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REAPPRAISAL OF THE HOLOTYPE OF *"TESTUDO" COSTARRICENSIS*, A TORTOISE SUPPOSEDLY FROM THE OLIGOCENE OR LOWER MIOCENE OF COSTA RICA

REEVALUACIÓN DEL HOLOTIPO DE *"TESTUDO" COSTARRICENSIS*, UNA SUPUESTA TORTUGA DEL OLIGOCENO O MIOCENO INFERIOR DE COSTA RICA

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ABSTRACT: *"Testudo" costarricensis* was described as a basal tortoise from the Oligocene or lower Miocene of Costa Rica and considered as evidence of a migration of tortoises from North America to South America to provide an ancestor to the modern genus *Chelonoides.* However, this was based on an incorrect reconstruction of the holotype carapace and plastron of continental *T. costarricensis*, which, when corrected, is identical to the North American Oligocene tortoise *Oligopherus laticunea*. Furthermore, there are no continental sedimentary rocks of Oligocene to Miocene age at the purported type locality nor does the matrix associated with the holotype of *T. costarricensis* match any sediment found there. *T. costarricensis* thus, apparently, is not a tortoise from the continental Miocene of Costa Rica. Instead, it was likely based on a specimen of *Oligopherus laticunea* from the United States.
Keywords: Costa Rica, tortoise, Miocene, turtles, *Testudo costarricensis, Oligopherus laticunea.*

RESUMEN: *"Testudo" costarricensis* se describió como una tortuga basal del Oligoceno o Mioceno Inferior de Costa Rica y se consideró como evidencia de una migración de tortugas de América del Norte a América del Sur para culminar con el género *Chelonoides* moderno. Sin embargo, esto se basó en una reconstrucción incorrecta del caparazón holotipo y el plastrón de *T. costarricensis* continental, que, cuando se analiza, es idéntica a la del Oligoceno norteamericano *Oligopherus laticunea*. Además, no hay rocas sedimentarias continentales de edad Oligoceno a Mioceno en la localidad del tipo del pretendido hallazgo, ni la matriz asociada con el holotipo de *T. costarricensis* concuerda con ningún sedimento encontrado allí. *T. costarricensis*, por lo tanto, parece no corresponder con una tortuga continental del Mioceno de Costa Rica; en su lugar, al parecer corresponde probablemente con un espécimen de *Oligopherus laticunea* de los Estados Unidos.
Palabras clave: Costa Rica, tortuga, Mioceno, tortugas, *Testudo costarricensis, Oligopherus laticunea.*

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INTRODUCTION

Testudo costarricensis was described and named in a lengthy article by Segura (1944) based on a single, ~80% complete fossil shell of a continental tortoise (family Testudinidae), purportedly from the Oligocene or lower Miocene of Costa Rica. It was widely and repeatedly cited as a Miocene Central American tortoise (e.g., Auffenberg, 1971; Coto and Acuña, 1986; Alvarado, 1994; Cadena et al., 2012), and became the basis of paleobiogeographic interpretations of the origin of South American continental tortoises (e.g., Auffenberg, 1971; Coto and Acuña, 1986). However, careful re-examination of the holotype shell of *T. costarricensis* in the collection of the Laboratorio de Paleontología de la Escuela Centroamericana de Geología, leads us to conclude that this specimen is a fossil of *Oligopherus laticunea* collected from the Eocene-Oligocene White River Group of the western United States.

HISTORY

The article that named "*Testudo" costarricensis*, Segura (1944), was originally published for a scientific and literary competition that was held by the Society of Natural Sciences and Pharmacy of the Republic of Guatemala. Apparently, the invitation to write the article came in 1942. Segura's (1944) description of a new tortoise species, including three low resolution photographs of the holotype, won the competition, and Segura received a gold medal from the President of Guatemala, with the following inscription: "Empowers Natural Sciences and Pharmacy, Guatemala Scientific Contest, Anniversary 1918- 1943, 18 set. 1943 Honor of Merit Prof. Alfonso Segura Paguaga."

Segura's manuscript was published in the monthly journal of *La Escuela de Farmacia* (Journal of the School of Pharmacy) in Guatemala in 1944. Segura had visited the Smithsonian Institution and the Wyoming desert (USA) for paleontological training between October 1941 and September 1942 (Alvarado, 1989, p. 279; Alvarado, 1994, p. 88-91), and later he sent a draft of the description and drawings in the article to Smithsonian paleontologist Charles W. Gilmore, who reviewed and accepted the proposed new taxon. The Costa Rican scientists Rómulo Valerio Rodriguez, Jorge León Arguedas, Vitalia Sáenz Bejarano, José Antonio Zavaleta, Eloisa de Segura and Surana Segura Paguaga also reviewed the manuscript.

According to Segura (1944; also see Alvarado, 1994), the turtle fossil was found by Adán Arce near Peralta de Limón in 1930. Subsequently, in December 1942, Mr. Ramón Ulloa (father and son) and Mr. Hugo Guzmán supposedly encouraged Mr. Arce to donate the fossil to the National Agricultural School in San José. Dr. César Dóndoli, head of the Section of Geology of the National Department of Agriculture (and considered the father of Costa Rican geology), then reportedly provided the turtle fossil to Segura for study.

The type description and locality of *"Testudo" costarricensis* were mentioned without critical review in several papers (e. g., Auffenberg, 1971, 1974; Coto and Acuña, 1986; Alvarado, 1994; Cadena et al., 2012; Lucas et al., 2007; Lucas, 2014; Lucas and Alvarado, 2017). Alvarado (1989, 1994), Lucas et al. (2007), Lucas (2014) and Lucas and Alvarado (2017) emphasized the historical significance of this find and the role of Alfonso Segura Paguaga (1913-2002) as the first native born paleontologist in Costa Rica.

Auffenberg (1971) and Coto and Acuña (1986) reclassified Segura's taxon as *Geochelone costarricensis.* Later, Coto y Pritchard (verbal communication cited by Alvarado, 1994) suggested that the fossil might represent a new genus, possibly of late Eocene age. Loveridge and Williams (1957), based on the erroneous reconstruction of Segura (1944), mentioned *"Geochelone costarricensis"* as an example of a tortoise species with the humeral pectoral sulcus crossing the entoplastron, but make no further reference to it.

Segura's (1944) original identification and description of the tortoise was used by Auffenberg (1971) to support his hypothesis of the origins of South American and Antillean tortoises. Thus, Auffenberg considered *"Geochelone" costarricensis* not to belong to the genus *Chelonoidis*, but possibly to be a transitional form between *Chelonoidis* and basal tortoises that retained

some features associated with *Indotestudo*. Unfortunately, these links were based on the incorrect reconstruction of the sutures and sulci by Segura (1944) as will be shown below (compare Figure 1A-C with D-F).

LOCALITY

According to Segura (1944), the turtle fossil was found at a place called Mile 52, near Peralta de Limón in east-central Costa Rica,

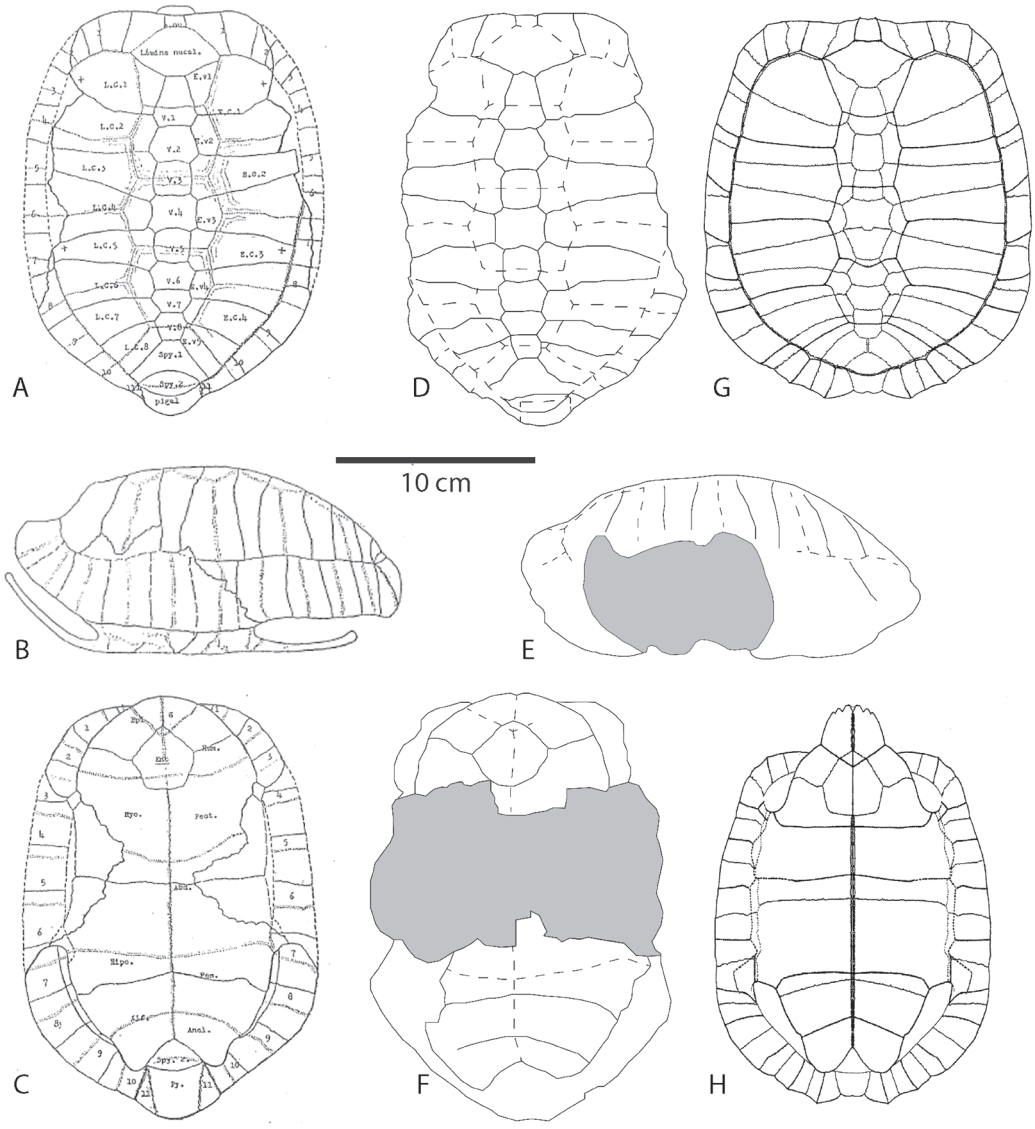

Fig.1: *Geochelone costarricensis* **A-C**, original reconstruction from Segura (1944); **D-F**, revised reconstructions. **G-H**, reconstruction of *Oligopherus laticunea* based on Hutchison (1996) A, D, G, dorsal view; B, E, lateral view; C, F, H, ventral view. **Abreviations: Anal**, anal scute; **Abd**, Abdominal scute; **fem**, Femoral scute; **Epi**, epiplastron; **Ent**, entoplastron; **G**, gular scute; **Hum**, humeral scute; **Hipo**, hypoplastron; **Hyo**, hyoplastron; **L.C.**, Left Costal; **V.**, neural; **Pect**, pectoral scute; ***Py***, pygal; **Spy,** suprapygal; **E.C.**, right costal; **Xic**, xiphiplastron.

and he stated that the holotype shell of *Testudo costarricensis* was found loose on Eocene marine sediments and below Quaternary volcanic deposits. Thus, he concluded that an Oligocene or perhaps early Miocene age of the tortoise fossil is possible. When Alvarado (1994) interviewed Segura in 1987, Segura affirmed that the fossil was found in 1930, although in his original paper of 1944 he never mentioned the year of the discovery.

According to the geological map of Madrigal (1985), in the vicinity of Peralta, marine shale, sandstone and calcarenites of likely Oligocene age are exposed and overlain by Quaternary volcanic rocks. However, Fernández (1987) assigned these marine strata an older, Paleocene-middle Eocene age and identified them as turbidites rich in volcanic debris deposited on the proximal continental slope. There are no reports near Peralta of continental sediments of Paleogene or Miocene age; the oldest continental strata there are of Pliocene and Quaternary age. A visit to the area by one of us (GEA) found no rocks consistent with the matrix associated with the holotype of *Testudo costarricensis*. The volcaniclastic rocks in the surrounding area are Quaternary lahar and debris flow deposits, as well as alluvial and colluvial deposits composed by rounded to angular fragments. These rocks do not resemble the sandstone matrix associated with *Testudo costarricensis* (Fig. 2).

The matrix inside the shell of the holotype of *Testudo costarricensis* is a medium-grained, clastic (not volcaniclastic) sandstone, which does not resemble the rocks that are exposed in the vicinity of Peralta de Limón. Therefore, the published locality and stratigraphic horizon of *T. costarricensis* seem unlikely, if not impossible, as the source of a Oligo-Miocene tortoise fossil.

DESCRIPTION AND TAXONOMY

The holotype of *Testudo costarricensis* (CF 2509) (Fig. 1-2) is a small (216 mm carapace length), moderately domed tortoise shell. Its preserved portion of the carapace includes the complete neurals, costals, nuchal, pygal and suprapygals as well as the anterior two and posterior four peripherals. The plastron is less complete, missing the medial portion between the two lobes and the posterior most portion of the anterior lobe. The fossil was evidently damaged sometime between the taking of the photograph published in Alvarado (1994, fig. 11) and the present, so that part of the plastron is now missing (Fig. 2). The remainder of the shell appears unchanged since the photographs of Segura (1944).

The nuchal is broad and pentagonal, with a roughly square cervical scute. This sutures to the first neural at the center of the first vertebral scute. The neural formula is 6-6-4-8-4-6-6-6, with the first neural enlarged, and the shorter sides of the anterior hexagonal neurals (n1-n2) facing toward the posterior end and toward the anterior end in the posterior three neurals (n6-n8). Neurals 3 and 5 are roughly square and are crossed by the anterior and posterior sulci of the third vertebral, respectively. Neural 1 sutures to the nuchal, neural 2, and costals 1 and 2. Neural 2 sutures to neurals 1 and 3 as well as costals 2 and 3. Neural 3 sutures to costal 3. Neural 4 is octagonal and sutures to costals 3, 4, and 5. Neural 5 contacts costal 5. Neural 6 contacts costals 5 and 6. Neural 7 contacts costals 6 and 7. Neural 8 contacts costals 7 and 8 as well as the anterior suprapygal. Neural 7 is divided roughly in half by the anterior sulcus of the 5th vertebral scute.

The costals are strongly wedged, as in all crown tortoises. The first costals contact the nuchal, at least two peripherals and the anterior lateral edges of neural 1. Costal 2 is expanded laterally and has the pleural 1-pleural 2 sulcus dividing it roughly in half. Costal 3 is constricted laterally, particularly lateral to the vertebral-pleural sulcus. Costal 4 is expanded laterally and divided roughly in half by the marginal 2-marginal 3 sulcus. Costal 5 is constricted laterally, and its proximal end is divided roughly in half by the vertebral 3-vertebral 4 sulcus. Costal 6 is expanded laterally and

divided roughly in half along most of its width by the marginal 4-marginal 5 sulcus. Costal 7 expands laterally, suturing to the anterior edge of the suprapygal. The insertion of the ribs into the peripherals is unclear. The costo-peripheral suture coincides with the pleural-marginal sulcus, as in most tortoises.

Peripheral 1 contacts costal 1, the nuchal and peripheral 2. The contacts of costal 2 are unclear beyond the anterior edge, which contacts costal 1 and peripheral 1. The fourth peripheral from the posterior end contacts costals 4 through 6. The third peripheral from the posterior end contacts costals 6 and 7. The second peripheral from the rear contacts costals 7 and 8. The posteriormost peripheral contacts costal 8 and the anterior suprapygal. The pygal is small, only contacting the posterior suprapygal and the posteriormost pair of peripherals.

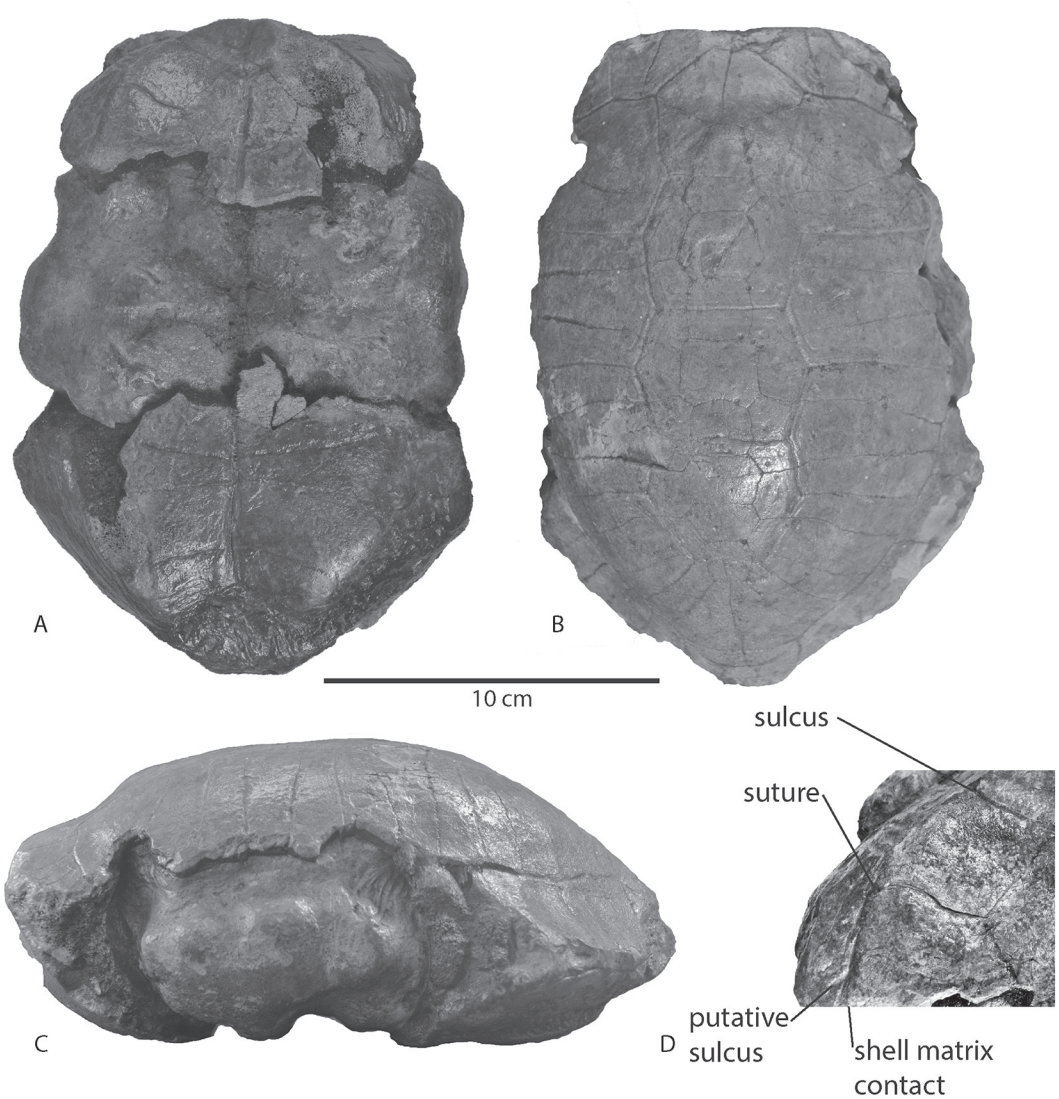

Fig. 2: **A-C**, Photographs of the holotype of *Testudo costarricensis*; and **D**, close-up of ventral view of the right epiplastron showing putative sulcus continuing onto the matrix A, ventral view; B, dorsal view; C, lateral view.

The epiplastra are about half the length of the anterior lobe of the plastron. They are significantly eroded on the left side, removing much of the surface of the bone. There is no significant anterior gular projection, as seen in many male tortoises. The entoplastron is diamond shaped, with the posterior point slightly abbreviated. The more anterior points join the epiplastron posterior sutures and the midline suture anteriorly. The entoplastron is overlapped by the gular scutes at its anterior extremity. The hyoplastron and hypoplastron are largely missing, preserving no evidence of their suture. The abdominal scutes extend into the posterior lobe of the plastron, just anterior to the suture with the xiphiplastron. Posterior to this, the posterior lobe is divided into two-thirds femoral and one-third anal scutes by two concave, posteriorly-oriented sulci. Two-thirds of the femoral scutes overlie the xiphiplastron and the rest overlie the hypoplastron.

T*estudo costarricensis* should be considered a junior synonym of *Oligopherus laticunea* (Hutchison, 1996) based on their osteological similarities, including a similar neural formula, the restriction of costal 1 to only contact neural 1, and the lack of anterior elongation of costal 1. Furthermore, the shallow concavity of the sulci outlining the femoral and anal scutes in *T. costarricensis* is significantly different than is seen in *Stylemys* (Hay, 1908; Hutchison, 1996). The posterior emargination of the plastron is deeper than in *Stylemys*. As stated by Auffenberg (1971), *T. costarricensis* lacks the derived traits of *Chelonoidis*, most importantly the absence of a cervical scute. *Chelonoidis* includes all South American and Caribbean tortoises. All of this together gives *G. costarricensis* distinct North American affinities. *T. costarricensis* is essentially identical to *Gopherus laticunea* (Hay, 1908; Hutchison, 1996), and we conclude that these taxa are synonymous.

PREVIOUS PHYLOGENETIC ANALYSIS

Coto and Acuña (1986), in their phylogenetic analysis of the taxonomic placement of *Geochelone costarricenesis*, differentiated this taxon from other tortoises based on a matrix of 18 characters. These characters, when present in *T. costarricensis*, are also present in *Oligopherus laticunea:*

1. Shell shape, specifically the presence of a concave lateral margin, was considered by Coto and Acuña (1986) to be apomorphic or derived in tortoises. This was stated to be present in *Testudo costarricensis,* but the relevant peripheral bones are not preserved in the holotype, so this feature cannot be confirmed.

2. Coto and Acuña (1986) regarded a smaller adult shell size than basal members of the family (e. g., *Hadrianus corsoni*) as apomorphic, including *Testudo costarricansis*. This smaller size is also seen in *Oligopherus laticunea.*

3. Coto and Acuña (1986) identify a narrow cervical scute intermediate in length as between the pleisiomorphic and derived states, but this is actually not different from the plesiomorphic state in the holotype of *Testudo costarricensis.* This is the same as in *Oligopherus laticunea.*

4. The depression or concavity of the neural plate posterior to the anterior margin is considered apomorphic relative to other North and South American tortoises by Coto and Acuña (1986). However, this trait is seen in all *Gopherus* and *Oligopherus*, as well as in *Testudo costarricensis* (Ernst and Lovich, 2009).

5. The neural formula of *Testudo costarricensis* was coded by Coto and Acuña (1986) as apomorphic relative to a plesiomorphic condition in *Stylemys*. This part of the morphology of the turtle shell has been widely suggested to be highly variable (Hay, 1908; Aufenburg, 1974) and should not be relied on for taxonomic identification or phylogenetic analysis. The neural formula of the holotype of *Testudo costarricensis* is identical to that of *Oligopherus laticunea.*

6. The contact of costal 1 with neural 2 was used by Coto and Acuña (1986) to separate *Testudo costarricensis* from other North American tortoises, but this feature in *T. costarricensis* is identical to that of *Oligopherus laticunea*. *O. laticunea* was left out of the analysis of Coto and Acuña (1986), which only included two more derived species of *Gopherus.*

7. Coto and Acuña (1986) note that the elongation of the anterior elements of the carapace, particularly costal 1, is absent in *Testudo costarricensis,* but this is similar to the state in *Gopherus brontops* and *Oligopherus laticunea.*

8. Two or three suprapygal plates was correctly coded by Coto and Acuña (1986) as two in *Gopherus* and other tortoises (Hay, 1908; Hutchison, 1996). So, this character is of no significance, as all taxa relevant to the relationships of *T. costarricensis* have the same morphology.

9. The fusion of midline scutes overlying the pygal bone is the same in T*estudo costarricensis, Oligopherus* and *Gopherus.*

10. The anterior gular region is described by Coto and Acuña (1986) as of intermediate breadth in *Testudo costarricensis* as well as in *Gopherus.* We agree with this assessment, and the morphology is identical to the state seen in *Oligopherus laticunea.*

11. Anterior elongation of the gulars is a sex-specific trait common to North American tortoises. According to suggested Coto and Acuña (1986), elongate gulars are absent in *Testudo costarricensis*, but given the similarities to *Oligopherus laticunea* it is likely that the holotype of T. *costarricensis* is a female lacking this male trait.

12. Position of the entoplastron relative to the humeral-pectoral sulcus was miscoded by Coto and Acuña (1986) based on the incorrect reconstruction of Segura (1944). In the holotype of *Testudo costarricensis*, the humeral pectoral scute was incorrectly drawn by Segura (1944) based on some surface damage misinterpreted to be a sulcus. This supposed sulcus is a mark on the surface of the bone that continues onto the adjacent matrix and thus cannot be interpreted as a feature of the bone (Fig. 2D).

13. Gular humeral sulcus crossing the entoplastron was identified by Coto and Acuña (1986) in *Testudo costarricensis*, but this is present in *Oligopherus laticunea* (American Museum of Natural History 1160: Hay, 1908, fig. 510), and a highly variable character in some other tortoise species.

14. Rectangular pectoral scutes was coded by Coto and Acuña (1986) as absent, but neither of the sulci outlining these scutes are preserved in the holotype of *Testudo costarricensis.* The humeral pectoral scute was incorrectly drawn by Segura (1944) based on some surface sculpture misinterpreted to be a sulcus.

15. The length of the anterior lobe relative to the posterior lobe of Testudo costarricensis is similar to that seen in *Oligopherus.*

16. The posterior extension of the anal scutes to either side of the midline was incorrectly described by Coto and Acuña (1986) as being substantially elongate in *Testudo costarricensis*, but they are only slightly elongate, as in *Oligopherus.*

17. An anal notch is absent in the North American tortoises sampled by Coto and Acuña (1986), but is present in the holotype of *Testudo costarricensis, Oligopherus laticuneus, Gopherus berlandieri*, and *G. agassizii.*

18. A recurved, weakly serrated margin of the carapace, as seen in the holotype of *Testudo costarricensis,* is again a common trait of the *Oligopherus laticuneus, Gopherus berlandieri*, and *G. agassizii* group.

The results of Coto and Acuña (1986) appear to have been biased by their limited taxon inclusion and unclear characters, such as character 4 (the depression of the nuchal) that vary in degree of development, but are coded by them as a simple presence/absence. In fact, the nuchal depression of *Testudo costarricensis* curves at this point to a degree very similar to turtles of the genera *Oligopherus* and *Gopherus*. Given the many similarities and the lack of any clear differences, we thus consider *Testudo costarricensis* to be a synonym of *Oligopherus laticunea.*

DISCUSSION

Based on the above, we conclude that the holotype of *Testudo costarricensis* is a specimen of continental *Oligopherus laticunea*, a common tortoise in the Eocene-Oligocene White River Group of the western USA, and that its published provenance is false. We add to this two observations: (1) the matrix of the holotype of *T. costarricensis* has been varnished in a manner similar to that commonly done by commercial collectors

of White River Group fossils; and (2) the preservation of the specimen, as a three-dimensional, nearly complete carapace and plastron filled with matrix, is also a characteristic preservation of White River Group tortoise fossils. So, how did a White River Group tortoise make its way to Costa Rica to be described by Segura (1944) as a new species of tortoise?

Segura received a scholarship to study at the National Museum of Natural History of the Smithsonian Institution from October 1941 to September 1942, under the tutelage of Wetmore, and with the collaboration of C. W. Gilmore, C. L. Gazin and G. Sternberg. During this time, Segura participated in fossil-collecting trips to Wyoming (Segura, 1944; Alvarado, 1994, and letters in the archives of Alvarado). Segura returned from the USA to Costa Rica in September 1942, and the turtle was donated to Dóndoli in December 1942, when Adán Arce presumably found the fossil. Thus, it seems most likely that *Testudo costarricensis* was a scientific hoax or an imported fossil that a non-Costa Rican person lost or gave as a gift to the local people along the railroad to the Caribbean Sea. The fact that this supposed Costa Rican tortoise remained in the scientific literature for more than 70 years can only be attributed to the fact that nobody critically re-examined the holotype prior to our research.

CONCLUSIONS

1. *Testudo costarricensis* is a synonym of *Oligopherus laticunea*.
2. The holotype specimen of *Testudo costarricensis* did not come from its stated type locality.
3. The holotype specimen of *Testudo costarricensis* was likely obtained in the United States, not in Costa Rica.
4. *Testudo costarricensis* is not a tortoise transitional between North and South American tortoises.

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