



Bioerosion traces on the Campanian turtle remains: New data from the lagoonal deposits of the Quseir Formation, Kharga Oasis, Egypt

**Magdy El Hedeny, Sara Moheesn, Abdel-aziz Tantawy, Ahmed El-Sabbagh,
Mohamed AbdelGawad, and Gebely Abu El-Kheir**

ABSTRACT

The uppermost part of the Campanian Quseir Formation of Kharga Oasis, Egypt, contains a concentration of turtle skeletal remains in a lagoon setting. They appear as three successive horizons (I–III), alternated between the variegated shales and the glauconitic mudstones and conglomeratic layers within the Hindaw Member. However, bones recovered in horizon III present a higher preservation potential than the others. Therein, turtle remains are represented by mostly complete shells, partial shells and many scattered and weathered shell fragments. The studied turtles lived in small ponds and marshes and were deposited as autochthonous to parautochthonous relics. Their bones display significant bioerosion signatures on both carapace and plastron. The morphological analysis of the bioerosion structures preserved revealed 11 ichnospecies, belonging to nine ichnogenera. Eight of these ichnotaxa are recorded for the first time in turtle bones of Egypt. The recognised bioerosional structures appear as borings, shallow chambers, grooves, and punctures produced by ticks, beetles, polychaete worms, fishes/crocodile, and gastropods. They were attributed to the ichnogenera *Karethraichnus*, *Cubiculum*, *Osteocallis*, *Radulichnus*, *Osteichnus*, *Osedacoides*, *Sulculites*, and *Machichnus*. In addition, some bite marks assigned to *Nihilichnus* also occur on a carapace peripheral. This grade of bioerosion was likely caused by relatively long exposure time before the final deposition or burial. In some cases, borings may be produced during the host's lifetime. The new material considerably expands the stratigraphic and geographic distribution of this trace fossil assemblage and reveals that their producers may have been able to survive in other palaeoenvironmental conditions.

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Magdy El Hedeny. Department of Geology, Faculty of Science, Alexandria University, Alexandria 21568, Egypt. magdy.elhedeny@alexu.edu.eg

Sara Moheesen. Geology Department, Faculty of Sciences, New Valley University, New Valley, Egypt. saramohesen1711@gmail.com

Abdel-aziz Tantawy. Geology Department, Faculty of Sciences, New Valley University, New Valley, Egypt. aatantawy@nv.aun.edu.eg

Ahmed El-Sabbagh. Department of Geology, Faculty of Science, Alexandria University, Alexandria 21568, Egypt. Corresponding author. ah.elsabbagh@alexu.edu.eg

Mohamed AbdelGawad. Department of Geology, Faculty of Science, Cairo University, Giza 12613, Egypt. mkabdelgawad@cu.edu.eg

Gebely Abu El-Kheir. Geology Department, Faculty of Sciences, New Valley University, New Valley, Egypt. gebely2006@sci.nvu.edu.eg

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INTRODUCTION

Upper Cretaceous deposits exposed in Kharga Oasis, in the Southern part of the Western Desert of Egypt, contain abundant vertebrate fossils in near-shore marine environments. Previous studies have led to the recovery and identification of crocodyliforms (cf. *Dyrosaurus*), dinosaurs (cf. *Spinosaurus*), turtles (*Podocnemis aegyptiacus* Andrews, 1900), lungfish (*Ceratodus* and *Protopterus*), bony fish, and sharks from the Mut Member, the lower part of the Quseir Formation (previously called the Mut Formation) from Dakhla Oasis (e.g., Churcher and de Iuliis, 2001; Claeson et al., 2014). Turtles of the Family Bothremydidae Baur, 1891 are among the most common fossil animals found at this locality. It represents an extinct family of side-necked turtles (Pleurodira) known from the Early Cretaceous (Albian) to the Eocene (Gaffney et al., 2006; Cadena et al., 2012). They were adapted to live in freshwater and brackish-coastal environments of North and South America, Europe, Africa, and India (Gaffney et al., 2001a, 2001b, 2006, 2007, 2009a, 2009b; Laurent et al., 2002; Gaffney and Tong, 2008; Lehman and Wick, 2010; AbdelGawad et al., 2023).

In Egypt, several authors have recorded members of the Family Bothremydidae from deposits at many localities, including the Campanian Quseir Formation, Kharga Oasis (e.g., AbdelGawad et al., 2019, 2023; Abu El-Kheir, 2020), the Maastrichtian Ammonite Hill Member of the Dakhla Shale, Abu Minqar (e.g., Lapparent de Broin and Werner, 1998; Abu El-Kheir et al., 2021) and the lower Cenomanian Bahariya Formation in Gebel El Dist, Bahariya Oasis (Lapparent de Broin, 2000; Abu El-Kheir, 2020). Despite studies having exam-

ined the taxonomy of the turtle assemblages in each locality, little is known about the palaeoecology and taphonomic signatures on these faunas, with their role as agents responsible for bone accumulations not fully understood.

Bioerosion (e.g., borings, grooves, scratch marks, tooth marks, and other evidence of feeding, reproduction, predation and scavenging on fossil material) is an important taphonomic process that has potential use as palaeoecological markers and can be significant for taphonomic studies of turtles (e.g., Behrensmeyer, 1978; Fiorillo, 1987, 1990; Tappan, 1994; Hasiotis, 2004; Tapanila et al., 2004; Zonneveld et al., 2022a, 2022b). So far, little attention has been paid to bioerosional traces on turtle bones. Owing to the fact that borings have not been described from the bones of modern turtles, the significance, origin, and frequency of borings in fossil turtles are still unclear (Zonneveld et al., 2022a, 2022b). The target of this study is to describe a suite of bioerosional traces on fossil bothremydid turtles collected from deposits of the uppermost Hindaw Member of the Quseir Formation of Kharga Oasis, Egypt (Figure 1) and to study their distribution on the plastron and carapace from palaeoecological and taphonomic perspectives. An attempt was made to distinguish if borings were produced during the host's lifetime (*in vivo*) or post-mortem.

LOCATION AND STRATIGRAPHIC CONTEXT

Excellent exposures of the Upper Cretaceous formations crop out in Kharga Oasis and its surrounding areas in the Southern parts of the Western Desert of Egypt (Ball, 1900; Beadnell, 1909; Said, 1962, 1990; Awad and Ghobrial, 1965; Her-

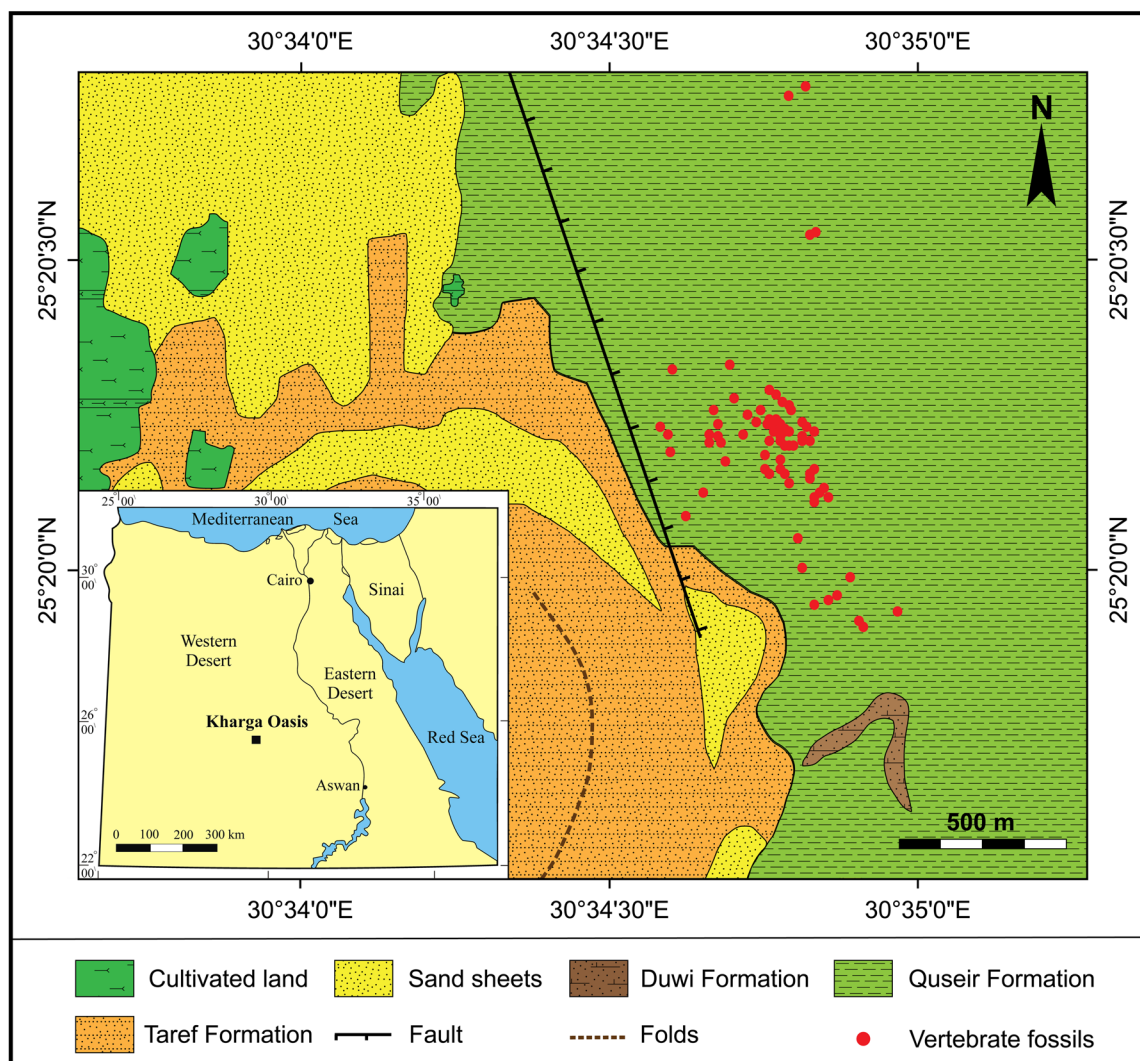


FIGURE 1. Simplified geological map of the study area with indication of the vertebrate distribution east of the Ganah village (modified after Abu El-Kheir, 2020; AbdelGawad et al., 2023).

mina, 1967, 1990). Among them, the Quseir Formation (Youssef, 1957) deposited during the Campanian, represents mixed limnic and marine conditions following an intense erosion period that started after the tectonically-controlled early Turonian regression (Awad and Ghobrial, 1965; Hendriks et al., 1984; Hermina, 1990). In the Southern parts of Egypt, the Quseir Formation is also known as the Variegated Shales (Said, 1961, 1962, 1990; Awad and Ghobrial, 1965) or the Mut Formation (Barthel and Herrmann-Degen, 1981).

In the Kharga area, the Quseir Formation unconformably overlies the Turonian sandstone of the Taref Formation and conformably underlies the upper Campanian/lower Maastrichtian phosphate-bearing Duwi Formation. The present work is based on the succession exposed in the Qarn

Ganah area (25°20'15"N, 30°34'45"E), about 10 km south of the Kharga city (Figure 1). In the study area, deposits are mainly composed of alternating shales and mudstones, attaining a thickness of about 26 m (Figure 2). Shales are variegated and laminated. Mudstones are grey to greyish green, silty, and glauconitic. Within this outcrop, and throughout Kharga Oasis, the two members of the Quseir Formation can be recognised readily in the field (e.g., Omara et al., 1976). They are from base to top: the Mut and Hindaw members (about 5 and 21 m thick, respectively).

Sedimentary deposits of the Quseir Formation in this new site contain distinctive Campanian reptile fossils mainly occurring in three successive horizons. Vertebrate fossils include lungfishes, turtles, crocodile bones, and some disarticulated skel-

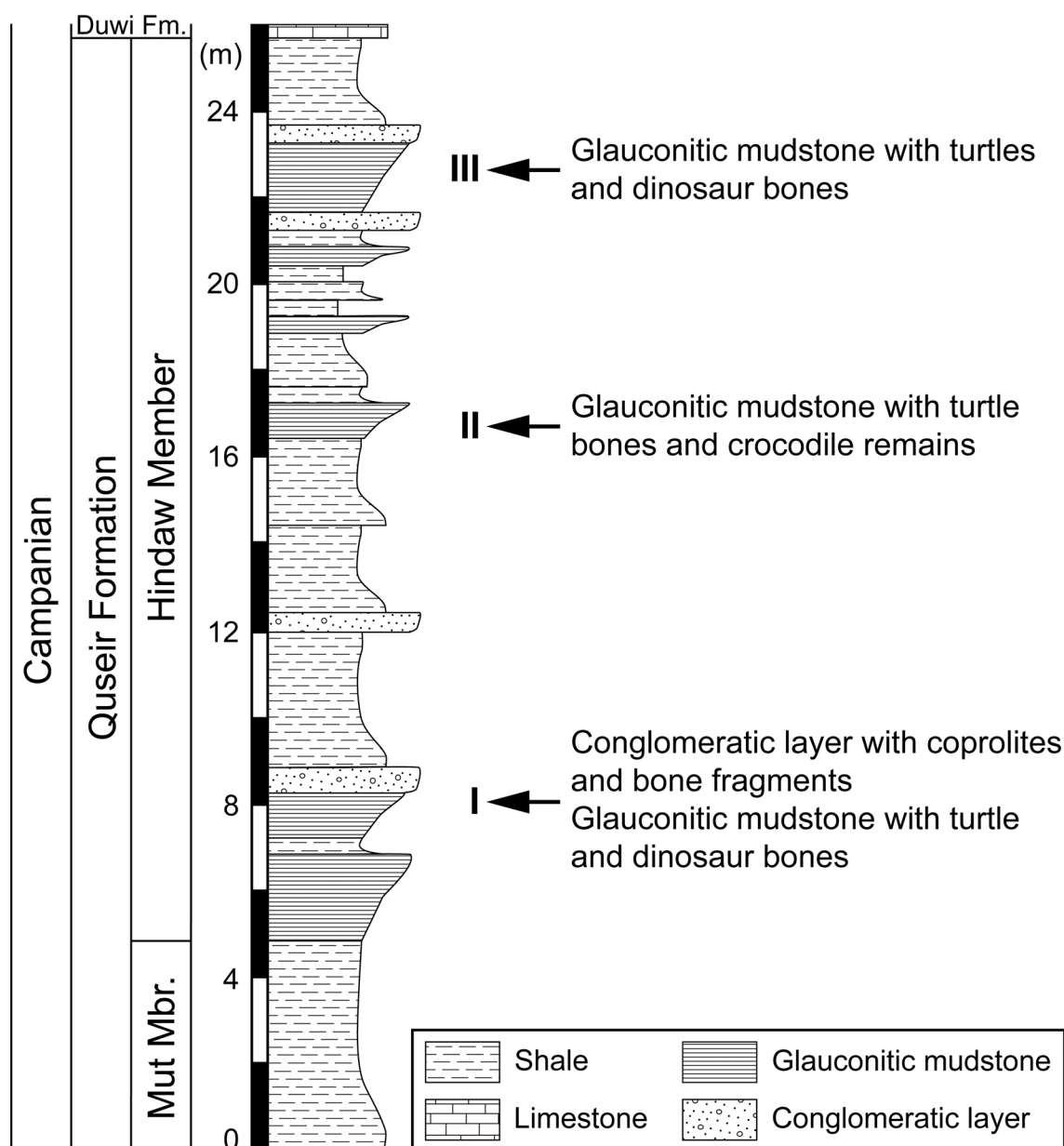


FIGURE 2. Lithological section of the Campanian Hindaw Member (the Quseir Formation) in the study area (modified after Abu El-Kheir, 2020). Arrows mark occurrences of the three turtle-bearing horizons (I–III) studied.

etons of dinosaurs. In addition, strata of the Hindaw Member are intercalated with four thin layers (0.3–0.5 m thick) of ferruginous conglomeratic sandstone, containing bone fragments and coprolites (Figure 2).

MATERIAL AND METHODS

Up to 50 turtle remains have been collected from three fossiliferous horizons of the Quseir Formation exposed in the Qarn Ganah area, Kharga Oasis; the majority of them belonging to horizon III. Turtle specimens are scattered, randomly oriented,

and unsorted. Most of the discovered materials are isolated plates; no cranial elements have been recovered thus far. However, two well-preserved, mostly complete shells that include both carapace and plastron were discovered.

In the laboratory, all specimens were gently cleaned under running water, scrubbing with a soft toothbrush. Then, each specimen was systematically screened for bioerosional traces using naked eye, a hand lens, and binocular microscope when necessary. Specimens were photographed with a Canon Power-Shot A3000 digital camera and the

SZ61TR-LED zoom stereo microscope. Determination of bioerosion structures was mainly based on criteria given by Vialov and Nesson (1974), Theinius (1988a), Mikuláš et al. (2006), Roberts et al. (2007), Karl et al. (2012), Xing et al. (2015), and Zonneveld et al. (2016, 2022a, 2022b).

Although taxonomic identification to ichnospecies level was possible for several specimens, the highly eroded specimens meant that in most cases specimens could only be identified to ichnogenus level. All specimens reported in this study are curated at the New Valley Vertebrate Palaeontology Center, New Valley University, New Valley, Egypt. Numbered turtle specimens are prefixed by NVP.

SYSTEMATIC ICHNOLOGY

At least 11 ichnospecies, representing nine ichnogenera, were identified, described and illustrated (Figures 3–5). Eight of these ichnotaxa have been recorded for the first time in Egypt (Table 1).

Ichnogenus *Nihilichnus*
Mikuláš et al., 2006

Type ichnospecies. *Nihilichnus nihilicus* Mikuláš et al., 2006

Diagnosis. Roughly triangular, circular or ovoid holes or external pits, occurring solitarily or in groups, which may show recurring patterns. Outer part of the margin of the cavity shows minute, irregular jags, resulting from a brittle deformation (Mikuláš et al., 2006).

Nihilichnus nihilicus Mikuláš et al., 2006
(Figure 3A)

Material. Three ellipsoid borings on a carapace fragment (NVP001).

Description. Circular, subcircular to ellipsoidal holes in outline, straight and perpendicular margin towards the outer and inner shell surfaces; not penetrating the cortical compact bone with minor irregular jags, diameter of holes ranges from 2 to 4 mm, situated 2 cm apart. No bioglyphes have been recorded.

Discussion. The presence of a set of grooves with irregular outlines in the studied specimen supports the assignment to the ichnofamily Machichnidae Wisshak et al., 2019 (which includes the ichnogenera *Machichnus*, *Nihilichnus*, *Linichnus*, *Knethichnus*, and *Mandaodonites*). Due to subsequent erosion of the superficial layers of the studied bone that leaves the internal-most section of the exposed traces, each groove exhibits a circular outline with minor irregular jags, allowing its assignment to the ichnogenus *Nihilichnus*. The

borings described show most of the morphological characters of the holotype described and illustrated by Mikuláš et al. (2006, p. 120, figure 6A–K). In general, *Nihilichnus* is known from terrestrial, palustrine, freshwater (reported herein), and marine environment (Rasser et al., 2016). Although it most commonly occurs on vertebrate bone substrate, it has also been recorded in other invertebrate skeletal substrate (molluscan shells) (Rasser et al., 2016; Ahmed et al., 2022).

Producer. The ichnogenus *Nihilichnus* represents putative bite marks on fossil bone. Crocodiles may be considered potential makers, as crocodylian remains are documented from the Quseir Formation (Abu El-Kheir, 2020). Similar cases have been reported previously by other authors (e.g., Milàn et al., 2011; Schwarz-Wings et al., 2014). Additionally, marine mammals, reptiles, and bony fish could be responsible for *N. nihilicus* (Irazaqui and Acosta Hospitaleche, 2022).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). It is also recorded from the Middle Triassic of Germany (Mujal et al., 2022), latest Triassic of Poland (Dzik et al., 2008; Niedźwiedzki et al., 2011), Kimmeridgian of Germany (Karl and Tichy, 2004), Lower Palaeocene of Denmark (Milàn et al., 2011), Eocene of Antractica (Irazaqui and Acosta Hospitaleche, 2022), Lower Miocene of Czech Republic and Egypt (Mikuláš et al., 2006; Zonneveld et al., 2022a), and Upper Miocene of Brazil (Di Gregorio et al., 2020).

Ichnogenus *Karethraichnus*
Zonneveld et al., 2016

Type ichnospecies. *Karethraichnus lakkos* Zonneveld et al., 2016

Diagnosis. Circular to subcircular and oval pits and holes bored into bony substrates. The hole may penetrate fully through the substrate or terminate within the substrate as a shallow, bowl-shaped pit or as a deeper shaft with a rounded, blunt, or pointed terminus (Zonneveld et al., 2016).

Karethraichnus lakkos Zonneveld et al., 2016
(Figure 3B, C)

Material. Four borings on a plastron (NVP002) and several bowl-shaped pits on three carapaces (NVP003–005).

Description. Simple shallow, circular to subcircular bores, bowl-shaped pits, sometimes closely spaced, and fused (Figure 3B) unbranched shafts into bone borings. They vary in diameter from 0.6 to 6 mm, 1–4 mm in depth. Depression sides are generally smooth, flattened to rounded.

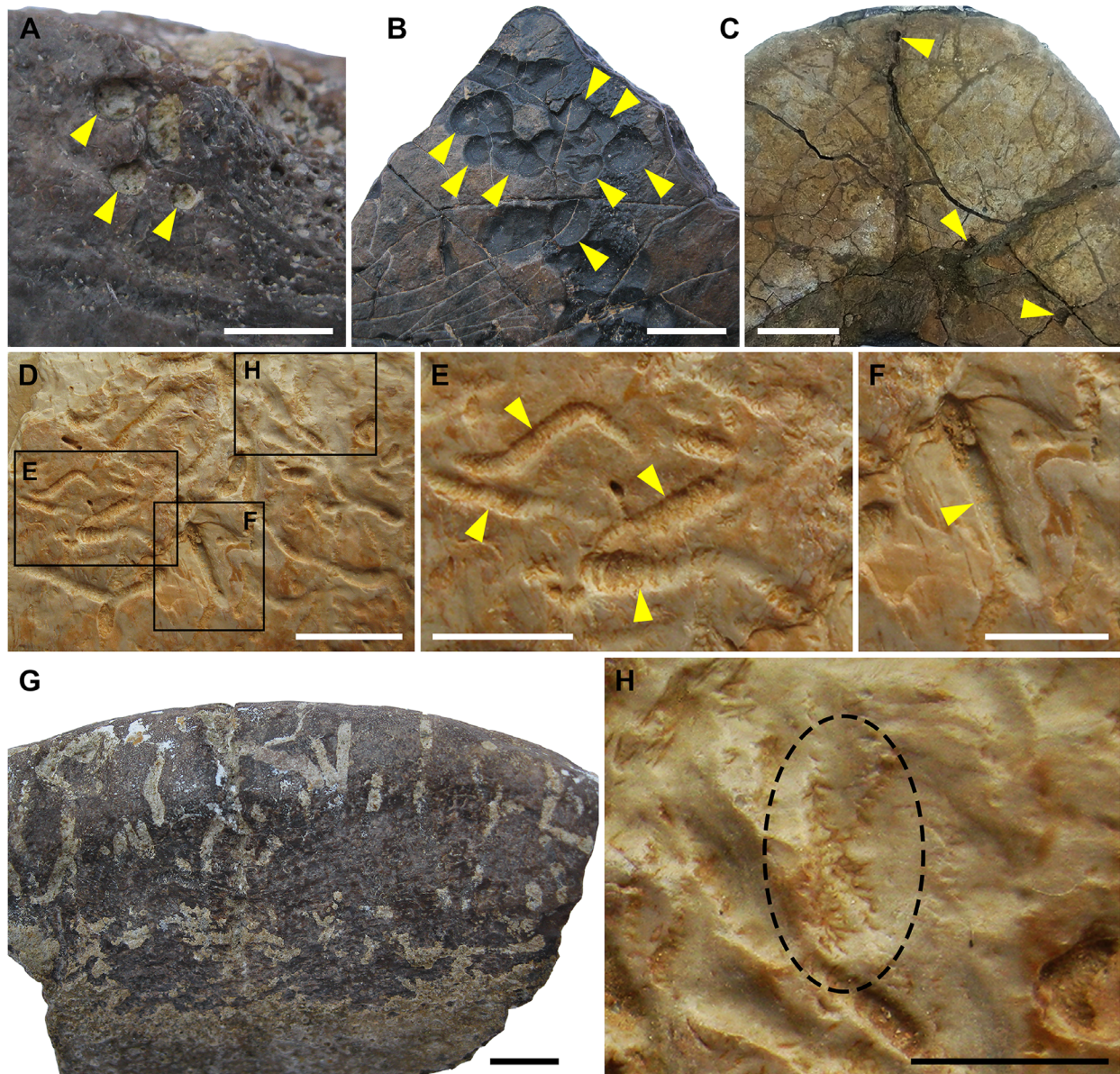


FIGURE 3. (A) *Nihilichnus nihilicus*, circular, subcircular to ellipsoidal non-penetrating holes (arrows) on the carapace peripheral. (B, C) *Karethraichnus lakkos*. (B) Cluster of bowl-shaped pits (arrows) of on the carapace peripheral. (C) Small rounded holes (arrows) of which are not completely penetrating the plastron fragments. (D) External surface of carapace peripheral containing three ichnospecies *Cubiculum ornatus*, *C. inornatus* and *Osteocallis mandibulus* (E, F, and H, respectively). (E) *Cubiculum ornatus* (arrows), showing the characteristic features of the ichnospecies with well pronounced bioglyphs. (F) *Cubiculum inornatus* (arrow), showing details of the morphological features the ichnospecies. (G) *Cubiculum* isp., showing borings arranged in groups of mostly parallel to each other and infilled with sediments. (H) *Osteocallis mandibulus* (ellipse), showing, randomly oriented surface borings with distinct arcuate (commonly paired) scratches in turtle skeleton. Scale bars equal 0.5 cm, except for B, D and G, which are 1.0 cm, and for C, which is 0.4 cm.

Discussion. *Karethraichnus lakkos* represents the third dominant trace fossil in the studied turtle bones. The specimens described show most of the morphological characters of the holotype of *K. lakkos* as described and illustrated by Zonneveld et al. (2016, p. 6, figure 6.1). This ichnospecies is com-

mon on the external surfaces of the plastron and carapaces of the majority of turtle shells. In the present study, *K. lakkos* appeared in two forms; one of them corresponds to small, unjagged rounded holes, not completely penetrative, apart from each other with varying distances and are not

occurring in sets, affecting the external surface of plastron fragments, especially at sulci between epidermal scales/plastron. The second form is slightly larger, consisting of shallow, bowl-shaped pits, closely spaced, and sometimes fused together on the external surfaces of carapace. Borings of the ichnospecies *K. lakkos* are only located in accessible places in living turtles (*in vivo*), such as external surfaces of the carapace and plastron, especially at marginal or lip areas. Although *K. lakkos* was first described from fossil shell bones of geoemydid turtles from lower Eocene non-marine strata of Wyoming (Zonneveld et al., 2016), it was observed also in both terrestrial tortoises and aquatic turtles from the Lower Miocene of Egypt (Zonneveld et al., 2022a).

Producer. Trace makers usually associated with *K. lakkos* include leeches and ixodid arthropods (ticks), which are known to feed on blood sinuses within shell bone, especially at sulci between epidermal scales (e.g., Siddall and Gaffney, 2004; Zonneveld et al., 2016). However, barnacles attaching onto a bone substrate are also a suggested producer of this ichnotaxon (Zonneveld et al., 2016, 2022b; Collareta et al., 2022).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). *Karethraichnus lakkos* has been recorded from the Lower Eocene of USA (Zonneveld et al., 2016; Adrian et al., 2021), Miocene of Peru, Italy and Egypt (Collareta et al., 2022; Collareta et al., 2023a; Zonneveld et al., 2022a), to Recent (Zonneveld et al., 2022b). This determination extends the stratigraphic range of the taxon at minimum to the Campanian.

Ichnogenus *Cubiculum*
Roberts et al., 2007

Type ichnospecies. *Cubiculum ornatus* Roberts et al., 2007

Diagnosis. Discrete ovoid borings in bone. Hollow, oval chambers with concave flanks bored into inner spongy and outer cortical bone surfaces. Chamber length three to four times greater than diameter. May be isolated, but observed more commonly in dense, sometimes overlapping concentrations. Walls commonly roughened, composed of shallow, arcuate (apparently paired) grooves (emended after Roberts et al., 2007).

Cubiculum ornatus Roberts et al., 2007
(Figure 3D, E)

Material. Up to 35 chambers on seven carapace remains (NVP006–012).

Description. Elongate, straight, or arcuate chambers with semi-circular ends, occurring in isolated dense and rarely overlapping concentrations. Boring long axes are parallel to the bone surfaces. Borings differ in their sizes; long axes: 1.8–10.8 mm; borings depth: 1.0–1.5 mm. Boring walls bear well-developed ornament (bioglyphs).

Discussion. The ichnospecies *Cubiculum ornatus* represents the most common ichnotaxon in our assemblage. Dimensions and overall form of the specimens closely match bone borings described from the Upper Cretaceous of Madagascar (Roberts et al., 2007). These borings represent pupation chambers made by dermestid beetles (Kitching, 1980; Martin and West, 1995; Hasiotis et al., 1999; Ozeki et al., 2020; Perea et al., 2020). The presence of these borings suggests that the turtle bones had a relatively long time of exposure, which was sufficient to allow beetles to posture, but not long enough to allow weathering to destroy them.

Producer. Generally, *Cubiculum* ichnospecies have been previously documented and interpreted as dermestid beetle borings in many palaeontological studies (e.g., Martin and West, 1995; Hasiotis et al., 1999; Laudet and Antoine, 2004; Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009; Saneyoshi et al., 2011).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). This ichnospecies has been recorded from the Middle–Upper Jurassic of South Africa (Britt et al., 2008; Xing et al., 2015), Upper Cretaceous of Brazil, Morocco (Ibrahim et al., 2014; Francischini et al., 2016) to Pleistocene of Brazil (West and Hasiotis, 2007; Dominato et al., 2009).

Cubiculum inornatus Xing et al., 2015
(Figure 3D, F)

Material. Four ellipsoidal chambers on a carapace remain (NVP006).

Description. Discrete, ellipsoidal borings in bone with marked concavity of flanks and bottom and marked constriction of walls in the upper area. Boring boundaries, wall and bottom are sharp and smooth. No bioglyphs or fillings were observed.

Discussion. In the present assemblage, *C. inornatus* is associated with other trace fossils; *C. ornatus* and *Osteocallis mandibulus*. *Cubiculum inornatus* resembles *C. ornatus* but is differentiated by having tapering ends and the absence of bioglyphs in their walls. *Cubiculum levis* Pirrone et al. (2014, p. 253, figure 3) differs from our specimens in having interior bowl-shaped morphology and a marked constriction of walls in the upper area.

Producer. Indeterminate osteophagous insect (Xing et al., 2015; Paes Neto et al., 2016).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). *Cubiculum inornatus* was recorded from the Middle Triassic of Brazil (Paes Neto et al., 2016) to Lower–Middle Jurassic of China and South Africa (Xing et al., 2015). The present determination greatly expands the stratigraphic range of *C. inornatus* to the Upper Cretaceous (Campanian).

Cubiculum isp.
(Figures 3G, 4F)

Material. Many boring clusters on five carapace remains (NVP0013–017).

Discussion. The present specimens are closely allied to *Cubiculum* isp. This is especially true for the general outline, dimension, and arrangement of borings. Borings are arranged in groups of three to five and parallel to each other, according to its major axis. However, due to sediment infilling and poor preservation, they could not be determined at the ichnospecific level.

Ichnogenus *Osteocallis*
Roberts et al., 2007

Type ichnospecies. *Osteocallis mandibulus* Roberts et al., 2007

Diagnosis. Shallow, meandering trail of arcuate grooves (apparently paired) bored into external (cortical) bone surfaces. May be single trail or network of randomly overlapping trails (Roberts et al., 2007).

Osteocallis mandibulus Roberts et al., 2007
(Figures 3D, H, 4A, B)

Material. Small trails on four carapace remains (NVP006, 019–021).

Description. Shallow, small trail of arcuate grooves, mostly formed of paired scratches (Figure 3H), sometimes consist of a network of randomly overlapping trails (Figure 4A, B). Ranging in width between 0.9 to 11 mm, generally less than 0.7 mm in length.

Discussion. This ichnotaxon was recorded for the first time in dinosaur bone from continental deposits of the Upper Cretaceous of Madagascar and Utah (Roberts et al., 2007). In the present study, *O. mandibulus* was recorded together with insect pupal chambers (*Cubiculum ornatus*; Figure 3D). Because similar bioglyph appeared in both ichnotaxa, the trace-making organisms are believed to be the same (Roberts et al., 2007). Palaeoecologically, *O. mandibulus* is found in nonmarine environmental settings (Paes Neto et al., 2016). The

presence of these borings suggests that the turtle bones had a relatively long time of exposure, which was sufficient to allow the silphid and histerid beetles to leave such a significant bone modification.

Producer. Necrophagous or osteophagous insects are considered to be the main producers of *O. mandibulus* (Roberts et al., 2007). They usually use their robust mouthparts for feeding.

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). *Osteocallis mandibulus* has been recorded from the Upper Triassic of Southern Brazil (Paes Neto et al., 2016), Upper Jurassic of Western Colorado (McHugh et al., 2020), the Upper Cretaceous of Utah and Madagascar (Roberts et al., 2007), and Lower Pliocene of Italy (Collareta et al., 2023b).

Ichnogenus *Radulichnus*
Voigt, 1977

Type ichnospecies. *Radulichnus inopinatus* Voigt, 1977

Diagnosis. Minute patches or shallow grooves with parallel or subparallel striae arranged side by side in transverse rows or irregularly distributed (Voigt, 1977).

Radulichnus inopinatus Voigt, 1977
(Figure 4C, D)

Material. Many arcuate bundles on three carapace remains (NVP019–021).

Description. Parallel to sub-parallel arcuate bundles closely spaced in groups, each group ranges from six to eight patches, covering some areas of the turtle skeletons.

Discussion. *Radulichnus inopinatus* occurs commonly on the external surfaces of the carapace of some turtle skeletons, uncovering the whole surfaces. In some cases, the studied ichnotaxon is associated with *Osteocallis mandibulus*. The latter ichnospecies differ from *R. inopinatus* by their small trail of arcuate grooves and sometimes consist of a network of randomly overlapping trails. Two ichnospecies of *Radulichnus* have been described: *Radulichnus inopinatus* and *R. transversus*. The second ichnospecies was characterised by parallel and short grooves (less than 1 mm in length) arranged in rows, concentrated in the central part of the inner surface of the valves of the clam species *Anomalocardia brasiliensis*. *Radulichnus inopinatus* corresponds to the marks left by gastropods, while *R. transversus* to those left by polyplacophorans (Lopes and Pereira, 2019). *Radulichnus inopinatus* has been recognised from

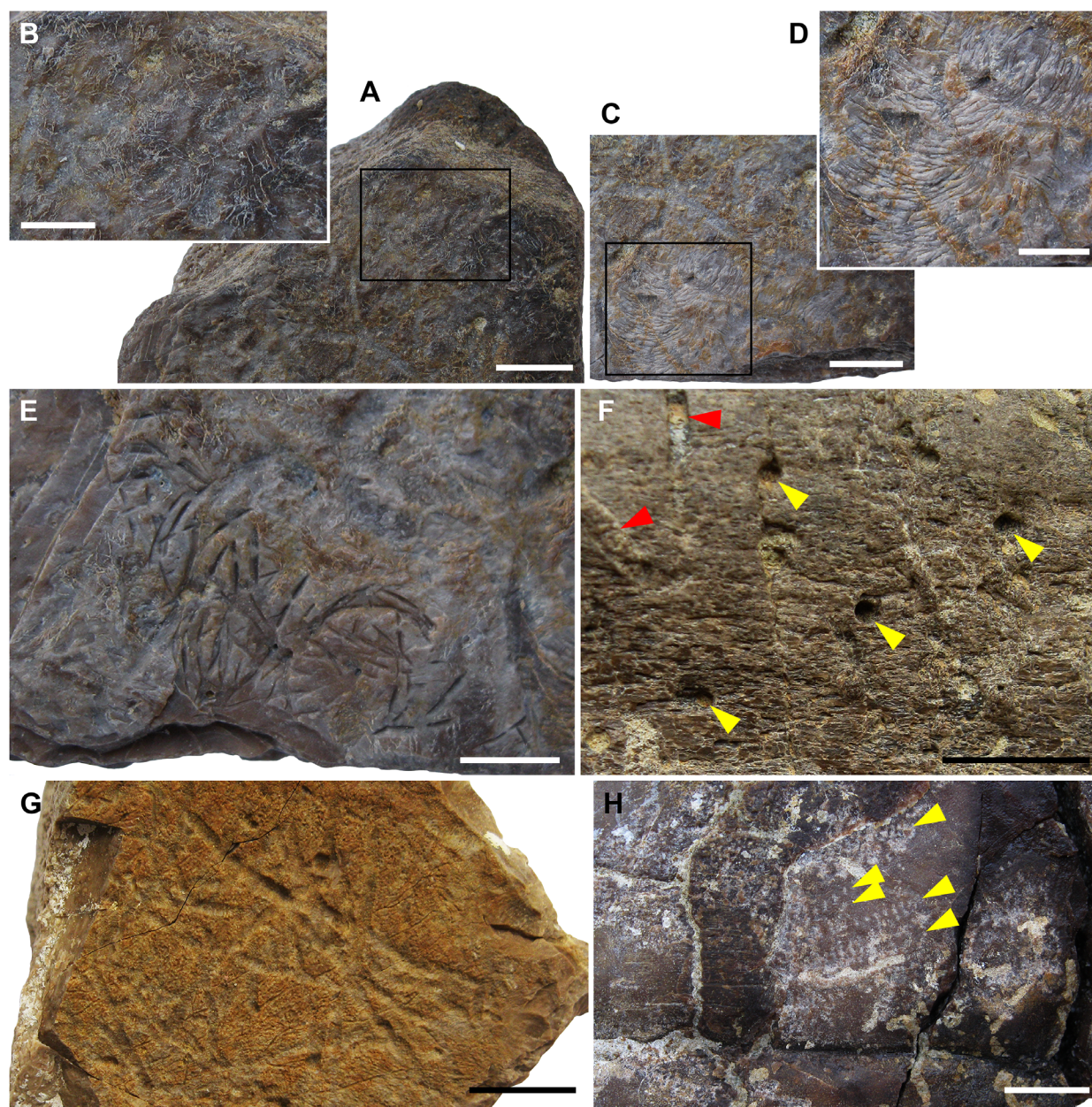


FIGURE 4. (A, B) *Osteocallis mandibulus*. (A) Small randomly oriented surface borings. (B) Close up view of A, showing small randomly oriented surface borings. (C, D) *Radulichnus inopinatus*, parallel to sub-parallel arcuate bundles closely spaced in groups. (E) *Osteichnus ossiobontum*, parallel borings with fused U-notches, inclined to the bone surface. (F) *Osedacoides jurassicus*, small simple borings in bone (yellow arrows) penetrating into the turtle bone. Note the occurrence of some *Cubiculum* isp. traces (red arrows). (G) *Sulculites bellus*, smooth, slender narrow, non-branched straight to curved grooves. (H) *Machichnus ?bohemicus*, shallow serial parallel or subparallel grooves (arrows) in carapace peripheral. Scale bars equal 1.0 cm, except for B, D, and E, which are 0.5 cm.

invertebrate shells (Lopes and Pereira, 2019), as well as from vertebrate remains (Jagt et al., 2020).

Producer. Invertebrate (chiefly molluscan) shells and polyplacophorans (chitons) (Voigt, 1977; Jagt, 2003; Gibert et al., 2007; Lopes and Pereira, 2019; Collareta et al., 2023b).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). *Radulichnus inopinatus* was previously recorded from the Middle Devonian of Germany (Bohatý, 2011), Maastrichtian of Netherlands and Belgium (Jagt, 2003; Mulder et al., 2005; Janssen

et al., 2013), Pliocene of France and Italy (Gibert et al., 2007; Collareta et al., 2023b), and Pleistocene of Southern Brazil (Lopes and Pereira, 2019).

Ichnogenus *Osteichnus*
Thenius, 1988a

Type ichnospecies. *Asthenopodichnium ossibiontum* (Thenius, 1988a)

Diagnosis. U-shaped burrows having a spreite (weblike construction) between the two limbs of the burrow, with a tube diameter of 3–5 mm, at an average notch length of 8–15 mm. Depth of U-constructions up to 7 mm (Thenius, 1988a).

Osteichnus ossibiontum (Thenius, 1988a)
(Figure 4E)

Material. Up to 25 borings on a carapace remain (NVP022).

Description. Cylindrical non-branched parallel borings with fused U-notches, inclined to the bone surface, cross-section long-oval at deeper levels with smooth interior surface. Dimensions vary between 3–8 mm long and between 1–3 mm in width. Depth of borings is ~2–3 mm.

Discussion. The specimens resemble the type ichnospecies *Asthenopodichnium ossibiontum* as described and illustrated by Thenius (1988a, p. 9, pl. 3, figures 1, 2) from the Miocene of Austria. The lithic-boring *Rogerella* Saint-Seine (1951) has closely similar features to the present osteic skeletal substrates ichnogenus. Unlike the producer of the present ichnogenus, barnacles of the Order Acrothoracica are considered to be the trace makers of *Rogerella* (e.g., Mikuláš, 1992).

Producer. Asthenopodinae mayfly larvae (Thenius, 1988a, 1988b; Britt et al., 2008; Ozeki et al.,

2020). In particular, the Asthenopodinae mayfly larvae, a subfamily of Polymitarcyidae, have been assigned to be the producer of the present ichnospecies (Thenius, 1979, 1988a; Jalvo and Andrews, 2016; Genise, 2017). Nowadays, species of this family live in moderate to high energy fluvial systems (Barber-James et al., 2008).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). Upper Jurassic of USA (Britt et al., 2008) to Middle–Upper Miocene of Austria (Thenius, 1988a, 1988b).

Ichnogenus *Osedacoides*
Karl et al., 2012

Type ichnospecies. *Osedacoides jurassicus* Karl et al., 2012

Diagnosis. Simple, basally thickened to branched borings in marine vertebrate bones with a single opening to the surface (Karl et al., 2012).

Osedacoides jurassicus Karl et al., 2012
(Figure 4F)

Material. Several circular borings on four carapace remains (NVP023–026).

Description. Simple, cylindrical borings, circular to semi-circular in cross-section, with a single entrance perpendicular to slightly inclined to the bone surface, closely spaced, bore diameter ranges between 1–4 mm.

Discussion. *Osedacoides* are simple, basally-branching borings in bone. They penetrate into bone as a shaft and branch at depth. *Osedacoides* are exclusively recorded in organic substrates (Karl, 2016).

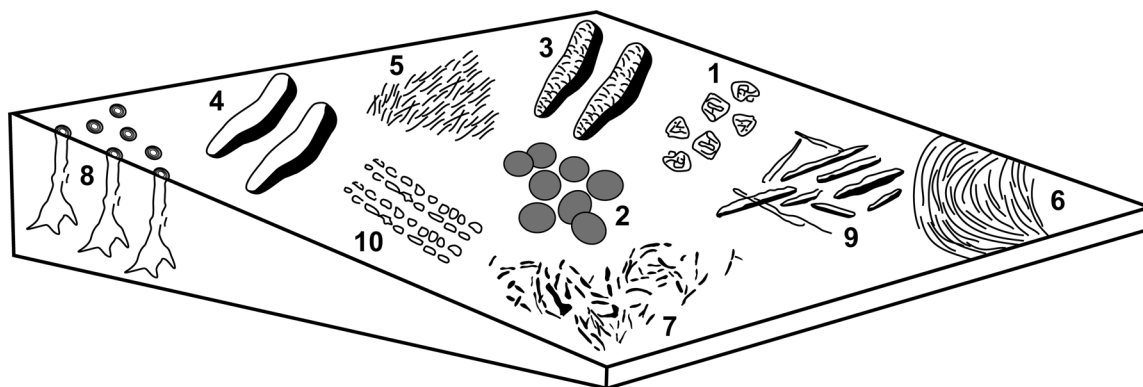


FIGURE 5. A sketch showing bioerosion traces colonising the turtle bones from the Campanian of the Hindaw Member (the Quseir Formation) in the Qarn Ganah area, Kharga Oasis, Egypt (1. *Nihilichnus nihilicus*, 2. *Karethraichnus lakkos*, 3. *Cubiculum ornatus*, 4. *Cubiculum inornatus*, 5. *Osteocallis mandibulus*, 6. *Radulichnus inopinatus*, 7. *Osteichnus ossibiontum*, 8. *Osedacoides jurassicus*, 9. *Sulculites bellus*, and 10. *Machichnus ?bohemicus*).

Producer. Osteophagous polychaetes (Karl et al., 2012).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). The type ichnospecies has been recorded from the Upper Jurassic (Middle Kimmeridgian) of Germany (Karl, 2016). This determination may extend the stratigraphic range of the taxon up into the Upper Cretaceous (Campanian).

Ichnogenus *Sulculites*
Vialov and Nessonov, 1974

Type ichnospecies. *Sulculites bellus* Vialov and Nessonov, 1974

Diagnosis. Furrows have a flat bottom and width from 0.18–0.5 mm or a little more, but usually about 0.3–0.4 mm. They are straight or curved; more often continuous, only rarely intermittent; sometimes single, sometimes forming chains of parallel systems. Groups of parallel furrows can be quite closely spaced to each other, being oriented in different directions. Another common type is curved and often intertwining relatively long furrows. Shorter depressions may be interspersed with them. The ends of the furrows either gradually narrow or abruptly break off (Vialov and Nessonov, 1974).

Sulculites bellus Vialov and Nessonov, 1974
(Figure 4G)

Material. Many narrow grooves on three carapace remains (NVP027–029).

Description. Smooth, slender, narrow, non-branched straight to curved grooves in the surface of bones. They occur solitarily or in clusters, sometimes crossing each other. Width ranges from 0.25–0.6 mm

Discussion. The specimens described show most of the morphological characters of the holotype of *S. bellus* as described and illustrated by Vialov and Nessonov (1974, p. 101, figures 1–4).

Producer. *Sulculites* most likely belongs to the category fodinichnia (Zonneveld, personal comm.). According to Vialov and Nessonov (1974), worms are suggested to be the main producer of this trace fossil.

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). *Sulculites bellus* is firstly recorded from the Albian of Eastern Uzbekistan (Vialov and Nessonov, 1974). This determination extends the stratigraphic range of the taxon up into the Campanian.

Ichnogenus *Machichnus*
Mikuláš et al., 2006

Type ichnospecies. *Machichnus regularis* Mikuláš et al., 2006

Diagnosis. Shallow serial parallel or subparallel grooves in turtle bone. The groove surface is smooth or longitudinally striated. Each series consists usually of dozens of grooves, which are typically uniform in shape and dimensions. The grooves are oriented perpendicular to substrate edge (Mikuláš et al., 2006).

Machichnus ?bohemicus Mikuláš et al., 2006
(Figure 4H)

Material. Three parallel scratches on a carapace remain (NVP030).

Diagnosis. Shallow, thin, discrete, parallel to subparallel, smooth-bottomed scratches. The scratches occur in small groups or series of corresponding width and length; width typically reaches 0.2–1.0 mm and usual length is up to 10 mm (Mikuláš et al., 2006).

Description. Shallow, thin, discrete, parallel to subparallel scratches. At the studied site, they occur on cortical bone of long bones or on the surfaces of antlers. The scratches occur in small groups. Within the series, they typically cover 10–50% of the surface. Each individual scrape is very short and does not overlap or approach any adjacent scrape. Length for each individual mark is typically greater (average 0.65 mm) than width. Each pair is approximately one millimetre apart.

Remarks. Scratches of the given morphology most likely occur during the feeding activity on soft tissues surrounding the bones. In the case of antlers, the scratches are interpreted as gnawing traces, as there is no digestible tissue to be consumed, except the felt on young antlers.

Discussion. The ichnofamily Machichnidae is characterised by a set of grooves, with somewhat irregular outlines on the cortical bone. This family is represented by five distinctive ichnogenera: *Machichnus*, *Nihilichnus*, *Linichnus*, *Knethichnus*, and *Mandaodonites*. Chumakov et al. (2013) erected three new ichnospecies, namely *Machichnus normani*, *M. harlandi*, and *M. jeansi*, for scratches on phosphorite nodules and pebbles from the Upper Cretaceous of England. Herein, the presence of shallow, thin, discrete, parallel to subparallel scratches that occur in small groups or series are undoubtedly assigned to the ichnogenus *Machichnus*. However, because of the smaller dimensions of each pair than the holotype of *M. bohemicus* described by Mikuláš et al. (2006), their ichnospecific determination is uncertain and needs more additional, well-preserved specimens to be confirmed.

TABLE 1. The studied bioerosional ichnotaxa reported on the turtle remains, stratigraphic range, impacted surface(s), their producers and ethological categories. * – ichnotaxa recorded for the first time in Egypt.

Trace fossil	Stratigraphic range	Impacted surface(s)	Trace makers	Ethological category
1. <i>Nihilichnus nihilicus</i> Mikuláš et al., 2006 (Figure 3A)	Middle Triassic–Lower Palaeocene	Carapace	Scavengers and predators (Milàn et al., 2011)	Praedichnia (predation or scavenging traces)
2. <i>Karethraichnus lakkos</i> Zonneveld et al., 2016 (Figure 3B, C)	Campanian (this study)–Recent	Carapace and Plastron	Multiple trace makers may produce similar traces (the ectoparasites ticks, barnacles (Zonneveld et al., 2016)	Fodinichnia
3. * <i>Cubiculum ornatus</i> Roberts et al., 2007 (Figure 3D, E)	Middle Jurassic–Pleistocene	Carapace	Larvae of dermestid beetles (Kitching, 1980; Martin and West, 1995; Hasiotis et al., 1999; Ozeki et al., 2020; Perea et al., 2020)	Pupichnia
4. * <i>Cubiculum inornatus</i> (Xing et al., 2015) (Figure 3D, F)	Campanian (this study)–Middle Triassic	Carapace	Indeterminate osteophagous insect (Xing et al., 2015; Paes Neto et al., 2016)	Pupichnia
5. * <i>Cubiculum</i> isp. (Figures 3G, 4F)	Campanian (this study)	Carapace	Dermestid beetles	Pupichnia
6. * <i>Osteocallis mandibulus</i> Roberts et al., 2007 (Figures 3D, H, 4A, B)	Upper Triassic–Lower Pliocene	Carapace	Feeding by osteophagous insects produced by silphid and histerid beetles (Roberts et al., 2007)	Fodinichnia
7.. <i>Radulichnus inopinatus</i> Voigt, 1977 (Figure 4C, D)	Middle Devonian–Pleistocene	Carapace	Gastropods and polyplacophorans (chitons) (Voigt, 1977; Jagt, 2003; Gibert et al., 2007; Lopesa and Pereira, 2019; Collareta et al., 2023a)	Pascichnia
8. * <i>Osteichnus ossiobontum</i> (Thenius, 1988a) (Figure 4E)	Upper Jurassic–Upper Miocene	Carapace	Attributed to osteophagous insects nymphs of mayflies (Thenius, 1988a)	Fodinichnia
9. * <i>Osedacoides jurassicus</i> Karl et al., 2012 (Figure 4F)	Upper Jurassic–Campanian (this study)	Carapace	Osteophagous polychaetes (Karl et al., 2012)	Fodinichnia
10. * <i>Sulculites bellus</i> Vialov and Nessov, 1974 (Figure 4G)	Albian–Campanian (this study)	Carapace	Unknown organisms, may be worms	Fodinichnia
11. * <i>Machichnus ?bohemicus</i> Mikuláš et al., 2006 (Figure 4H)	Campanian (this study) –Lower Palaeocene	Carapace	Rodent probably teeth of fishes and crocodile (Mikuláš et al., 2006; Mikuláš and Dvořák, 2010)	Praedichnia (predation or scavenging traces)

Producer. The ichnospecies *Machichnus bohemicus* is interpreted as a biting trace, possibly made by crocodylians (Mikuláš et al., 2006; Mikuláš and Dvořák, 2010). This ichnospecies is suggested to be produced by mechanical action of carnivore teeth (e.g., fishes and crocodiles) on the bones (Bieńkowska-Wasiluk et al., 2013; Irazoqui and Acosta Hospitaleche, 2022).

Stratigraphic and geographic distribution. Campanian of the Qarn Ganah, Kharga Oasis (this study). *Machichnus bohemicus* has been recorded

from the Middle Danian (Lower Palaeocene) of Denmark (Milàn et al., 2011), Eocene of West Antarctica (Irazoqui and Acosta Hospitaleche, 2022) and Miocene of Czech Republic (Mikuláš et al., 2006). This determination extends the stratigraphic range of the ichnotaxon through at minimum the latest Maastrichtian. In addition, Muij et al. (2022) identified bite traces on tetrapod bones from the Middle Triassic of Southwestern Germany that were identified as *Machichnus*-like traces.

PALAEOECOLOGY AND POST-MORTEM ALTERATIONS

The Quseir Formation was deposited in terrestrial and brackish environments that graded to a shallow shelf (Ward and McDonald, 1979; Hermina, 1990). It contains vertebrate remains of fishes, crocodiles, dinosaurs, mosasaurids, and turtles in the Campanian deposits (Abu El-Kheir, 2020). In the Qarn Ganah area, the uppermost part of the Hindaw Member (the Quseir Formation) is formed of about 35 m of variegated shale alternating with glauconitic sandstone and siltstone. Turtle concentrations appeared in this member in three successive horizons (Figure 2), alternated between the variegated shales and the glauconitic mudstones and the conglomeratic layers. The bones found in such deposits indicate a supratidal marsh environment, concordant with the occurrence of side-necked turtles (Bothremyidae) (Abu El Kheir, 2020; AbdelGawad et al., 2023).

In the study section, more than 50 moderately to well-preserved turtle remains are recorded. They are distributed in very small areas along the three fossil-bearing horizons (Figure 2). While horizons I and II contain fragmentary and highly weathered turtle remains, samples gathered from horizon III represent the highest concentration of moderately to well-preserved turtle remains in the study section. This massive concentration of turtle skeletons may be due their habit of living in small pond and marshes (AbdelGawad et al., 2023). Such shallow, nutrient-rich ponds were exposed to sunlight with little water flowing through it. Many plant remains were recorded in the grey glauconitic mudstone of the study area (Figure 6A–D). In general, glauconite contains many trace elements that serve as necessary micro-nutrients for the plant growth (e.g., El-Habaak et al., 2016). Accordingly, turtles may have lived at the margin of the pond, with a high density of plants (Mahmoud, 2003). However, pond turtles are omnivorous and will eat anything available, including other turtles.

This concentration may be responsible for greater densities of turtles in horizon III (Figure 6D). The associated crocodiliforms might have lived together with turtles in this pond, with very little or without transportation of fossil elements by the currents. The study area was incised laterally by fluvial sandstone meandering channels, which may have transported the separated elements of sauropod dinosaurs into the existing pond.

In the field, the turtle fossils of the Qarn Ganah area are represented by complete shells, partial shells and many scattered and little-weathered

turtle shell fragments. No significant transport or bone sorting is observed, and both complete and fragmentary bones in the assemblages show the same biostratigraphic features. Vertebrate fossils with rounded or polished edges are absent. These features suggest mass mortalities of turtles, and burial before many shells disarticulated. All these observations indicate that we are dealing with little-transported, autochthonous to parautochthonous concentration of turtle remains.

In the turtle-rich layer (horizon III; Figure 6D), turtles are almost in a similar taphonomic condition, with many shells mostly intact and subjected to little weathering. No cranial turtle remains are recorded and only a few limb bones are collected from the surface of the fossil bearing layers. These elements may have been transported by currents to other sites after the exposure of the turtle skeletons (Brand et al., 2000). The majority of turtle shells are partially buried in the sediments, as the buried portion is still associated while the exposed part is disarticulated, indicating an erosional process of skeletons after removal of the sediments (Brand et al., 2000). Few complete turtle shells were collected from the third horizon. The turtle shells in the turtle-rich layer have a normal position, where the carapace is up and plastron is down, which means that these turtles were not moved along with the currents. All turtle remains display very little abrasion, confirming a small-scale transportation of fauna.

Herein, bioerosion is informative as a general indicator of exposure time of the turtle skeletons at the sediment-water interface before the final burial. It is remarked that most bioerosive structures are recorded in the carapaces, indicating little transportation and relatively prolonged period of exposure prior to deposition, while bioerosion in the plastrons are fewer, reflecting post-mortem period of colonisation. It has been noticed that bioeroders occurred both on carapace and plastron, preferring carapace surfaces.

The evidence of predators and bioerosion are quite well recorded in turtle shells of the study area. Signs of insect feeding represent the predominant bioerosional structures in the turtle bones. This reflects an increased insect activity and a high consumption of the nutrient-rich spongy tissue, causing loss of large areas of the turtle bone surface. The infestation by insect larvae is well pronounced in turtle bones of this study, which indicates longer exposure times before the final deposition or burial. This is confirmed by the work of Lopes and Ferigolo (2015) who indicated that

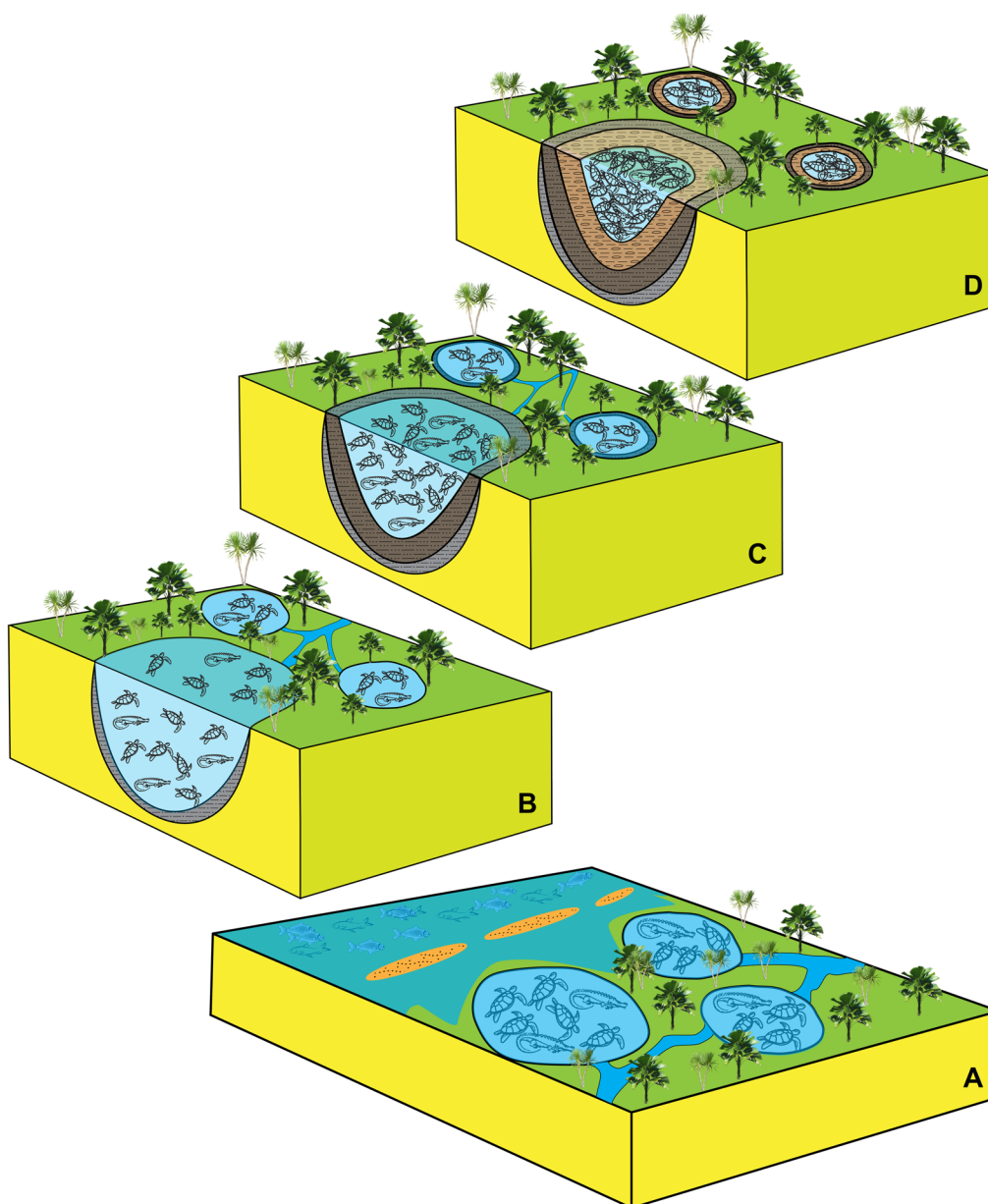


FIGURE 6. Palaeoecology and post-mortem stages of the three turtle-bearing horizons in the Qarn Ganah area, Kharga Oasis, Egypt. (A) A sketch showing the proposed life of side-necked turtle (*Bothremydidae*) living in small isolated ponds during the Campanian time. (B–D) A proposed model for the formation of the three horizons of turtle concentrations.

bones protected by flesh and skin until the final burial displayed no infestation by insects. The scarcity of bioerosional traces that could be attributed to predators or scavengers (e.g., *Nihilichus*) indicates that carnivory was an unessential element in the bioerosion of turtle remains. On the other hand, the record of *Osedacoides* that were produced by *Osedax* worms implies that the bone was still fresh and contained enough usable organic matter to support the colonisers.

Although the presence of any bioerosive records on turtle bones almost always indicates post-mortem production, the presence of some structures (e.g., *Karethraichnus* and *Nihilichnus*) may be indicative of the opposite. The presence of these borings suggests that the turtle bones had a relatively long time of exposure, which was sufficient to allow the silphid and histerid beetles to leave such a significant effect on their bones. *Karethraichnus lakkos* borings are formed as a result of

various activities of parasitic organisms that should be produced *in-vivo* rather than post-mortem (Zonneveld et al., 2016). In addition, the ichnogenus *Nihilichnus* was recorded on a carapace fragment of a tortoise that may have been emplaced pre- or post-mortem on the host animal (Zonneveld et al., 2022a).

The bioerosive assemblages in the studied bones indicate that they were deposited in a low-energy environment, with low rates of sedimentation. It is suggested that bioeroder activities most probably occurred immediately after the death and accumulation on the substrate of the turtle remains, but before the carapace was overturned by large scavengers.

CONCLUSIONS

1. The uppermost part of the Campanian Quseir Formation (the Hindaw Member) of Kharga Oasis, Egypt, contains a high concentration of turtle skeletal remains that lived in small ponds and marshes and were deposited as autochthonous to parautochthonous relics.
2. The turtle skeletal remains display significant bioerosional structures, indicating that they were utilised by predators and scavengers.
3. Common signs of insect feeding reflect increased insect activity and a slightly prolonged time of exposure prior to final sedimentation.
4. Nine ichnogenera (*Nihilichnus*, *Karethraichnus*, *Cubiculum*, *Osteocallis*, *Radulichnus*, *Osteichnus*, *Osedacoides*, *Sulculites*, and *Machichnus*), representing 11 ichnospecies, were identified. Eight of these ichnotaxa are recorded for the first time in Egypt.
5. The recognised bioerosional structures appeared as borings, shallow chambers, grooves and punctures produced by ticks, beetles, polychaete worms, fishes/crocodiles and gastropods.
6. Such bioerosion traces were likely caused by relatively long exposure time before the final deposition or burial. In some cases, borings may have been produced *in vivo*.
7. The new material considerably expands the stratigraphic and geographic distribution of this trace fossil assemblage and reveals that their producers may have been able to survive in other palaeoenvironmental conditions.

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