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Testudo amphithorax Cope Referred to *Stylemys*[1]

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The testudinine turtle fauna of the White River Formation is of considerable interest, since it marks the first appearance of several important New World tortoise genera (*Geochelone*, *Stylemys*, and *Gopherus*). Furthermore, a number of species of tortoises referred to these genera from these beds have been described on the basis of very fragmentary materials. Thus, additional information on shell architecture and the configuration of various elements that comprise the axial and peripheral portions of the skeleton may be helpful in the determination of the validity and relationships of the several described forms.

One of the species for which such information is highly desirable is *Testudo amphithorax* Cope (1873). An almost complete specimen of fossil tortoise in the University of Colorado Museum (U.C.M. No. 20575) has been compared with the material on which Cope based *amphithorax* (A.M.N.H. Nos. 1139, 1145, 1147) and is referred to this species without any doubt. It was collected by James Mellinger, close to the type locality of the species (Weld County, Colorado, near the head of Horse Tail Creek, Horse Tail Creek Member, White River Formation, Lower Oligocene). It consists of a complete shell and almost all the postcranial skeleton of an adult male specimen. A poor skull, not articulated with the cervical vertebrae, but with the shell when the collection was donated to

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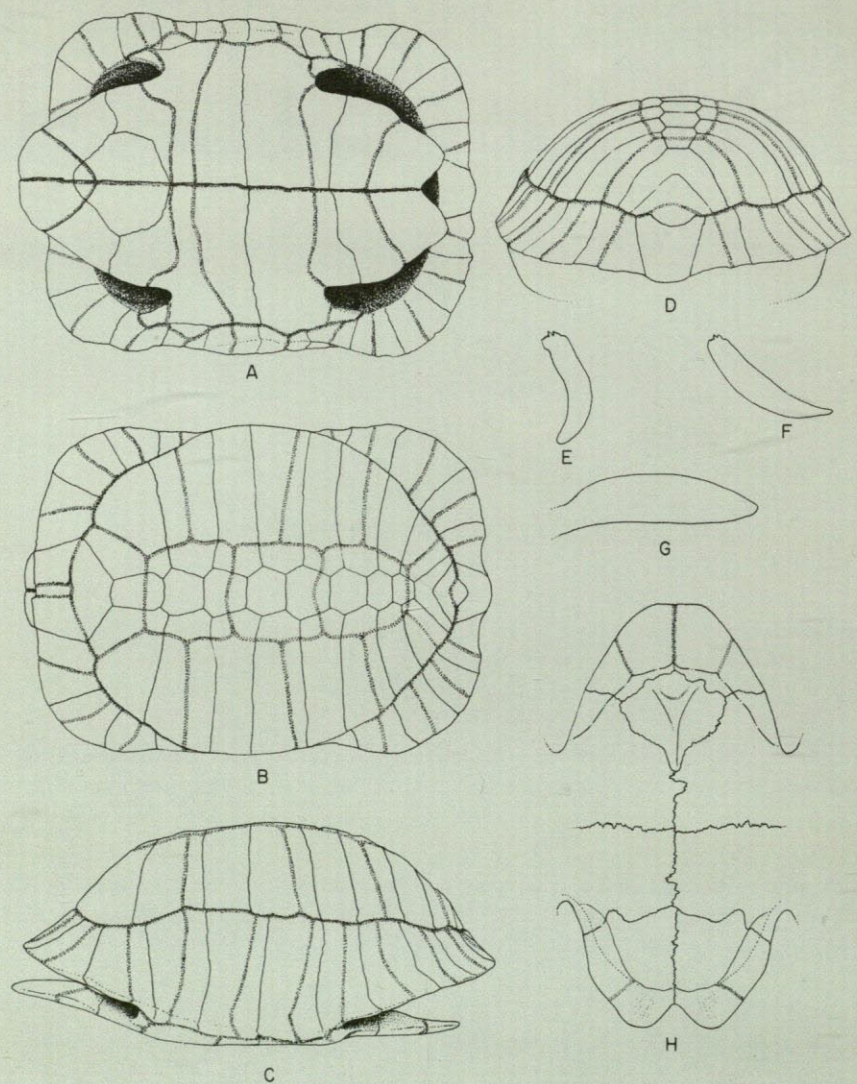

FIG. 1. Adult *Stylemys amphithorax* (U.C.M. No. 20575), from near head of Horse Tail Creek, Weld County, Colorado, Horse Tail Creek Member, White River Formation, Lower Oligocene. A–D. Ventral, dorsal, lateral, and posterior view of shell. E. Cross section of pygal. F. Cross section of ninth peripheral. G. Cross section of epiplastral lip. H. Internal view of plastron.

the Museum, may belong with the specimen. In every detail on which comparisons can be based this specimen is identical to the type material of *amphithorax*.

The shell is complete (fig. 1), though slightly flattened on the left side. In form the carapace is moderately narrow and strongly arched in all directions. The length of the carapace is 511 mm., and the width approximately 351 mm. The anterior border is concave along the nuchal and part of the first peripheral elements; then it passes into a broad curve to the lateral surfaces. The nuchal scute is 13 mm. wide and 46 mm. long (16 by 36 in A.M.N.H. No. 1139, the type of *amphithorax*). A rather deep groove runs along the lower ends of the bridge peripherals, as in the type of *amphithorax*. The upper border is 76 mm. wide and excavated for the reception of the second suprapygal. The lower border is 45 mm., and the length 78 mm. The first suprapygal is bifurcate, with the upper border 23 mm., the lower 112 mm. As in the type, the rear part of the carapace slopes downward and backward at an angle of about 45 degrees, and the carapacial sulci are narrow and only slightly impressed.

The neurals are not greatly differentiated. The first is elongated and oval; the remaining ones are hexagonal, the fourth having lateral sutures almost equal in length. The neurals are all wider than long. The costals are not highly differentiated, with only costals 3 and 4 alternately wider and narrower.

The pygal is wedge-shaped. The vertical edge is narrower and truncated; the dorsal edge, notched for the reception of the second suprapygal.

The plastron has a total length of 487 mm. The width of the anterior lobe at its base is 230 mm., and the length is 150 mm. The lip projects only slightly beyond the anterior end of the carapace. The lower surface is concave, with the epiplastral beak only slightly raised above the lowest portion of the plastron (figs. 1G and 2). The remaining middle and posterior portions of the plastron are concave, indicating that the specimen was probably an adult male. The free edges of the anterior lobe converge in an almost continuous fashion and are only slightly truncated anteriorly. The posterior lobe is 147 mm. long from its base, and 225 mm. wide. The sides are rather parallel for over half of its length, where they turn inward and backward, forming an obvious angle. The xiphiplastral notch is moderately developed.

The gular sulcus extends onto the entoplastron, and the humeropectoral sulcus just touches it. The entoplastron is roughly pentagonal in shape and wider than long.

The bridge is 190 mm. wide, and the costal ribs do not extend into pits in the peripherals.

TABLE 1
SHELL MEASUREMENTS (IN MILLIMETERS)
OF *Stylemys amphithorax* (U.C.M. No. 20575)

Length of nuchal scute	46
Width of nuchal scute	13
Length of vertebral scute 2	97
Width of vertebral scute 2	101
Length of vertebral scute 4	109
Width of vertebral scute 4	90
Length of vertebral scute 5	113
Width of vertebral scute 5	145
Length of gular scute	113
Length of humeral scute	85
Length of pectoral scute	26
Length of abdominal scute	135
Length of femoral scute	62
Length of anal scute (midline)	61
Depth of xiphiplastral notch	28
Length of entoplastron	113
Width of entoplastron	121
Length of hypoplastron	93
Length of xiphiplastron (midline)	100
Anterior width of nuchal bone	90
Greatest width of nuchal bone	130
Length of nuchal bone	112
Length of neural 1	74
Width of neural 1	40
Length of neural 2	45
Width of neural 2	55
Length of neural 4	40
Width of neural 4	56
Proximal end of pleural 3	51
Distal end of pleural 3	36
Proximal end of pleural 4	40
Distal end of pleural 4	69
Greatest length of epiplastron	131
Greatest thickness of epiplastral lip	26
Width of both epiplastra	207
Length of hypoplastron	87
Greatest width of epiplastron	110
Greatest external thickness of xiphiplastron	34

The skull, probably associated with the shell, is not nearly complete. Though the general shape is somewhat discernible, only the palatal region is complete. The general proportions of the skull seem similar to those of *osborniana*. The palatal region is highly vaulted. The vomer is arched, with a median ridge. There is a ridge on the midline of the premaxilla, though

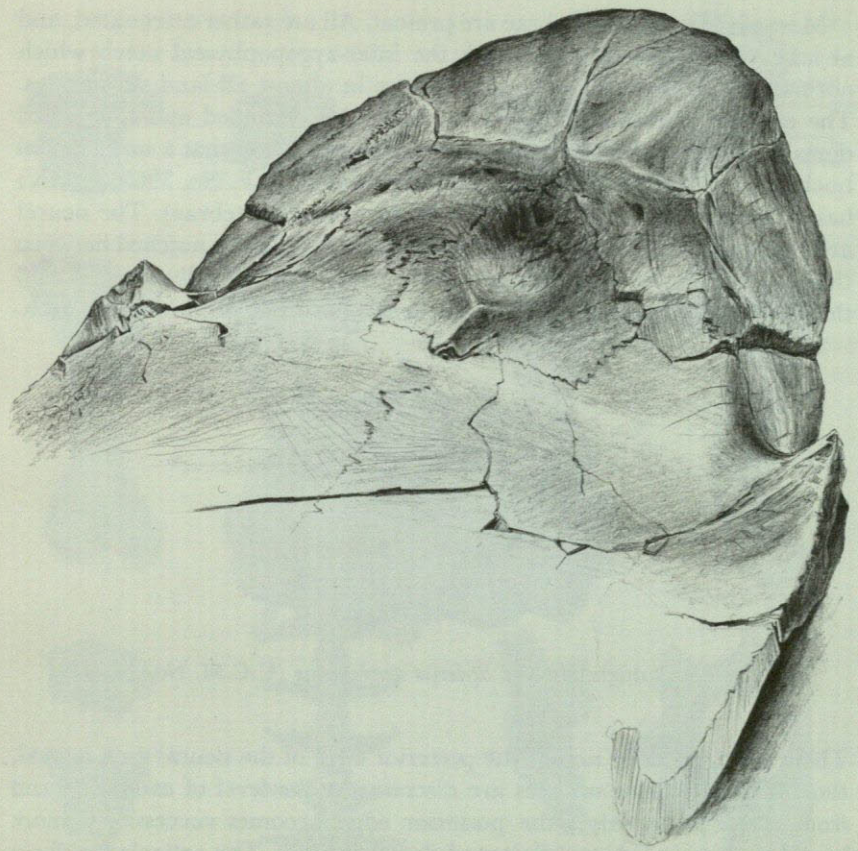

FIG. 2. Internal view of anterior part of plastron of adult *Stylemys amphithorax* (U.C.M. No. 20575).

it is not so strongly developed as is that of *Gopherus*. As in most other testudinines, the alveolar surface is provided with two ridges and two grooves. The outer ridge is separated from the inner one by the wider groove. What remains of the jugal arch indicates that it was narrower than that in *osborniana*, and more similar to that in *impensa*.

The remainder of the skeleton is more or less articulated within the shell. The pelvis is in its natural position and is essentially complete. The ischial processes are much more strongly developed than in any testudinine species for which the pelvis has been figured. Both ischia are greatly thickened ventromedially, so that they come into broad contact with the plastron. The ventral pubic processes are well developed (fig. 4M).

Most of the caudal vertebrae are present. All are rather attenuated, and at least the middle members lack the inter-zygopophyseal notch which normally separates the post-zygopophyses in almost all land vertebrates. The eleventh and twelfth (?) are considerably flattened and roughened dorsally. The transverse processes are not elongated, so that a supracaudal buckler was probably absent. A second specimen (U.F. No. 3967, fig. 4K) has a fair part of the tail complete (eight caudal vertebrae). The neural arch of caudal 1 is broken off. That of caudal 2 is slightly notched between the post-zygopophyses. There is a fairly strong keel dorsally. In caudal 3 the keel is reduced to a small boss near the posterior portion of the arch.

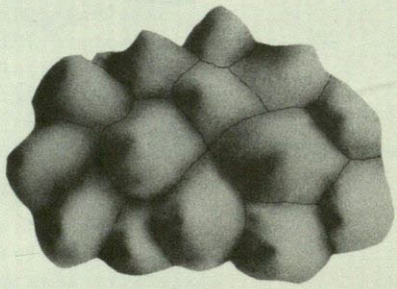

FIG. 3. Fused thigh patch of *Stylemys amphithorax* (U.C.M. No. 20574).

There is no posterior notch; the posterior edge of the neural arch is oval, though the articular surfaces are discrete. At the level of caudal 6 (and from there posteriorly), the posterior edge becomes successively more broadened, rounded, and flattened dorsoventrally. The articular surfaces fuse, so that the entire posterior edge of the neural arch comes in contact with the continually distinct prezygopophyseal processes of the next posterior vertebrae. The very end of the tail in *amphithorax* remains unknown.

A specimen in the University of Colorado collections (U.C.M. No. 20574), represented by a plastron and some peripherals, has, in definite association, a fused thigh patch (fig. 3) similar to that described for *crassiscutata* and *rexroadensis*.[1]

Cervical vertebrae 1 and 2 are articulated. Cervical 2 has a single concave articulation anteriorly, biconvex posteriorly. The first dorsal vertebra has been badly prepared, and its shape cannot be determined

[1] A more fragmentary thigh patch was, before final preparation, previously mistakenly interpreted as a caudal buckler (Auffenberg, MS).

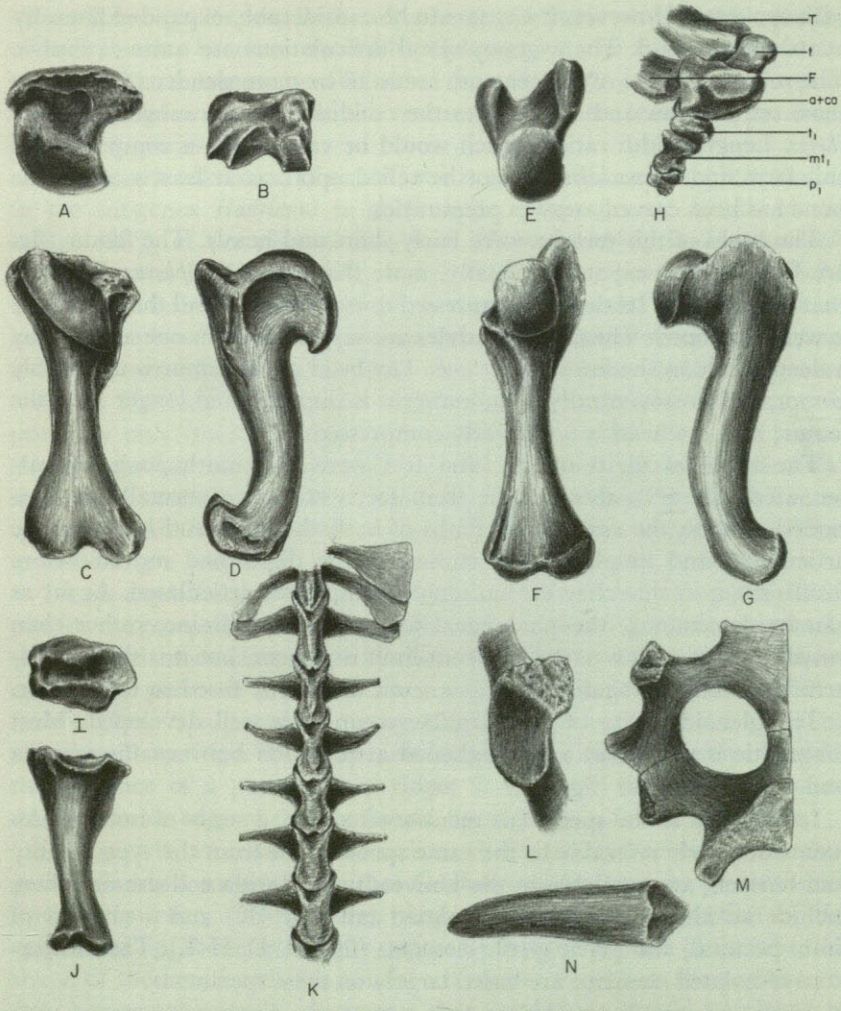

FIG. 4. Various skeletal parts of *Stylemys amphithorax*. A–D. Proximal, distal, internal, and anterior views of femur (U.F. No. 3968). E–G. Proximal, internal, and anterior views of humerus (U.C.M. No. 20575). H. Part of hind foot (U.F. No. 3972). I–J. Proximal and internal views of tibia (U.F. No. 3973). K. Anterior caudal vertebrae (U.F. No. 3967). L. Glenoid cavity (U.F. No. 3975). M. Internal view of right half of pelvis (U.C.M. No. 20575). N. Terminal digit of hind foot (U.C.M. No. 20575). *Abbreviations:* a+ca, astragalus plus calcaneum; F, femur; mt1, metatarsal I; p1, phalanx I; T, tibia, t, tibial; t1, tarsal I.

with accuracy. However, it appears to be considerably expanded laterally at its anterior end. The zygopophyseal articulations are quite extensive. The middle portion of the centrum seems to be more slender than that of most testudinines and approaches the condition in the subgenus *Monachelys*. Length-width ratios, which would be valuable in a comparison of this form and *Monachelys*, cannot be relied upon, as at least some of the bone has been carved away in preparation.

The limbs of this tortoise were fairly short and heavy. The femur (fig. 4A–D) is slightly expanded distally, more than that of *Gopherus*, less than that of *Geochelone*. Its shaft is compressed dorsoventrally, and the tuberosity is well developed. The distal condyles are separated from one another by a deep notch on the internal surface. The head of the femur is noticeably compressed dorsoventrally. The humerus is slimmer, and longer than the femur; and the head is not greatly compressed.

The terminal digits of the hind feet were apparently long and attenuated (fig. 4N); those of the front feet were more normally proportioned. Almost the entire hind limbs of both the right and left sides are articulated and in place. Unfortunately, the digits had moved before fossilization, so that they are no longer completely articulated. As far as can be determined, the phalangeal formula is testudinine, rather than emydine. The carpus of the left front limb is present, but it is slightly disarranged. The astragalus and calcaneum are firmly fused to each other.

The glenoid cavity of the scapular complex is well developed. Most diagnostic is the broad and roughened articulation between the scapula and the precoracoid (fig. 4L).

In addition to the specimens mentioned above, a series of isolated elements definitely referable to the same species, and from the type locality and horizon, are available in the University of Florida collections. These include an almost complete articulated tail (fig. 4K) and a number of limb, pectoral, and pelvic girdle elements (fig. 4A–D, H–L). The illustrations of isolated elements are based largely on these specimens.

DISCUSSION

Both of the University of Colorado specimens described above are placed in the species *amphithorax* Cope on the basis of correspondence in all important characters (shape and proportions of the nuchal scute, pygal and second suprapygal, groove at the base of the peripherals, and almost all characters associated with the plastron) with the type specimen of the species. The intermediate nature of the nuchal scute (between that of the type of *ligonia* and that of the type of *amphithorax*) suggests that these

White River species may be found to be synonymous when better material of both species becomes available. However, in the type of *ligonia* the epiplastral beak is more parallel-sided than that of any of the specimens of *amphithorax* known so far. For this reason *ligonia* is here tentatively retained as a valid species.

The generic allocation of *amphithorax* is not a simple matter. It is similar to the subgenus *Hadrianus* in shell shape, proportionate length of the bridge (38% of the plastral length in *Hadrianus*, 44% in *Hesperotestudo* [fide Gilmore, 1915], and 37% in *amphithorax*), position of the posterior buttress, and the presence of only hexagonal neurals. The pleurals are less differentiated than those of even the most primitive species of *Hesperotestudo* known, but are more so than those of *Hadrianus*. *Geochelone primaeva* from the Madison Valley fauna (?) possesses all hexagonal neurals, but is probably only distantly related to *amphithorax*. Unlike *Hadrianus*, *amphithorax* lacks paired supracaudal scutes. However, paired supracaudal scutes are not confined to *Hadrianus*, being known in both fossil and Recent species of both *Testudo* and *Geochelone*. From *Cymatholcus*, *amphithorax* differs in possessing a longer tail and differently shaped caudal vertebrae.

Testudo amphithorax differs from *Stylemys nebrascensis* in lacking peripheral pits for the reception of the costal ribs and in possessing a proportionately thinner and more elongate shell. Like *Stylemys* and *Gopherus*, *amphithorax* apparently possesses a premaxillary ridge, though it is faint. It differs from *Chelonoides* in possessing hexagonal neurals throughout and in having a premaxillary ridge. Probably most indicative of its relationships (besides the presence of a premaxillary ridge) is the very shallowly excavated dorsoposterior edge of the epiplastral lip (fig. 2), as found in *Stylemys*.

Owing to its somewhat intermediate character, *amphithorax* is not altogether clearly a member of either *Geochelone* or *Stylemys* (as presently defined). However, the thickness, shape, and shallow excavation of the epiplastral lip, the length of the exposed proximal portion of the ribs, the shape of the femur and the caudal vertebrae, as well as the presence of only hexagonal neurals, all suggest that *amphithorax* should be placed in the genus *Stylemys*. If correctly placed, it differs from all other members of the genus in having a much narrower nuchal scute. In addition, it apparently differs from *nebrascensis* (its presumed closest relative) in being more elongate, in lacking peripheral bridge pits, and possibly in attaining a larger size.

So far, *Stylemys amphithorax* is known only from the White River Oligocene of northeastern Colorado. There is some evidence that it is the only species of *Stylemys* in the Colorado Titanothere beds. It seems less often encountered in the Oreodon beds of the same area, where it is said to

occur with the more common *S. nebrascensis* (Galbreath, 1953). The latter point should be thoroughly investigated, since the available information suggests that *amphithorax* is probably the direct linear ancestor of *nebrascensis*.

Testudo uintensis Gilmore (1915) has long been considered the earliest member of the genus *Geochelone* (as restricted by Loveridge and Williams, 1957) in the New World. The type and only known specimen of this species is somewhat crushed, but the shell architecture is very similar to that of *amphithorax* (in those characters in which the two species can be compared). A reëxamination of *uintensis* will probably show that this species is incorrectly placed in *Geochelone*, and that it is the earliest known member of a small series of forms including the Lower Oligocene *amphithorax* and the Middle Oligocene *nebrascensis*.

Through the courtesy of the following individuals and institutions (with abbreviations used as indicated), I have had an opportunity to study almost all the better material of *Stylemys amphithorax* available: Dr. Edwin Colbert, the American Museum of Natural History (A.M.N.H.); Dr. Clayton Ray, University of Florida (U.F.); and Dr. Peter Robinson, University of Colorado Museum (U.C.M.).

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