MT PAL.2012.0.10 the anal-femoral sulci join the midline at 30–45°; in MT PAL.2012.0.10, that sulcus proceeds from the lateral margin in a nearly straight line that joins the midline at nearly a 90° angle.

PHYLOGENETIC ANALYSIS

Cladistic analyses of *Testudo antiqua* and its close relatives were conducted using a modified version of the character matrix used in Lapparent de Broin et al. (2006b, 2006c). The following five modifications were made to the character/taxon matrix: First, *T. antiqua* was re-scored based upon all of the available Hohenhöwen specimens. Second, two additional characters were added (i.e., characters 18 and 19) that pertain to the shape of vertebral scute 5 and the position of the femoral-anal sulcus relative to the apex of the anal notch. These characters were also scored for *T. graeca* (SMF 73784, SMNS 6819, SMNS 6858), *T. marginata* (SMF 67576, SMF 50975), *T. hermanni* (SMNS 10681, SMNS 11011, SMNS 6687), *T. horsfieldii* (SMF 62339, SMNS 6874), *Indotestudo forstenii* (SMF 73267), *Indotestudo elongata* (SMF 71585), and *Manouria impressa* (SMF 69777) based on personal observations. *Paleotestudo canetotiana, T. kazachstanica*, and *T. lunellensis* were scored for character 18 based upon figures published in Lapparent de Broin et al. (2006b). *Ergilemys bruneti, T. hermanni boettgeri*, and *T. kazachstanica* were scored for character 19 using figures published in Lapparent de Broin et al. (2006b). Third, *I. forstenii* (SMF 73267) and *T. kleinmanni* (SMF 65095) were added to the data set. Fourth, "*T. antakyensis*" was omitted from the data set, because Parham et al. (2006b) provided molecular evidence that this taxon is firmly situated within the species *T. graeca*. Fifth, preliminary analyses indicated that the Pleistocene *T. kenitrensis* behaves as a "rogue taxon" so it was also excluded from the analyses. See Appendix 1 for a complete list and description of characters and Appendix 2 for the character matrix. The matrix was analyzed using PAUP*, v. 4.0b10 (Swofford, 2002). PAUP settings were as follows: 1) all characters left at equal weight and were not ordered; 2) branches were set to collapse if minimum length equals zero; and 3) shortest trees were computed via a branch and bound search. The analysis with reduced taxonomic sampling resulted in one most parsimonious tree (Fig. 11).

For unknown reasons, we could not precisely reproduce the reported strict consensus tree of Lapparent de Broin et al. (2006c) using their original matrix. Their cladograms were generated using Windows based TNT, but specific settings for the strict consensus tree were not provided, so perhaps there is a subtle difference in our settings and theirs. Nonetheless, our strict consensus with their original scoring is very similar in overall topology, especially in the collapse of the three extant clades into a polytomy, so we are not concerned with the minor differences we observed.

DISCUSSION

The Testudo antiqua *population*.—A thorough analysis of all known *Testudo antiqua* specimens from the Hohenhöwen locality strongly suggests that they are all representatives of a single species. While there is obvious variation among the specimens, none exhibits a diagnostic suite of characters that distinguishes it from the others. Such polymorphic variation is also observed within extant populations of *Testudo* sp., a fact that is discussed at length by Lapparent de Broin et al. (2006b, 2006c). For example, they pointed out that the humeral-pectoral sulcus is posterior to the entoplastron in 24 observed *T. graeca* specimens, but coincides with the posterior border of entoplastron in 17 others. In *T. hermanni* they observed 19 with the humeral pectoral sulcus posterior to the entoplastron, four with contact at the posterior border of entoplastron, and two that intersected the entoplastron. They reported similar situations with five other characters: the gular pocket, the hinge, the suprapygal arrangement, the pygal shape, and the cervical scute. We confirmed many of those observations with extant representatives of *Testudo*. For example, our analysis showed that the suprapygal condition varies amongst *T. graeca*, with two museum specimens exhibiting a single trapezoidal suprapygal and a third a boomerang-shaped suprapygal 1 embracing suprapygal 2 such that suprapygal 1 contacts the pleural-marginal sulcus. Delfino et al. (2009) figured a *T. graeca* whose suprapygal 1 embraces suprapygal 2 in the same fashion, and those authors also note and discuss significant intraspecific variation of several characters amongst the eight osteological specimens used in their analysis. The suprapygal embrasure also varies amongst *T. horsfieldii,* as seen in those illustrated by Lapparent de Broin et al. (2006b) and in our own observations of *T. horsfieldii*.

We observed significant variation in a number of characters within the *T. antiqua* population from Hohenhöwen. We observed variation in the numbers of neurals (with two specimens exhibiting seven neurals and the rest eight), the shape of vertebral scute 5 (of seven specimens that display this character, one has a flask-like shape vertebral scute 5, as in *T. horsfieldii*, and the others have a rounded trapezoidal shape, as in *T. hermanni*), contact between the humeral-pectoral sulcus and the entoplastron (in the four specimens retaining this character, three have the sulcus posterior to the entoplastron and in one it intersects the posterior border of the entoplastron), the sinuosity of the humeral-pectoral scute (two of seven specimens retaining the character have pronounced sinuosity as seen in *T. hermanni* figured in Lapparent de Broin et al., 2006b). Thus, it is clear that there is significant overlap of many supposedly diagnostic characters within and between species in these closely related animals, so much so that it is very difficult if not impossible to correctly diagnose a single fossil individual to species level.

Phylogenetic analysis.—For our phylogenetic analyses we added two characters and two taxa, *I. forstenii* and *T. kleinmanni*, to the matrix of Lapparent de Broin et al. (2006b, c), while removing two taxa, *T. kenitrensis* and *T. antakyensis*. *Testudo kleinmanni* was included in order to establish relationships amongst all Mediterranean tortoises, and *I. forstenii* was included to strengthen the *Indotestudo* clade. However, we did not include *Malacochersus tornieri* (Siebenrock, 1903), because it cannot be scored for most characters, due to the fact that its shell is so highly reduced. Our scoring for *T. antiqua* differed for character 16 (character 15 of Lapparent de Broin et al., 2006b, 2006c), which pertains to the fusion of the twelfth marginal (supracaudal) in internal view. There are no internal views of the pygal region for any of the *T. antiqua* specimens, so we scored '?' in place of '1'. We also entered a score of '1' instead of '2' for character 17 (character 16 of Lapparent de Broin et al., 2006b, 2006c) because we could find no evidence for a true sulcus in the fused twelfth marginal scute on the only specimen with an intact pygal (MT PAL.2012.0.10). PAUP analysis of our matrix yielded a single, most parsimonious tree that places *T. antiqua* into a basal polytomy with the three extant clades of *Testudo* (i.e., the *T. hermanni* clade, the *T. graeca/marginata/kleinmanni* clade, and the *T. horsfieldii* clade; Fig. 11). Our results are broadly consistent with those of Lapparent de Broin et al. (2006b, 2006c), but disagree in placing *T. antiqua* at the base of *Testudo*, instead of along the *T. hermanni* lineage. Given that our analysis primarily differs from that of Lapparent de Broin et al. (2006b, 2006c) in the scoring of *T. antiqua*, this difference is likely the result of our updated scoring based on all available specimens.

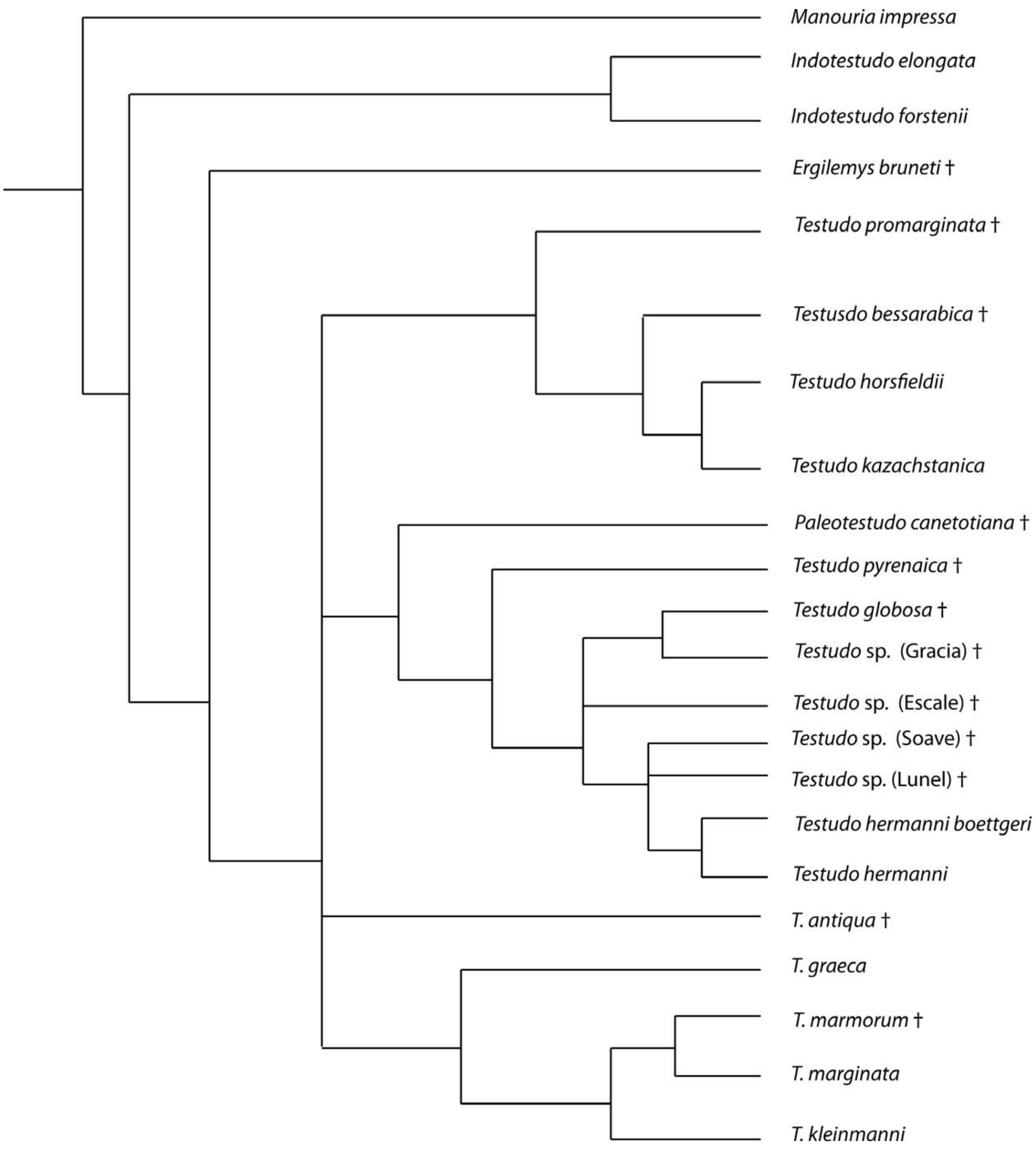

FIGURE *11*—Single most-parsimonious tree using the modified character/taxon matrix of Lapparent de Broin et al. (2006b, 2006c). TL= 57 steps; CI=0.667, RI=0.782. See methods section for PAUP settings and parameters. The informal names Gracia (middle Pleistocene, Spain), Escale (middle Pleistocene, France), Soave (middle Peistocene, Italy), and Lunel (Pleistocene, France) refer to regions from which fragmentary material used in the Lapparent de Broin et al. (2006b, 2006c) study (but not yet referred to a genus) was collected. Extinct species are indicated with a cross.

Two recent molecular phylogenies have focused on resolving relationships within the *Testudo* clade. Parham et al. (2006a) used complete mitochondrial genomes to explore phylogenetic relationships amongst all Mediterranean tortoises, whereas Fritz and Bininda-Emonds (2007) used three mitochondrial genes and two nuclear genes to do the same for all tortoises. The results of both analyses are comparable, although differences exist, particularly in regards to the question of whether *Testudo* (sensu Fritz and Bininda-Emonds, 2007) is paraphyletic relative to *Indotestudo* and *M. tornieri* (Parham et al., 2006a) or whether *Testudo* forms a monophyletic clade that is sister to *Indotestudo* and *M. tornieri* (Fritz and Bininda-Emonds, 2007). Our morphological analysis more closely agrees with the topology of Fritz and Beninda-Emonds (2007) in hypothesizing the monophyly of a clade *Testudo* relative to *Indotestudo*, but our analysis is uninformative in regards to *Malacochersus* because this taxon could not be included.

If *Indotestudo* and *M. tornieri* are ignored, our analysis broadly agrees with those of Parham et al. (2006a) and Fritz and Bininda-Emonds (2007) in finding strong support for a clade containing only the three hinged species (*T. marginata*, *T. kleinmanni,* and *T. graeca*) and in its inability to resolve the relationships between

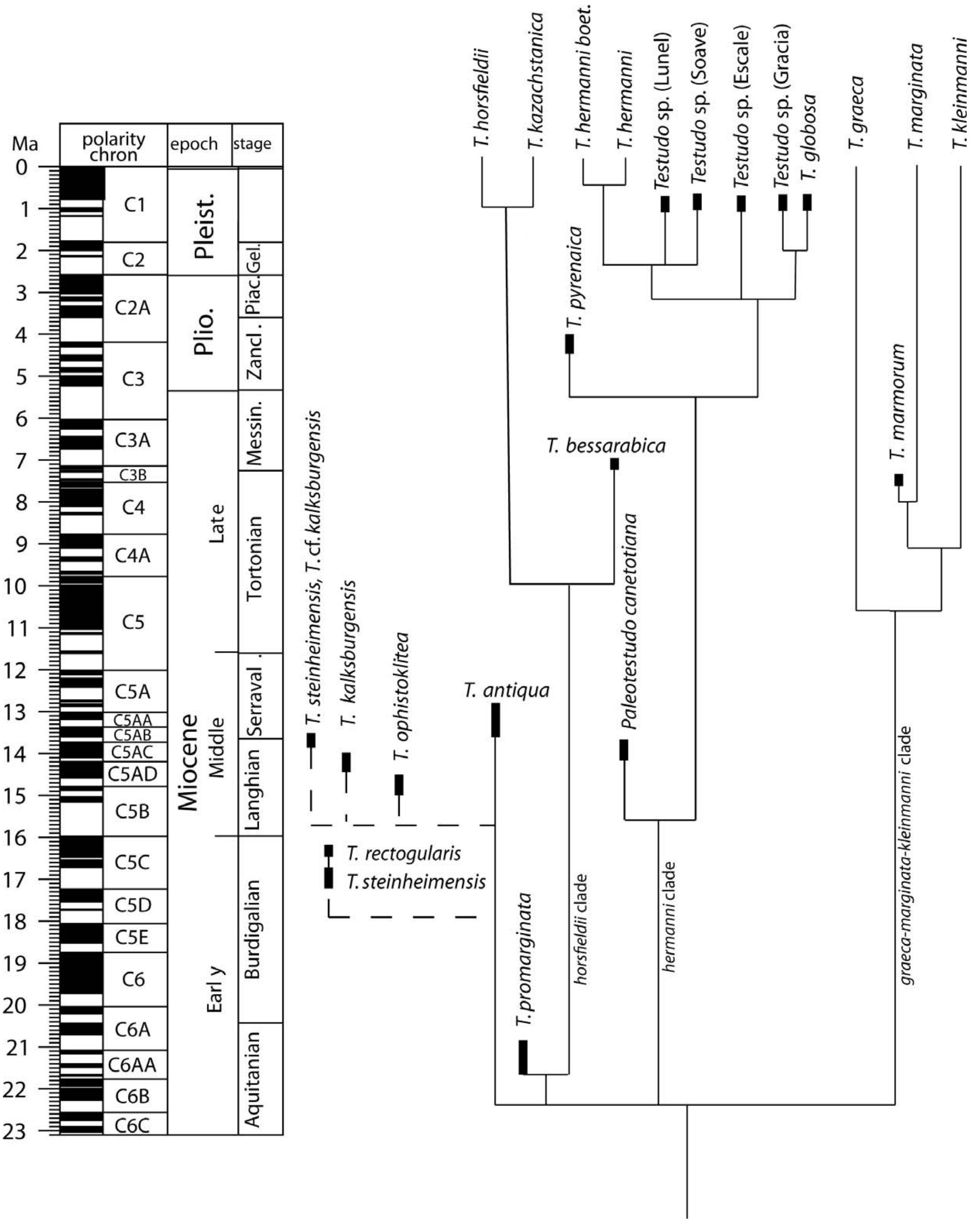

FIGURE 12—Locality and chronology of European fossil tortoises used in the phylogenetic analysis discussed in this report. *Testudo globosa* (Upper Valdarno, Italy), *Testudo lunellensis* (Cova de Gràcia, Spain), *Testudo pyrenaica*, (Serrat d'en Vaquer, France), *Testudo bessarabica* (Taraklia, Republic of Moldova), *Testudo marmorum* (Pikermi, Greece), *Paleotestudo canetotiana* (Sansan, France), *Testudo antiqua* (Hohenhöwen, Germany), *Testudo steinheimensis T.* cf. *kalksburgensis*, (Steinheim, Germany), *Testudo kalksburgensis*, (Kalksburg Austria), *Testudo ophistoklitea* (Gammelsdorf, Germany), *Testudo rectogularis* (Sandelzhausen, Germany), *Testudo steinheimensis* (Altenstadt, Germany), *Testudo promarginata* (Frankfurt-Nordbassin, Germany). Dashed lines on the cladogram represent relationships not analyzed in the phylogenetic analysis presented here. The informal names Gracia (middle Pleistocene, Spain), Escale (middle Pleistocene, France), Soave (middle Pleistocene, Italy), and Lunel (Pleistocene, France) refer to regions from which fragmentary material used in the study (but not yet referred to a genus) was collected.

the three primary clades of *Testudo* (i.e., the *T. hermanni* clade, the *T. graeca/marginata/kleinmanni* clade, and the *T. horsfieldii* clade). The Parham et al. (2006a) study conducted a relative-rate analysis, which suggested that this polytomy is neither soft nor hard, but is instead caused by the rapid divergence of *M. tornieri*. Our analyses did not include *M. tornieri* and also resulted in that polytomy, suggesting that the nodes might be collapsing for different reasons in the morphological and molecular phylogenies. Alternatively, it also remains possible that this lack of resolution indicates a true star radiation at the base of the *Testudo* clade. In keeping with that notion, we were unable to identify any unambiguous autapomorphies in *T. antiqua*, and it is possible that *T. antiqua* exhibits the ancestral morphology of the turtles that gave rise to the *Testudo* crown clades.

The early fossil record of Testudo.—The evolution of extant Mediterranean tortoises remains ambiguous, though the current study does cast some light on possible relationships. Our cladistic analysis using morphological characters suggests that *T. antiqua* rests firmly within the *Testudo* clade. However, our analysis does not resolve its precise position in the clade, nor the precise relationships between the three modern clades (Figs. 11, 12). While our analysis has shed some light on the phylogenetic relationships between *T. antiqua* and some *Testudo* fossils, the taxonomy is still in need of extensive revision, particularly among early representatives of the clade. Many specimens (including holotypes) are fragmentary, making it difficult to conduct rigorous cladistic analyses with those specimens. Also, the plasticity of characters within species has been and continues to be a significant impediment to clear diagnoses required for taxon assignment.

Our preliminary examinations of many early to middle Miocene representatives of *Testudo* suggest that at least some of these taxa will eventually be referred to *T. antiqua*. An example is the earliest known member of the *Testudo* clade, *T. promarginata* Reinach 1900 from the early Miocene. Photographs of *T. promarginata* in Broin (1977) show what appear to be two discrete taxa, and it is not clear which one is actually *T. promarginata*. One of these taxa shares many characters with *T. antiqua* (a rounded anterior epiplastral margin and humeral, morphology of the pectoral sulcus, and many shared carapacial characters*)*, while the other displays several unique autapomorphies that might suggest a separate species. Another example is the holotype of another Miocene tortoise, *T. rectogularis* Schleich, 1981, which consists of a fragmentary carapace and plastron that is missing the anterior portion of the epiplastron (the gular region). This material is insufficient for a complete diagnosis, but is consistent with our diagnosis of *T. antiqua*. Schleich (1981) also referred a number of specimens to *T. rectogularis* from the Sandelzhausen locality in southern Germany, of which all but one (a specimen with a broad and blunt anterior epiplastral margin) show character morphologies consistent with *T. antiqua*.

Schleich (1981) also reported *T. steinheimensis* Staesche, 1931 material from the Altenstadt locality, Germany, now known to be late early Miocene (Prieto et al., 2009), making it roughly contemporaneous with the early Miocene *T. rectogularis*. The Altenstadt specimen lacks the anterior margin of its epiplastron, but in its available characters is also consistent with our diagnosis of *T. antiqua*. *Testudo antiqua* is also roughly contemporary with a number of other fossils turtles from central Europe (see Fig. 11.2): *T. opisthoklitea* Schleich, 1981 (Gammelsdorf near Landshut, Germany), *T. kalksburgensis* Toula, 1896 (Kalksburg near Vienna, Austria), *T. kalksburgensis* var. *steinheimensis* (Staesche 1931), and *T. canetotiana* Lartet, 1851 (Sansan, Department Gers, France). *Testudo opisthoklitea* appears to share many characters with *T. antiqua* and can probably be synonymized with that taxon. The holotype *T. kalksburgensis* and *T. kalksburgensis* var. *steinheimensis* both consist of a fragmentary plastra that, except for a slightly less rounded anterior epiplastron, are consistent with *T. antiqua*. *Testudo canetotiana* is another closely related tortoise similar to *T. antiqua* except for three subtle characters in the anterior epiplastron (the blunt anterior margin of the epiplastron, extension of the epiplastral lip to the border of the entoplastron in a visceral view, and a somewhat narrower anterior lobe) of *T. canetotiana* (Lapparent de Broin, 2000). In summary, while the work by de Broin (1977), Schleich (1981), and Lapparent de Broin (2006a, 2006b, 2006c) has greatly contributed to our understanding of these tortoises, significant taxonomic revision is still necessary.

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APPENDIX 1

Character descriptions

Characters 1–17 were taken from Lapparent de Broin et al. (2006b) and can be briefly summarized as follows: character 1=general shape of the carapace; character 2=bridge height to lateral keel; 3=hypo-xiphiplastal hinge; 4=coincidence of pleural-marginal sulcus with costal-marginal suture; 5=neural number; 6=suprapygal type; 7=suprapygal arrangement; 8=pygal shape; 9=shape of dorsal epiplastral lip; 10=epiplastral excavation and epiplastral lip; 11=abdominal-femoral sulcus position; 12=elevation of bone under gular scutes; 13=cervical scute; 14=width of vertebral series; 15=fusion of twelfth marginal internal view; 16=fusion of twelfth marginal external view; 17=union of the trochanters of the femur; 18=shape of vertebral scute 5; 19=anal-femoral sulcus contact with anal notch. Significantly more extensive character descriptions for these characters can be found in Lapparent de Broin et al. (2006b). Note that character numbering in Lapparent de Broin et al. (2006b) begins with 0 and ours begins with 1.

Two new characters are included in this analysis, and scoring was as follows: character 18, shape of vertebral scute 5. 0=trapezoidal, narrow anteriorly with rounded posterior border; 1=hexagonal or heptagonal as in *Indotestudo forstenii* and *I. elongata*, respectively; 2=flask shaped, narrow anteriorly with rounded posterior border, as in *T. horsfieldii*. Character 19, anal-femoral scute contacts or nearly contacts apex of anal notch. 0=absent; 1=present.

A number of the character descriptions in Lapparent de Broin et al. (2006b, 2006c) are sufficiently complex to warrant an explanation of our interpretations:

Character 1 (0 of Lapparent de Broin et al. 2006b) pertains to the general shape of the carapace excluding the anterior borders. It has four states, all with complex descriptions that essentially capture the degree of doming and length of the carapace. State 0 we took to be the condition in *Manouria impressa*, state 1 the condition in *Indotestudo* spp., state 2 that in *T. graeca* and *T. hermanni*, state 3 that in *T. marginata*, and state 4 that in *T. horsfieldii*. We found it very difficult to distinguish between *Indotestudo* spp. and *T. marginata* for this character.

Character 7 (6 of Lapparent de Broin et al. 2006b), pertaining to the suprapygal configuration, has three states. State 0 we interpreted to be the basal condition for Testudinidae, with a narrow, trapezoidal suprapygal 1 and a wide, roughly hexagonal suprapygal 2, as seen in *Manouria impressa*. State 1 we interpreted to be the situation when suprapygal 1 embraces the lenticular suprapygal 2 on its anterior margin, and the pygal embraces it on its posterior border, as seen *Indotestudo* spp.. State 2 was scored for those individuals whose suprapygal 1 embraces the semi-lenticular suprapygal 2 anteriorly. Since suprapygal 2 is semi-lenticular, its border with the pygal is straight.

Character 8 (7 of Lapparent de Broin et al. 2006b), pertaining to suprapygal shape, is a character which we found to be partially redundant with character 7 but nevertheless captured some additional nuances that occur in the configuration and shape of suprapygals. State 0 was assigned to those species who scored 0 or 1 for character 7 (i.e., those whose suprapygals 1 and 2 overall border does not form a trapezoid with straight edges). State 1 we took to be the situation when the collective outline of 1 and 2 is trapezoidal and when a semi-lenticular suprapygal 2 is embraced by suprapygal 1.

Character 10 (9 of Lapparent de Broin et al. 2006b) pertains to the dorsal view of the anterior epiplastron (epiplastral lip). State 0 is the condition found in the outgroup *Manouria impressa*, with virtually no lip and very shallow excavation, state 1 is marked by the elongated (anterior-dorsal) epiplastral lip found in the Oligocene *Ergilemys bruneti*, state 2 in *Indotestudo* spp., and state 3 in all members of the *Testudo* clade, including *T. horsfieldii*. We also note that our two *Indotestudo* specimens (*I. elongata* and *I. forstenii*) were very different in this charcter from those figured in Lapparent de Broin et al. (2006b).

Character 11 (10 of Lapparent de Broin et al. 2006b) attempts to capture four aspects of the epiplastral lip and the deep excavation underneath: The position of the overhanging lip with respect to the entoplastron, whether the lip is horizontal or sloped upward posteriorly, the extent to which the lip overhangs the excavation, and the shape of the excavation. This character was difficult to score. We interpreted state 0 as the condition with no upward slope toward the rear of the animal, as seen in *Manouria* and *Indotestudo*. State 1 we scored when there is an upward slope to the lip (posteriorly) but it does not overhang the excavation. State 2, we scored when there was an upward slope posteriorly, significant overhang that does not reach the anterior border entoplastron, and marked by a flat bottom to the excavation, as seen in *T. hermanni* group and the *T. horsfieldii* group. State 3 occurs in *T. marginata* and *T. graeca*, and is marked by upward slope posteriorly, and the 'gular pockets.'

The other characters were straightforward and their descriptions easy to interpret, and since our scorings were in the end nearly identical to those reported for both extant turtles and the fossils at hand, it appears that our interpretations are reasonable.

APPENDIX 2—Character matrix after Lapparent de Broin (2006b, 2006c) with two additional taxa (*Indotestudo forstenii* and *Testudo kleinmanni*) and two additional characters (18 and 19). The informal names Gracia (middle Pleistocene, Spain), Escale (middle Pleistocene, France), Soave (middle Peistocene, Italy), and Lunel (Pleistocene, France) refer to regions from which fragmentary material used in the study (but not yet referred to a genus) was collected. Ages were taken from de Lapparent de Broin et al. (2006b)

Taxon	Character			
Manouria impressa	00000	00000	00000	0000
Indotestudo elongata	10001	01002	01000	1101
Indotestudo forstenii	10001	01002	11001	11?1
Ergilemys bruneti	20001	01001	01000	21?0
Testudo promarginata	20001	02203	12000	1102
Testudo canetotiana	20201	02103	22100	1110
Testudo antiqua	20001	12103	22000	?1?0
Testudo pyrenaica	20001	02103	22121	?210
Testudo globosa	20001	0230?	?2001	?2??
Gracia	20001	0220?	?2001	?2??
Escale	20001	?2303	22101	121?
Soave	20001	02213	22101	?2??
Lunel	20001	02313	22101	2210
Testudo hermanni boettgeri	20001	12313	22101	2210
Testudo hermanni hermanni	20001	12313	22101	2210
Testudo graeca	20011	22103	32000	1101
Testudo marmorum	30111	02103	?3000	11??
Testudo marginata	30111	22203	33010	1100
Testudo bessarabica	41001	02113	?2010	11??
Testudo horsfieldii	41001	22210	32210	1102
Testudo kazachstanica	41001	22203	22110	1102
Testudo kleinmanni	20001	12230	33311	11?0