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US ISSN 0006-9698

CAMBRIDGE, MASS. SEPTEMBER 20, 1973 NUMBER 405

A FOSSIL TRIONYCHID TURTLE FROM SOUTH AMERICA

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ABSTRACT. A hyoplastron of a large trionychid turtle from the middle Pliocene (Huayquerian) Urumaco Formation of northern Venezuela constitutes the first indisputable record of a member of this family from South America. The reported occurrence of a trionychid from the late Cretaceous or Paleocene of Patagonia (*Trionyx argentina* Ameghino 1899, *nomen dubium*) cannot be substantiated. The species represented by the Venezuelan fragment was presumably a waif immigrant from Central America that was unsuccessful, very possibly owing to competitive exclusion, in establishing an enduring foothold in South America.

Living trionychid turtles are known from Africa, Asia, the Indo-Australian archipelago and North America. Paleontological evidence indicates that this group formerly had an even more extensive distribution. Fossil forms are known from parts of Africa, Asia, and North America where they no longer occur, and remains are found in European Tertiary deposits as well. Until now, with one dubious exception (discussed below), no members of the family, living or fossil, have ever been encountered in South America. Discovery of an unquestionable trionychid fragment from late Tertiary sediments in Venezuela during the summer of 1972 is therefore of considerable interest.

The specimen (Museo de Ciencias Naturales, Caracas, no. 238) was recovered from the upper part of the lower member of the Urumaco Formation about twelve kilometers WSW of Urumaco and .75 kilometer north of Kilometer 153 on the oil pipe line running from Punta Gorda to the Paraguaná Penin-

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sula. It was found on the surface, together with parts of a pelomedusid that was in the process of weathering out. The Urumaco Formation (Gonzales de Juana *et al.*, 1970: 612–613) is now believed to be of Huayquerian age (Pascual and de Gamero, 1969; Wood and de Gamero, 1971). Outcrops are restricted to a relatively small area in the northern part of the state of Falcón. The vertebrate fauna, for the most part not yet described (see, in addition to the publications cited above, Royo y Gomez, 1960, and Sill, 1970), consists of numerous aquatic reptiles (some half dozen species of both crocodilians and turtles), a testudinine, fish, and various kinds of mammals. The depositional environment was in the main a near-shore marine one, with fluctuations involving a variety of paralic and near-shore continental conditions.

The find consists of a large, well-preserved hyoplastron (Figure 1). Its sculptured external surface, covered with anastomosing ridges, is characteristic of trionychids. These rugosities, coupled with the distinctive outline of the bone, leave no doubt regarding the familial reference. Dimensions are as follows: width along the hyo-hypoplastral suture = 22.2 centimeters; length at narrowest part = 7.3 centimeters; greatest dorsoventral thickness along hyo-hypoplastral suture = 2.8 centimeters. From the condition of the sutural surface, it is clear that the hyo- and hypoplastra were distinct bones rather than fused as is the case in various genera of the family. The hyoplastron appears to be unusually thick for its size, the thickness/width ratio being 0.126. Measurements of shell thickness are scarcely ever given in the literature. A few T/W ratios can roughly be estimated from the figures and sporadic measurements given by Hay (1906) for North American fossil trionychids; these range from 0.083 to 0.019. The hyoplastra of those living forms available to us are as follows regarding this ratio: *Lissemys punctata,* 0.087; *Chitra indica,* 0.081; *Trionyx hurum,* 0.067; *T. sinensis,* 0.079; *T. cartilagineus,* 0.090; *T. spinifer* (6), 0.107–0.064; *T. ferox* (4), 0.081–0.070; *T. muticus* (2), 0.077–0.049. This, of course, is a wholly inadequate sample, but as far as it goes it confirms our impression that the Urumaco hyoplastron is unusually thick. Further, the sample suggests that thickness decreases, relatively, with age; in all species of which we have more than one specimen the smallest individual has the highest ratio and the largest the lowest. The thickness of the Urumaco specimen is not, we accordingly suspect, due to size.

This hyoplastron is sufficiently distinctive for reasonable as-

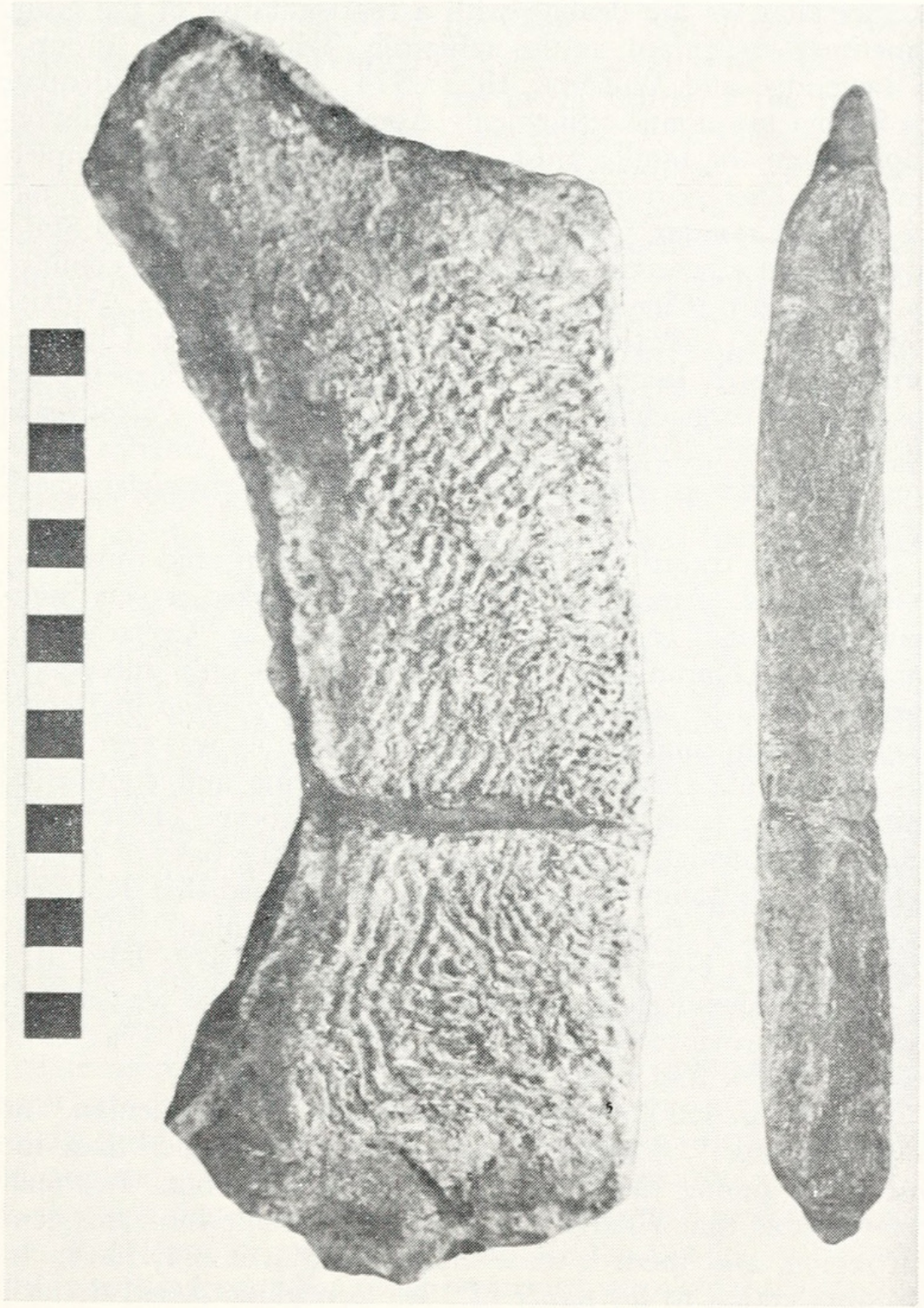

Figure 1. Trionychidae, gen. et sp. indet. Ventral and posterior views of hyoplastron. Scale in centimeters.

surance that we are dealing with a representative of the group sometimes recognized as the subfamily Trionychinae (group I of Loveridge and Williams, 1957: 414), but quite inadequate for further taxonomic refinement. Assessment of precise relationships within the family must await discovery of more complete material. The geographically nearest living species of the family are *Trionyx spinifer*, whose range extends from the United States down into northeastern Mexico, and *T. ater*, which is confined to the Cuatro Cienegas Basin of central Coahuila, Mexico (Webb, 1962). Neither attains great size; in fact, the Urumaco form was clearly larger than any of the living American species. Some fossil trionychids (*e.g.*, the late Paleocene *Paleotrionyx quinni* Schmidt, 1945) are known from North America, however, whose size is comparable to that of the Venezuelan specimen.

The earlier record of a South American trionychid must now be considered. Ameghino (1899: 10) published a very summary "diagnosis" of *Trionyx argentina* from the "Cretaceous of Patagonia (Guaranitic Formation)." In his only subsequent mention of it, he stated that *Tryonix* [sic] *argentina* had come from the "Sehuenian" (1900: 216). No locality was ever given. His "Guaranitic Formation" included marine and continental strata ranging from Cretaceous to early Oligocene (Deseadan), and his "Sehuenian" formed part of it. On the basis of his last statement concerning the age it could be assumed that *T. argentina* came from the type area of the "Sehuenian" (now the Mata Amarilla Formation, Coniacian; Leanza, 1972: 695, 701) on the Río Shehuen (or Sehuen or Chalía) in the west-central part of the province of Santa Cruz, and Feruglio (1949a: 257) believed that it had. This is not certain, however.

In 1898 (p. 121) Ameghino included in his "Sehuenian," or "Piso Sehuense," deposits occurring in regions other than the type area, among them the Río Chico del Chubut. It would seem possible that *T. argentina* could have come from this general region, and there is some indication that it may have. In the introduction to his paper of 1899 Ameghino stated that all species proposed in it had been collected by his brother Carlos since the manuscript of his paper of 1898 (to which 1899 was a supplement) had been delivered to the printer, which was done at the end of July, 1897 (letter from F. Ameghino to D. de la Fuente, August 7, 1897; *in* Torcelli, 1935: 688). By that time Carlos Ameghino's collecting activities had centered on northern Santa Cruz and Chubut. Reporting on the results of

his expedition of 1898–99 to the Golfo de San Jorge, he wrote (letter to Florentino, February 15, 1899; *in* Torcelli, 1935: 106) that he had found "more or less in the center of the gulf . . . characteristic fossils (sharks, chelonians, crocodiles, etc., the same as those of Sehuen and Lake Argentino)." These chelonian remains could have included the material on which *T. argentina* was based. Florentino's statement (1899) that a trionychid had just been found ("acaba de encontrarse") could be so interpreted. At any rate, years later, Staesche (1929) described turtle fragments collected, together with crocodilian remains, by von Huene near the center of the gulf, "mainly at Cabo Peligro," and several of these answer to Ameghino's "diagnosis" of *T. argentina* in one respect, vermicular sculpturing. Staesche believed the age of these specimens to be Late Cretaceous, but the bed from which they came was the *banco negro inferior* at the base of the Río Chico Formation or perhaps at the top of the Salamanca Formation (Feruglio, 1949b: 27, fig. 87), both of which are now considered to be Paleocene in age. Turtle remains, according to Feruglio, commonly occur in this bed or beds in the region of the gulf. Against the possibility that *T. argentina* may have been recovered from this area, however, is the fact that by 1900 (p. 119) Ameghino had begun to make a distinction between the "Sehuenian" and the beds in Chubut containing *Ostrea pyrotheriorum* (now the Salamanca Formation). As in the case of *Niolamia argentina* (Simpson, 1938), also described in 1899, no conclusion can now be reached as to the precise age and locality of *T. argentina*, although we regard Paleocene and the gulf as being the more likely alternative.

The affinities are even more uncertain. Ameghino's "diagnosis" reads, in free translation, "*Trionyx argentina* n. sp., size small, surface of shell with vermicular sculpturing, ossification incomplete, without scute sulci."[1] No information was given as to the type material. This is wholly inadequate to define a species of *Trionyx* or even to demonstrate the familial assignment. Other turtles have what could be termed vermicular sculpturing; what is meant by "incomplete ossification" is not clear; and the absence of sulci is not a certain indication that scutes were lacking. The specimen or specimens on which the taxon was based

[1]". . . de talla pequeña y superficie de la coraza con esculptura vermicular pero de osificación incompleta y sin surcos externos que indiquen la presencia de escudos corneos."

would appear to have been lost; Wood failed to encounter them in the course of an examination of the turtle remains in the Ameghino collection. Consequently, we regard *"Trionyx argentina"* as a *nomen dubium* and we feel that the existence of a late Cretaceous or Paleocene South American trionychid has not been demonstrated.

The specimen described here is thus the only definite record of a trionychid for the continent. Representatives of the family did obtain a foothold there, but for how long and in what manner? During 1970 Wood spent four months in South America examining collections of fossil turtles ranging in age from Cretaceous to Pleistocene and nowhere saw so much as a fragment that could be identified as a trionychid. The extensive collections made in the late Oligocene and later Miocene of Colombia by University of California parties include turtle remains but no representative of this family. Among the hundreds of turtle specimens in all stages of completeness seen by us in the Urumaco Formation only this one trionychid fragment was found.[1] On the face of it, therefore, it would seem possible that the invasion was a Huayquerian event and only briefly successful in the geological sense of the word. Why this should have been so is puzzling, for the great river systems of South America encompass habitats surely suitable for members of the family. Simpson (1943: 423) has suggested that trionychids and chelids may be ecologically incompatible. Chelids are clearly an old South American group in the sense of Dunn (1931). Wood has in hand undescribed material from the early Eocene Casamayor of Argentina.[2] Undescribed chelids have recently been discovered at Tremembé, in Brazil, now known to be a deposit of early Oligocene, Deseadan, age (Paula Couto and Mezzalira, 1971). Specimens occur in the Oligocene and in the Miocene of Colombia (Stirton, 1953: 614) and have long been known from Paraná. We have good material of *Chelus* from the Urumaco Formation, and additional undescribed material of this same genus has been found in Pliocene deposits along the upper reaches of the Juruá River in the territory of Acre, Brazil. The Chelidae was not the only family that could have provided

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[1]It was collected midway in the season and a very close watch for others was maintained thereafter.

[2]Ameghino "diagnosed" three species of *Platemys* from his "Guaranítico" in 1899, but these records are *nomina dubia* and the specimens evidently lost.

competition to invading aquatic turtles.[1] Pelomedusids, also Old South American forms, are known in the continent from the late Cretaceous on and are very numerous in the Urumaco deposits. The demonstrated failure of trionychids to maintain themselves in South America could be interpreted in terms of competitive exclusion. Chelids and pelomedusids have evolved together in South America throughout the Cenozoic, and in the course of this time no doubt parceled out between them a wide variety of habitats. That they would have completely saturated the continent is unlikely, but such diversification would have lengthened the odds against an invader. The species represented by our Urumaco trionychid may well have had the misfortune to encounter upon arrival a comparably adapted resident and have failed to compete successfully with it. It was, indeed, similar in size to the commonest Urumaco pelomedusid, *Podocnemis venezuelensis* Wood and de Gamero.

Such mammalian remains as occur in the Urumaco Formation are all of South American type, a finding in accord with Argentinian evidence suggesting a Montehermosan date for the joining of the American continents. On this basis, then, the Venezuelan trionychid would appear to have been a waif immigrant carried by ocean currents. Members of the family may well be rather prone to such accidents. There is some evidence that several of them enter brackish or even salt water (summary and references in Neill, 1958: 26–27). These would be particularly liable to hazards of this kind, but tolerance for saline waters need not necessarily be prerequisite. The African *Trionyx triunguis* also occurs in rivers and swamps along the eastern Mediterranean littoral. Flower (1933: 754) has suggested that this extension results from individuals being swept to sea by Nile floods and carried eastward by the prevailing current. The ancestor or ancestors of the Venezuelan trionychid presumably came from Central America, the nearest land area, and arrived in South America at approximately the same time as did the extinct *Cyonasua* group of the Procyonidae. No trionychid now

[1]At the present time there is one area in which chelids and trionychids come together. This is southern New Guinea where the wide-ranging trionychid *Pelochelys bibroni* has established itself — rather recently in Darlington's opinion (1957: 210). There it is in contact with several chelids. So far as we are aware no information is available on possible interactions, but direct competition would seem unlikely. *P. bibroni* is a large species, much larger than any New Guinean chelid.

lives in Central America — it is a decidedly odd fact of distribution that all living North American species of *Trionyx,* in contrast to a number of their Old World congeners, are extratropical. None has been recorded fossil there, but in view of our abysmal ignorance of the Tertiary vertebrates of the region no weight can at present be given to their absence.[1]

This note records a momentary success in range extension resulting from waif dispersal. Such transitory events must surely have been commoner than those more enduringly successful, but in the nature of things the chances are against their entry into the fossil record. They could have played a part in furthering distribution. In the case of organisms such as freshwater turtles each new toehold gained, for however brief a time, in a suitable environment would have provided a potential base for further waif dispersal. The distribution of pleurodirans, for example, may have been to some degree forwarded in this way.

ACKNOWLEDGMENTS

Our field work in Venezuela was made possible by National Science Foundation Grant no. GB–32489x to Patterson, and by the generous cooperation of the Escuela de Geología, Universidad Central de Venezuela, and the Ministerio de Minas y Hidrocarburos. We are indebted to Profesora María Lourdes Diaz de Gamero, Dr. Clemente Gonzales de Juana, Dr. A. Bellizzia G., Professor John Gibson-Smith, Dr. Edgardo Mondolfi, Sr. Blas Gonzalez, and our companions in the field: Messrs.

[1]Webb (1962: 584) has credited Mullerreid (1943) with recording a fossil trionychid of unknown provenance from Mexico. Actually, that author mentioned seeing the internal mold of an unidentified turtle. The owner of the specimen, which has probably been lost, stated that he had found it on the Mesa de Capolla, a short distance SSW of Tuxtla Gutierrez, Chiapas. Cretaceous and early Tertiary sediments are present there, and Mullerreid believed that the mold had come from the latter. With the exception of the Oligocene or Miocene testudinine *Geochelone costarricensis* (Segura) (Auffenberg, 1971), this is the only published record of a Tertiary turtle from Central America. (In addition, we know of undescribed material from two Tertiary localities in Panama; no trionychids are included among the specimens.) Aguilera (1907: 241) listed *Tryonix* [sic] sp. as occurring with marine invertebrates in Turonian deposits at Peyotes, Coahuila. This is the only North American fossil record of the family south of the United States. It requires confirmation, and is in any event within the present range of *T. spinifer emoryi.*

Arnold D. Lewis (the finder of the specimen here discussed), Daniel C. Fisher, Robert W. Repenning, and Michael F. Stanford. The participation of Messrs. Fisher, Repenning, and Stanford was due, respectively, to the generous provision of a summer scholarship from the Department of Geological Sciences, Harvard University, and of grants from the Shell Oil Company and the Creole Petroleum Corporation. Wood's work in South America during 1970 was supported by the National Geographic Society.

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