

A new genus and species of gigantic marine turtles (Chelonioidea: Cheloniidae) from the Maastrichtian of the Harrana Fauna–Jordan

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7 figures

Abstract

Marine turtle fossils are extremely rare in the Muwaqqar Chalk Marl Formation of the Harrana Fauna in comparison to the relatively rich variety of other vertebrate fossils collected from this locality. This paper reports and describes the remains of an extinct marine turtle (Chelonioidea) which will be tentatively assigned to a new genus and species of marine turtles (Cheloniidae Bonaparte, 1835) *Gigantatypus salahi* n.gen., n.sp.. The new genus represented by a single well–preserved right humerus, reached remarkably large proportions equivalent to that of *Archelon Wieland*, 1896 and represents the first to be found from this deposit and from the Middle East. The specimen, which exhibits unique combinations of features is characterized by the following morphological features not found in other members of the Cheloniidae: massive species reaching over 12 feet in length; a more prominently enlarged lateral process that is situated more closely to the head; a ventrally situated capitellum; a highly laterally expanded distal margin. The presence of these features may warrant the placement of this new species in a new genus. The specimen also retains some morphological features found in members of advanced protostegids indicating close affinities with the family. Several bite marks on the ventral surface of the fossilized humerus indicate shark–scavenging activities of possibly *Squalicorax* spp..

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Abbreviations

C	capitellum	1	distal side
f	fossa	2	interior lateral side
h	head	3	proximal side
lp	lateral process	4	exterior lateral side
mp	medial process		

Institutional abbreviations

ERMNH	Eternal River Museum of Natural History, Amman–Jordan
JPMC	Jordan Phosphate Mines Company, Amman
ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania

1. Systematic palaeontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Chelonioidea Bauer, 1893
Family Cheloniidae Bonaparte, 1835
Genus *Gigantatypus* n. gen.
Species *salahi* n. sp.

Type species and specimen: *Gigantatypus salahi* Kaddumi, 2006. Right humerus deposited in the private collection of the author under the number ERMNH 1076 and intended to be a part of a forthcoming privately owned and registered museum of natural history.

Diagnosis: Gigantic marine turtle not less than 3.5 meters in length; massive 67 cm long and straight humeri with a moderately flattened shaft; expanded distal humeral region 30 cm in width; enlarged lateral process that is situated in very close proximity to the humeral head; humeral head elevated above medial process; well ventrally situated radial capitellum.

Etymology: Giganta-, Greek for 'gigantic' and typus is Greek for 'type', referring to this as a new gigantic type of marine turtles.

2. Introduction

Fossil records indicate that marine turtles that are well adapted to marine life with flipper-like forearms made their first appearance in the Jurassic some 200 million years ago (Fernandez & De la Fuente, 1993; Hirayama, 1997). The Cretaceous witnessed more distribution and diversification of marine turtles with the Chelonioidea superfamily, likely reaching the peak of its diversity during the Campanian stage (Weems, 1988; Hirayama, 1997). It was during the same era that the following families became well-established: Dermochelyidae, Protostegidae, and Cheloniidae. The three previous families are recognized by most authors with each comprising a relatively distinct and well-defined clade (Lehman & Tomlinson, 2004). Hirayama (1995, 1998) distinguished two superfamilies of marine turtles, the Chelonioidea (containing both Toxochelyidae and the Cheloniidae families) and the Dermochelyoidea (containing both Dermochelyidae and Protostegidae). All of these turtles possess modified limbs that allow for an underwater flying propulsion mode (Hirayama, 1997). Each of the previous subfamilies is characterized by several synapomorphies.

For the purpose of this study, only those characters pertaining to the humeri of different groups will be listed. In the Cheloniidae, the lateral process of the humerus is enlarged into a V-shaped structure. In the Dermochelyidae (Baur, 1888), the humeral process is elongate with an anterior projection. A lateral humeral process that is restricted to the anterior margin of the shaft with a median concavity in its proximal surface characterizes Protostegidae Cope, 1872. In this paper, Hirayama (1995, 1998) will be followed in the distinction of the superfamilies, and a new genus and species of marine turtles will be assigned to the Cheloniidae.

3. Geological setting

The Muwaqqar Chalk Marl Formation, where the bone was collected (figure 1), was invoked by Masri (1963) after the town of Muwaqqar which is about 30 km west of AlHarrana area. As the name implies, the formation (figure 2) is composed of chalks and marls and represents the oldest outcrop in the locality dating back to the Maastrichtian Upper Cretaceous and is topped by the Eocene Umm Rijam Chert-Limestone Formation which is mainly composed of chalk and chert. Overall, the formations are of composite lithology with chalks being the main component of the rock units. The Muwaqqar Chalk Marl Formation, composed of the same lithology, is exposed in the Azraq area in Wadi Usaykhim some 85 kilometers east of the Harrana area (Al Harithi & Ibrahim, 1992), Tilal al Fulug, and Qa Khana. Ibrahim (1996) indicated the formation thickness in Tilal al Fulug to be 30 meters, 10.5 meters in Qa Khana, and 10.5 meters South East of Qasr AlHarrana. The exposed parts of the formation in the study area, as measured by Hunjul (2001) range between 15 to 23 meters. Microfaunal analysis by the Subsurface Geology Division of the Natural Resources Ministry, conducted on samples from the Usaykhim section indicated a Maastrichtian age. The same results were reached on an assemblage studied from the Qa Khana section.

Although all exposed sections of the Muwaqqar Chalk Marl Formation studied in different areas contain fossiliferous concretions, their size and faunal and floral content differ greatly from those found in the study area which will be referred to in this manuscript as the 'Harrana Fauna' due to its close proximity to Qasr al Harrana

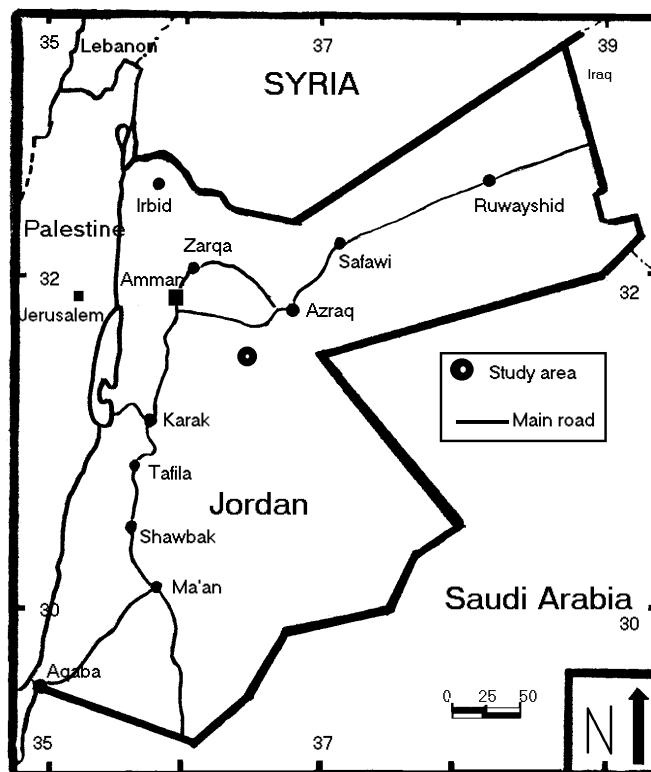


Figure 1. Location map of study area. Drawing by the author.

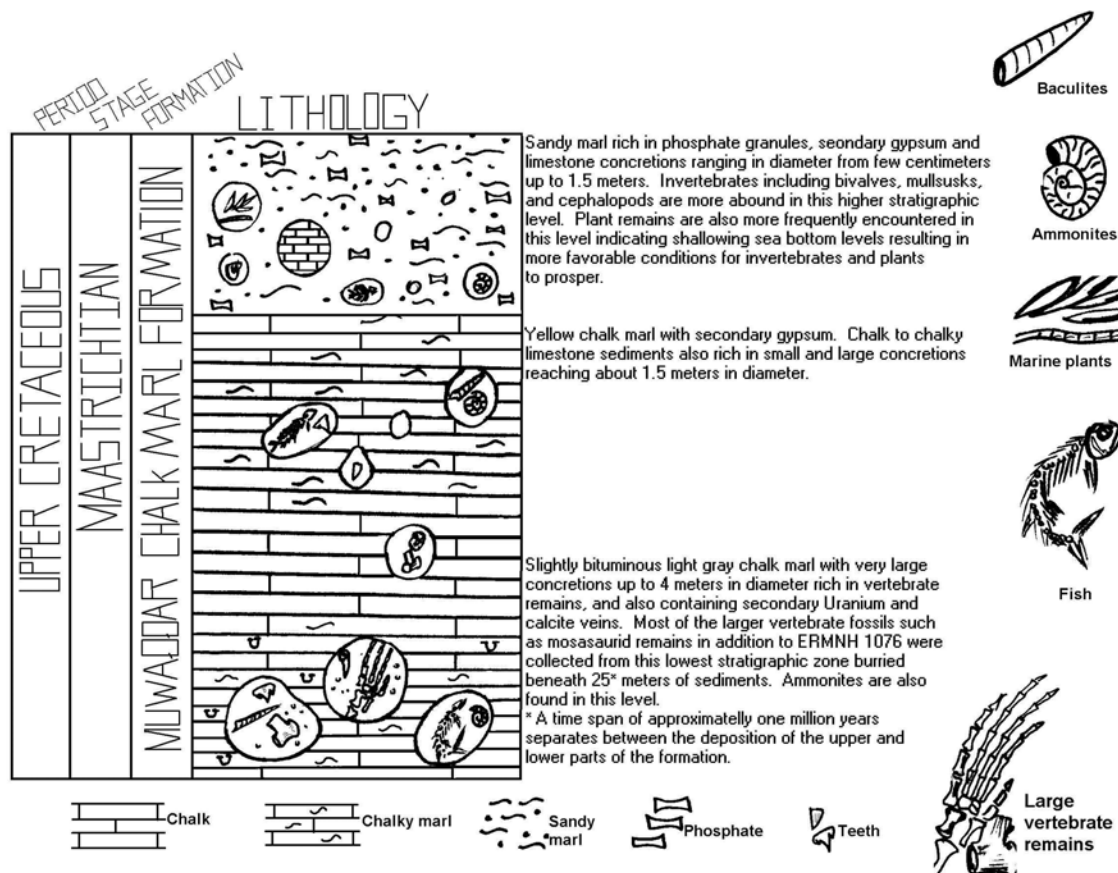


Figure 2. A generalized stratigraphic column of the Muwaqqar Chalk Marl Formation measured in Wadi Al Dab'i of the Harrana Fauna. Drawing by the author .

and the occasional fascinating vertebrate and invertebrate fossils discovered within its concretions. The most important and intriguing geological feature of the Harrana Fauna section of the Muwaqqar Chalk Marl Formation is the presence of very large and massive micritic limestone concretions reaching as wide as 4 meters in diameter. The concretions are buried at different depths, reaching well over 20 meters under beds of gypsiferous and dark grey bituminous marl, granular phosphate and sandy limestone. The outer surface of some of the concretions is covered with a thin layer of trace uranium.

4. Faunal assemblage

The concretions come in a variety of sizes contain a variety of exceptionally well-preserved fossils that are usually not affected by the earth's compression factors and in many instances still retain superbly clear anatomical detail of their soft tissue. The great majority of fossils found are imbedded in a manner parallel to the lamination and, among the fauna fish are usually the most affected by compression. Some of the discovered fossils were obliquely embedded indicating very soft and muddy bottom conditions. Fish fossil finds in the Harrana Fauna indicate that a diverse group of fish existed in the southeastern margin of the Tethys during the Maastrichtian age of the upper Cretaceous. Among the fish assemblage teleosteans are most abundant in terms of percentage and are represented either by complete specimens, fragments, teeth or scales. The following families were identified by author: Enchodontidae represented by several taxa including *Enchodus elegans* and *Enchodus libycus*; Eurypholidae indet.; Dercetidae represented by the genera *Dercetis* and *Stratodus apicalis* which is represented by the first and only complete cranial skeleton discovered to date; Saurodontidae represented by at least two different genera including *Saurodon* Hays, 1830 and *Saurocephalus* Harlan, 1824; Ichthyodectidae indet. Though rare, remains of fish belonging to the Beryciformes (Dinopterygoidea) were also discovered. Several other species and genera with undetermined affinities were also discovered among the faunal assemblage of the Harrana fossils. Although selachian remains were also found in the concretions, they are not as common as fish and are mostly represented by teeth with only very rarely partially complete or complete articulated skeletons found. Most common among selachians are the remains of *Squalicorax pristodontus* and *Cretolamna biauriculate*. Well-preserved remains of undetermined myliobatoid rays were also found. Undetermined enigmatic tiny 2 mm selachian teeth with three lateral cusplets and a broad massive root are among the shark assemblage of the Harrana fossils.

Remains of marine reptiles are mostly represented by disarticulated skeletons and teeth. They are usually unaffected by compression factors, are very well-preserved and show clear anatomical bone surface detail. Marine reptiles identified to date include: mosasaurids, plesiosaurids and marine turtles. Among the marine reptiles, mosasaurids are the most abundant followed by marine turtles with the remains of plesiosaurids being the least abundant. Mosasaurids are represented by several genera including *Clidastes* Cope, 1868, *Mosasaurus hoffmanni* Mantell, 1829, *Liodon anceps*, *Platecarpus* indet., *Tylosaurus* indet., in addition to a new species and genus of small durophagous mosasaurs similar to carinodens represented by a 12 cm long partial dentary with teeth. With only five specimens discovered including the one in study, marine turtle remains found in the Harrana Fauna are considerably less than the mosasaurid remains discovered from the same deposit. Uniquely, plesiosaurids are represented by a single well-preserved, but partial polycotyloid skull. The specimen represents a definite early Maastrichtian age distribution of the family within the southeastern margin of the Tethys. Other vertebrate fossils, though rare, include pterosaurs found within the concretions (of which the author collected a fine specimen represented by an uncrushed and well-preserved wing bones on July of 2003). Pterosaurs from the deposit are also represented by an incomplete well-preserved notarium. Non-vertebrate fossils, which are usually more common in the upper horizons of the formation, include ammonites and baculites, brachiopods, gastropods and occasionally well-preserved carbonized imprints of marine plants.

The collection of specimens from the Harrana Fauna was a result of ten year fossil collection and excavation in the locality carried out by author. The diversity of the floral and faunal content of the deposit is immense and future studies will significantly increase the number of identified taxa. The fossil assemblage of the Harrana Fauna will significantly increase our paleogeographical awareness filling several gaps between several Cretaceous Tethyan and non-Tethyan assemblages including the near by Hajula, Hakel and Namoura in Lebanon (Forey *et al.*, 2003), Ein Yabrud in the West Bank, Jebel Tselfat in Morocco (Arambourg, 1954), the assemblages of the Cretaceous Western Interior Sea of the United States and Canada, and El Rosario in Mexico Wolfgang *et al.* (2005).

5. Material and methods

The specimen described is a right humerus, ERMNH 1076, and 67 cm long (figures 3, 4, 5), collected by the author on November 25th, 2005 from the Maastrichtian Muwaqqar Chalk Marl Formation of the Harrana Fauna, Jordan. As indicated by the very large size of specimen in addition to the fully ossified articular surfaces

of humeral elements, ERMNH 1076 belonged to a mature individual at the time of death. The specimen exhibits very fine surface detail with superbly preserved cortical bone that is not abraded. The bone, which was found during quarrying, was initially broken in a manner perpendicular to the axis into two halves. Each portion was completely encased in a thick limestone matrix. The extra limestone was cut away far from the bone, followed by removing the hardened limestone overlying the ventral surface of the humerus. Once the ventral surface of the bone was exposed on the two halves, they were glued back together. As a result of the jackhammer used in quarrying to split open the concretions, damage was caused to the ventral surface of the humerus where the drill bit penetrated the bone. The original penetration took place just lateral to the pectoral crest and slightly distal to the medial process causing irreparable damage to the original bone. The damaged area is about 4 cm in greatest width decreasing distally to form a small fracture line. Proximally, the damaged area also became narrower passing through the fossa at a width of 8 mm and through the internal side of the large head. To mask and reconstruct the damaged area, a mixture of white cement with colour oxide and a strong bonding agent was prepared and poured into the large open cavity and allowed to completely cover the internal exposed bone. The dorsal surface of the humerus is still imbedded in a thick chalky-marl matrix as no further preparation was conducted on this side.

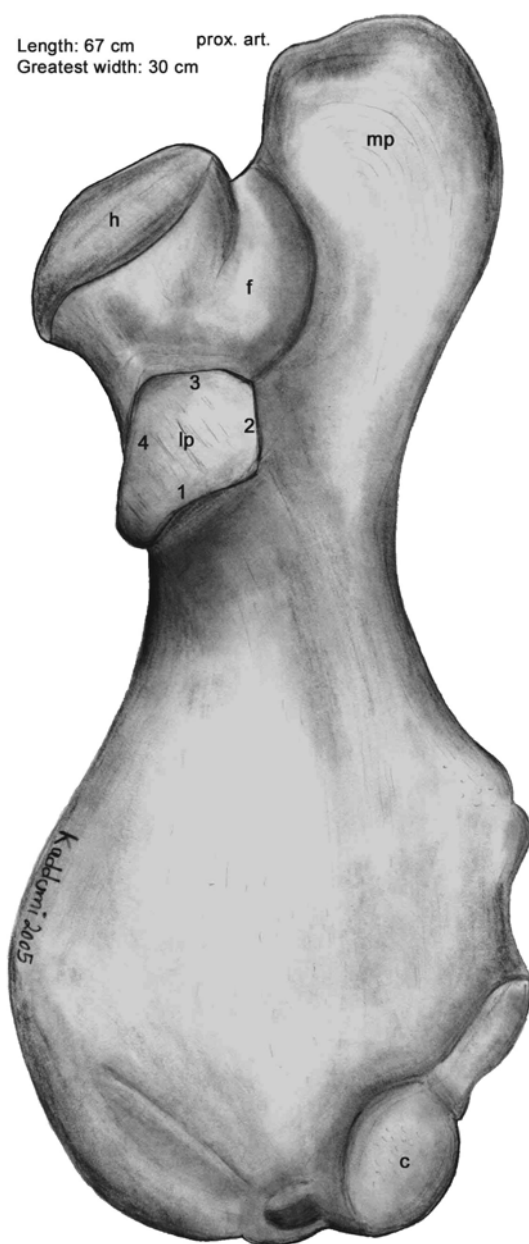


Figure 3. *Gigantatypus salahi* n.gen., n.sp. (ERMNH 1076). Ventral margin of right humerus from the Maastrichtian of the Muwaqqar Chalk Marl Formation. Drawing by the author.



Figure 4. *Gigantatypus salahi* n. gen., n.sp. (ERMNH 1076). Ventral margin of the right humerus from the Maastrichtian of the Muwaqqar Chalk Marl Formation of the Harrana Fauna. Photograph by the author.



Figure 5. *Gigantatypus salahi* n. gen., n.sp. (ERMNH 1076). Right humerus: proximal margin showing the head, medial process and pectoral crest. The arrow points to the 2nd shark tooth mark on the proximal region of pectoral crest. Photograph by the author.

6. Description

ERMNH 1076 is a well-preserved right humerus, medium brown in coloration. The humerus is uncrushed and still perfectly retains its natural bone contour and curvature despite the damage done by the quarry's jackhammer (see above). The total length of humerus is 67 cm (measured on the ventral side) with a maximum width of 30 cm (measured slightly proximally to the distal most margin). The bone is divided into four main regions: a proximal articular surface (figure 5), a large pectoral crest, a shaft, and a distal articular surface. Overall, the bone is very large with highly expanded distal and proximal regions. The proximal articular area is divided into three main areas, two prominent lateral tuberosities (head and medial process) with a deep and moderately long fossa in between. The width of the proximal region is 27 cm. The medial process is wider and longer than the head being 14 cm long (as measured to the proximalmost margin of the pectoral crest), and 12 cm wide (measured from its exterior lateral margin to the margin of fossa). The medial process is dorsoventrally flattened being more flattened externally (3.7 cm) and gradually widening internally, reaching a maximum width of 9 cm. The medial process has moderately deep and long grooves for the attachment of the flipper abductor and extensor muscles. These grooves are oriented in a distal-proximal fashion. The proximalmost margin of the medial process extends 2.8 cm further proximally past the head. The ventralmost margin of the medial process is slightly lower than head. In lateral view, the medial process projects slightly dorsally at a very low angle in relation to the axis of the shaft. The head is slightly offset and characteristically massive with a large sub-circular face, facing more proximally than ventrally. The width of the subcircular face of the head is 11 cm. The dorsoventral length of this face cannot be accurately determined since the dorsal margin of head is still imbedded in matrix, though it is expected to be no less than 12 cm. The head projects ventrally from the axis of the shaft at a low angle, and thus the head's plane of motion is at a greater angle to the shaft.

The lateral process is large with pronounced ridges. It begins well up on the shaft and rises distinctly close to the head and opposite the medial process with a distance of only 5 cm separating its summit from the proximally situated head. The lateral process (figures 3 [lp], and 7 [2]), which is situated just distal to the head, has a very large summit sub-quadrilateral in outline with four sides (1-4) two of which (1, 3) nearly parallel. The lengths of the sides are: 1 = 9 cm, 2 = 4.7 cm, 3 = 5.5 cm, 4 = 8.5 cm. The exterior distal margin of summit strongly curves laterally from the remaining flat summit. Exterior distal margin with three prominent scars for muscle insertions measuring consecutively 2 cm x 0.8 cm, 2.5 cm x 1.1 cm, 2 cm x 0.5 cm. Four edges lead to the summit of the lateral process, a notably high and wide distal edge emerging from the humeral shaft, a smaller and not as wide interior lateral edge, and two shorter edges leading to the proximal and exterior lateral margins of summit. The lateral process projects from the axis of the shaft at a high angle (45°) and grows ventrally and proximally with a summit facing more ventrally with a slight exterior lateral inclination. The summit and distal margin of lateral process (edge facing the distal margin of humerus and leading to the summit) has prominent scars for the insertion of the very strong pectoral flipper protractor muscles needed for propulsion. The middle margin of the distal edge is slightly concave. Concaved area measures 2.5 cm in greatest width, 2.5 cm in length, and 0.5 cm in depth.

Distally, and beyond the head region, the humerus narrows down to a straight, distinctly wide (15 cm), and moderately dorsoventrally flattened shaft (approximately 8 cm). Prior to uniting the two halves of the broken humerus together, the cortical bone thickness of the shaft region was observed to be much thicker than that of the humeral extremities (not less than 2 cm thick for each of the dorsal and ventral margins). Beyond the shaft region, the cortical bone thickness becomes notably slimmer (not exceeding a few millimeters in thickness). Highly porous and cancellous bone was observed in the shaft region sandwiched between the thick cortical bone. The cancellous bone extends proximally passing through the pectoral crest and continues almost to midway of head region. Distally, it extends only slightly proximally to entepicondyle. The remaining internal bone of extremities is very compact, not porous, and very light in coloration unlike the brown spongy bone. The dorsoventrally flattened distal end of the humerus is markedly wide (30 cm) which is broader than the proximal region (27 cm). The supinator region is broad and the entepicondyle is also broadly expanded. The entepicondyle foramen is absent. Located distally and projecting more ventrally is the ulnar condyle, which has a circular articulation joint. The articular surface with a saddle shaped trochlea. Distal exterior lateral margin of humerus slightly twisted ventrally. A moderately large U-shaped and deep foramen is present in the distal margin of humerus next to capitellum (as illustrated).

7. Discussion

ERMNH 1076 from the Harrana Fauna exhibits a unique combination of morphological features that are similar to the general form of the cheloniid (*Cheloniidae*) humerus. Both have an enlarged deltoid crest that is situated distally and in close proximity to the head process, opposite the medial process; a wide and deep fossa between the medial process and the head; enlarged medial process extending beyond the humeral head; a large

sub-spherical head approximately 20° offset from the bone shaft and with a proximal surface more proximally projected than ventrally. Such morphological features merit the placement of this new species within Cheloniidae. However, several differences occur between this holotype and modern and extinct members of the family. Some of the major differences include: the massive humeral size, a more prominently enlarged lateral process that is situated more closely to the head, a characteristically highly laterally expanded distal margin more so than any other modern or extinct family of turtles. Based on these differences, this new species qualifies to be placed in a new genus of Cheloniidae. It is interesting to note that the lateral process of ERMNH 1076 is particularly similar to the lateral process of the late Cretaceous turtle *Allopleuron hoffmanni* (Gray, 1831) from the Maastrichtian type area (Mulder, 2003: plate 44, figure 2). The lateral process in *Gigantatypus salahi* (ERMNH 1076) is more closely situated to the head than in *Al. hoffmanni*. The lateral process in dermochelyids is placed farther distally and projects farther laterally. Also in dermochelyids, the humerus is more notably flattened than in *G. salahi*. Unlike cheloniid humeri which have relatively thick cortical bone around a cancellous core, the humerus of dermochelyids is mainly composed of cancellous bone with relatively very little cortical bone. In Protostegidae Cope, 1872, the lateral process is similar in being restricted to the anterior portion of the shaft but differs markedly in the structure. Despite the anterior placement of the lateral process, it is not close to the proximal region of the head as in *G. salahi*. Also, *G. salahi* lacks the medial concavity in the proximal margin of the lateral process which is considered a distinct feature found in the humeri of Protostegidae (Hirayama, 1992). Although the humeral shaft of *G. salahi* is widened as in advanced protostegids and dermochelyids, it is not as dorsoventrally compressed and flattened which is considered a typical feature of the two previous families. When viewed ventrally, the humerus of *G. salahi* is more straight than the humeri of protostegids and dermochelyids. In addition to the highly specialized humeri and massive size that both protostegids and the new species in study reached, a ventrally situated radial capitellum is common to both families (which is situated more dorsally in Cheloniidae). The humeral head elevated above the medial process in *G. salahi* is a condition different from derived Cheloniidae and basal protostegids and dermochelyids.

Interestingly, ERMNH 1076 also exhibits resemblance to the enigmatic upper Cretaceous partial humerus of *Atlantochelys mortoni* (ANSP 9234) identified as a marine turtle bone and named by Agassiz (1849) without any further description. Three views of the specimen were later figured by Leidy (1865) and presumed to be the humerus of *Mosasaurus*. Two of the views illustrated by Leidy were re-illustrated after him in this manuscript (figure 6 [2–3]) for comparisons. *Atlantochelys mortoni*, which was considered a protostegid by Hirayama (1997) and has a proximal margin that is similar in the general outline and form to *G. salahi*. Both humeri are massive in size and belonged to gigantic marine turtles. Both specimens possess a long, deep and moderately wide fossa between the lateral process, head, and medial process; an enlarged lateral process that is situated at a very close proximity to the head; a medial process that projects proximally past the articular surface of the head; an enlarged head that is elevated above the medial process. Such similarities pertaining to both humeri suggest affinities with protostegids. However, several morphological differences are present between both specimens, which include:

- Distally and beyond the head's region, the humerus of *At. mortoni* narrows down to a notably constricted shaft in comparison to the distinctly wide shaft of *G. salahi*. In *At. mortoni*, the proximal region's width is 2.76 times greater than width of shaft in comparison to 1.8 times in *G. salahi*. The narrow-waist of *At. mortoni* is a primitive feature and the broad and flattened shaft of *G. salahi* is a synapomorphy of the Cheloniidae, Dermochelyidae, and Protostegidae.
- The proximalmost margin of the medial process in *At. mortoni* extends further proximally past the articular surface of the head than in *G. salahi*.
- The medial process of *G. Salahi* is laterally wider and, in lateral view (figure 6 [1]), the dorsoventral thickness of its proximal extremity is notably thicker and with a pronounced difference in shape. Also, the medial process projects slightly dorsally. In *At. mortoni*, it is almost straight.
- In *G. Salahi*, the face of the humeral head is more proximally projected (figure 6 [4]) than ventrally. In *At. mortoni*, it is more ventrally and externally projected (figure 6 [3]).
- The lateral process of *G. salahi* is more massive, with a large and broad summit facing more proximally than ventrally. The lateral process of *At. mortoni* is not as massive and with a smaller summit facing more ventrally. In lateral view the internal lateral margin (the edge leading to the summit of lateral process) of *G. salahi* is notably wider than the corresponding element in *At. mortoni*. The lateral process of *At. mortoni* projects further ventrally from the body of the humerus.
- The lateral process of *At. mortoni* projects at a greater angle in relation to the axis of the shaft than in *G. salahi*.

As of yet, only one specimen of *At. mortoni* has been collected and it is unfortunate that it is missing its entire distal margin. Due to its constricted shaft, it is likely there would have been more acute differences between it and holotype in the morphology of the distal humeral region.

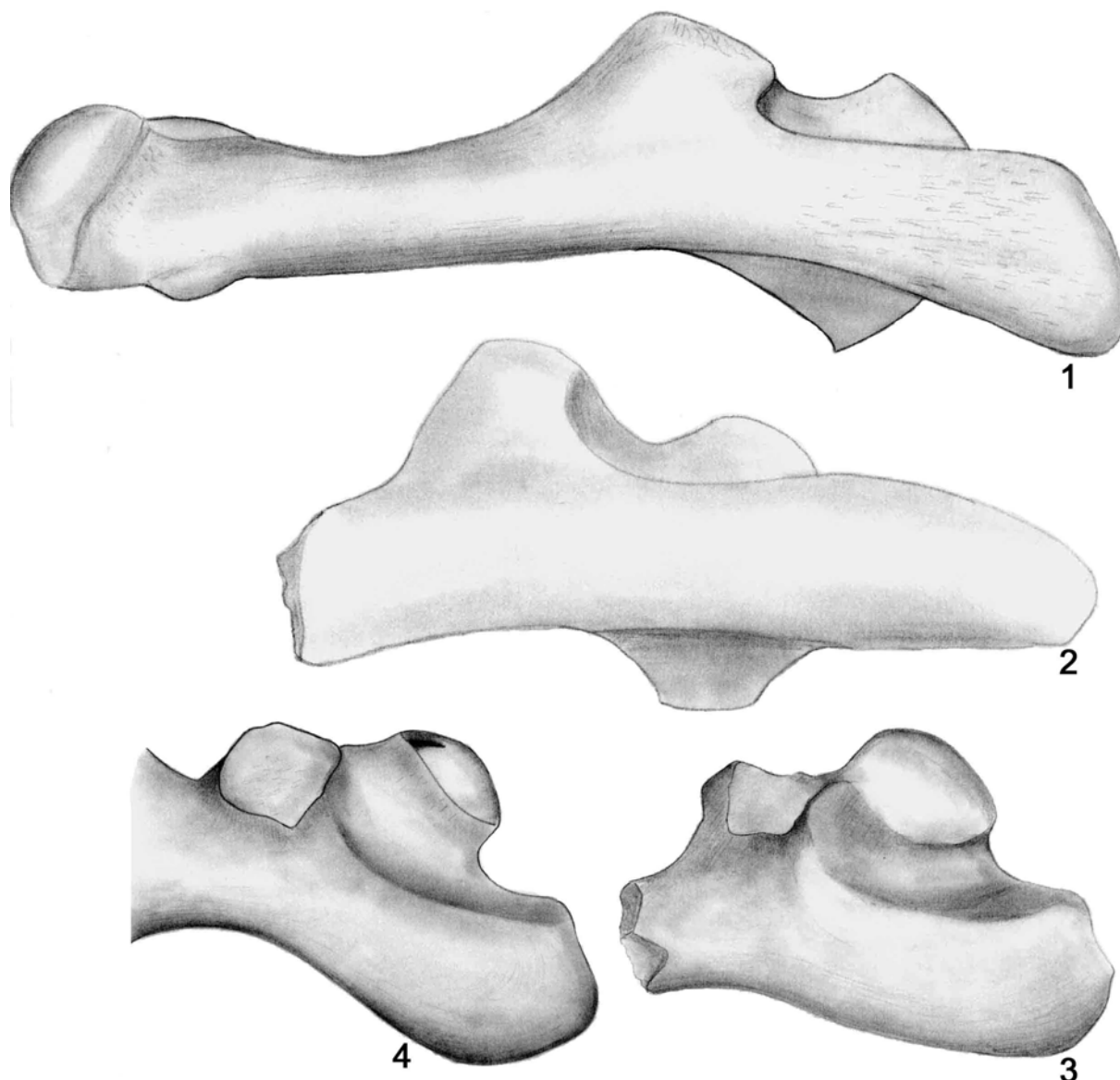


Figure 6. 1: *Gigantatypus salahi* n. gen., n.sp. (ERMNH 1076) in lateral view; 2: *Atalantochelys mortoni* in lateral view (after Leidy, 1865); 3: proximal extremity of *Atalantochelys mortoni* (after Leidy, 1865); 4: proximal extremity of *Gigantatypus salahi* n. gen., n.sp. (ERMNH 1076) drawn from an anterior ventrolateral view matching the drawing angle by Leidy. Drawings by the author.

8. Size

Measured from the proximalmost to the distalmost margin, the humerus in study is 67 cm long. If we were to estimate the total length of the forelimb, based upon estimates of complete cheloniids, we can arrive at an estimated 35 cm long ulna. According to Zangerl & Sloan (1960) and Zangerl *et al.* (1988), the ulna is typically 45–55% the length of the humerus and the radius is equal to 55–65% the length of the humerus in cheloniids. If we were to consider the lowest percentage, the radius of *Gigantatypus salahi* is 33 cm in length. Considering the length of the hand, including the carpals, metacarpals and phalanges, to be at an average of 3.1 times greater than the length of the radius, the hand of the new species in study will be 105 cm long. Adding all the figures together, 105+33+66, we arrive at the average total length of the arm which is 205 cm.

Considering the average total length of the body in turtles from snout all the way to the tip of the tail to be 5.44 times longer than humerus, the total estimated length of *Gigantatypus salahi* will be 3.64 meters long (11.95 feet). It is important to consider the variations relevant to the ratio of body parts in different groups of marine turtles. Therefore, the above is only an estimate based upon other genera from the Cheloniid family. The actual length may fall a little shorter or possibly a little longer than the estimated value and a more accurate determination of size will only be attainable with the discovery of more related skeletal remains. Nevertheless,

one fact remains certain: this ancient marine turtle was a giant among others, comparable in size to *Protostega gigas* Cope (1871) and *Archelon ischyros* Wieland (1896). Our new specimen may actually exceed by a bit the largest *Protostega* found to date, a 3.4 meters giant exhibited in the Dallas Museum of Natural History. The largest *Archelon* discovered to date is 4.6 meters long (Mike Everhart, Marine turtles from Western Interior Sea, www.oceansofkansas.com).

9. Shark bites

ERMNH 1076 is also noteworthy because it shows evidence of scavenging or predation by sharks or other aquatic predators. Two clearly distinguished tooth marks on the lateral process are visible. The first mark is located on the interior ventral margin near the summit (figure 7.1) and the second is located right on the proximal most narrow margin of summit 7 cm away from the first (figure 7.2). Both bite marks are slightly curved, 22 mm long, 2.5 mm deep and lack serration grooves. Although it is impossible to determine beyond any doubt what taxon caused the tooth marks, especially when no teeth or partial teeth were found imbedded in the bone nor in the matrix surrounding the bone, we can speculate as to the most likely attributors. The two probable candidates are both sharks, either *Squalicorax* or *Cretolamna*, whose remains were found in the concretions of the Harrana Fauna (personal observation). Based on fossiliferous evidence and data available on the behaviour of Cretaceous sharks (see below), *Squalicorax* is a more likely candidate attributing to such injuries. In addition, the occurrence of *Squalicorax pristodontus* Agassiz (1843) in the type area was much more common than members of *Cretolamna* (personal observation). Teeth of *S. pristodontus* from the type area were found by author in association with a very large and disarticulated scavenged remains of a *Leiodon anceps* Owen (1840) skull, which was most likely scavenged after the reptile's death. Fossil evidence indicates members of *Squalicorax* were scavengers of dead carcasses including those of mosasaurs during the upper Cretaceous Schwimmer *et al.* (1997).

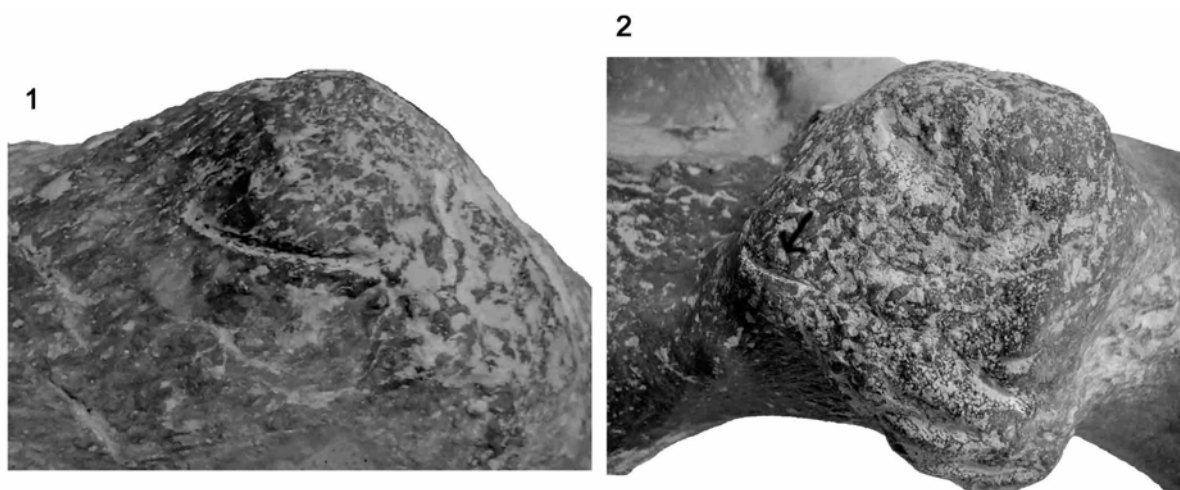


Figure 7. Bite marks of a large shark on the lateral process of *Gigantatypus salahi* n. gen., n.sp. (ERMNH 1076) from the Maastrichtian of the Muwaqqar Chalk Marl Formation. 1: bite mark on the interior lateral edge; 2: bite mark on the proximal margin. Photograph by the author.

Toxochelyid turtle remains preserved as stomach contents of *Squalicorax falcatus* (Agassiz, 1843) were reported by Druckenmiller *et al.*, (1993). *Squalicorax* tooth marks found on the humeri of several species of turtles, including the giant *Protostega gigas* Cope (1872) and *Desmatochelys lowii* Williston, (1894) were documented by Schwimmer *et al.* (1997). Shimada & Hooks (2004) reported the discovery of *Cretoxyrhina mantelli* Agassiz, 1843 tooth marks associated with the peripheral bones of a large *P. gigas* in addition to the discovery of five imbedded *C. mantelli* broken teeth tips in a very large *P. gigas* humerus. Everhart (2005) reported the presence of deep serrated *Squalicorax* bite marks on the humerus of a protostegid in the collection of the University of Wisconsin–Madison. Many of the turtle remains discovered around the world are usually fragmentary remains of dismembered carcasses.

In the case of the material in study, decisively determining if the bite marks occurred as a predatory or non-predatory shark attack is almost impossible. It is evident from available data on modern sharks that predatory attacks on marine turtles do occur. Simpfendorfer *et al.* (2001) reported that the tiger shark population along the Australian coast appears to consume at least several thousand sea turtles yearly. The predation of sea turtles by white sharks is limited (Fergusson *et al.*, 2000). Nevertheless, *Gigantatypus salahi* may have sustained

the teeth injuries due to post mortem scavenging behaviour. The tooth marks present on the humerus do not exhibit any bone healing and tissue repair, therefore, determining if the turtle was bit shortly before, during or after being killed is impossible. Had the bones showed some tissue repair, then we could be certain the injuries were sustained while alive and the animal survived the attack allowing time for injuries to heal.

10. Conclusions

With its very large, stout, dorsoventrally flattened and highly distally widened humerus, *Gigantatypus salahi* had powerful flippers that acted like wide oars, giving an incredible thrust to this massive animal. In addition, the highly developed lateral process and its low radial crest that provided strong holds for muscular attachments must have aided the turtle with powerful swimming capabilities and adaptations equivalent to the members of *Protostegidae*. With such features, *G. salahi* was capable of traveling long distances within the shallow warm subtropical southeastern margin of the Tethys which at the time was filled with fauna and flora. New satellite remote sensing techniques combined with moderns Geographic Information Systems has indicated that extant marine turtles can travel very long distances. An extant captive loggerhead marine turtle, when released, traveled 11,500 kilometers from Santa Rosalita in Mexico's Baja California to Sedai Bay in Japan (Nicholls *et al.*, 2000). Distances covered by *Chelonia mydas* in the Mediterranean region range from 320 to 2200 kilometers in periods ranging from 8 to 44 days (Godley *et al.*, 2002).

It is known that modern sea turtles feed on a variety of food sources including sea grasses, algae, mollusks, and jellyfish, which were all abundant in Tethys margin of the Harrana Fauna. The diet of *Gigantatypus salahi* could have included any of the previous items but determining beyond doubt will only be attainable with the discovery of more related material, particularly cranial elements. Finding a specimen with its last meal fossilized in its gastrointestinal tract would help shed some light on such a subject. The rich Harrana's margin of the Tethys could have been utilized by these turtles as foraging grounds during their migration. Being far from the coastline, their nesting grounds could have been in any of the islands to the north in the Syrian margin of the Tethys, or to the south of the Harrana where marine turtle remains are more abundant or in costal grounds few hundred kilometers to the south or to the west. The similarities between the fossil assemblages of the southern margin of the Tethys below 20° N paleolatitude strengthens the possibility this new taxon of marine turtles could have been in migration anywhere from the vast northern or northeastern coastal regions of Cretaceous Africa.

Due to the rarity of fossilized marine turtle remains in the area, and the nature of their fragmentary remains, little is known of their occurrence within the Maastrichtian Harrana Fauna region of the Tethys. Within the past decade, only five fragments belonging to at least two different families (including the species in this study) were collected by author from the locality. One of the collected specimens consists of seven articulated cervical vertebrae identified as belonging to basal cheloniids. We know from fossil evidence this region teemed with several genera of mosasaurs, with some reaching well over seven meters in length, forming formidable predators to even the largest and hardest marine turtles at the time. Such a menacing presence would have caused at least some of the more vulnerable marine turtles to avoid these areas and seek refuge in safer grounds. Also, the oxygen-rich, shallow, warm and sunlight-penetrated waters of the Harrana's margin of the Tethys opened the way for an array of marine plants to prosper and reach immense sizes (personal observation). Such a lush environment provided the mosasaurs with ideal ambushing grounds, which for a turtle to pass through such an area could have meant suicide. Despite all the danger, the highly rich environment was an irresistible lure.

Remains of marine turtles mainly represented by costal plates are more abundant in the Maastrichtian Hassa Phosphorite Formation some 50 miles to the south of the Harrana Fauna. The lack of complete marine turtle specimens and the nature of the disarticulated remains may be an indicator of predation by other vertebrates such as sharks and mosasaurs, which infested the waters of the Tethys during the Maastrichtian right before their sudden disappearance alongside the dinosaurs. In general, due to their usually smaller size, low speed, and lack of defensive capabilities, it seems that marine turtles may have been more subject to predatory attacks. The fossil record has preserved plenty of fine examples of such behaviour.

Marine turtle remains closely related to cheloniids represented mainly by large costal plates (10 cm wide and 20 cm long) and a single vertebra kept in Amman (JPMC) were reported by Bardet & Pedra Suberbiola (2002). The cervical vertebra is low and wide resembling those of cheloniids and different from those of dermochelyids and protostegids (Zangerl, 1953; Hirayama & Chitoku, 1996). The procoelous centrum bearing a reniform to elliptic articular surface was interpreted as being the fifth or the eighth of a cheloniid cervical series (Bardet & Pedra Suberbiola, 2002). Similar cervical material from the late Cretaceous phosphates of Syria was reported by Bardet *et al.* (2000). A new genus and species (*Karkaemys arabicus*) of side-necked marine turtles (Pleurodira, Bothremydidae) was reported and described from the Maastrichtian Upper Cretaceous Wadi Umm Ghudran Formation of Jordan by Zalmout *et al.* (2005).

Certainly, the importance of the discovery of a gigantic cheloniid marine turtle from the Middle East cannot be overstated. The extreme rarity of such material from this region of the world, and to that matter from the Maastrichtian Tethys as a whole, has kept our knowledge of this group of marine turtles rather poor and incomplete. The discovery of this new species increases our knowledge on the diversification, distribution, and phylogeny of Cretaceous marine turtles. Similar to mosasaurids, it is evident that certain groups of aquatic turtles, such as the cheloniids, reached immense sizes close to the end of the Cretaceous. So far, as evidenced by their limited radiation and geographical distribution, members of these giant marine turtles appear to have been highly restricted to specific and limited ecosystems.

While members of this new species and genus of Cheloniidae probably did not survive the K–T boundary, such was the fate of protostegids and other families of turtles. Other members of Cheloniidae, though much smaller in size, survived the Cretaceous mass extinction and continued on with new generations that remained until our present day.

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