PaleoBios 33: 1–13, March 8, 2016

PaleoBios

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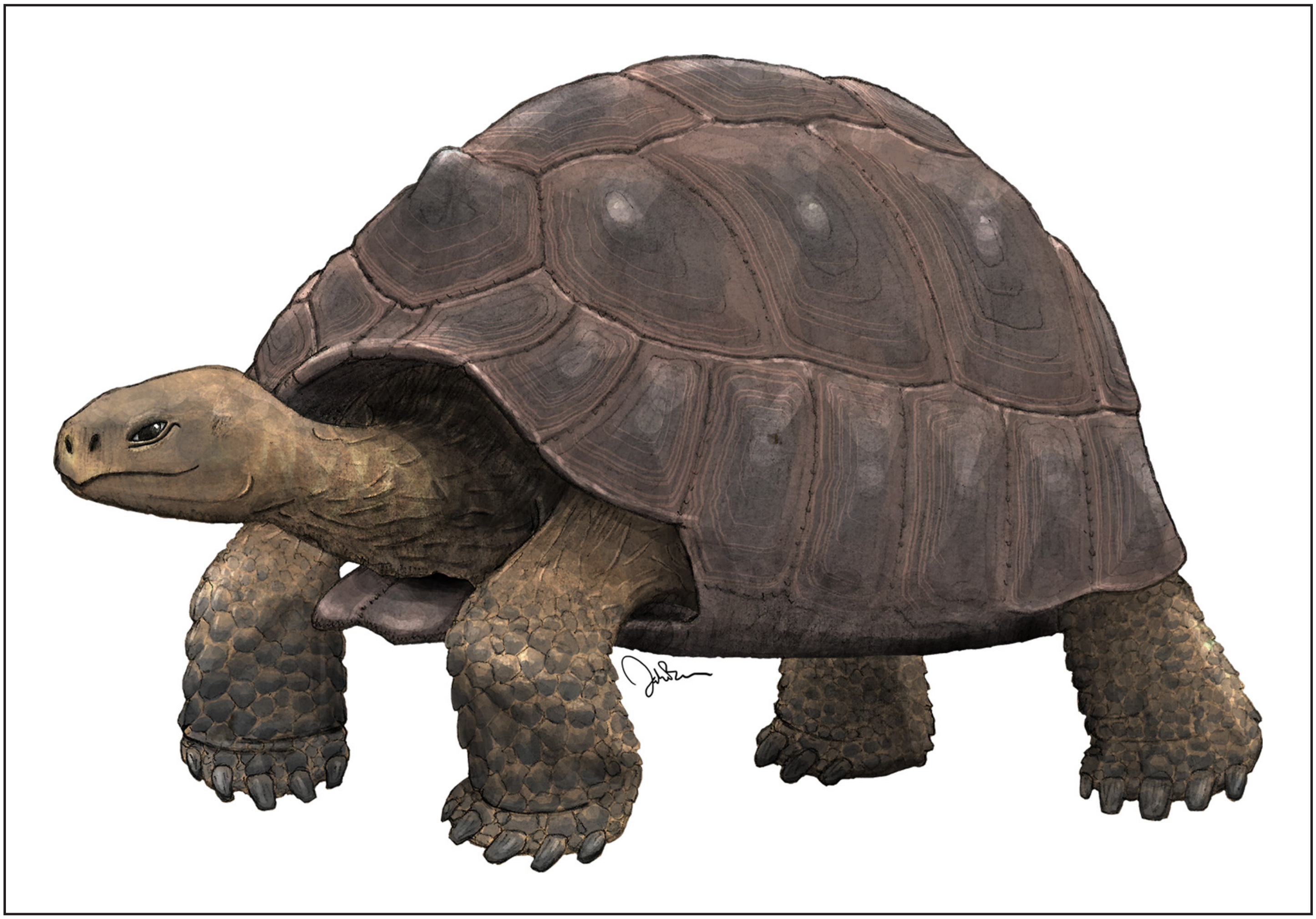

Jacob Biewer, Julia Sankey, Howard Hutchison, Dennis Garber (2016). A fossil giant tortoise from the Mehrten Formation of Northern California.

Cover illustration: Artistic rendering by Jacob Biewer of the giant tortoise, *Hesperotestudo orthopygia* (Cope, 1878), from the Miocene of northern California.

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A fossil giant tortoise from the Mehrten Formation of Northern California

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Hesperotestudo is a genus of giant tortoise that existed from the Oligocene to the Pleistocene of North and Central America. Recorded occurrences in the United States are plentiful; however, California seems to be an exception. Literature on *Hesperotestudo* in California is limited to faunal lists in papers, with few detailed descriptions. Here we review the literature on the genus, describe and identify specimens found in the upper Mehrten Formation (late Miocene-early Pliocene) exposed in the Central Valley of California at Turlock and Modesto Reservoirs, Stanislaus County, and address their implications for early Pliocene California biogeography and climate. All fossils described are from the collections of the University of California Museum of Paleontology (UCMP). The largest specimen from the Mehrten is a peripheral from an animal with an estimated carapace length over one meter. The specimens were compared first to modern material of *Gopherus*, the only other tortoise genus from the late Miocene-early Pliocene of California, and then to measurements from the literature of the three species of *Hesperotestudo* to which it could most likely be referred: *H. osborniana, H. orthopygia, and H. campester.* Based on characteristics and measurements of the carapace and plastron, these specimens are assigned to *H. orthopygia. Hesperotestudo orthopygia* is a species known primarily from the Great Plains region, so its presence in California during the late Miocene-early Pliocene indicates that it expanded west into California at this time. Large tortoises are not very tolerant of frost conditions, possibly indicating a relatively frost free climate for this area at the time. This agrees with previous estimates of annual temperature records based on plant fossils from the upper Mehrten Formation, in particular the presence of *Persea,* an avocado relative, which is also frost sensitive.

Keywords: Tortoise, *Hesperotestudo, orthopygia,* California, Miocene, Pliocene, Mehrten

INTRODUCTION

Hesperotestudo Williams, 1950 is a clade of giant tortoise that existed from the Oligocene to the Pleistocene of North and Central America (Meylan and Sterrer 2000). Fossils have been documented and described across the United States, on the island of Bermuda, as far south as El Salvador, and as far north as Saskatchewan, Canada (Auffenberg 1962, Holman and Tokaryk 1987, Meylan and Sterrer 2000, Cisneros 2005, Bourque et al. 2012). In the past, *Hesperotestudo* was considered a sub-genus of *Geochelone* Fitzinger, 1835. Today *Geochelone* is restricted to a few species in Africa and Asia, so what was once called *Geochelone* in North America is now recognized as a distinct genus, *Hesperotestudo*. *Hesperotestudo* is most closely related to two other North American genera: *Gopherus* Rafinesque, 1832 and *Stylemys* Leidy, 1851 (Franz 2014, Meylan and Sterrer 2000). The ancestor to these three genera first appeared in the New World during the early Eocene, crossing over from Eurasia when the climate was wetter and warmer. Drier conditions in the late Eocene of North America were likely a strong driving force toward these modern lineages that were more tolerant of arid environments. All three genera existed in California; however, *Stylemys* and *Hesperotestudo* went extinct during the middle Miocene and Pleistocene respectively, while the *Gopherus* lineage is still extant today (Franz, 2014).

There are many fossil *Hesperotestudo* specimens and publications that describe or list the genus in North America, including in many parts of the United States (Williams et al. 1952, Auffenberg 1962, 1963, 1971, 1974, Fry 1973, Bourque et al. 2012). However, there is relatively little published information on specifically California occurrences of the genus. Authors generally only include *Hesperotestudo* in their faunal lists, with no detailed descriptions of material or discussion of the genus (Boessenecker and Poust 2015, Brattstrom 1961, Casteel and Hutchison 1973, Jefferson 2001, Miller and Downs 1974, Wagner and Prothero 2001, Murray 2008, Tseng et al. 2009).

Brattstrom (1961) is one of the few published papers that includes illustrations and descriptions of tortoises from California. Of particular relevance, Brattstrom (1961) describes specimens of large tortoises from various Pliocene sites

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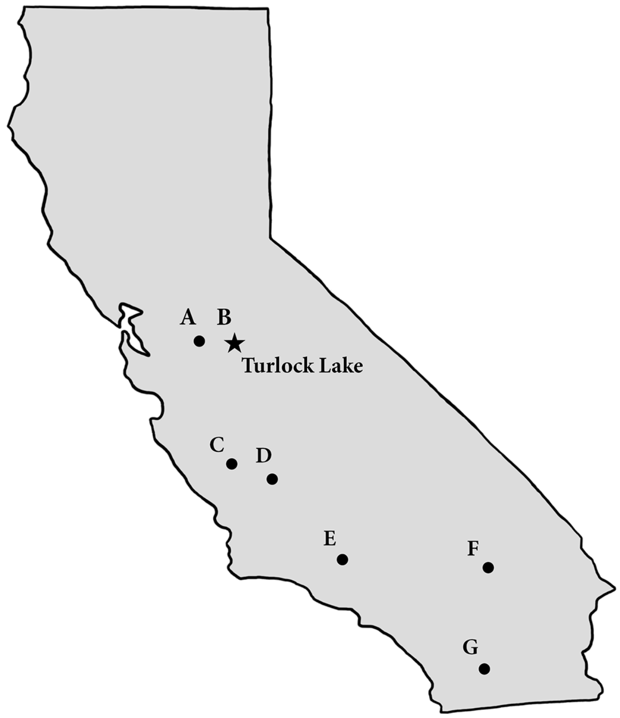


Figure 1A-G. Map of published *Hesperotestudo* localities in California. **A.** Ingram Creek, Miocene (Clarendonian), San Pablo Formation (Brattstrom 1961). **B.** Turlock Lake, late Miocene-early Pliocene (Hemphillian), Mehrten Formation (Casteel and Hutchison 1973, Wagner 1981). **C.** Monocline Ridge, middle Miocene (Barstovian), Temblor Formation (Tseng and Stewart 2009) **D.** Kettleman Hills, upper Pliocene-Pleistocene, Tulare Formation (Boessenecker and Poust 2015). **E.** Hungry Valley, Hemphillian, lower Hungry Valley Formation (Miller and Downs 1974). **F.** Gypsum Ridge, unnamed formation, late Blancan-early Irvingtonian (Wagner and Prothero 2001). **G.** Vallecito Creek–Fish Creek, Pliocene-Pleistocene, Hueso and Tapiado Formations (Jefferson 2001, Murray 2008).

in California, including "many fragments of the shell and limbs of a very large tortoise" from Ingram Creek, Stanislaus County, California (UCMP V3952/36080). We have briefly examined this specimen in the UCMP collections, and it is recorded as from the San Pablo Formation and Clarendonian (North American Land Mammal Age). It is definitely from a large tortoise (*Hesperotestudo*) and is similar in size to the *Hesperotestudo* specimens described here from the upper Mehrten Formation.

Casteel and Hutchison (1973) include *Hesperotestudo* in a short paragraph summarizing the fauna found from the upper Mehrten Formation (Hemphillian) at Turlock Lake, California (the focus of this paper). In Tseng and Stewart (2009), *Hesperotestudo* appears in a preliminary faunal list of the Monocline Ridge Assemblage (Temblor Formation; middle Miocene; Barstovian). Boessenecker and Poust (2015), justify a freshwater or non-marine environment for a section of the Tulare Formation (Pliocene/Pleistocene; Kettleman Hills) from the presence of *Hesperotestudo* in the assemblage. In their systematic discussion of the Hemphillian-aged local fauna from the Hungry Valley-Peace Valley area of the Transverse Range (north-west corner of Los Angeles County), Miller and Downs (1974) note carapace fragments they identify as *Geochelone* based on them being "heavier and thicker than in *Gopherus*." These fragments most likely belong to *Hesperotestudo*. Wagner and Prothero (2001) list *Hesperotestudo* cf. *H. campester* from Gypsum Ridge (Marine Corps Air Ground Combat Center; late Blancan-early Irvingtonian). Murray (2008) lists a few elements of *Hesperotestudo* that had been originally misidentified as bear and mammoth material. The specimens are from the Hueso and Tapiado Formations; Vallecito Creek–Fish Creek Section of Anza-Borrego Desert, California, and are Plio-Pleistocene in age. Jefferson (2001) also refers to *Geochelone* specimens from Vallecito Creek–Fish Creek as well but these are likely *Hesperotestudo*.

We compiled all published records of *Hesperotestudo* from California in a distribution map (Fig. 1). We found these publications using two methods. First, we searched the fossil databases for published records of *Hesperotestudo* in the University of California Museum of Paleontology, Berkeley and the Natural History Museum of Los Angeles County collections. Second, we searched for publications online using the key words *Hesperotestudo*, California, Miocene, and Pliocene. Although the map is preliminary, it provides a foundation to our current knowledge on which to build with publications we may have missed, and the many museum specimens of *Hesperotestudo* that have yet to be recorded in the literature.

GEOLOGIC SETTING

The Mehrten Formation (Miocene-Pliocene) is an andesitic volcanic-sedimentary unit exposed in the low foothills of the Sierra Nevada along the eastern margin of the northern San Joaquin Valley of California, from Sacramento to Merced. Numerous vertebrate fossil sites occur in the upper Mehrten Formation exposed in and around Turlock Lake and Modesto Reservoir, Stanislaus County (Fig. 2). Mammals from the uppermost Mehrten are numerous and well documented, including for example, many specimens of horse, camels, giant sloths, and mastodons (Wagner 1981). There are also many fossils of turtles, amphibians, and fish, including the giant tusk-tooth salmon *Oncorhynchus rastrosus* Cavender and Miller, 1972.

Most fossils found in the Mehrten Formation come from its uppermost division, the Modesto Reservoir Member,

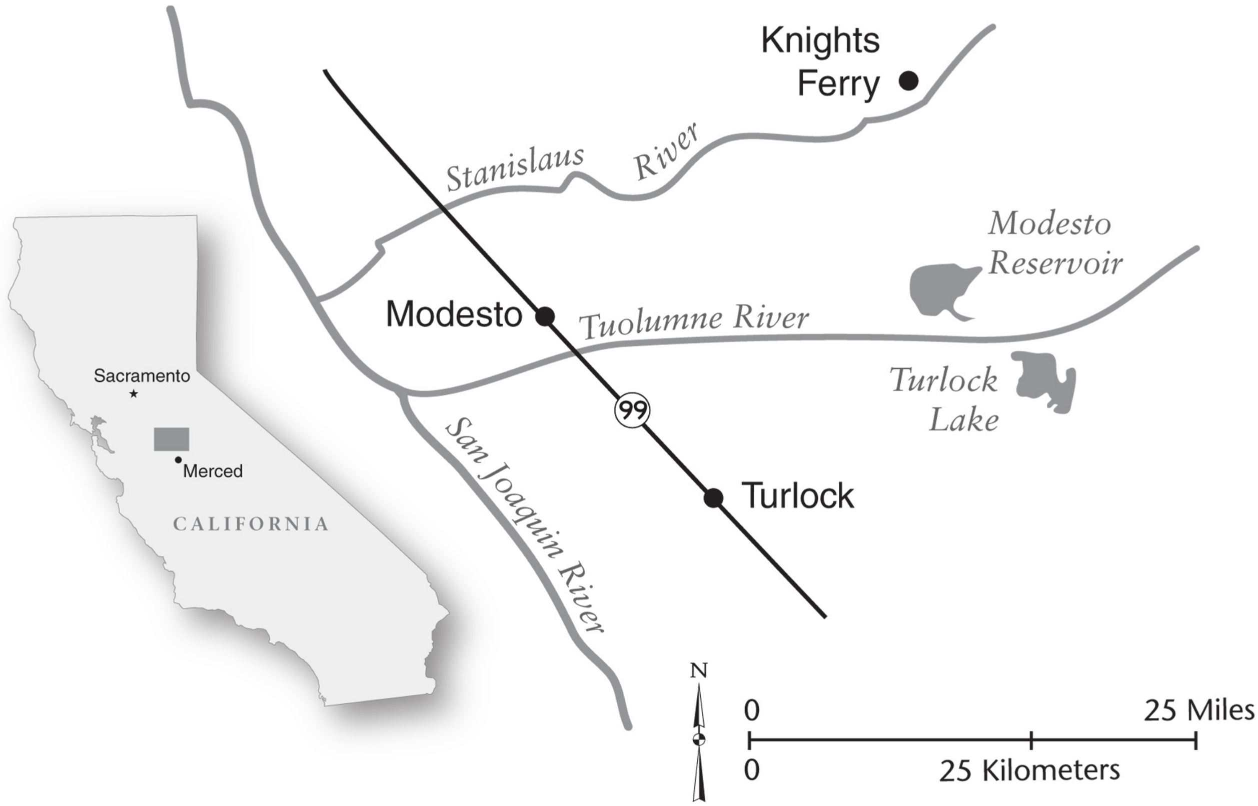


Figure 2. Central Valley of California showing locations of Turlock Lake and Modesto Reservoir.

which will be referred to in this paper as the upper Mehrten Formation (Fig. 3). The upper Mehrten Formation is Hemphillian and approximately 5 Ma (Wagner 1981) based on two lines of evidence: 1) correlation to the Pinole Formation based on similarities in the mammalian faunas and 2) a dated tuff within the Pinole Formation, approximately 5 Ma. The Pinole is part of Hh4, the last phase of the Hemphillian LMA, which straddles the Miocene-Pliocene boundary (Tedford et al. 2004).

The Mehrten Formation consists primarily of andesitic sedimentary deposits representing stream, lake, and floodplain environments. In places, such as the Knights Ferry area, the Mehrten Formation is interfingered with volcanic flows that had their source to the east of the current-day Sierran crest near the Little Walker Caldera (Wagner 1981). The fossils from Turlock Lake and Modesto Reservoir come from tuffaceous siltstones and sandstones representative of a river flood plain depositional environment, with the presence of possible lahar deposits. The tortoise material from Modesto Reservoir comes from one small island in the middle of the reservoir (UCMP V71138). According to a preliminary geologic map of Turlock Lake by Marchand and Wagner (1980), all of the Turlock Lake tortoise sites, with one exception, come from the same geologic sub-unit of the upper Mehrten Formation mapped as Tmo. They describe

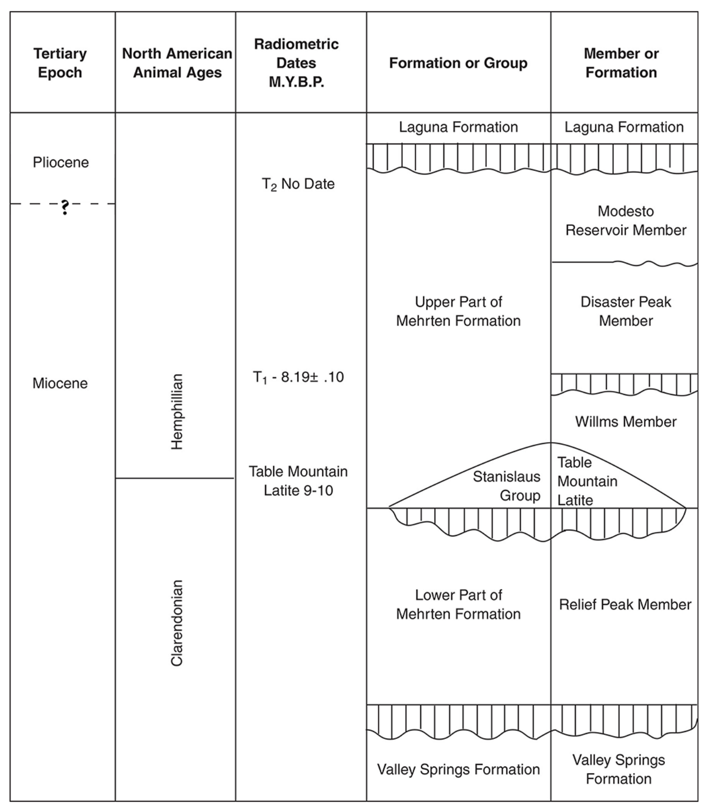
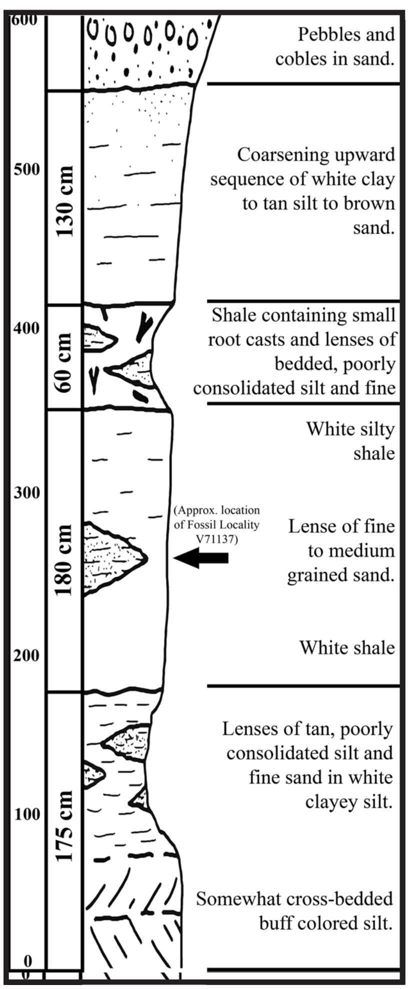


Figure 3. Stratigraphy of the Mehrten Formation and adjacent formations. Modified from Wagner (1981).

Figure 4. Photograph of island tortoise site (UCMP V71137). Arrow points to stratigraphic position of the site.



Tmo as brown sandstone, siltstone, and conglomerate that unconformably overlies pinkish siltstone. A majority of the larger and more complete tortoise specimens from Turlock Lake come from an island within the lake (UCMP V71137; Fig. 4). This fossil site is a cliff face that is exposed over a large portion of the island's southern shore (Fig. 5). Close to and stratigraphically above another tortoise locality at Turlock Lake (V81248) there are cross-bedded sands, gravels, and cobble size rip-up clasts of pink silt above a sharp, erosional unconformity cutting into flood plain deposits. These deposits are evidence of a large river we have termed the "Proto-Tuolumne," after the nearby river. They likely signal a change in the topography to one of higher relief where previously there had been much lower relief indicated by fossil *Orthodon microlepidotus* Ayres, 1854, the Sacramento Blackfish, which avoided fast moving rapids, and the remains of plants that grew in and around flood plains (Casteel and Hutchinson 1973, Axelrod 1980). There are also lenses of water lain tuff in a few locations around the lake. These tuffs are heavily weathered, making it difficult to obtain usable samples, but could potentially be used to better constrain the age of the upper Mehrten Formation at Turlock Lake.

Two sites in the upper Mehrten Formation at Turlock Lake produced numerous fossil leaves of shrubs and trees such as oaks and sycamores. These plant fossils provide information

◀ **Figure 5.** Stratigraphic column of island site (UCMP V71137).

on the riparian biomes that existed in the area at the time. The most common plant remains belong to species that were largely confined to the borders of streams and lakes (Axelrod 1980). Based on the present day locations of taxonomically closest species, there are two main plant communities represented: oak savannah and river floodplain (Axelrod 1980). These habitats, which occupy slightly higher elevations than in the Central Valley today, were relatively lower due to the more mild conditions during the early Pliocene. The Central Valley was wetter, with an estimated 635 mm of rainfall throughout the year (Axelrod 1980), double the current average annual rainfall for central California. Unlike today, a larger portion of this rainfall would have fallen during the summer months. Additionally, the temperatures were milder, with average July temperature approximately 22°C and average January temperature approximately 9°C (Axelrod 1980) (today these are approximately 25°C and 8°C respectively). These differences would have been due to the lower elevation of the Coast Ranges, which today produce a rain shadow effect in the Central Valley (Axelrod 1980).

The numerous and well preserved fossil tortoise specimens from the upper Mehrten Formation at Turlock Lake and Modesto Reservoir are important for two reasons. First, they allow a species level identification to *Hesperotestudo orthopygia* Cope, 1878. This species is best known from the Great Plains, suggesting that it expanded into California during the late Miocene to early Pliocene. Second, large tortoises today do not live in areas with severe winters. The presence of large tortoises in the Central Valley of California during the early Pliocene suggests that paleoclimatic conditions were milder than at present, which is supported by the paleobotanical evidence.

MATERIALS and METHODS

Many vertebrate and plant fossils were collected from the upper Mehrten Formation at Turlock Lake and Modesto Reservoir by Dennis Garber in the 1970s and subsequently deposited at the UCMP and LACM. The tortoise fossils described here are from the collections of UCMP. The tortoise fossils come from seven localities in and around Turlock Lake and Modesto Reservoir. From these sites there are 19 specimen numbers representing over 50 pieces of plastron and carapace (Table 1). Identification of the tortoise specimens is based on comparison to the only two known testudinid genera in the late Miocene and Pliocene of California: *Hesperotestudo* and *Gopherus.* To determine genus, the material from the Mehrten Formation was measured with digital calipers and compared against modern skeletal *Gopherus* housed at the University of California Museum of Vertebrate Zoology (MVZ) and to equivalent measurements of *Hesperotestudo* from the literature. Features of the plastron most closely resemble those of the subgenus *Hesperotestudo* of Auffenberg (1963), which includes *H. orthopygia, H. osborniana* Hay, 1905, and *H. campester* Hay, 1908, so the material was next compared to measurements of these three species from Hay (1908) and Oelrich (1952). A large portion of the material cannot be identified or can only be generally identified as belonging to the plastron or carapace.

Table 1. List of UCMP locality and specimen numbers for material of *Hesperotestudo,* upper Mehrten Formation, Turlock Lake and Modesto Reservoir (Dallas-Warner Reservoir), Stanislaus County, CA.

Locality Name	Locality Number	Specimen Number
Turlock Lake General	V65711	232060
Turlock Lake General	V65711	232061
Turlock Lake	V6878	132084
Turlock Lake 10	V71137	132086
Turlock Lake 10	V71137	134831
Turlock Lake 10	V71137	137148
Turlock Lake 10	V71137	95918
Dallas-Warner Reservoir 1	V71138	132055
Dallas-Warner Reservoir 1	V71138	134832
Dallas-Warner Reservoir 1	V71138	136528
Dallas-Warner Reservoir 1	V71138	137147
Dallas-Warner Reservoir 1	V71138	95919
Dallas-Warner Reservoir 1	V71138	95920
Turlock Lake 11	V81248	131793
Turlock Lake 11	V81248	131794
Turlock Lake 11	V81248	132087
Turlock Lake 11	V81248	134830
Turlock Lake 13	V90007	136527
Turlock Lake 14	V90008	136526

Institutional Abbreviations

UCMP, University of California Museum of Paleontology, Berkeley; **MVZ**, University of California Museum of Vertebrate Zoology, Berkeley; **CSUS**, California State University Stanislaus; **LACM**, Natural History Museum of Los Angeles County.

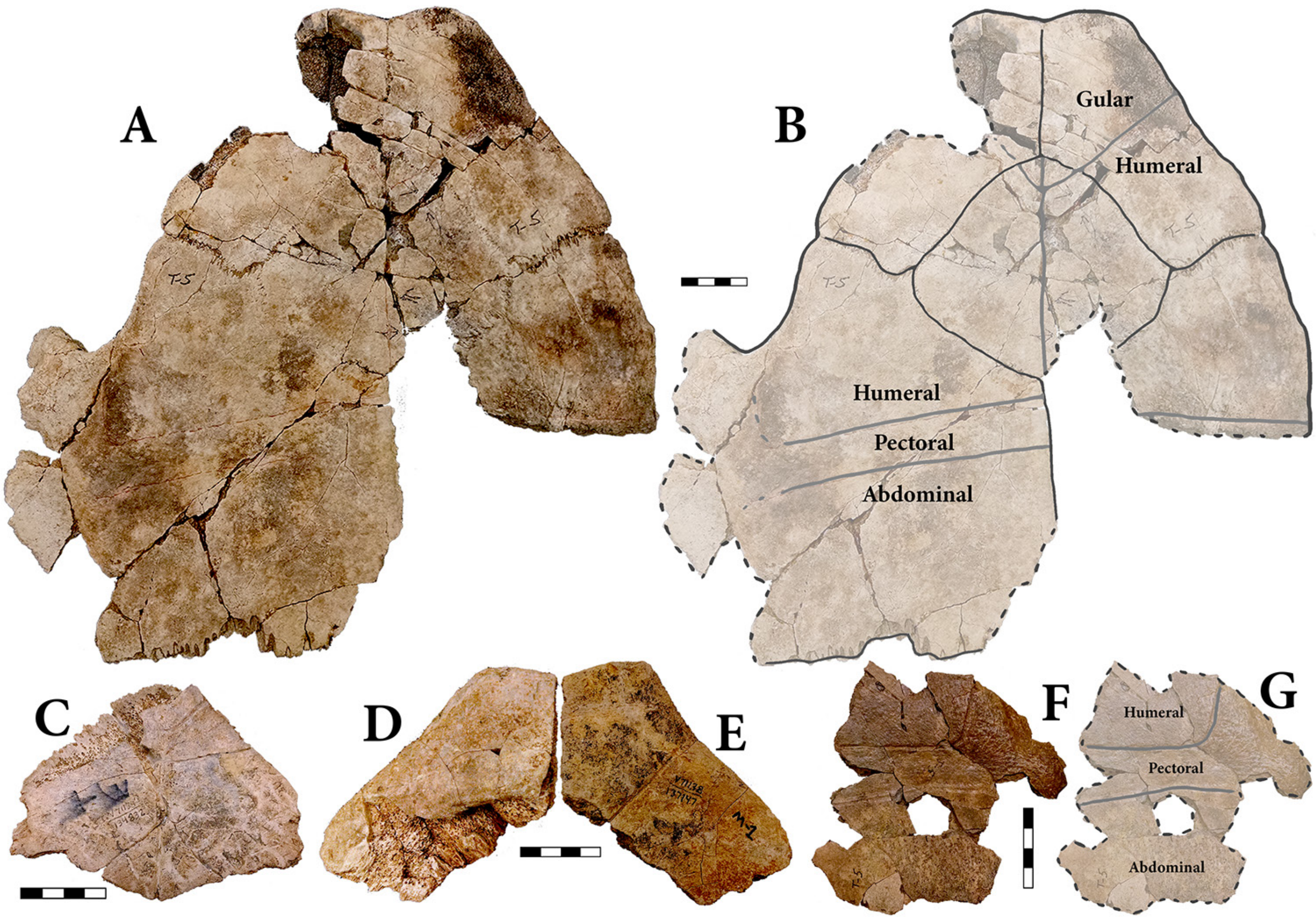


Figure 6A-G. Elements of the anterior plastron. **A.** Ventral view of UCMP 131794, anterior plastral lobe including left and right epiplastra, entoplastron, right and partial left hyoplastron. **B.** Locations of sutures, dark grey and sulci, light grey. **C.** Entoplastron, UCMP 134832. Ventral view of sulci, separating humeral scales and gular scales visible. **D.** Dorsal View of left epiplastron, UCMP 137147. **E.** Ventral view showing sulcus between gular and humeral scales. **F.** Ventral view of Partial left hyoplastron, UCMP 95919, showing sulci between humeral, pectoral, and abdominal scales. **G.** Location of sulci. Scale bars=4 cm.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768
TESTUDINES Batsch, 1788
TESTUDINIDAE Gray, 1825
HESPEROTESTUDO Williams, 1950
Hesperotestudo orthopygia (Cope, 1878)
Figs. 6-12

Xerobates orthopygius Cope, 1878: 393.
Testudo orthopygia (Cope, 1878): Hay, 1899:349.
Geochelone (Hesperotestudo) orthopygia (Cope, 1878): Williams, 1950:30.
Hesperotestudo orthopygia (Cope, 1878): Holotype—AMNH 5868.

Referred specimens—UCMP: 232060, 232061 (V65711); 132084 (V6878); 136086, 134831, 137148, 95918 (V71137); 132055, 134832, 136528, 137147, 95919, 95920 (V71138); 131793, 131794, 132087, 134830 (V81248); 136527 (V90007); 136526 (V90008).

Description

Epiplastron—There are epiplastra from two individuals present in the assembled material: UCMP 131794 (Fig. 6A, B), a complete left and mostly intact right attached to the adjacent plastral elements, and UCMP 137147 (Fig. 6D, E), an isolated left from a smaller individual. From the anterior end to about 60 mm posterior, they thicken dramatically: to 37 mm for the former specimen and 35.5 mm for the latter. At this point there is a sudden drop off forming the epiplastral excavation, a ridge below which there is an anterior excavation that gently slopes down to the relatively uniform thickness of the rest of the plastron. This ridge and midline

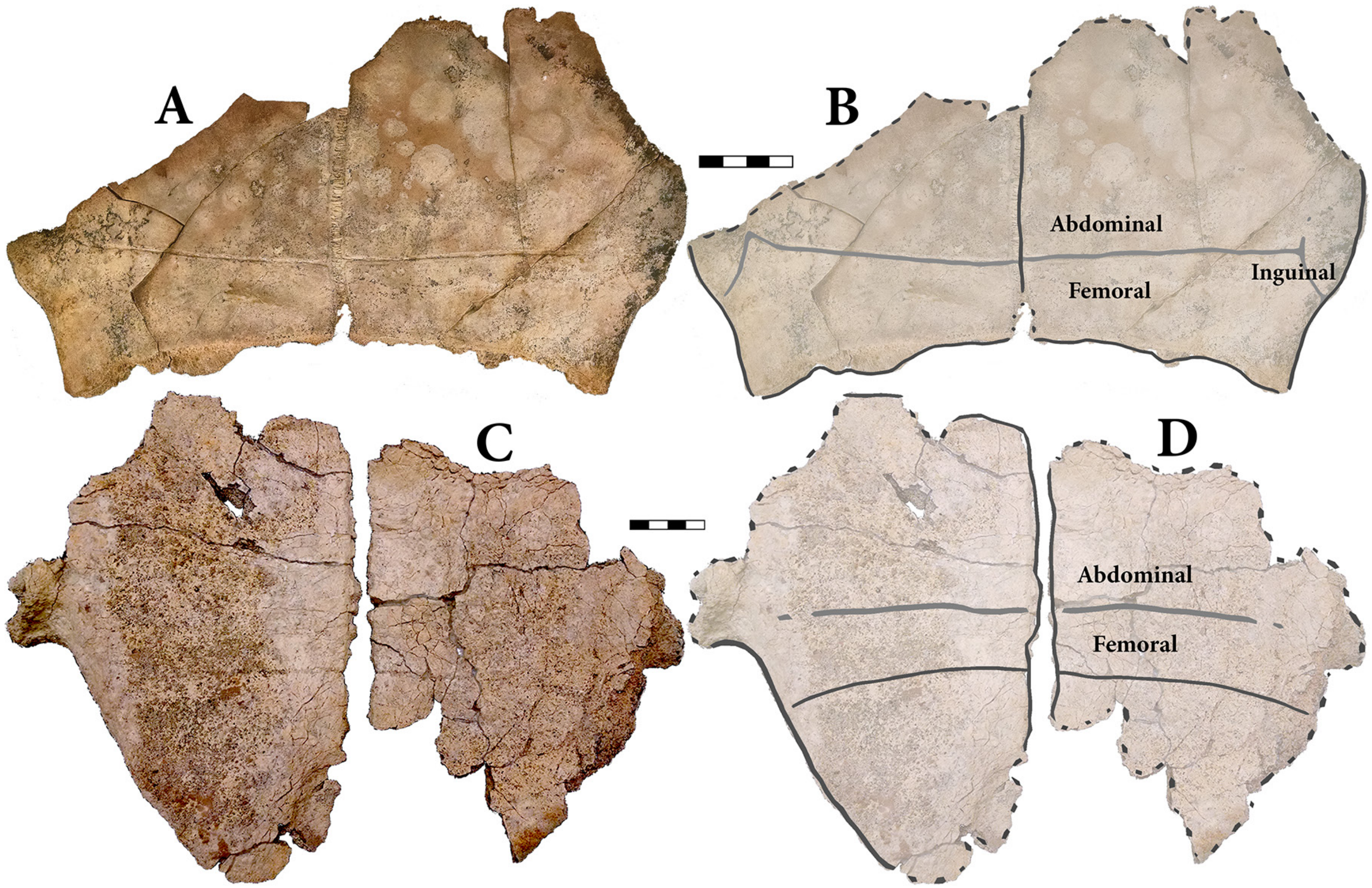


Figure 7. A. Ventral view of articulated right and partial left hypoplastron, UCMP 136527. **B.** Locations of sutures and of sulci between abdominal, femoral, and inguinal scales, UCMP 136527. **C.** Ventral view of posterior plastron including most of left and right hypoplastron and xiphiplastron, UCMP 134830. **D.** Locations of sutures and sulci between abdominal and femoral scales, UCMP 134830. Scale bars=4 cm.

Table 2. Shell measurements (in mm) of the Mehrten Formation tortoise material in comparison with those of *H. osborniana* and *H. orthopygia* from Hay (1908) and *H. campester* from Oelrich (1952). *Estimated.

	Mehrten Formation	Hay (1908)		Oelrich (1952) Campester (*rexroadensis*)	
		osborniana	*orthopygia*		
	UCMP 95919	AMNH 5868	AMNH 3929	UMMP 28124	KU
Pygal Free Margin Width	44	80	75	-	-
Pygal Dorsal Width	53	114	-	-	-
Pygal Length	70	83	75	125	-
	UCMP 131794				
Hyoplastron Midlength	148	140	115	145	137
Entoplastron Length	100	153	110	-	187
Entoplastron Width	130	210	160	-	195
Pectoral in Midline	27	10	18	44	42
Maximum Plastron Length	620*	710	515	777	710
	UCMP 95918				
Peripheral Thickness	37	23	34	57	-
	UCMP 134831				
Costal Thickness	15	-	8	22	-

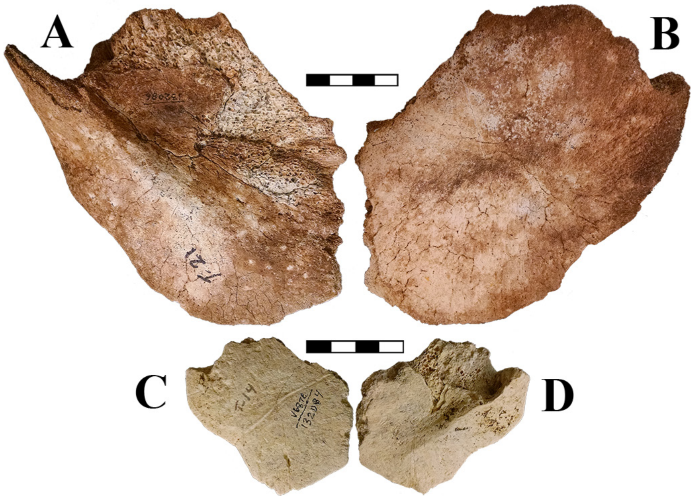


Figure 8A-D. Two xiphiplastra. **A.** Dorsal view of UCMP 132086, a left xiphiplastra. **B.** Ventral view of UCMP 132086 showing sulcus between femoral and anal scales. **C.** Ventral view of UCMP 132084, right xiphiplastron showing sulci. **D.** Dorsal view of UCMP 132084. Scale bars=4 cm

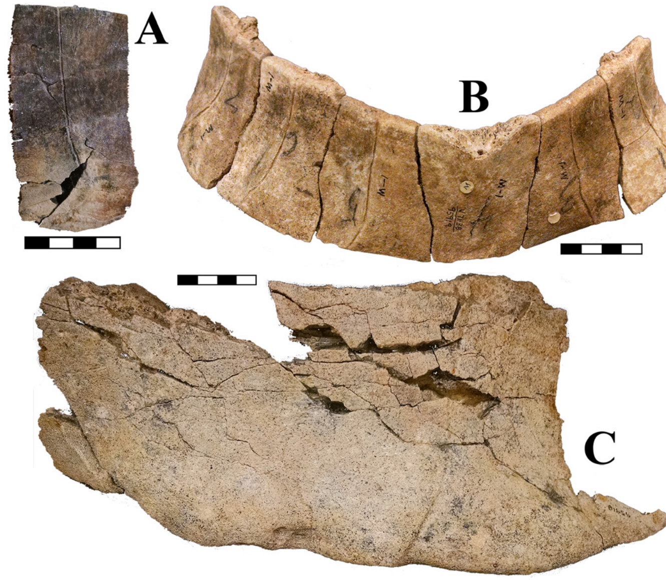


Figure 9A-C. Peripherals. **A.** Right peripheral 5, lateral view, UCMP 97986. **B.** Pygal, left and right peripheral pairs 10-11, and left peripheral 9, posterior view showing sulci separating marginal scales, UCMP 95919. **C.** Lateral view, two articulated partial left peripherals, UCMP 95918. Scale bars=4 cm.

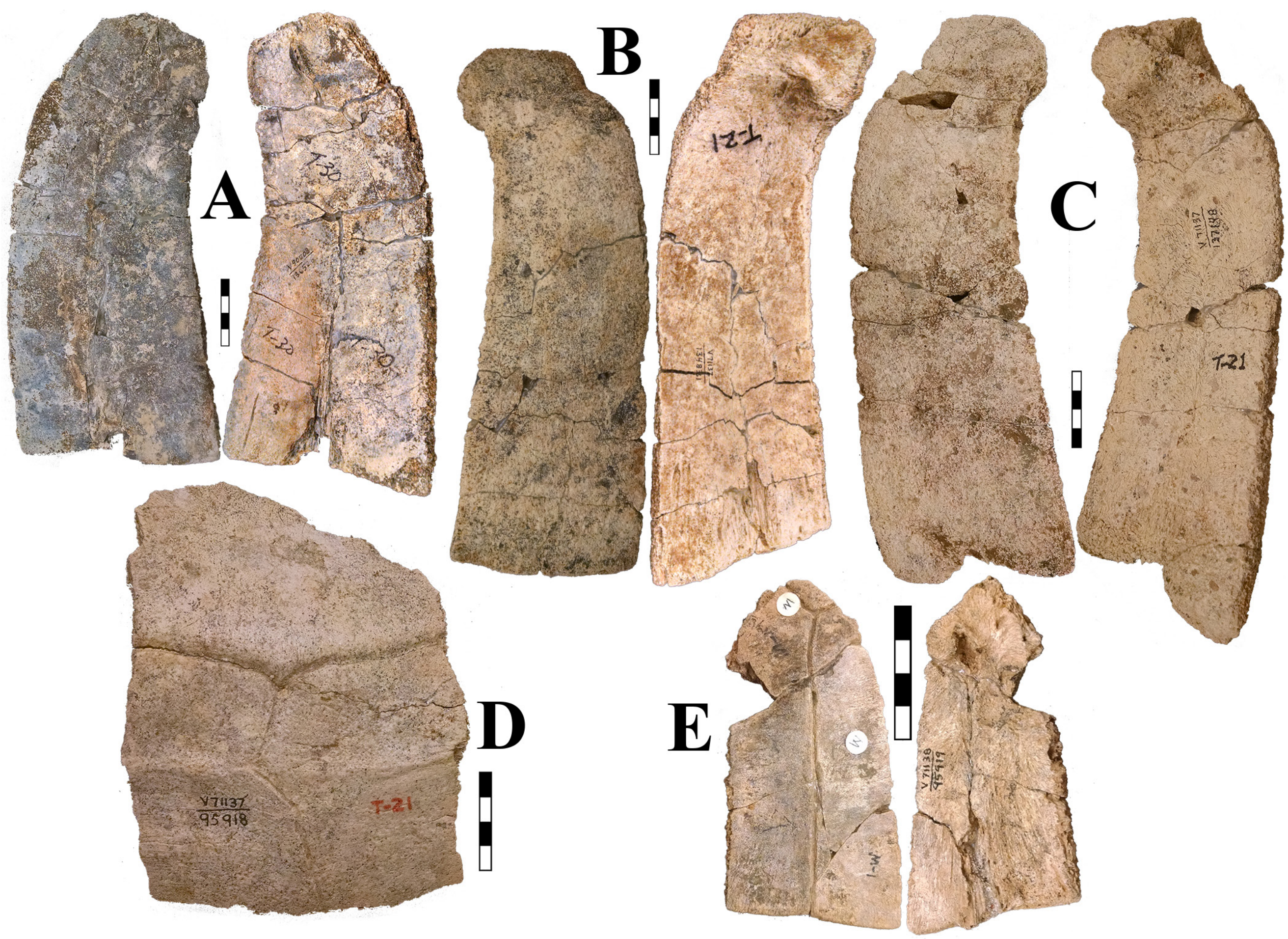
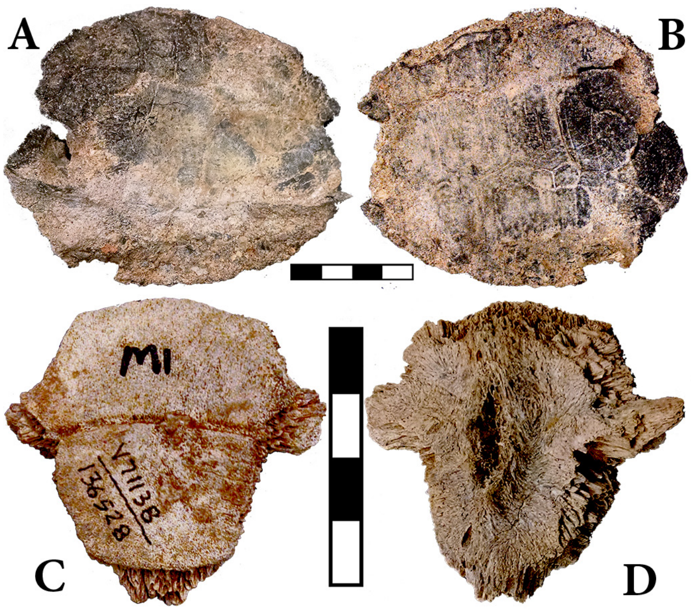


Figure 10A-E. Identified costals in external and visceral views. **A.** UCMP 136526. **B.** UCMP 134831. **C.** UCMP 137148. **D.** UCMP 95918. **E.** UCMP 95919. Scale bars=4 cm.



◀ **Figure 11. A.** Ventral view of juvenile shell with sulci divisions of plastron partly visible, UCMP 131793. **B.** Dorsal view, suture and sulci visible, UCMP 131793. **C.** Dorsal view of neural 8, showing sulcus, UCMP 136528. **D.** Ventral view of UCMP 136528 showing neural arch scar. Scale bar=4 cm.

thickening taper laterally. These epiplastra would take up 57.5 mm and 72.8 mm of the total midline plastron length respectively. The anterior margin between the anterior tips of the epiplastra forms a shallow v-shaped concave emargination. On both specimens, the sulci dividing the gular and humeral scales are visible and deeply impressed.

Entoplastron—There are also two entoplastra present: one part of an articulated anterior plastral lobe, UCMP 131794 (Fig. 6A, B), and the other isolated, UCMP 134832 (Fig. 6C). Both are roughly diamond-shaped with a broad and rounded posterior and sharper anterior point. Their inner surfaces are concave and thinner by a few millimeters at the center (scapula attach site) relative to the edges. They are wider than long, 130 mm by 100 mm for UCMP 134832 and 149

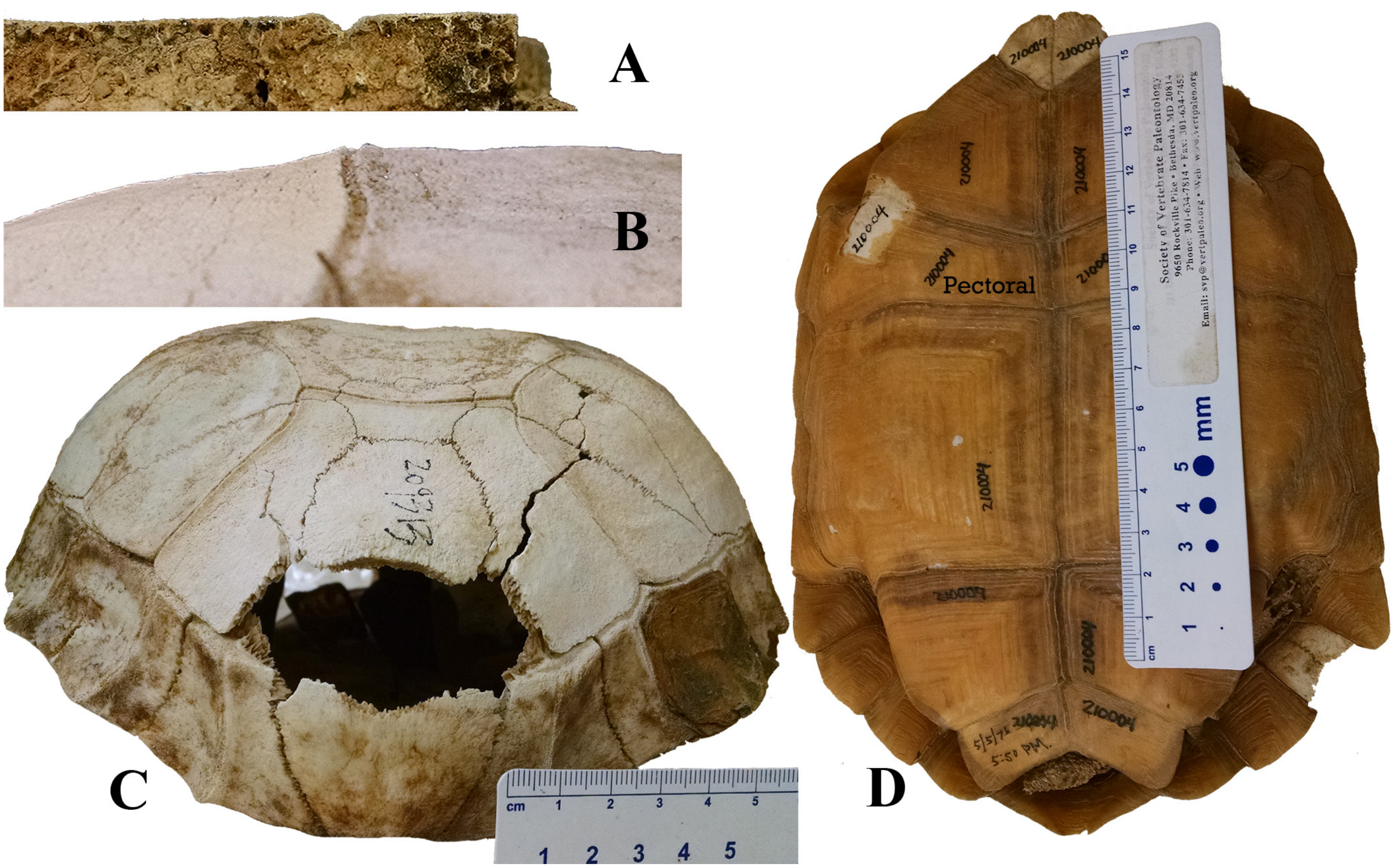


Figure 12A-D. A. Cross-section of Mehrten carapace with sulcus pressed into bone, UCMP 134832. **B.** Profile of *Gopherus* carapace, edges of sulci are perched, MVZ 209313. **C.** Posterior view of *Gopherus agassizi* carapace showing shape of pygal and perched sulci, MVZ 209313. **D.** Ventral view of a *Gopherus agassizi* plastron showing length of the pectoral scale in the midline relative to total length of the plastron, MVZ 209313.

Table 3. Measurements of modern *Gopherus* shell elements compared to equivalent measurements from the material of the Mehrten Formation. *Estimated.

MVZ #	Pectoral Scale Width	Plastron Length	Ratio of Length to Scale
210020	19.1	219.6	11.5
210009	18.8	232.8	12.4
210010	10.1	240.1	23.8
210003	15.5	192.1	12.4
210004	17.6	196.7	11.2
Average	16.2	216.2	13.3
Mehrten	27.0	622*	23.0
	Pygal Width	Pygal Height	Shell Thickness
210070	36.9	27.5	2.9
209345	41.2	31.8	3.0
209313	42.7	25.1	4.3
209364	34.3	18.4	2.5
209343	36.3	28.2	3.1
Average	38.3	26.2	3.2
Mehrten	50.0	65.0	7.0

mm by 123 mm for UCMP 131794, a trait seen in both *H. osborniana* and *H. orthopygia* (Table 2).

Hyoplastron—UCMP 131794 (Fig. 6A, B) includes an intact right hyoplastron, that preserves a portion of the bridge, and anterior half of a left hyoplastron. UCMP 95919 (Fig. 6F, G) is a partial left hyoplastron lacking the left bridge. On UCMP 131794, the hyoplastra measure 150 mm at the midline. The distance across the base of the anterior plastral lobe (between the right and left axillary notch) is 308 mm. The hyoplastra are thinnest, 8-9 mm, near the midline and near the suture with the hypoplastron. They are thickest, 26 mm, near the free border at the sutures with the epiplastra. On UCMP 131794 the sulci between the pectoral and abdominal scales are visible on the right (Fig. 6A, B). Both these sulci are visible on UCMP 95919 (Fig. 6F, G). The pectoral scales narrow at the midline to about 27 mm and 24 mm respectively, and maintain this narrowness until widening markedly near the bridge.

Hypoplastron—There are two pairs of hypoplastra. UCMP 136527 (Fig. 7A, B) is an articulated left and right hypoplastra missing a section of the right anterior edge, and UCMP 134830 (Fig. 7C, D) consists of disarticulated left and right hypoplastra that are missing varying portions of their anterior margins and bridges. Both are thickest at the bridge and then thin to 7 - 10 mm at the thinnest part near the midline. There is a linear bulge on each that extends perpendicular to the midline between the bridges that are 14 mm and 16 mm thick respectively. The hypoplastra measure roughly 159 mm and 136 mm along the midline respectively. The sulci separating the abdominal, femoral, and inguinal scales are visible on the ventral sides (Fig. 7B, D). There is extensive contact between the femoral and inguinal scales (Fig. 7B, D).

Xiphiplastron—There is a partial pair of xiphiplastra attached to the previously mentioned disarticulated hypoplastra, UCMP 134830 (Fig. 7C, D), as well as two isolated elements, UCMP 132086 and UCMP 132084 (Fig. 8A-D). The joined pair is intact with the exception of the posterior left side. They are thickened dorsally on the free margin to about 25 mm forming a ridge which then quickly curves down and thins toward the midline to 9 mm. On the ventral side of the disarticulated specimens the sulci between the femoral and anal scales are distinctly visible (Fig. 8B, C). This sulcus is obscure on UCMP 134830.

Peripherals—Of the many peripheral fragments present in the collection, only three specimens can be placed as to carapace position. UCMP 97986 (Fig. 9A) is a right peripheral 5. UCMP 95919 (Fig. 9B) consists of the pygal, the peripheral pairs 10 and 11, and the left peripheral 9. The third, UCMP 95918 (Fig. 9C) is a large segment of two left peripherals missing the dorsal edge. While the pygal has a relatively flat outer surface, the free margins of the peripherals progressively flare anterolaterally, giving them a curved surface. Each of the peripherals has intermarginal sulci that cross them from dorsal to ventral margins and curve anteriorly near the lateral margin. The pygal lacks intermarginal sulci, has a relatively rectangular shape that is taller than wide, 71 x 45 mm at the free margin and 53 mm dorsally. There is a difference in thickness among individual specimens measured at their thickest point. UCMP 95918 is 37 mm thick and nearly twice as thick as UCMP 95919 (23.3 mm). UCMP 95919 has a width of 54 mm measured along the free margin while UCMP 95918 is 146 mm wide.

Costals—There are five costals in the material from the Mehrten Formation: UCMP 136526 (Fig. 10A),UCMP 134831 (Fig. 10B), UCMP 137148 (Fig. 10C), UCMP 95918 (dorsal part) (Fig. 10D), and UCMP 95919 (Fig. 10E). The costals in Figure 10A-C and E have the same elongate shape and about the same thickness, 15 mm, with the exception of the smaller specimen that is only 6.7 mm thick. The fifth (Fig. 10D), which belongs to the same animal as the large peripherals, has a maximum thickness of 27 mm before thinning to 15 mm. The origin of the rib head on the four complete specimens (UCMP 134831, UCMP 137148, UCMP 136526, UCMP 95919) occurs about 19 mm (15 mm for the smaller specimen) away from the dorsal suture. The sulci separating the pleural and vertebral scales are visible on all four, in some places lightly and in others deeply impressed.

Juvenile—UCMP 131793 (Fig. 11A, B) is the crushed carapace and plastron of a young tortoise, lacking most or all of the free margins. It is 103 mm long and 92 mm wide as preserved. The bones, inferred scales, and sulci between them are generally visible on each side.

Neural—There is a single small neural, UCMP 136528 (Fig. 11C, D). On the underside the neural arch is visible. An intervertebral sulcus traverses the dorsal surface scales. The greater length than width, lateral sutural projections indicating intercostal articulation and presence of an intervertebral sulcus suggest neural 8.

DISCUSSION

Identification

The material of the Mehrten Formation fossil tortoise is much larger and thicker than equivalent elements from *Gopherus* and appears closer in many features to *Hesperotestudo.* The free margin of the carapace is thicker and more rounded than in *Gopherus*. We compared the large peripheral (Fig. 9C) to measurements from relevant figures in Hay (1908) and estimate a total carapace length of approximately 1200 mm. Sulci on the carapace and plastron are deeply impressed into the bone (Fig. 12A). These impressed sulci are reminiscent of the condition in *Hesperotestudo* and unlike *Gopherus* where they are perched above the general plane of the surface as raised ridges (Fig. 12B). In *Hesperotestudo* and in the Mehrten specimens, the entoplastron is wider than long (Table 2). One of the most defining characteristics of *Hesperotestudo* is the narrowness of the pectoral scale. *Gopherus* has a wide pectoral scale relative to its body length (Fig. 12D, Table 3). Among the *Hesperotestudo* examined, *H. osborniana* has the narrowest pectoral scale and *H. campester* the widest, with the pectoral scale of *H. orthopygia* ranging between the two (Table 2). The Mehrten specimens more closely resemble *H. orthopygia* in narrowness of the pectoral scale (Table 2). The Mehrten fossils more closely match Hesperotestudo by having extensive contact between these two scales (Fig. 7A,B). In *Hesperotestudo* there is extensive contact between the femoral and inguinal scales while in *Gopherus* there is little contact. The Mehrten fossils more closely match *Hesperotestudo* by having extensive contact between these two scales. The pygal and peripherals in *Hesperotestudo* are taller than wide and rectangular in shape (Hay 1908) while in *Gopherus* they are wider than tall and trapezoidal (Fig. 12C, Table 3). The Mehrten specimens more closely match the described pygal shape of *Hesperotestudo* than *Gopherus* (Fig. 9B), and are similar to measurements of *H. osborniana* and *H. orthopygia* (Hay 1908) (Table 2). In most *Hesperotestudo*, there is a thinning of the carapace (Hay 1908). Thinning of the carapace is seen in the Mehrten material as well as in the literature describing *H. osborniana*, and *H. orthopygia* (Hay 1908). However, this thinning of the shell is a trait that is not seen in *H. campester* (Oelrich 1952) (Table 2). In *Gopherus*, the origin of the rib head on the costals is extremely close to the dorsal suture, while in *Hesperotestudo* they are more distally located. The locations of the rib heads on the Mehrten specimens more closely match *Hesperotestudo*.

The Mehrten tortoise material is diagnosed as *Hesperotestudo* based on the thicker shell, large size, impressed sulci, more rectangular shaped pygal that is taller than wide, and the narrowness of the pectoral scale in the midline relative to body length. The extreme narrowness of the pectoral scale in the Mehrten specimens is indicative of *Hesperotestudo* of Auffenberg (1963). Among species of *Hesperotestudo*, the material most closely resembles *H. orthopygia*, *H. osborniana*, and *H. campester* in three ways. The entoplastron is wider than long, there is extensive contact of the femoral and inguinal scales, and the pygal is rectangular shaped. The early Pliocene age of the Mehrten specimens matches more closely the species *H. orthopygia* and *H. campester*, than it does *H. osborniana,* a species that lived during the Miocene. The hyoplastron takes up a larger proportion of the total length in *H.*

orthopygia and *H. osborniana* as compared to *H. campester*. The pectoral scale is not as extremely narrowed as in *H. osborniana* and not as wide as in *H. campester*. Based on this evidence we place the Mehrten specimens in *H. orthopygia*.

Climate

Tortoises can be good indicators of climate. The presence of fossils from a large reptile like *Hesperotestudo* in this area possibly shows that there was little to no frost present throughout the year because giant tortoises are not tolerant of heavy frost conditions (Hibbard 1960, Fry 1973). This agrees with the paleoclimate interpretations based on the plant fossils of the Mehrten Formation, especially *Persea coalingensis* Axelrod, 1944, a relative to the avocado, which is not frost tolerant (Axelrod 1980).

CONCLUSIONS

This paper describes and identifies the numerous and well preserved fossils of a large tortoise from the upper Mehrten Formation (early Pliocene) of California. We identify the tortoise as *Hesperotestudo orthopygia*, a tortoise best known from the Great Plains of the United States. This is the first thorough description of *Hesperotestudo* from California. We based our identifications on the following characteristics: the shorter, wider entoplastron, long midline length of the hyoplastron, more rectangular shaped pygal, extensive contact of the femoral and inguinal scales, and similarity of age (early Pliocene), with previously described material (Hay, 1908; Oelrich, 1952). Because *H. orthopygia* is a species best known from the Great Plains region of the United States, its presence in the Central Valley of California during the late Miocene-early Pliocene indicates hat it migrated west at this time. In addition, extant, large, non-burrowing, tortoises are not frost tolerant, and this supports the paleobotanical evidence that this area had a milder climate during the early Pliocene than today.

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