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Vertebrate paleontological exploration of the Upper Cretaceous succession in the Dakhla and Kharga Oases, Western Desert, Egypt

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Abstract

The Campanian and Maastrichtian stages are very poorly documented time intervals in Africa's record of terrestrial vertebrate evolution. Upper Cretaceous deposits exposed in southern Egypt, near the Dakhla and Kharga Oases in the Western Desert, preserve abundant vertebrate fossils in nearshore marine environments, but have not yet been the focus of intensive collection and description. Our recent paleontological work in these areas has resulted in the discovery of numerous new vertebrate fossil-bearing localities within the middle Campanian Qusier Formation and the upper Campanian-lower Maastrichtian Duwi Formation. Fossil remains recovered from the Campanian-aged Quseir Formation include sharks, rays, actinopterygian and sarcopterygian fishes, turtles, and rare terrestrial archosaurians, including some of the only dinosaurs known from this interval on continental Africa. The upper Campanian/lower Maastrichtian Duwi Formation preserves sharks, sawfish, actinopterygians, and marine reptiles (mosasaurs and plesiosaurs). Notably absent from these collections are representatives of Mammalia and Avialae, both of which remain effectively undocumented in the Upper Cretaceous rocks of Africa and Arabia. New age constraints on the examined rock units is provided by 23 nannofossil taxa, some of which are reported from the Duwi Formation for the first time. Fossil discoveries from rock units of this age are essential for characterizing the degree of endemism that may have developed as the continent became increasingly tectonically isolated from the rest of Gondwana, not to mention for fully evaluating origin and diversification hypotheses of major modern groups of vertebrates (e.g., crown birds, placental mammals).

1. Introduction

Post-Cenomanian deposits from the Late Cretaceous of continental Africa are scarce (Haughton, 1963; Dingle et al., 1983; Mateer et al., 1992) and limited to only a few geographically restricted localities. Whereas the expanding terrestrial/freshwater vertebrate record from the 'Middle' Cretaceous (~Aptian-Cenomanian) has improved considerably in recent years (e.g., Sereno et al., 2004; Gomani, 2005; Sereno and Brusatte, 2008; Gottfried et al., 2009; Cavin et al., 2010; O'Connor et al., 2010; Gorscak et al., 2014; Sertich and O'Connor, 2014), our understanding of biotic dynamics leading up to and through the K-Pg boundary in Africa and Arabia remains extremely limited. Moreover, the few vertebrate fossils that are known from the Late Cretaceous of Africa derive from temporally restricted stratigraphic intervals, precluding direct comparison of faunas. This issue is particularly problematic for the latest Cretaceous, where the rate of new discoveries pales in comparison with earlier parts of the Cretaceous record.

The Late Cretaceous is of great interest for paleontologists as it coincides with a number of significant global-level faunal changes, and culminates in the extinction of many vertebrate (e.g., nonavian dinosaurs, marine reptiles) and invertebrate (e.g., ammonites) groups. The final two stages of the Cretaceous (Campanian and Maastrichtian) represent a time when Gondwanan fragmentation culminated in the near-complete isolation of most of the southern landmasses and Africa in particular (e.g. Müller et al., 1993; Smith et al., 1994; Scotese, 1998; Hay et al., 1999; Pletsch et al., 2001 and Scotese, 2001), offering a significant mechanism that could have profoundly influenced the evolutionary trajectories of numerous terrestrial vertebrate clades. However, our working knowledge of the African terrestrial biosphere and vertebrate diversity during this critical period of isolation is currently too limited to allow for meaningful comparisons of faunal patterns that have been documented in the Late Cretaceous on other landmasses. Moreover, the current sampling bias also precludes a critical evaluation of hypotheses positing the origin of major vertebrate groups prior to the Cretaceous-Paleogene boundary (e.g., Ericson et al., 2006; Meredith et al., 2011; Jetz et al., 2012; Jarvis et al., 2014; although see Prum et al., 2015 for a recent synopsis regarding the temporal origin of modern birds).

1.1 Background

Recently-developed Gondwana-wide (e.g., Sereno et al., 2004; Krause et al., 2006; Ali and Krause, 2011) and Africa-specific (e.g., O'Connor et al., 2006; Sertich and O'Connor, 2014; Gorscak and O'Connor, In Review) models related to Cretaceous biogeography can only be tested and refined through intensification of paleontological work in the uppermost Cretaceous deposits exposed on the continent. One of the most promising regions where such data may be collected corresponds to the sparsely vegetated circum-Saharan areas that preserve varied depositional settings (e.g., fluviatile, estuarine, near-shore marine, etc.) like the Western Desert of Egypt. Rigorously characterizing biotas (e.g., Claeson et al., 2014) that are unearthed from these units should provide insight into physical processes at both local and regional scales (e.g., timing of Gondwanan fragmentation, subdivision of large terrestrial landforms by marine transgressions, etc.) thought to influence terrestrial/freshwater communities during this time.

The Upper Cretaceous deposits along the Abu Tartur Plateau (Fig. 1), and in particular near the Dakhla and the Kharga Oases, hold great promise for the recovery of fossil vertebrates that are necessary for characterizing latest Cretaceous African faunas. New discoveries are essential for formally evaluating biogeographic models or characterizing the relative endemicity/increasing provincialism (e.g., Sereno et al., 1994, 2004) that may have existed on the African continent more generally during the Late Cretaceous. The Dakhla Oasis is situated in the southern part of the Western Desert about 150 km west of the Kharga Oasis, south of the Abu Tartur Plateau. A number of vertebrate clades have been noted from Cretaceous rocks in this region, either having been documented directly (e.g., Churcher, 1995; Rauhut et al., 1997; Lapparent de Broin and Werner, 1998; Churcher, 2006; Lamanna et al. 2004; Smith and Lamanna, 2006) or referred to indirectly as part of geological reports (e.g., Awad and Ghobrial, 1965; Klitzcsh, et al., 1979; Hendriks et al.,1984).

It has already been documented that sediments of the middle Campanian Quseir Formation exposed along the Abu Tartur Plateau (Fig. 1) preserve remains of freshwater gastropods, reptiles, dinosaurs, and terrestrial plant matter (Hendriks et al., 1984). The Quseir Formation reaches a maximum thickness of 70-90 m near the Dakhla Oasis and consists primarily of variegated shale (Hermina, 1990). Thus far, very little focused paleontological work has been conducted in this area due in large part to its remote location. Previous reconnaissance work in the eastern part of the Dakhla Oasis has led to the recovery and identification of crocodyliforms (cf. *Dyrosaurus*), dinosaurs (cf. *Spinosaurus*), turtles ("*Podocnemis*" *aegypticus*), lungfish (*Ceratodus* and *Protopterus*), bony fish, and sharks from the Quseir Formation (Churcher and De Iuliis, 2001; Claeson et al., 2014). With the exception of lungfish, however, none of these fossils have been described in any additional detail.

The upper Campanian/lower Maastrichtian Duwi Formation (Fig. 2) overlies the Quseir Formation and underlies the Maastrichtian-Paleocene Dakhla Formation (Tantawy et al., 2001), and contains phosphate beds in a sequence of alternating claystone, sandstone, siltstone, and conglomerate (Hermina, 1990). Dinosaur material (e.g., a single theropod tooth) from the Duwi Formation has been reported, but with unknown provenance other than it was recovered near Idfu in the Nile Valley (Smith and Lamanna, 2006). The Maastrichtian/Paleocene Dakhla Formation consists mainly of shales with sandstones, siltstones and marls, and preserves vertebrates and fossil wood (Tantawy et al., 2001). A femur of a sauropod dinosaur was collected from the Maastrichtian subunit (Ammonite Hill Member) of the Dakhla Formation just west of Mut by German geologists decades ago (Rauhut and Werner, 1997), but no further collecting has since been undertaken by vertebrate paleontologists.

Given the potential of these units for yielding vertebrate remains, the Mansoura University Vertebrate Paleontology (MUVP) project was initiated to carry out exploratory fieldwork in the poorly-sampled vertebrate-bearing strata of Egypt's Western Desert. Six expeditions conducted to date have identified numerous fossil-bearing localities, with specimens ranging from fragmentary material to complete cranial and postcranial skeletons.

1.2 Abbreviations

Institutional abbreviations: **MUVP**, Mansoura University Vertebrate Paleontology Center at the Geology Department, Faculty of Science, Mansoura University, Egypt.

2. Geographic and Geological setting

2.1 Basic Sedimentology and Stratigraphy

Upper Cretaceous outcrops are accessible in multiple areas near both the Dakhla Oasis and the Kharga Oasis, southern Egypt (Fig. 1). The lithostratigraphic sequences in this area include a variety of depositional environments, ranging from fluviatile and estuarine to numerous distinct marine facies, most of which preserve vertebrate fossils characteristic of their respective settings (Klitzcsh et al., 1979; Hendriks et al., 1984; Hermina, 1990; Klitzsch and Schandelmeier, 1990; Tantawy, et al., 2001; Mahmoud, 2003).

In the present study, the uppermost Cretaceous (Campanian-Maastrichtian) succession exposed north of the village of Tineida about 40 km east of Mut (capital of Dakhla Oasis) was measured and is represented by three major rock units (from older to younger): Qusier, Duwi and Dakhla formations (Fig. 2, 3A). The section described herein was established based on novel field investigations that included: (1) a detailed description of the rocks, (2) a determination of the acid insoluble residue, and (3) by considering the distribution of fossils in the investigated units. These new observations were in turn integrated within the extensive regional stratigraphic and sedimentologic framework developed by Hermina (1990). The type section of the Quseir Formation (lower-middle Campanian) is located at Gebel Atshan in the Quseir area, Red Sea Coast (Youssef, 1957). The sediments of the Quseir Formation from the Dakhla Oasis area document fluvial, brackish, and restricted marine settings, and are divided by Hermina (1990) into the ~30 m brick-red mudstone and fissile purple shale-dominated Mut Member and the 20-35 m overlying variegated shale El Hindaw Member, containing alternating ferruginous-glauconitic sandstones, a green siltstone, and brown and grey sandy claystones. Near the village of Tineida, a ~30 m thick unit assigned to the upper part of the Quseir Formation is exposed, consisting of slope forming variegated shale (purple, gray and green) alternating with hard bands of sandstones and siltstones (Fig. 3B and C). There are a few thin phosphatic beds with evidence of bioturbation (e.g., burrows) intercalated in the upper part of the succession (Fig. 3D). Petrified wood was also noted in these same units (Fig. 3E). Evidence of charcoal from the Quseir Fm. has recently been used to infer the presence of paleo-wildfires during the Campanian in northern Africa (El Atfy et al., 2016). A few invertebrates (molluscs and gastropods) were collected from horizon T13. The vertebrate fossils described in this report were collected mainly from the T9-T12 horizons (Fig. 2) of the Quseir Formation including fish, turtle, crocodyliform, and dinosaur remains (Table 1).

The Duwi Formation (upper Campanian-lower Maastrichtian) has its type section at the Gebel Duwi in the Quseir area, Red Sea Coast (Youssef, 1957). It is a phosphate-bearing unit that conformably overlies the Quseir Formation. In the studied succession, the base of Duwi Formation is composed of ~3 m thick cliffs forming the phosphate beds, alternating with thin layers of shale and siltstone (Fig. 3F and G). Each of the phosphate beds is characterized by the ichno-taxon *Thalassinoides* at its base (Fig. 3H). The fossil content of the lower part of the Duwi Formation preserves a diversity of shallow-shelf fossils such as shark teeth, the mosasaur *Globidens*, and other marine reptiles. The upper part of the Duwi Formation is composed of a ~10 m thick layer of argillaceous limestone (60% carbonate at the base) and fissile carbonaceous shale (75% mud at the top) representing a deep marine facies; it includes well-preserved remains of osteichthyan fishes and marine reptiles (e.g., partial mosasaur skulls and associated skeletons) (Table 1).

2.2 Nanoplankton studies and age constraint

Rock samples were collected from each layer of the Quseir and Duwi formations and from the base of Dakhla Formation in the village of Tineida section (Fig. 1-2). An evaluation of nanoplankton content was performed using the simple smear slide technique (Bown and Young, 1998). Semi-quantitative abundance estimates of nanofossils were made (Table 2). The nanofossil biozonation of Sissingh (1977, 1978) as refined by Perch-Nielsen (1985) is generally accepted as the standard scheme for the Cretaceous and was used in the present study. The first occurrence (FO) of *Quadum trifidum* was used to define the base of *Quadum trifidum* Zone (CC22). *Qadrum trifidum* is stratigraphically important species for the late Campanian (Perch-Nilsen, 1985; Bown, 1998).

An examination of the Quseir Formation rock samples yields no nanoplankton at the study area. However, late Campanian calcareous nanofossil assemblages were identified for the first time from the upper part of the Duwi Formation (Fig. 2). A total of 23 nanofossil taxa were identified from the sampled rocks (Table 2; Fig. 4). The identified calcareous nanofossils indicate that the middle-upper Duwi Formation is late Campanian (73 Ma) in age, corresponding to Zone CC22 (*Qadrum trifidum*) of Sissingh (1977, 1978) and UC15 d of Burnett (1998).

The analysis of the calcareous nanofossil content (Fig. 4) of the Duwi Formation reveals that the dominant assemblages include: *Ceratolithoides aculeus, Stradneria crenulala, Lucianorhabdus cayeuxii, Microrhabdulus decoratus, Quadrum trifidum, Rhagodiscus angustus, Watznaueria barnesae,* and *Calculithus obscurus*. These taxa indicate a near-shore marine environment and a warm surface water paleotemperature (Thierstein, 1976; Roth, 1978; Doeven, 1983 and Faris, 1992).

3. Vertebrate Fossils

The fossiliferous units exposed in the Dakhla and Kharga oases have produced a notable collection of terrestrial/freshwater and marine fossil vertebrates from localities that are dated to be uppermost Cretaceous (~73 Ma) in age. The new localities contain a diversity of post-Cenomanian, Upper Cretaceous terrestrial/freshwater/marine vertebrates representing members of several major clades, including fishes, turtles, crocodyliforms, marine reptiles, and non-avian dinosaurs (Table 1; Figs. 5-6). Notable among the latter are both sauropod and theropod dinosaurs that were recovered from deposits near the village of Tineida (Dakhla Oasis) and Baris (Kharga Oasis). Below we provide an overview of the discoveries to date.

3.1. Quseir Formation Fauna

3.1.1. Fishes

Fish material from the Quseir Formation is best represented by numerous, mostly isolated lungfish tooth plates, as detailed in the recent paper by Claeson et al., (2014).

Sarcopterygii Romer, 1955

Dipnoi Müller, 1844

Ceratodontiformes Berg, 1940

Lepidosirenidae Bonaparte, 1841

The lepidosirenid lungfish remains were only collected by surface prospecting in the Quseir Formation. The new materials include partial and complete tooth plates, along with additional partial jaw elements of the taxa *Lavocatodus protopteroides*, *Lavocatodus humei*, *Lavocatodus giganteus*, and *Protopterus nigeriensis*. The new hypodigm and its biogeographic implications were discussed and evaluated in more detail by Claeson and colleagues (2014).

3.1.2 Testudines

Turtle material has been collected from all fossiliferous levels of the Quseir Formation exposed in the Dakhla and the Kharga oases. The majority of the discovered materials are isolated plates; no cranial elements have been recovered thus far. However, a well-preserved, mostly complete shell that includes both carapace and plastron was discovered from the base of Quseir Formation near the road between Baris and Ezbit Duch, south of Kharga Oasis.

Testudines Linnaeus, 1758

Pleurodira Cope, 1865

Pelomedusoides indet. Cope, 1868

(Fig. 5A)

The specimen (MUVP 179) consists of a relatively complete shell (CL = ca. 50 cm) lacking most of the peripheral ring and the epiplastra. The pelvis is sutured to the shell, a cervical scute is absent, reduced mesoplastra are present, and at least six large neurals fully separate the costal series. The specimen is therefore tentatively referred to Pelomedusoides indet. (Gaffney et al., 2006).

3.1.3 Crocodyliformes

Numerous crocodyliform specimens referable to neosuchia have been recovered from different horizons of the Quseir Formation. The materials include cranial and postcranial elements that were collected from both Dakhla and Kharga Oases. The preservation ranges from being fully replaced by gypsum (maintaining only the general shape of the bone) to well-preserved. These remains can tentatively be referred to Neosuchia, with numerous cranial and postcranial elements indicative of at least two distinct taxa. To date, no definitive remains of Dyrosauridae, as reported elsewhere (e.g., Lamanna et al., 2004), have been recovered from the Quseir Formation of Dakhla or Kharga Oases.

Eusuchia Huxley, 1875

Crocodylia Gmelin, 1789

cf. Gavialoidea Hay, 1930

(Fig. 5B-C)

Other specimens (e.g. MVUP 186) pertain to a long snouted form similar in overall morphology to 'thoracosaur' gavialoids (Eusuchia) based on the presence of circular supratemporal fenestra, dorsoventrally flattened crania, and distinct anterior projections on the postorbitals. Relatively complete cranial remains (MUVP 180) recovered near Baris await preparation, but will permit thorough diagnosis of the taxon. It is possible that this form is the source of previous reports of Dyrosauridae from the Quseir Formation (Churcher and De Iuliis, 2001; Lamanna et al., 2004)

Crocodylomorpha Hay, 1930

Crocodyliformes Hay, 1930 (sensu Clark, 1986)

Neosuchia Clark in Benton and Clark, 1988

(Fig. 5D, E)

Materials assigned to an as yet undescribed basal neosuchian crocodyliform were collected from the Quseir Formation in the Dakhla Oasis area. The remains include dorsal vertebrae, fragmentary cranial elements, and a left dentary. The taxon is distinguished by a low, straight dentary with a short symphysis, contributions of the splenials to the mandibular symphysis, and conical teeth. Closely associated cranial remains include a jugal with a distinct mediolaterally wide anterior process and multiple tooth waves in the maxilla. Associated vertebrae (MUVP 10-11) are amphicoelous, suggesting a basal position among neosuchians. Other collected materials include a partial skull and various limb elements (MUVP 12 to MUVP 37) assignable to multiple individuals.

3.1.4 Dinosauria

Numerous saurischian dinosaur specimens (Fig. 5F-H) have thus far been collected from the Quseir Formation in both the Dakhla and Kharga Oases. The specimens include a variety of axial postcranial and appendicular elements referable to Theropoda and Sauropoda. In the village of Tineida area (Dakhla Oasis), sauropod teeth, an isolated sauropod tibia (?) (Fig. 5H) missing its ends, and the proximal ends of semi-articulated sauropod tibia and fibula (Fig. 5G) have been recovered. In the Baris area (Kharga Oasis), isolated materials referable to Sauropoda include a partial humerus (Fig. 5F), a femur, two cervical vertebrae, and partial ribs. A proximal left fibula of a theropod dinosaur was also collected from the Baris area. Most significantly, an associated skeleton of a titanosaurian sauropod is currently undergoing preparation and will be the focus of a future report.

3.2 Duwi Formation Fauna

3.2.1 Fishes

Fossil fishes are among the most common vertebrates preserved in the Duwi Formation. The collected material ranges from isolated teeth and cranial fragments to partial/complete skulls and skeletons of both Chondrichthyes and Osteichthyes. The chondrichthyan materials are mainly shark and sawfish teeth that are found in different horizons and are generally consistent with earlier reports (e.g. Dominik and Schaal, 1984; Kassab and Mohamed, 1996). Of particular note are the occurrence of multiple clades of actinopterygians.

Telostei Müller, 1844

Ichthyodectiformes Bardack and Sprinkle, 1969

Ichthyodectoidei Romer, 1966

Saurodontidae Cope, 1871

(Fig. 6A)

A remarkable saurodontid fish (MUVP 183) was recovered from the Duwi Formation and consists of a nearly complete skull, partially articulated axial skeleton and pectoral fin, and numerous dissociated components of the vertebral series. MUVP 183 was recovered from a marine calcareous shale bed in the upper part of the Duwi Formation near the village of Tineida, Dakhla Oasis. Although flattened, the specimen is very well-preserved. The edentulous unpaired predentary bone, a neomorphic ossification projecting from the lower jaw and extending beyond the anterior margin of the upper jaw, is not preserved. The specimen is an exceptionally large saurodontid and represents the first record of Saurodontidae from Africa (Youssef et al., 2011).

Teleostei Müller, 1844

Aulopiformes Rosen, 1973

Enchodontoidei Berg, 1940

Enchodontidae Lydekker, 1889

cf. *Enchodus* Agassiz, 1835

(Fig. 6B)

Enchodus has also been reported before from Cenomanian deposits of the Bahariya Oasis, Egypt (Allam, 1986), but has not been documented or illustrated. An associated partial cranium and lower jaw, including right and left dentaries and right ectopterygoid, and a number of unidentifiable elements were collected from the upper part of the Duwi Formation near the village of Tineida, Dakhla Oasis. The collected material (MUVP 59) is the most complete and first recorded material of *Enchodus* from the Campanian of Egypt (Holloway et al., 2013). Moreover, several scattered teeth and other possible skull fragments that likely pertain to *Enchodus* were collected from the same horizon. These materials are currently under more detailed study (Holloway et al., in prep) and will form the basis of a separate contribution.

3.2.2. Reptiles

3.2.2.1. Squamates (Mosasauridae) and other "marine reptiles"

Although a number of sauropterygian (e.g., plesiosaur (MUVP 184)) fossils (Fig. 6C) have been identified, documented in-situ, and collected from the Duwi Formation, most represent isolated vertebrae that have relatively limited anatomical information for use in assigning the materials to lower taxonomic levels. These are known from both the upper and the lower parts of the Duwi Formation exposed near the village of Tineida, Dakhla Oasis. There are also abundant materials of well-preserved marine squamates that include cranial, dental, and postcranial materials.

Squamata Oppel, 1811

Mosasauridae Gervais, 1853

Mosasaurinae Gervais, 1853

(Fig. 6 D, E)

Isolated cranial, dental, and postcranial elements, in addition to multiple associated mosasaur skeletons, have been identified throughout the study area. Most specimens were noted by GPS and will require additional field investigation and excavation prior to assignment to the lower level ranks. One isolated specimen can be referred to genus level.

Squamata Oppel, 1811

Mosasauridae Gervais, 1853

Mosasaurinae Gervais, 1853

Globidensini Russell, 1967

Globidens Gilmore, 1912

(Fig. 6F)

A single isolated tooth (MUVP 185) has a conical shape and is short and robust with a bulbous crown. The apex of the tooth is situated at the midpoint of the crown. The surface of the tooth is ornamented by fine and densely arranged striations. The base is broken and does not preserve the root. The tooth (Fig. 6A) was collected from the hard phosphate band of the lower part of the Duwi Formation exposed near the village of Tineida, Dakhla Oasis.

4. Discussion and Conclusions

The Late Cretaceous biosphere experienced a number of significant faunal changes and represents a critical interval for understanding one of the key transitional periods (Cretaceous-Paleogene) of vertebrate faunal evolution on the planet. Recent fossil discoveries from Upper Cretaceous (Campanian and Maastrichtian) deposits on Afro-Arabia are not only extremely rare, but also limited to a few geographically restricted areas. Thus, continental Africa has contributed relatively little to the development of our understanding of global scale patterns of vertebrate evolution during the Late Cretaceous.

Fossil vertebrates recovered thus far from outcrops surrounding Dakhla and Kharga oases yield from deposits estimated at ~73 Ma based on nanoplankton biostratigraphy. Paleontological efforts have resulted in the discovery of numerous (~ 100) new fossil-bearing localities that represent a variety of different palaeoenvironments. Groups represented include sharks, rays, actinopterygian and sarcopterygian fishes, turtles, marine reptiles (mosasaurs and plesiosaurs), crocodyliforms, and saurischian dinosaurs. Specimens range from isolated elements, partial-compete skulls to semi-articulated skeletons.

Continuing reconnaissance paleontology and geology in the areas adjacent to the Dakhla and Kharga Oases should provide significant new insights into the vertebrate faunas that inhabited northern Africa during the last part of the Cretaceous Period. Recovery of mammal fossils, and of more complete archosaur materials, from the Campanian terrestrial deposits of the Qusier Formation would help to fill major gaps in Africa's Turonian- Paleocene record of vertebrate evolution, and must remain a top priority for paleontological work in Egypt. On a regional scale, placing the new fossils into both environmental and temporal contexts will contribute baseline data on community structure in northern Africa during the Cretaceous-Paleogene transition and will assist with characterizing faunal dynamics leading up to the end-Cretaceous extinction event.

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TABLES

Table 1. Faunal list of vertebrate groups collected from Upper Cretaceous Quseir and Duwi formations of Dakhla and Kharga oases.

Table 2. Calcareous nanofossil assemblage from the upper Campanian Duwi Formation. These samples were collected just north of the village of Tineida (Fig. 1). The code used in this study is translated as follows: **C** (common), one to ten specimens per fov (field of view); **F** (frequent), one specimen per fov; **R** (rare), one specimen per eleven to twenty fov.

FIGURES

Figure 1. Location (A) and geologic map (B) of the Dakhla and Kharga Oases in the Western Desert, southern Egypt, to illustrate main lithological units of the Upper Cretaceous-Paleogene succession. Modified after El Khawaga et al., (2005). The dashed box on **A** corresponds to the general location depicted in **B**.

Figure 2. Stratigraphic section measured north of the village of Tineida, Dakhla Oasis, Western Desert, Egypt, showing the lithostratigraphy of the Quseir, Duwi, and base of the Dakhla formations. See Figure 1 for specific location of measured section.

Figure 3. Photos illustrating relationships among stratigraphic units and fossil bearing layers. A, Overview of exposures in the Dakhla Oasis study area depicting the superpositional relationships of the Quseir, Duwi, and Dakhla formations. B, Overview of the Quseir Formation, with white dotted line indicating the contact between the Quseir Formation and overlying Duwi Formation. C, Close-up of variegated shale of the Quseir Formation and contact (white arrow) with the Duwi Formation. D, Phosphatic bands in the Quseir Formation. E. Silicified wood in the Quseir Formation. F, Duwi Formation exhibiting lower phosphate band with upper argillaceous limestone layers that preserve marine reptiles and fishes described herein. G, Phosphate bands of the Duwi Formation preserving chondrichtyan and

mosasaur (e.g., cf. *Globidens*) materials and the sharp contact with the underlying Quseir Formation. H, *Thalassinoides* ichnofossils at the base of the phosphate bands of the Duwi Formation.

Figure 4. Calcareous nanoplankton fossils recovered from the upper part of the Duwi Formation. A-B, *Arkhangelskiella cymbiformis* Vekshina (1959). C-D, *Aspidolithus parcus constrictus* (Hattner et al., 1980). E-F, *Quadrum trifidum* (Stradner in Stradner & Papp, 1961). G, *Quadrum sissinghii* Perch-Nielsen (1984b). H, *Micula decussata* Vekshina (1959). I, *Retecapsa crenulala* (Bramlette & Martini, 1964). J, *Cribrosphaerella ehrenbergii* (Arkhangelsky, 1912). K, *Zygodiscus spiralis* Bramlette & Martini (1964). L, *Calculites obscurus* (Deflandre, 1959). M, *Lithraphidites carniolensis* Deflandre (1963). N, *Zeugrhabdotus pseudanthophorus* (Bramlette & Martini, 1964). O, *Manivitella pemmatoidea* (Deflandre in Manivit, 1965). P, *Eiffellithus eximius* (Stover, 1966). Q, *Reinhardtites anthophorus* (Deflandre, 1959). R, *Microrhabdulus decoratus* Deflandre (1959). S, *Lucianorhabdus cayeuxii* Deflandre (1959). T, *Watznaueria barnesae* (Black in Black & Barnes, 1959).

Figure 5. Representative turtle, crocodyliform and saurischian dinosaur material recovered from the middle-upper Campanian Quseir Formation. A, A near-complete turtle shell (MUVP 179) in dorsal view. B, Partial cranium (MUVP 186) of a gavioloid in dorsal view (anterior to the top of the image). C, Volume rendered image of skull roof and mandibular fragment of cf. gavialoid (MUVP 180) in dorsoventral projection view. D, Dissociated appendicular

materials (MUVP 30- MUVP 37) of a large-bodied crocodyliform. E, Isolated dorsal vertebra (MUVP 11) of crocodyliform in right lateral view. F, Isolated right humerus (MUVP 181) of a sauropod dinosaur in anterior view (proximal end toward the left of the image). G, Associated tibia (left) and fibula (right) (MUVP 182) of a sauropod dinosaur. H, Isolated limb bone (MUVP 200) of a sauropod dinosaur. The lens cap in G is ~ 7 cm in diameter. **Abbreviations**: **fr**, frontal; **pa**, parietal; **stf**, supratemporal fenestra.

Figure 6. Fish (A-B) and representative marine reptile material (C-F) recovered from the upper Campanian Duwi Formation. A, Saurodontid fish (MUVP 183) preserving most of the skull and postcranial skeleton, right lateral view. B, Associated partial cranium and lower jaw of *Enchodus* (MUVP 59) in the field. The white lines trace the outline of the lower jaw. C, Isolated vertebrae of plesiosaur (MUVP 184) and other unidentifiable sauropterygian remains. D, Associated mosasaur vertebrate scattered as surface materials (*not collected*). E, Isolated mosasaur vertebrae in cranial (anterior) view (*not collected*). F, Isolated tooth (MUVP 185) of a mosasaur (cf. *Globidens*) from the lower phosphate unit of the Duwi Formation. The paint brush is C-D is 5 cm wide and the lens cap in E is ~ 7 cm in diameter.

Table 1. Faunal list of vertebrate groups collected from Upper Cretaceous Quseir and Duwi formations of Dakhla and Kharga Oases.

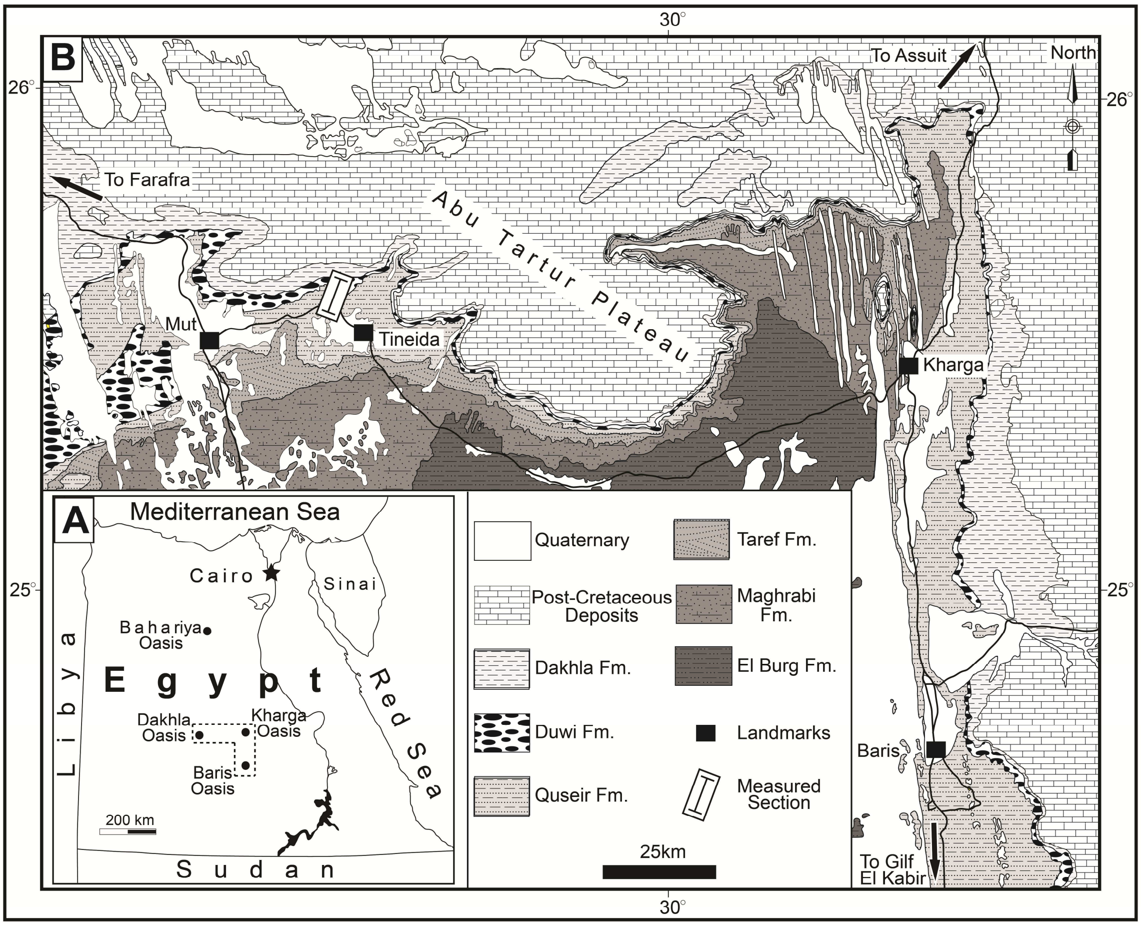
Quseir Formation

- Osteichthyes
  - Sarcopterygii
    - Dipnoi
      - Ceratodontidae
- Sauropsida
  - Testudines
  - Archosauria
    - Crocodyliformes
      - Dyrosauridae
      - ?Neosuchia
      - Eusuchia
        - ?Gavialoidea
    - Dinosauria (nonavian)
      - Saurischia
        - Theropoda indet.
        - Sauropoda
          - Titanosauria

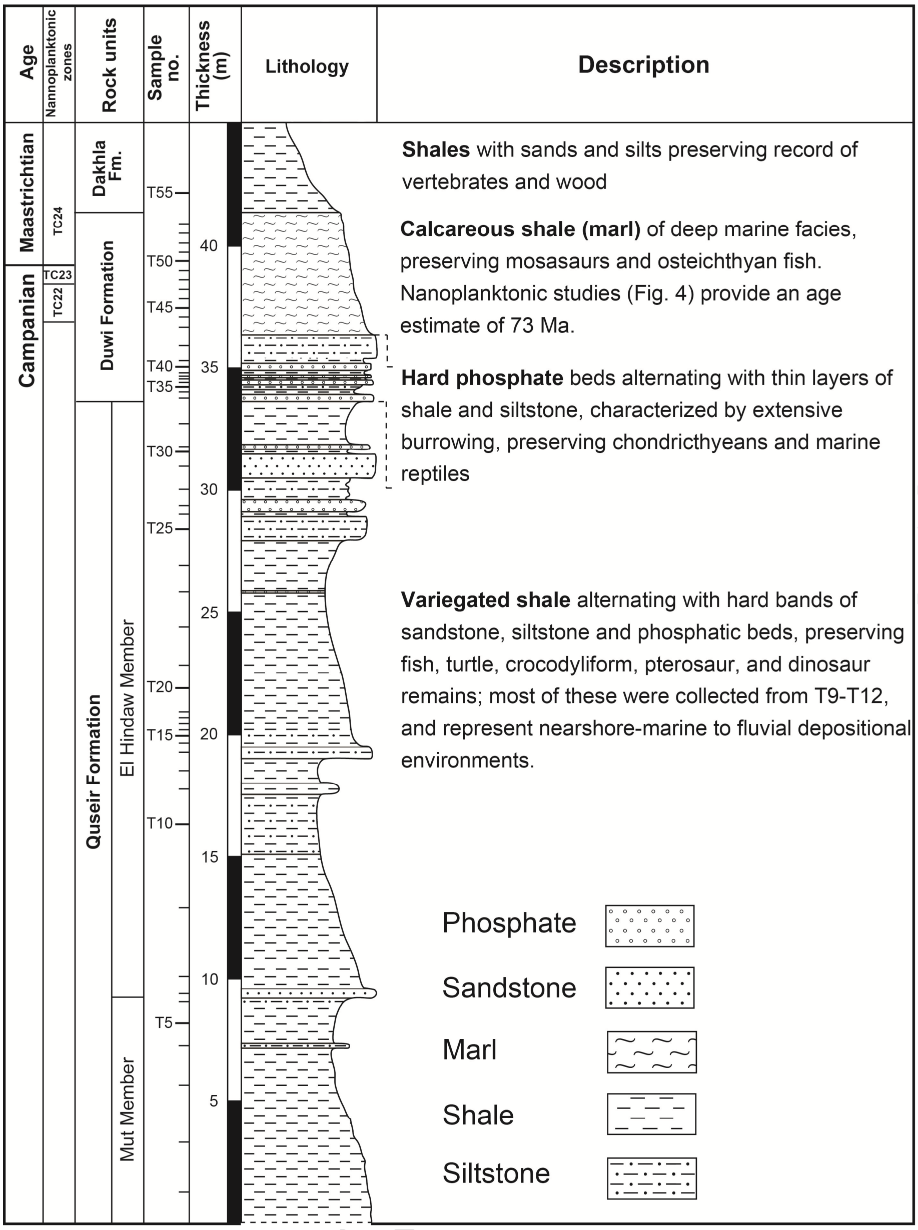
Duwi Formation

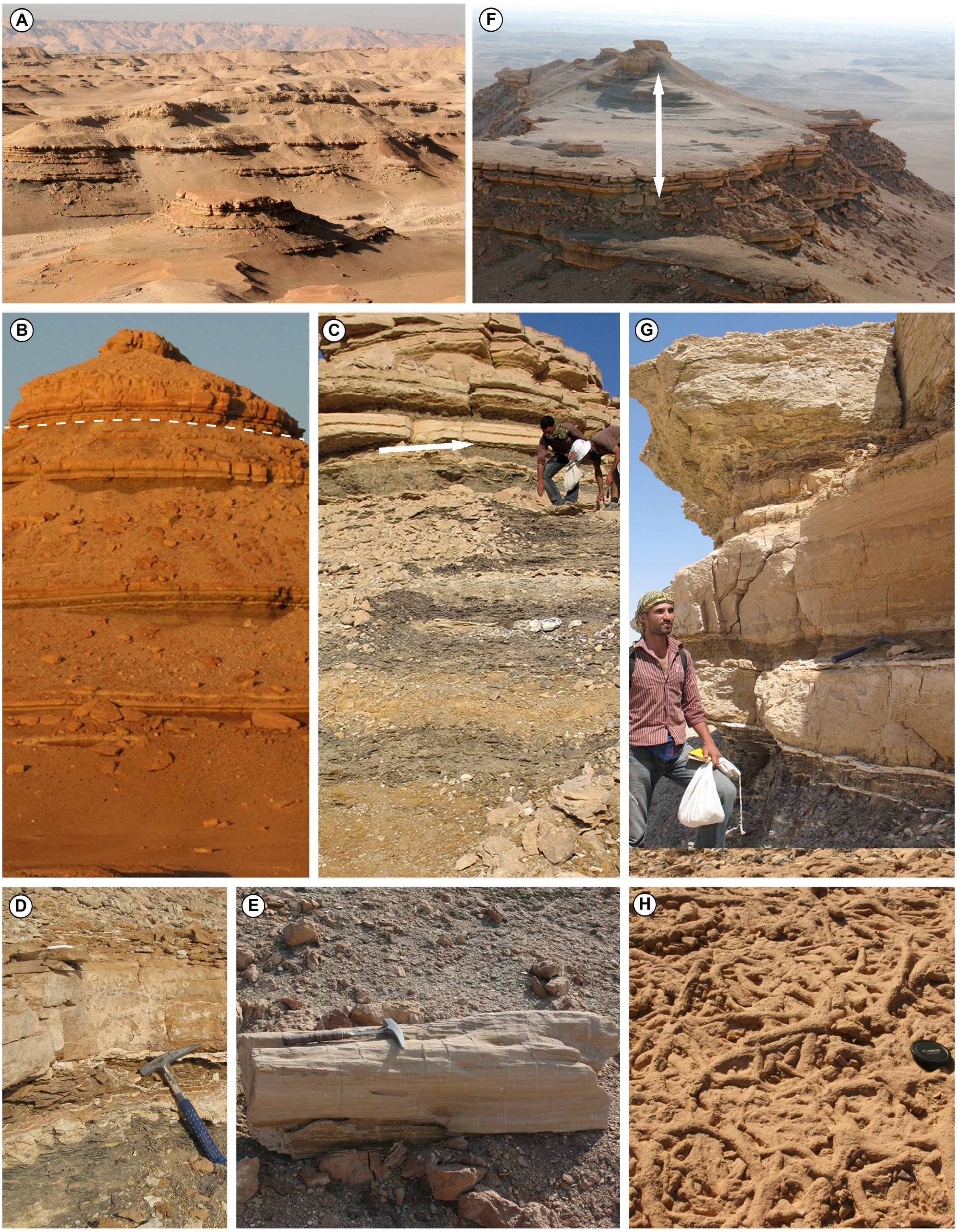
- Chondrichthyes
- Osteichthyes
- Actinopterygii
    - Teleostei
      - Saurodontidae
- Sauropsida
  - Sauropterygia
- Squamates
  - Mosasauridae
      - cf. Globidens

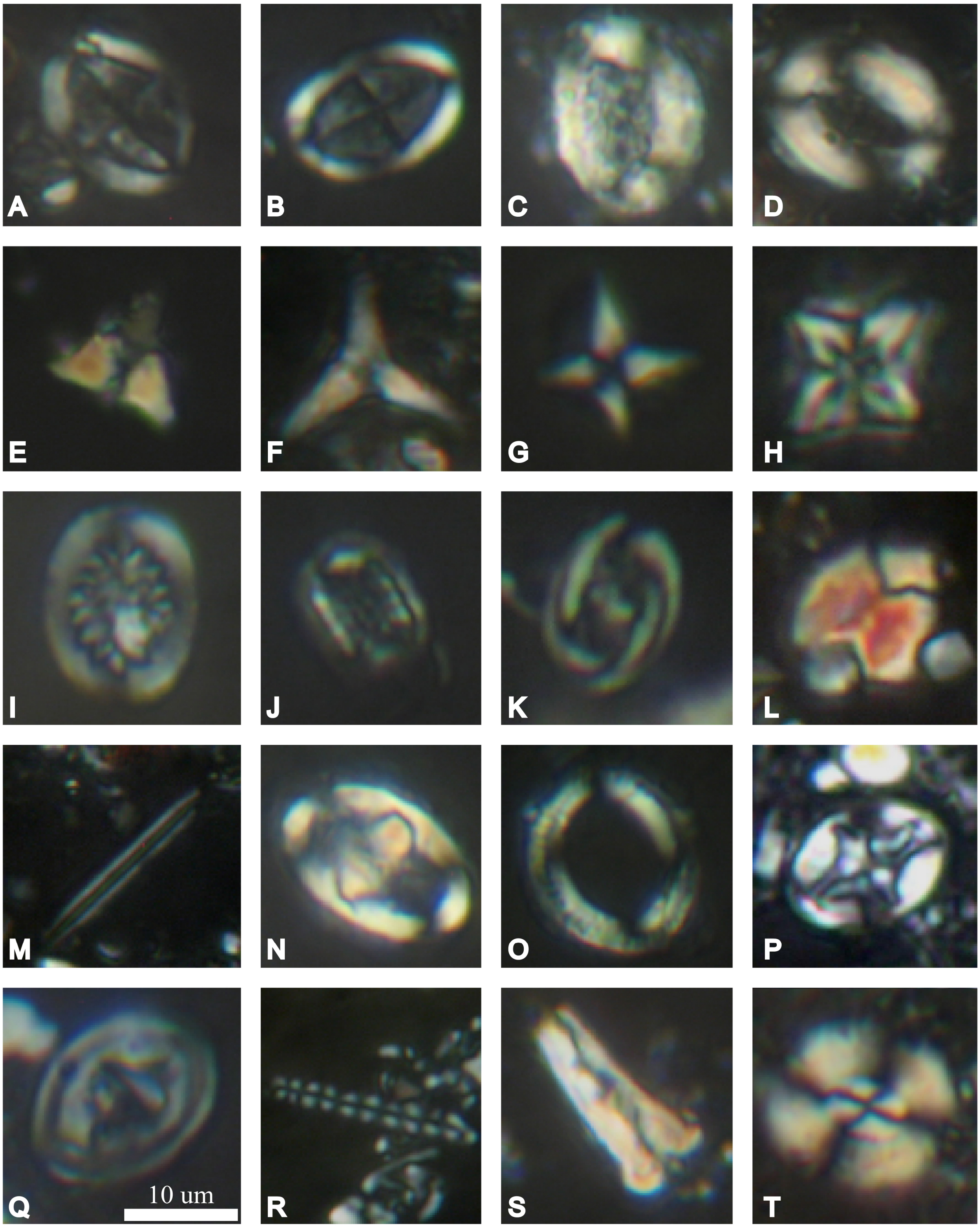
No.	Taxon name	Specimens/field of view
A	*Ahmuellerella octoradiata*	R
B	*Arkhangelskiella cymbiformis*	R
C	*Aspidolithus parcus constrictus*	R
D	*Calculithus obscurus*	R
E	*Ceratolithoides aculeus*	F
F	*Stradneria crenulala*	F
G	*Cribrosphaerella ehrenbergii*	R
H	*Eiffellithus eximius*	R
I	*Eiffellithus gorkae*	R
J	*Eiffellithus turriseiffelii*	R
K	*Glaukolithus diplogrammus*	R
L	*Lucianorhabdus cayeuxii*	F
M	*Microrhabdulus decoratus*	F
N	*Micula decussata*	R
O	*Petrarhabdus copulatus*	R
P	*Predscosphera cretacea*	R
Q	*Quadrum trifidum*	F
R	*Reinhardtites anthophorus*	F
S	*Reinhardtites levis*	R
T	*Rhagodiscus angustus*	F
U	*Tranolithus phacelosus*	R
V	*Watznaueria barnesae*	C
W	*Zeugrhabdotus pseudanthophorus*	R

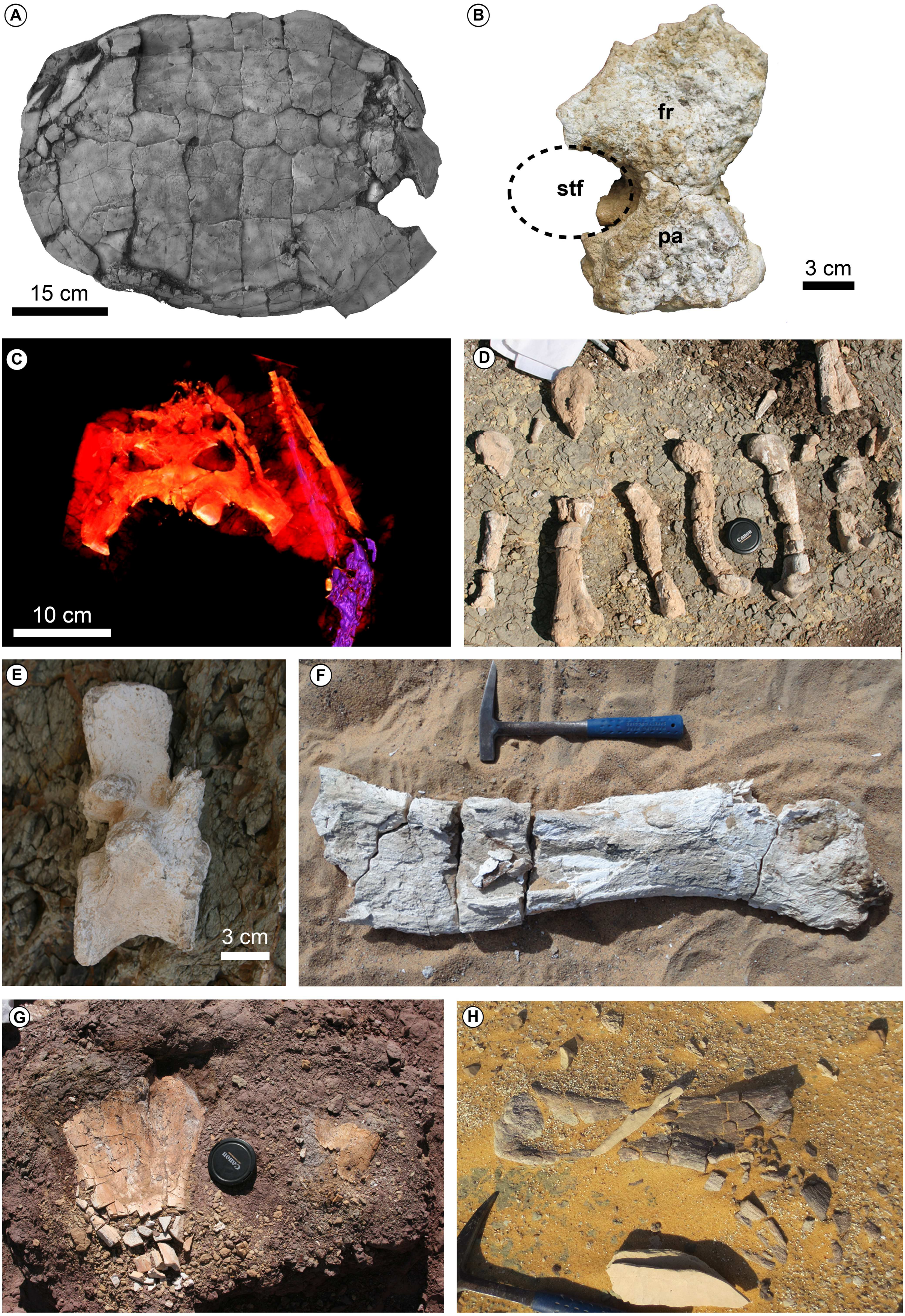


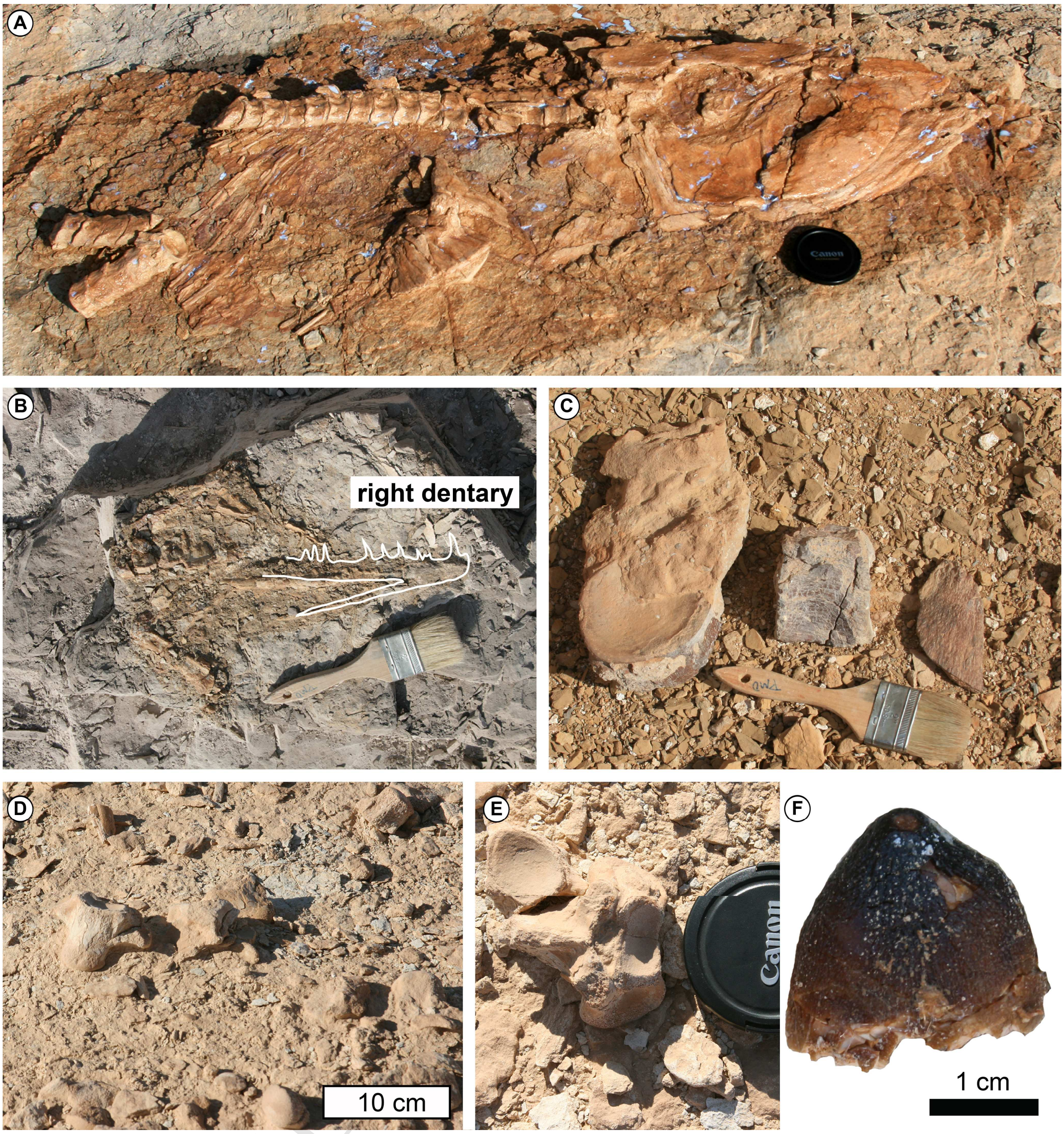
B
30°
26°
To Assuit
North
To Farafra
Abu Tartur Plateau
Mut
Tineida
Kharga
Baris
To Gilf El Kabir
25°
A
Mediterranean Sea
Cairo
Sinai
Bahariya Oasis
Egypt
Libya
Red Sea
Dakhla Oasis
Kharga Oasis
Baris Oasis
200 km
Sudan
Quaternary
Post-Cretaceous Deposits
Dakhla Fm.
Duwi Fm.
Quseir Fm.
Taref Fm.
Maghrabi Fm.
El Burg Fm.
Landmarks
Measured Section
25km


Age
Nannoplanktonic zones
Rock units
Sample no.
Thickness (m)
Lithology
Description
Maastrichtian
Campanian
TC24
TC23
TC22
Dakhla Fm.
Duwi Formation
Quseir Formation
El Hindaw Member
Mut Member
T55
T50
T45
T40
T35
T30
T25
T20
T15
T10
T5
40
35
30
25
20
15
10
5
Shales with sands and silts preserving record of vertebrates and wood
Calcareous shale (marl) of deep marine facies, preserving mosasaurs and osteichthyan fish. Nanoplanktonic studies (Fig. 4) provide an age estimate of 73 Ma.
Hard phosphate beds alternating with thin layers of shale and siltstone, characterized by extensive burrowing, preserving chondricthyeans and marine reptiles
Variegated shale alternating with hard bands of sandstone, siltstone and phosphatic beds, preserving fish, turtle, crocodyliform, pterosaur, and dinosaur remains; most of these were collected from T9-T12, and represent nearshore-marine to fluvial depositional environments.
Phosphate
Sandstone
Marl
Shale
Siltstone


A
F
B
C
G
D
E
H


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
10 um
R
S
T


A
15 cm
B
fr
stf
pa
3 cm
C
10 cm
D
E
3 cm
F
G
H


A
B
right dentary
C
D
10 cm
E
F
1 cm

Highlights

- Vertebrate paleontological work on Qusier and Duwi formations from the Late Cretaceous of Egypt
- The fossil bearing localities occur within the middle Campanian- early Maastrichtian
- New age constraints on the examined rock units based on nannofossil taxa
- Fossil remains include sharks, rays, actinopterygian and sarcopterygian fishes, turtles, and rare terrestrial archosaurians, including dinosaurs and crocodiles