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The First Side-Necked Turtle (Pleurodira, Bothremydidae) from the Campanian (Late Cretaceous) of Egypt †

Mohamed AbdelGawad [1,*], Adán Pérez-García [2], Ren Hirayama [3], Sara Mohesn [4], Abdel-Aziz Tantawy [4] and Gebely Abu El-Kheir [4]

1 Geology Department, Faculty of Science, Cairo University, Giza 12613, Egypt
2 Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, Avda. Esparta s/n, 28232 Madrid, Spain
3 School of International Liberal Studies, Waseda University, Nishiwaseda 1-7-14, Shinjuku-ku, Tokyo 169-0051, Japan
4 Geology Department, Faculty of Sciences, New Valley University, New Valley 72511, Egypt
* Correspondence: mkabdelgawad@cu.edu.eg
† urn:lsid:zoobank.org:act:7EFC0CF3-8101-4A5B-865A-249ABA524298;
urn:lsid:zoobank.org:pub:C475DDB9-AB10-4893-AA85-8DB7F1B2724D;
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Abstract: The Quseir Formation is an Upper Cretaceous (Campanian) deposit in the Kharga oasis of the Southwestern Desert (Egypt). This formation comprises a clastic sequence of bioturbated mudstone and sandstone intercalations, including rare scattered and fragmented vertebrate remains such as shark teeth, dinosaur remains, and turtle plates. These deposits indicate a supratidal marsh environment. A complete shell of a turtle discovered from the Quseir Formation, at the Kharga oasis, is attributed here to Bothremydini (Pleurodira, Bothremydidae), and determined as a new taxon: *Khargachelys caironensis* gen. et sp. nov. This form represents the only Bothremydini member currently identified in the Campanian record not only of Egypt but also of North Africa. Therefore, it helps fill the missing evolutionary gap from the Late Cretaceous pleurodires in Egypt and in North Africa.

Keywords: Campanian; Quseir Formation; Kharga; Bothremydini; *Khargachelys caironensis* gen. et sp. nov

Citation: AbdelGawad, M.; Pérez-García, A.; Hirayama, R.; Mohesn, S.; Tantawy, A.-A.; Abu El-Kheir, G. The First Side-Necked Turtle (Pleurodira, Bothremydidae) from the Campanian (Late Cretaceous) of Egypt. *Diversity* **2023**, *15*, 284. https://doi.org/10.3390/d15020284

Academic Editor: Jürgen Kriwet

Received: 25 December 2022
Revised: 2 February 2023
Accepted: 4 February 2023
Published: 16 February 2023

1. Introduction

The Late Cretaceous attracts great attention from paleontologists as its end coincides with the mass extinction of many vertebrate groups, including several groups of reptiles such as non-avian dinosaurs and plesiosaurs [1–9]. Given the potential of the Upper Cretaceous sediments for yielding vertebrate fossil remains, Cairo University and New Valley University members collaborate to carry out exploratory fieldwork in the vertebrate-bearing strata of the South Western Desert, Egypt.

The vertebrate horizons in the Late Cretaceous of Egypt are concentrated in the Western Desert. There are three main horizons: the first is the Cenomanian horizon which is concentrated in Baharyia Oasis, which is known for the most famous dinosaur remains in Egypt and other vertebrates such as fishes, crocodiles, and Squamata [10,11]; the second is the Campanian horizon in Kharga and Dakhla Oases which contain dinosaurs [4], fishes, and marine lizard remains [1]; the third is the Maastrichtian horizon in Dakhla and Farafra Oases which contains fishes and marine lizard remains [6,8,9]. All three horizons contain turtle remains [12].

The diversity of Bothremydidae in the Late Cretaceous record of Africa is relatively poorly known, the information about the Egyptian representatives being extremely scarce. Due to the breaking up of Pangea, the distribution of the non-marine turtles exhibits distinct paleobiogeographic distribution patterns [13].

The bothremydids may have lived in different environments, indicating by the recording of their remnants from several sediments with diverse paleoenvironments, such as freshwater and littoral marine environments. The secondary adaptation to littoral marine environments gave them the ability for dispersal between different continents, the origin of all or most of the Bothremydidae lineages being located in the southern hemisphere, but most of them also reaching the northern hemisphere [14,15]. The bothremydid turtles attained a great level of variety and vast range throughout the Cretaceous and Paleogene, and are especially well registered throughout the Late Cretaceous, from the Cenomanian to the Maastrichtian [16,17].

In the Mesozoic record of the African continent, bothremydid representatives have been described in both the Cenomanian and the Maastrichtian records. The Cenomanian taxa correspond to *Galianemys whitei* and *Galianemys ermingeri*, from the Kem Kem Formation of Morocco [16,18], and *Akoranemys madagasika*, from Madagascar [19]. A relatively large diversity has been identified for the Maastrichtian, including *Nigeremys gigantea* and *Ilatardia cetiotesta*, from Niger [20–23], and the presence of *Zolhafah bella* and *Arenika krebsi* from Egypt [14].

Turtle diversity in the Late Cretaceous of Egypt is poorly described and a relatively large gap of time is present between the oldest and youngest references to bothremydid remains. The following is the vertical distribution of the turtle fauna from the Late Cretaceous in Egypt; the distribution is in a geological chronological order: in the Cenomanian, Lapparent de Broin [22] reported the presence of "*Apertotemporalis baharijensis*", a putative Bothremydidae in Baharyia Oasis in the Baharyia Formation currently identified as *nomen nudum* (see [17]). Recent studies on the Baharyia fauna reported the presence of a turtle assemblage (fragmentary materials) containing Araripemydidae Bothremydidae; and a marine Chelonioidea (see [10]). In the Campanian age, Sallam et al. [1] reported the appearance of Pelomedusoides in the Southwestern Desert in South Kharga Oasis.

In the Maastrichtian age, Lapparent de Broin and Werner [14] reported a turtle assemblage with the presence of at least four taxa (i.e., the bothremydids *Zolhafah bella*, *Taphrosphys* cf. *sulcatus*, and *Arenila krebsi*, and the cryptodiran *Tasbacka* sp.) in the Ammonite Hill Member in the South Western Desert. Additionally, in the Maastrichtian, Abu El-Kheir et al. [8] reported the presence of a gigantic Pan-Cheloniidae (sea turtle) from the Dakhla Formation in the Abu Minqar area in the Southwestern Desert.

A turtle specimen studied here represents a new bothremydid record from Egypt. It corresponds to the first relatively complete shell of a bothremydid turtle from the Campanian record of Egypt, from the Quseir Formation in the Southwestern Desert. This well-preserved shell is attributed to a new taxon. Its systematic analysis is seen to fill the poor turtle record from the Upper Cretaceous in Egypt. The description of this specimen from the Southwestern Desert of Egypt as a new bothremydid turtle provides a wider distribution range and diversity for this clade in Africa and in the southern continents.

Anatomical abbreviations: Ab, abdominal; An, anal; c, costal; Eg, extragular; ent, entoplastron; ep, epiplastron; Fe, femoral; Gu, gular; hp, hypoplastron; Hu, humeral; hy, hyoplastron; M, marginal; ms, mesoplastron; n, neural; nu, nuchal; p, peripheral; Pc, pectoral; Pl, pleural; py, pygal; spy, suprapygal; V, vertebral; xi, xiphiplastron.

Institutional abbreviations: NVP, New Valley Vertebrate Paleontology Center, New Valley University, Kharga, Egypt.

2. Geological Setting

The present study area is located east of Ganah village, about 10 km south of the Kharga oasis (South Western Desert, Egypt), where the basal part of the Quseir Formation is exposed (Figure 1).

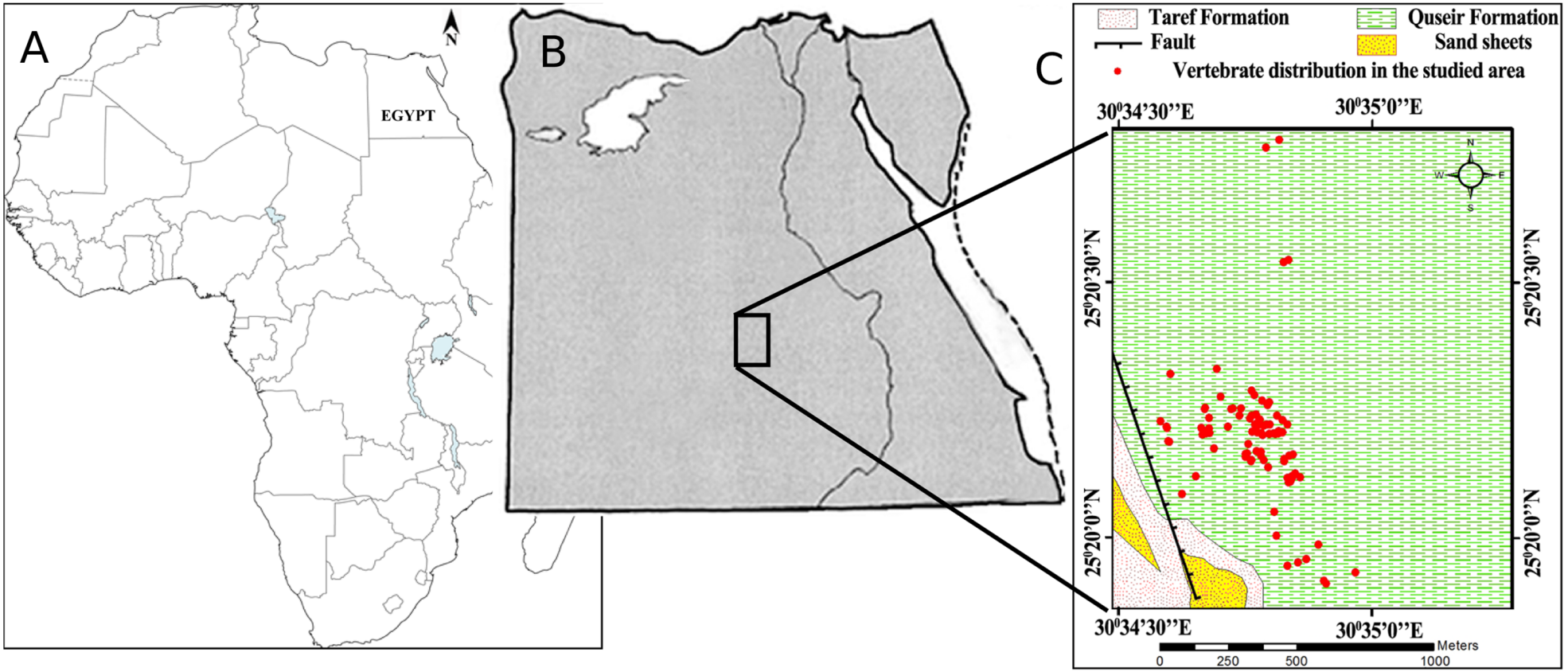

Figure 1. Map of Africa showing the location of Egypt (**A**); map of Egypt showing the location of the studied area in a rectangle (**B**) and a detailed map for the studied area showing the vertebrate distribution east of Gennah village in Kharga Oasis, Southwestern Desert, Egypt (**C**).

The present bone-bearing layers in the south of Kharga belong to the middle Campanian Quseir Formation [24–26]. The Quseir Formation extends between Kharga and Baris, attaining a thickness varying between 60 and 80 m [27]. According to Hermina [28], the Quseir Formation is divided into two members, Mut Member, and Hindaw Member. The Mut Member represents the lower part of the Quseir Formation, consisting of about 30 m thick red brick mudstone and gray fissile shale, which contain the present bone-bearing layers. The Hindaw Member overlies the Mut Member and is composed of about 30 m thick glauconitic claystone intercalated with gray siltstone and sandstone in thin layers [28]. From the nannoplankton analysis [1], the Quseir Formation is referred to as the late Campanian age. According to research on polymorphs and palynofacies, it is thought to have been deposited under fluvio-lacustrine and restricted shallow marine environments [25].

The Upper Cretaceous successive facies of Qarn Ganah are represented from the bottom to the top by the Taref Formation (Coniacian-Santonian), Quseir Formation (Campanian) and the lower part of Duwi Formation (Campanian). The Taref Formation represents the main floor of the north and south west of Kharga oasis. It is represented in the study area by small, isolated hills, highly affected by tectonic activities and extended along Darb El Arbaien, especially between Kharga and Beris oases. The Taref Formation is formed in the study area by about 50 m cross-bedded, coarse to medium grain size fluvial sandstone, occasionally intercalated with thin layers of claystone [29].

The claystones, siltstones, and sandstones of the Quseir Formation [24] (Mut Formation [29]) unconformably overlie the sandstones of the Taref Formation (Coniacian–Santonian age). The Quseir Formation covers extensive areas in Kharga and Dakhla depressions and appears, with varying thicknesses, to make up the foothills of the bordering scarps [30]. In the Kharga area, the basal succession characterized by clay and sandstones provides evidence of terrestrial and brackish environments, grading to a shallow shelf [30]. The upper sediments are mainly varicolored, mottled, silty, and sandy claystones, reflecting prodeltaic shallow shelf facies. In general, the Quseir Formation indicates a gradual, occasionally stagnating transgression. The Quseir Formation fauna includes freshwater gastropods, remains of freshwater reptiles, abundant terrestrial plant debris, and dinosaur remains. These faunas are embedded in the basal sediments, indicating limnic conditions [27,30,31].

Hermina [28] suggested that the Quseir Formation was deposited in terrestrial and brackish environments that graded to a shallow shelf. Hendriks [27] divided the Quseir Formation (Mut Formation [29]) between Kharga and Beris into two main facies: tidal flat facies, consisting of 25 to 45 m of tidal flat deposits, topped by 20 to 40 m thick inner shelf facies. Mahmoud [25] studied the palynofloras of the lower part of the Quseir Formation, between Kharga and Beris, near Bullaq area. He recorded an abundance of water ferns and freshwater algae, supporting the occurrence of moisture in warm humid paleoclimate.

The lithologic exposure here represents the ground of the study area without distinctive cliffs, showing the succession of the Quseir Formation, except in the human excavations, which have exposed about 5 to 7 m thick variegated shale intercalated with thin layers of sandstones, with fragments of turtles, crocodiles, shark teeth, and coprolites. These layers are covered by about 2 m thick grey–purple mudstone, representing this locality's bone-bearing horizon. This layer is rich in turtle shells, sauropod, and crocodile remains in addition to some fish bones, plant remains, and coal. It is intercalated by medium to coarse-grained, cross-bedded sandstone fluvial channels. A small exposure of a thin phosphate layer, rich in shark teeth and fish bones, covers a small part of the lower succession. The sand sheets and the vegetation cover a large part of the study area.

The Quseir Formation is conformably overlain by the Duwi Formation [24,29]. This Formation is the phosphate-breaking horizon in the Western Desert of Egypt [24]. It is composed of shallow marine, 30 m thick dark gray laminated shale, intercalated with successive phosphate layers. Duwi Formation in the study area is represented by thin layers of phosphatic marl, containing an abundance of different taxa of shark teeth, fish bones, and turtle bone fragments.

Most of the recorded turtle fossils of the Campanian deposits in the Qarn Ganah area are embedded in the upper part of the Quseir Formation, Hindaw member. The turtle shells are embedded close to each other, thus appearing in large numbers in a small area.

Many turtle skeletons are deposited in normal positions and others in inverted positions. Most of the turtle skeletons are found disarticulated, but they are intact without scattering, which means that they are highly affected by erosion after exposure [32].

The turtle bones are slightly abraded, indicating short-distance movement with the current [5]. The turtle fossils are associated with scattered elements of dinosaur elements and partial crocodile skeletons and rare fishbones.

The presence of the intact skeletons of turtles and the heavy limb bones of dinosaurs and crocodiles displaying a low stage of abrasion and the palynomorphs which were recorded by Mahmoud [25] reveals that these animals lived around and near the margins of a pond or small lake, surrounded by dense vegetation and deposited in a fluvio-lacustrine environment [5,25].

3. Materials and Methods

The anatomical and systematic study of a relatively complete and articulated shell without the skull of a Bothremydini turtle from the Late Cretaceous (Campanian of the Quseir Formation, in the Kharga Oasis) in the South Western Desert, Egypt is performed here. The turtle material is housed in the New Valley Vertebrate Paleontology Centre of New Valley University, Kharga Oasis, New Valley governorate (Egypt), with the collection number NVP005. The precise locality in which the discovery of NVP005 occurred is Ganah village, Kharga Oasis, New Valley governorate, Egypt.

The shell has very slight fractures and small shifting by the host compact claystone rocks. The shell was removed from the hosting rock and contained in a plaster jacket. The cleaning and the restoration of the specimen were undertaken by different size air scribes and small needles, using PVA and glue as adhesive and hardener materials. Photographs were taken using a digital camera (Af-S Nikkor 24–120 mm 1:4 G ED VR; Nikon) and lens (Af-S Nikkor 70–00 mm 1:28E FL ED VR; Nikon) in normal light. The specimen had been collected within a project funded by STDF (34811; PI: Dr. Mohamed AbdelGawad).

A first-hand analysis of the specimen has been performed. This shell has been described in detail. NVP005 is here represented by photographs of the specimens in two views, i.e., dorsal and ventral views (Figure 2). In addition, schematic drawings of the shell are included in the figure. The complete margins of the plates and scutes are represented in these drawings by continuous black lines. The margins of the scutes are represented by thicker gray lines.

The morphological characters recognized in NVP005 are analyzed in detail, to establish the systematic attribution of the specimen. It is recognized as attributable to a new genus and species of Bothremydini, *Khargachelys caironensis* gen. et sp. nov. Therefore, the specimen is identified as the holotype of the species.

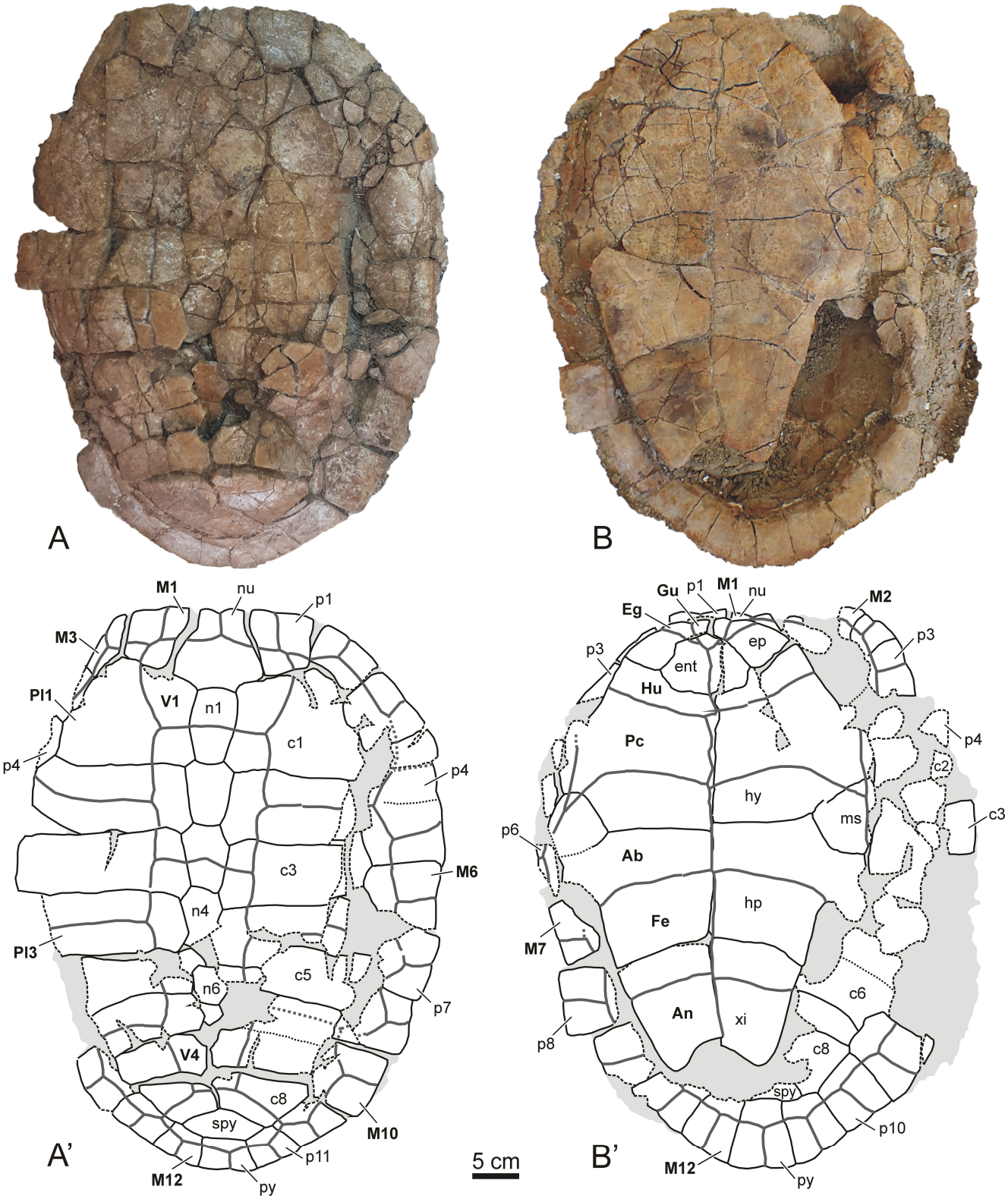

Figure 2. NVP005, the shell of the bothremydid turtle *Khargachelys caironensis* gen. et sp. nov., from the Campanian age of Kharga Oasis, South Western Desert, Egypt, in dorsal (**A**,**A'**) and ventral (**B**,**B'**) views.

4. Systematic Paleontology

Testudines Batsch, 1788 [33]
Pleurodira Cope, 1864 [34]

Pelomedusoides Cope, 1868 [17]
Bothremydidae Baur, 1891 [35]
Bothremydini Gaffney, Tong and Meylan, 2006 [17]
Khargachelys caironensis gen. et sp. nov
(Figure 2)

Holotype: NVP005, complete carapace and plastron.

Etymology: "Kharga" honors Kharga Oasis, where the specimen was collected; "chelys" is Greek for, turtle; "caironensis" honors Cairo, the capital city of Egypt, and honors Cairo University.

Type locality and horizon: Qarn Gennah (Kharga oasis); Quseir Formation; Campanian age [36].

Diagnosis: Member of Bothemydini that differs from the other representatives of this clade by the following character combination: long shell close to 60 cm in length; oval-shaped carapace, reaching its widest point at the fifth peripherals; narrow and shallow nuchal emargination; seven neurals; almost as long and wide as the first pair of peripherals; first vertebral scute being the widest of the vertebral series; second to the fourth vertebrals noticeably longer than wide; first pair of marginals overlapping half the lateral nuchal margins; anterior margin of the plastron reaching the anterior carapace edge; anterior plastral lobe wider than the posterior one; twice as wide as long entoplastron; entoplastron width equivalent to almost half the anterior plastral lobe width; extragulars overlapping the entoplastron; humero-pectoral sulcus located behind the epiplastra, showing a relatively long distance between them; pectoral scutes overlapping the anterior region of the mesoplastra.Description: The carapace is almost complete but partially broken (Figure 2). The damaged and crushed parts are due to the pressure from the overlying sediments. The carapace is estimated to be about 580 mm long and 430 mm wide. The height of the carapace cannot be estimated due to the compression, but it still has a high domed shape. It is an oval-shaped carapace, longer than wide, that reaches its widest point at the fifth peripheral level and then narrows to the posterior end. The nuchal is slightly wider than long, and its anterior margin width is about half the maximum width of the plate. The nuchal emargination is narrow and shallow. This specimen shows seven neurals. Neural 1 is rectangular, longer than wider, with slightly curved margins. Neurals 2 to 6 are hexagonal, longer than wide, and show short antero-lateral margins. Neural 7 is pentagonal. The neural series reach the seven costals. The first costal pair is almost twice as large anteroposteriorly as the second pair. The peripherals 1 are almost as long and wide. The posterior peripherals are relatively short, longer than wide. The suprapygal is pentagonal, and the pygal is rectangular, longer than wide. This taxon lacks a cervical scute. The subpentagonal first vertebral scute is the widest of the vertebral series. The hexagonal second to the fourth are noticeably longer than they are wide. The first pair of marginals overlaps half the lateral length of the nuchal.

The well-preserved plastron is articulated with the carapace (Figure 2B). It is about 450 mm in length and 300 mm in width. The anterior plastral margin almost reaches the anterior margin of the carapace. The anterior lobe shows a lateral and anterior subrounded margin. It is wider than the posterior lobe, and its length is almost half its width. The posterior lobe length is twice that of the anterior lobe. Its lateral margin is sub-straight, tapering posteriorly. The plastral bridge anteriorly reaches the third pair of peripherals, posteriorly being developed at least to the seventh pair. A shot medial contact is recognized between both epiplastra. The entoplastron is twice as wide as long. The width of the entoplastron is almost half the maximum width of the plastral anterior lobe. A pair of subpentagonal mesoplastra are laterally located. The anal notch is almost twice as wide as long, being U-shaped. The pelvis is sutured to both the carapace and plastron. The anterior margin of the extragular scute is slightly wider than each extragular. The gular reaches the humerals, preventing medial contact between the extragulars. The extragulars overlap the entoplastron. A relatively long distance separates the pectorals from both the entoplastron and the epiplastra. However, these scutes show a relatively long overlap with

the mesoplastra. The anal scutes are completely developed on the xiphiplastral, away from the sulci between that pair of plates and the hypoplastra.

5. Results

Characters such as the first pair of costal plates approximately twice as long as the second one; the presence of fewer than eight neural plates, resulting in the medial contact with the last pairs of costals; axillary buttresses reaching the third peripherals; the presence of relatively small lateral mesoplastra; and absence of a cervical scute, allow the identification of the specimen studied here as a member of Bothremydidae [15,17,37–40]. It can be attributed to Bothremydidae by the presence of a relatively short and wide anterior plastral lobe, shared with the members of Bothremydini, but not with those of its sister group Taphrosphini, and the absence of overlap of the pectoral scutes on the epiplastron [15,17]. Within the lineage of Bothremydini, the specimen analyzed here cannot be attributed to any previously defined taxon (see Discussion).

The currently known members of Bothremydini in Europe are: (1) *Algorachelus peregrina* [15], from the uppermost middle-lower most upper Cenomanian of Spain and Portugal; (2) *Foxemys trabanti*, from the Santonian of Hungary; (3) *Foxemys mechinorum* [41], from the upper Campanian–lower Maastrichtian of France and Spain; (4) *Elochelys perfecta* [42], from the Campanian of France; (5) *Polysternon provinciale* [43], from the Campanian of France; (6) *Iberoccitanemys atlanticum* [44] from the upper Campanian–lower Maastrichtian of France and Spain; (7) *Rosasia soutoi* [45], from the upper Campanian–lower Maastrichtian of Portugal. (8) *Palemys bowerbankii*, [46], from the Lower Eocene of London, England; (9) *Tartaruscola teodorii*, [40], from the Early Eocene of France. In North America this lineage is known by: (1) *Algorachelus tibert* ([39]), from the uppermost Cenomanian of Utah (USA); (2) *Chedighaii barberi* [47], from the Campanian of Eastern and Central USA; (3) *Palauchelys montellanoi* [48], from Upper Campanian of Olmos Formation, Mexico; (4) *Chedighaii hutchisoni* [17], from Late Campanian of New Mexico, (USA); (5) *Bothremys cooki* [17,49], from the Maastrichtian of New Jersey (USA). From South America region; (1) *Puentemys mushaisaensis* [50], from the Paleocene of Colombia. From Asia are: (1) *Algorachelus parva* ([51]), from the Cenomanian of Palaestine; (2) *Bothremys arabicus* [16], from the Santonian of Jordan. From Africa are: (1) *Bothremys kellyi*, [17] from the Early Eocene of Morocco; (2) *Araiochelys hirayamai* [17], from the Paleocene of Morocco; (3) *Bothremys maghrebiana* [17], from the Early Paleocene, of Morocco; (4) *Akoranemys madagasika* [19], from the Upper Cenomanian of Madagascar.

6. Discussion

The specimen analyzed here differs from all members of Bothremydini so far described. The carapace is oval-shaped, similar to *Algorachelus peregrina* [15] (Cenomanian; Spain and Portugal); *Puentemys mushaisaensis* [50] (Paleocene, Colombia); *Chedighaii barberi* [47] (Campanian, Eastern and Central USA); *Rosasia soutoi* [45] (upper Campanian–lower Maastrichtian, Portugal).The nuchal plate is almost hexagonal and wider than long as in *Algorachelus peregrina* [15]; *Chedighaii barberi* [47]; and *Rosasia soutoi* [45], while those of *Foxemys mechinorum* [41] (upper Campanian–lower Maastrichtian, France and Spain) and *Polysternon provinciale* [43] (Campanian, France) are trapezoidal. The nuchal emargination is narrow as in *Rosasia soutoi* [45] and *Polysternon provinciale* [43], and unlike *Chedighaii barberi* [47] which lacks a nuchal emargination. The first pair of costals is formed by plates twice as long as the second pair, as in *Algorachelus peregrina* [15]. The attachment of the inguinal buttress to the fifth costal pair is long and extends onto it, which is similar to *Algorachelus peregrina* [15]. The pygal is rectangular as in *Rosasia soutoi* [45] and unlike *Chedighaii barberi* [47], which is square shaped, and *Algorachelus peregrina* [15], which is trapezoidal.

The anterior plastral margin reaches a level close to the anterior margin of the carapace which is like *Algorachelus peregrina* [15], and it is unlike most of the Bothremydidae, where the anterior margin of the plastron does not reach the anterior margin of the carapace. The anterior lobe is wider than the posterior lobe which is similar to *Foxemys mechinorum* [41];

Polysternon provinciale [43]; *Rosasia soutoi* [45]; *Chedighaii barberi* [47] and *Araiochelys hirayamai* [17](Paleocene, Morocco).

The bridge is anteroposteriorly longer than the anterior lobe and shorter than the posterior one and is thus similar to *Chedighaii barberi* [47], and different from *Foxemys mechinorum* [41]; *Polysternon provinciale* [43]; and *Rosasia soutoi* [45] where the bridge is longer than the posterior lobe. The anal notch is twice as wide as it is long and U-shaped similar to *Algorachelus peregrina* [15]; *Foxemys mechinorum* [41]; *Araiochelys hirayamai* [17] and *Chedighaii barberi* [47].

The length of the epiplastral symphysis is shorter than the length of the entoplastron like *Foxemys mechinorum* [41]. The gulars extend into the entoplastron as in *Rosasia soutoi* [45] and differ from *Foxemys mechinorum* [41]; *Polysternon provinciale* [43]; *Chedighaii barberi* [47]; and *Elochelys perfecta* [42] (Campanian, France). The pectoral scutes do not reach either the epiplastron or entoplastron and differ from *Elochelys perfecta* [42]; *Chedighaii barberi* [47]; and *Foxemys mechinorum* [41].

The entoplastron is twice as wide as long similar to *Algorachelus peregrina* [15]. The humeral-pectoral sulcus is posterior to the entoplastron similar to *Rosasia soutoi* [45] and unlike *Foxemys mechinorum* [41]; *Polysternon provinciale* [43] and *Chedighaii barberi* [47].

The posterior end of the entoplastron does not reach the anterior margin of the bridge as in *Rosasia soutoi* [45] and unlike *Foxemys mechinorum* [41] and *Polysternon provinciale* [43]. The pectoro-abdominal suture is partially across the anterior margin of the mesoplastron, unlike in *Foxemys mechinorum* [41] and *Araiochelys hirayamai* [17] and similar to *Algorachelus peregrina* [15]; *Polysternon provinciale* [43], *Rosasia soutoi* [45] and *Chedighaii barberi* [47]. The humero-pectoral sulcus is located in the upper portion of the hyoplastron and is posteriorly located to both the ento-hyoplastral and the epi-hyoplastral sulci and similar to *Polysternon provinciale* [43], *Rosasia soutoi* [45] and *Araiochelys hirayamai* [17].

Therefore, NVP005 represents a new member of Bothremydini, *Khargachelys caironensis* gen. et sp. nov. *Khargachelys caironensis* represents the first appearance of the bothremydids in the Campanian deposits of Africa, which may fill the gap of the fossil record of the Bothremydidae between the Cenomanian and the Maastrichtian periods.

7. Conclusions

The described turtle shell here, from the Quseir Formation of Kharga Oasis, in the South Western Desert (Egypt), represents the first record of Bothremydidae (Pleurodira) from the Campanian age in Egypt and in Africa. The Campanian deposits in the Kharga area indicate a supratidal marsh environment, concordant with the occurrence of such aquatic turtles. The specimen is attributed to a new genus and species of Bothremydini, *Khargachelys caironensis* gen. et sp. nov. This specimen brings new data to the poorly known diversity of turtles from the Late Cretaceous of Egypt.

The restricted brackish water environments and the gradual shallow shelf together with fossils such as freshwater gastropods and palynofloras, support indications of the ability of Bothremydidae to reside in different environments, such as freshwater and coastlines. The diversity of the paleoenvironments of the Bothremydidae enabled them to reach a wide distribution in both the northern and southern continents during the Late Cretaceous, along the coastlines of the Atlantic Ocean, breaking the barriers of the vicariance pattern of evolution.

Author Contributions: Conceptualization, M.A., A.P.-G. and G.A.E.-K.; methodology, M.A., A.P.-G., S.M. and G.A.E.-K.; validation, M.A., R.H., S.M., A.-A.T. and G.A.E.-K.; formal analysis, M.A., A.P.-G. and S.M.; investigation, G.A.E.-K.; resources, A.-A.T. and G.A.E.-K.; data curation, M.A., S.M. and G.A.E.-K.; writing—original draft preparation, M.A., A.P.-G., R.H., S.M. and G.A.E.-K.; writing—review and editing, M.A., A.P.-G., R.H., S.M., A.-A.T. and G.A.E.-K.; visualization, G.A.E.-K.; supervision, M.A., A.-A.T. and G.A.E.-K.; project administration, G.A.E.-K. All authors have read and agreed to the published version of the manuscript.

Funding: The Spanish Ministerio de Ciencia e Innovación (PID2019-111488RB-I00) has funded the professional English edition of this research.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We would like to thank Cairo University and New Valley University for their support.

Conflicts of Interest: The authors declare no conflict of interest.

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