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MANGROVE-DWELLING CRABS (DECAPODA: BRACHYURA: NECROCARCINIDAE) ASSOCIATED WITH DINOSAURS FROM THE UPPER CRETACEOUS (CENOMANIAN) OF EGYPT

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ABSTRACT—Brachyuran decapods (crabs) are rarely preserved in coastal environments and have not been documented in close association with dinosaur fossils. A crab referable to the Necrocarcinidae Förster, 1968, is here described from the Cenomanian Bahariya Formation, Bahariya Oasis, Egypt. The occurrence of a crab in a mangrove setting in association with terrestrial vertebrates is extremely unusual in the fossil record. Review of decapod occurrences from the region has resulted in placement of *Portunus* sp. of Roger (1946) within the Raninidae de Haan, 1839, and *Lophoraninella cretacea* (Dames, 1886) into the Galatheoidea Samouelle, 1819. The crabs of the Bahariya Formation were probably scavengers, feeding on vegetation and other organic material and were possibly a food source for fish and other vertebrates and invertebrates in the environment.

INTRODUCTION

Brachyuran decapods (crabs) from coastal habitats are rarely preserved in the fossil record, largely due to the rapid disintegration of the animals caused by decomposition and scavenging as well as the limited potential for burial. Crabs form an important component of the food chain in modern marine ecosystems and may have played an important role in marine environments as early as the Jurassic, when crabs are first known with certainty in the fossil record (Glaessner, 1969). The material described here provides rare documentation of crabs from a paralic, vegetated ecosystem interpreted as a low energy, mangrove coast, dominated by the tree fern *Weichselia reticulata* (Stokes and Webb) Fontaine (see note under Systematic Paleontology). It is thought to have been ecologically similar to modern mangrove habitats (Dominik, 1985; Lacovara et al., 2000; Smith et al., 2001). The unit preserving the crabs has also yielded chondrichthyans, osteichthyans, turtles, plesiosaurs, squamates, crocodyliforms, dinosaurs, various invertebrates, and plants (Stromer, 1915, 1931, 1932, 1934, 1936; Weiler, 1935; Werner, 1989; Lejal-Nicol, 1990; Lejal-Nicol and Dominik, 1990; Smith et al., 2001), and thus provides detailed information regarding this coastal ecosystem. Only anecdotal evidence has been reported of decapods associated with dinosaurs and other terrestrial animals, and in those cases, the decapods were lobsters and ghost shrimp (Gallagher et al., 1986; Gallagher, 1993; Kuehne, 1993). Heckert et al. (1999) reported a decapod associated with dinosaurs in Triassic deposits of New Mexico; however, those fossils do not appear to be decapods (R. M. Feldmann, personal commun.). Thus far, no confirmed crabs have been reported associated with dinosaur fossils.

Relatively few fossil decapods are known from the Middle East and it appears that no Cretaceous decapods have been reported from Egypt. Late Cretaceous decapods in Syria, Lebanon, and Israel have been collected from fish-rich shales, similar to the occurrence of the material reported here (Glaesser, 1945; Roger, 1946; Remy and Avnimelech, 1955; Förster, 1968; Larghi and Garassino, 2000). Some of these decapods have been referred to genera within the Necrocarcinidae (Larghi and Garassino, 2000). The preservation of these specimens is generally similar to that of the new Egyptian material; the decapods are flattened and poorly preserved as carbonized and oxidized material.

The remainder of the decapod occurrences from the region are Eocene in age. Nötling (1885) and Lőrenthey (1909) described Eocene decapod faunas from Egypt, and Collins and Morris (1973), Anderson and Feldmann (1995), and Collins et al. (1999) have reported Eocene brachyurans from North Africa, all of which were collected from carbonate rocks. The previously reported Cretaceous faunas are dominated by macruran decapods (shrimp and lobsters) and primitive podotreme crabs, while the Eocene faunas are dominated by more derived heterotreme crabs. This may reflect environmental differences as well as the decline of macrurans and the radiation of the heterotreme brachyurans during the Tertiary (Glaessner, 1969; Schram, 1986; Schweitzer, 2001b; Schweitzer et al., 2002).

STRATIGRAPHIC AND DEPOSITIONAL SETTING

Crab fossils were found within the lowest portion of the exposed Bahariya Formation in a blue-gray indurated shale. The decapod remains were located between 0.5 and 3.0 m from a titanosaurian sauropod dinosaur caudal vertebra. Lenticular and wavy bedding within the shale indicate deposition by tidal currents. Detrital plant leaves and stems are common in this lithosome. The underlying unit is a loosely consolidated sand and mud with flaser-bedding and subvertical rhizoliths. Separating the units is an iron-concreted mangrove paleosol containing many horizontal rhizoliths that form a laterally extensive fossilized root mat.

The succession of environments began with a tidal channel colonized by mangrove vegetation, including *Weichselia* (Table 1). The developing mangrove soil was buried by an aggrading mud flat, which also buried crab, plant, and dinosaur remains. Finally, mangrove vegetation recolonized the area and the overlying soil developed.

The tidal flat facies containing crab fossils is part of a depositional setting we interpret as a low-energy, mangrove coast, situated along the southern shore of the Tethys Sea. In analogous modern mangrove settings often dominated by *Rhizophora* or *Avicennia*, mud-dwelling portunid, grapsid, sesarmid, and ocypodid crabs, predominantly of the genera *Scylla*, *Cardisoma*, *Sesarma*, *Uca*, and *Ucides*, are ubiquitous (Jones, 1984; Smith et al., 1989; Tan and Ng, 1994; Keenan et al., 1998; Hogarth, 1999; Ellison and Farnsworth, 2001).

SYSTEMATIC PALEONTOLOGY

Note.—The authorship of *Weichselia reticulata* has been difficult to verify. The original paper in which the trivial name was

TABLE *1*—Description of stratigraphic section from which crabs were collected. * denotes unit with crab fossils.

Thickness	Unit	Description	Environment
0.05 m	Iron-concreted paleosol	Root mats and wood fragments	Mangal
*1 m	Mud	Lenticular to wavy bedding; crabs, dinosaur vertebra, leaf impressions	Tidal flat (low energy)
0.07 m	Iron-concreted paleosol	Root mats and wood fragments (*Weichselia*)	Mangal
1.5 m	Sand and mud	Flaser bedding	Tidal channel (moderate energy)

introduced has been considered to have been written by Stokes and Webb (1824). That manuscript bears no mention of those two authors; neither are they listed anywhere in the volume as verified by reference experts at the Kent State University and Ohio State University libraries. Further, Seward (1894), who definitively catalogued Wealden floras to that time, was also unable to verify the initials of these two authors and notes that their names did not occur in the title of their paper (p. 171). Thus, the first initials of Stokes and Webb are unknown, and the derivation of these two people as the author is enigmatic. We have followed Alvin (1971) in the authorship for *Weichselia reticulata*.

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily CALAPPOIDEA H. Milne Edwards, 1837

Discussion.—The Necrocarcinidae was referred to the Calappoidea by Schweitzer and Feldmann (2000) based largely upon carapace shape and ornamentation. However, necrocarcinids have long slender appendages, while calappids do not. At least one family within the Dorippoidea, the Dorippidae, has very long second and third pereiopods and short first pereiopods (Holthuis and Manning, 1990), as do necrocarcinids with preserved appendages. Some extant dorippoids inhabit mangrove habitats as well (Tan and Ng, 1994). It seems possible that the Necrocarcinidae may be better referred to the Dorippoidea; however, formalization of that transfer must await examination of better-preserved material.

Family NECROCARCINIDAE Förster, 1968

Discussion.—The material reported here is poorly preserved but is referred to the Necrocarcinidae for several reasons. Roger (1946) reported several macruran and anomuran decapods from the Upper Cretaceous (Cenomanian) fish-beds of Lebanon. He also described several brachyurans, including *Geryon hadjoulae* Roger, 1946 (Geryonidae, Colosi, 1923). Larghi and Garassino (2000) subsequently referred *G. hadjoulae* to *Orithopsis* Carter, 1872, within the Necrocarcinidae, and illustrated additional material from Cenomanian deposits in Lebanon (fig. 1). Remy and Avnimelech (1955) described a necrocarcinid crab from Campanian rocks of Israel, and Förster (1968) described several genera assignable to the Necrocarcinidae from the Cenomanian fish-beds of Lebanon. In addition, the preservational style of the new material is nearly identical to that of material described and illustrated by Roger (1946) and Larghi and Garassino (2000). Thus, it seems overwhelmingly likely that the Egyptian material is also of necrocarcinid crabs.

Although little is known about necrocarcinid appendages, they are well-preserved in the Lebanese material described by Roger (1946) and Lebanese material illustrated by Larghi and Garassino (2000). The appendages and their individual articles in the Egyptian material described here are longer than those of the Lebanese material illustrated by Larghi and Garassino (2000). This is most readily observable in the dactyls, which are three to four times as long in the Egyptian material as in the Lebanese material. Necrocarcinid crabs, including the Lebanese material, have small first pereiopods and chelae and long third maxillipeds, where known, as do the new specimens from Egypt. Although the length of the appendages differs somewhat, the possession by necrocarcinids of short first pereiopods and mani and long second and third pereiopods makes referral of the Egyptian material to the Necrocarcinidae the most parsimonious action until more and better preserved material is collected.

Members of the Majoidea Samouelle, 1819, are also characterized by possession of extremely elongate pereiopods 2–5, elongate dactyls of the pereiopods, short first pereiopods as compared to the length of the other pereiopods, and an elongate, well-ornamented carapace (Rathbun, 1925; Sakai, 1976). The material described here possesses these features. However, modern majoids do not inhabit mangrove-like environments, possibly because they cannot tolerate low salinities (P.K.L. Ng, personal commun.).

Paguroids, or hermit crabs, often have elongate pereiopods and dactyli of pereiopods; however, the fossil record of this group is known primarily from the major and minor chelae of the first pereiopods and in only rare cases (e.g., Schweitzer and Feldmann, 2001) are other pereiopods known. The dorsal carapace, as far as is known to the authors, has never been described from the fossil record. Thus, the possibility of these fossils belonging to the Paguroidea seems remote, especially since the dorsal carapace is preserved in one of the Egypt specimens, several minor pereiopods are preserved in three specimens, and a chela is preserved in only one.

Galatheoids, an anomuran group, have an elongate carapace and can have elongate appendages. However, the appendages of these animals are rarely preserved, and if they are, they are usually fragmentary. The only reasonably intact galatheoid appendages known to the authors are currently under study by one of us (CES). The first chelate pereiopods of galatheoids are long and often much longer than the remainder of the pereiopods. This condition is not seen in the new specimens, in which the last pereiopod is much longer than the first.

Modern mangrove habitats are populated with large numbers of grapsid, sesarmid, and ocypodid (fiddler) crabs (Hogarth, 1999) and a limited number of dorippid crabs (Tan and Ng, 1994). However, the former three groups have appendage morphologies that immediately exclude the Egyptian material from them. Within the Grapsidae MacLeay, 1838, the appendages are short, with broad meri and short dactyli. Within the Ocypodidae Rafinesque, 1815, the appendages are short, and the major cheliped is enormous, often much larger than the body of the animal. Thus, the fossils are clearly excluded from either of these two families. A small number of genera belonging to the Portunidae Rafinesque, 1815, inhabit modern mangrove settings (Warner, 1977; Hogarth, 1999); however, portunid crabs are wider than long, have appendages of relatively short or moderate length and have broad and typically paddle-like dactyls on the appendages. The new material exhibits none of these and is therefore not referable to the Portunidae.

Members of the Homolodromiidae Alcock, 1899, and Homolidae de Haan, 1839, have elongate appendages and are known from Cretaceous records. However, it seems unlikely that the material belongs to either group. Members of the Homolodromiidae have extremely elongate dactyls on the second and third pereiopods, but the fourth and fifth are reduced and chelate. There is no evidence of chelae other than on the first pereiopod in the new material and the elongate appendages appear to be the posteriormost appendages, either the fourth or fifth pereiopod. The chelae of the first pereiopods of homolodromiids are slender and small, unlike the stout chelae preserved in the new material. Both fossil and Recent records of the Homolodromiidae are from sandy, shallow to deep-water, tectonically active settings (Feldmann and Wilson, 1988; Guinot, 1995), clearly very different from the environment in which the new fossils were recovered. Within the Homolidae, the appendages are elongate, but the dactyls are as long as or shorter than the other individual elements of the appendages; the dactyls of the new material are much longer than any other single appendage element. Additionally, fossil as well as Recent homolids primarily inhabit deep water settings (Guinot and Richer de Forges, 1995; Schweitzer, 2001a); however, some fossil homolids inhabited shallow and epicontinental seas (Collins, 1997). Thus, environmental preference cannot be used as the only factor to exclude the fossils from the Homolidae.

Members of the Raninidae de Haan, 1839, exhibit an elongate carapace. However, the appendages of raninid crabs are short and typically have dorso-ventrally flattened elements, unlike the appendages in the new material. In addition, the chelae of raninid crabs are often unusually shaped, displaying a fixed finger positioned nearly perpendicular to the manus. The new material exhibits a fixed finger than extends straight distally from the manus, thus making the overall morphology of the chela very different from raninid chelae.

Glaessner (1945) described several decapod taxa from Cretaceous, fish-rich beds of Syria. Most of that material belongs to macruran taxa; however, the new material is not referable to any of those taxa. Based upon the morphology of the chela and appendages and the orientation of the appendages with respect to the carapace, the new material is not referable to any macruran groups and must be a brachyuran. On examination, a specimen (MB.A.229a, b) of the single brachyuran reported by Glaessner (1945), *Lophoraninella cretacea*, deposited in the Museum für Naturkunde Berlin Paläontologisches Museum, Humboldt-Universität zu Berlin, likely belongs to the Galatheoidea, which are typified by transversely-ridged ornamentation on the dorsal carapace. This feature does not appear to be present on the new material.

Portunus sp. was reported by Roger (1946); however, examination of that material (RO3873) deposited in the Muséum National d'Histoire Naturelle, Paris, indicates that it is referable to the Raninidae, a group that cannot accommodate the Bahariya material as discussed above. Specimen RO3873 exhibits an elongate carapace and a markedly elongate buccal cavity, typical of all raninids and not typical of *Portunus* or any other portunid crabs. Remy and Avnimelech (1955) described a lobster-like macruran decapod, which has subsequently been referred to the Stomatopoda Latreille, 1817, the mantis-shrimps (Hof, 1998).

Genus and species indeterminate
Figure 1

Description.—Carapace very poorly preserved, small, approximately 7.4 mm long and 4.5 mm wide. Third maxillipeds appear longer than wide. Chela of first pereiopod stout; manus about as long as high, outer surface coarsely granular; fixed finger narrowing markedly distally, with triangular teeth on occlusal surface; movable finger narrowing distally, with triangular teeth on occlusal surface; first pereiopod much shorter than other appendages. At least 2 pereiopods other than first preserved, probably pereiopods 2 and 3; each extremely elongate, longest 25.2 mm total length; basis and merus of longest appendage 7.6 mm long, merus much longer than high; carpus and manus of longest appendage 8.8 mm long, manus much longer than high; dactyl 8.8 mm long, very much longer than high; articles of pereiopods appear finely granular.

Material examined.—The specimens, CGM 81126–81128, are deposited in the Egyptian Geological Museum, Cairo, Egypt.

Occurrence.—Specimens were collected from Upper Cretaceous (Cenomanian) rocks of the Bahariya Formation (See Ball and Beadnell, 1903; Dominik, 1985; Lacovara et al., 2000), Bahariya Oasis, Egypt, about 320 km southwest of Cairo (Fig. 2). The material was collected from locality BDP 2001–13 (28°26.412′N, 28°55.935′E), 1.2 km north-northeast of the type section of the Bahariya Formation at Gebel el Dist (Stromer, 1914).

Discussion.—The three specimens upon which the description is based have been flattened and altered into an iron oxide which rapidly disintegrates upon contact. Few of the original fine structures of the carapace or appendages are observable; however, the outline of the appendages is clear. It is probable that the long pereiopods are the second and third which, are long in necrocarcinids; the fourth and fifth pereiopods in necrocarcinids are small and carried dorsally (C. Larghi, personal commun.). Unfortunately, there is no evidence of the fourth and fifth pereiopods in the fossils. The extremely long appendages and dactyls are distinctive and presumed to be diagnostic for this animal; thus, fossils collected in the future can easily be compared to this material as long as appendages are preserved.

DISCUSSION

Crabs have not previously been reported closely associated with dinosaurs. Additionally, the observation of fossil crabs in a mangrove depositional setting is unusual; occurrences include early middle Miocene decapods from Japan (Karasawa, 1992, 1993; Karasawa and Inoue, 1992), and Quaternary sub-fossils (Idris, 1989). Pleistocene decapods from Guam were possibly preserved in a mangrove setting (Kesling, 1958). Crabs that inhabit coastal habitats, e.g., ocypodes, grapsids, and majoids, are rarely preserved as fossils because of their susceptibility to mechanical disarticulation and scavenging by other animals. The preservation of crabs in Bahariya sediments suggests rapid burial in quiescent conditions. The tidal couplets in which the crabs were buried indicate an accumulation rate of about 8 mm per tidal cycle, or 1.6 cm per day, assuming semidiurnal tides. Additionally, the fine sediment size suggests deposition by slow-moving currents. These conditions probably allowed the gentle burial of these small crabs within a 24-hour period, providing a rare opportunity for their preservation in an environment in which they are seldom recorded.

The Bahariya Formation records a highly productive Cenomanian coastal ecosystem, populated by a number of very large tetrapod species (Smith et al., 2001) that would have required a substantial trophic base. Crabs are an important part of the modern marine food web (Warner, 1977) and are eaten by fish and other invertebrates such as octopi. Crabs and other decapods provide a large amount of nutrition, especially protein, relative to their size; thus, the crabs in the Bahariya ecosystem may have served as an important food source for larger invertebrates, fish, turtles, and perhaps small terrestrial vertebrates inhabiting the area. Weiler (1935) reported that the fish fauna of the Bahariya Formation was dominated by benthic species with dentition suitable for grating or grinding; thus, they would have been well adapted to eating crabs. It is not hard to imagine that small terrestrial vertebrates, perhaps even juvenile or small dinosaurs, used the crabs as an important food resource.

Additionally, modern mangrove-dwelling crabs are important detritivores in that biome. Sesarmid crabs, for example, directly consume 30–80 percent of fallen plant material in most mangrove forests (Robertson et al., 1992). In addition to consuming leaf

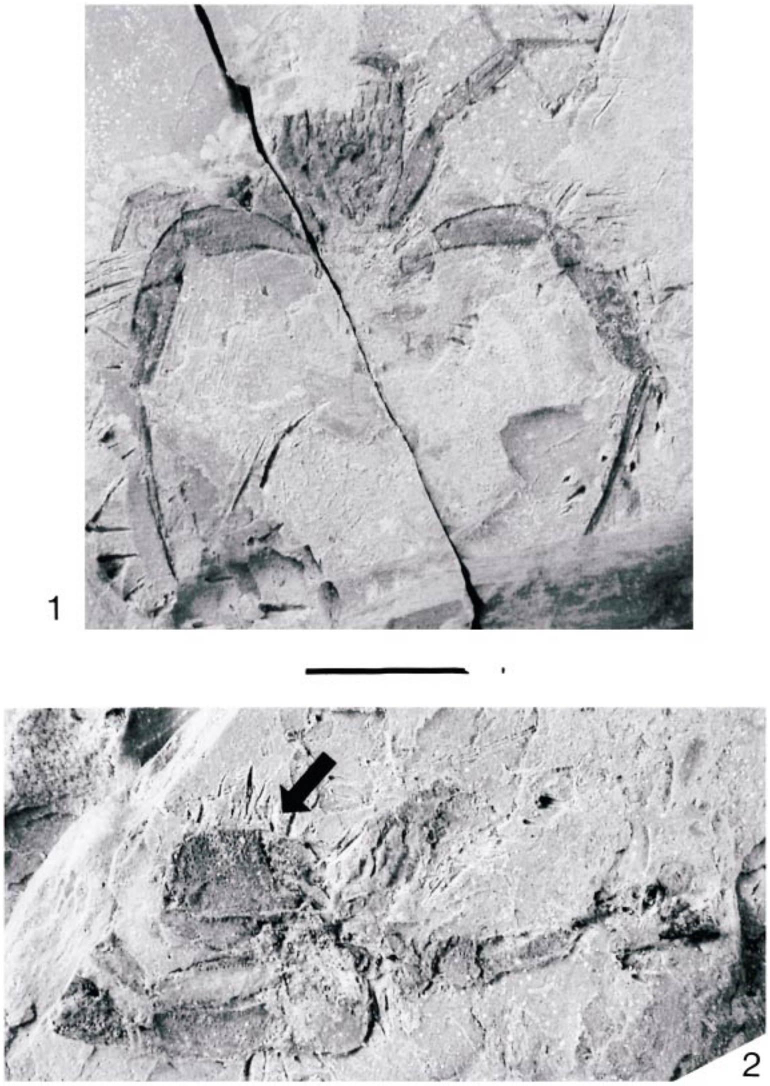

FIGURE *1*—Brachyuran crab referred the Necrocarcinidae. *1,* CGM 81126, posterior portion of carapace with what appear to be the fourth and fifth pereiopods. Note extreme length of pereiopods and dactyls of fifth pereiopods, indicated by arrows. *2,* CGM 81127, fragmented carapace and first pereiopod with major chela indicated by arrow. Scale bar equal to 1 cm.

litter and propagules, grapsoid crabs also browse directly on mangrove vegetation (Warner, 1967; Beever et al., 1979; Farnsworth and Ellison, 1991). Modern mangrove roots provide habitat for burrowing crabs, which in turn oxygenate and nutrify the peaty substrate (Smith et al., 1991; Ellison and Farnsworth, 2001).

The crabs in the Bahariya environment were probably feeding on abundant vegetation or through extraction of organic material from the muddy bottom. The crabs could have been using the vegetation not only as a food source, but also as a means of camouflage; for example, dorippid crabs that inhabit modern mangroves carry leaves over their back as camouflage (Ng and Tan, 1986; Ng, 1987). The proximity of vertebrate fossils to the crab fossils suggests that they may also have scavenged vertebrate carcasses. The extremely elongate appendages of the Bahariya crabs may have facilitated walking on vegetation, mud, or possibly both, by distributing the body weight over a broad surface area (Warner, 1977). Bahariya Formation mangrove paleosols contain many rhizoliths in addition to leaves and stems, which could have provided abundant habitat for Cenomanian crabs. Like their modern counterparts, these paleosols are heavily burrowed, probably in part due to the activity of crabs. As is the case for modern mangrove-dwelling crabs, necrocarcinids may have played a key role in the development and maintenance of the Cretaceous mangrove biome.

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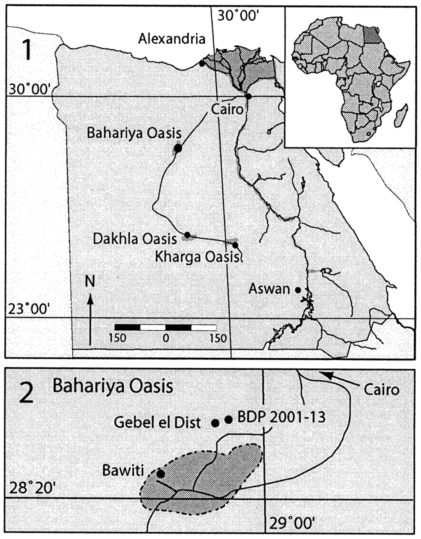

FIGURE 2—*1*, location of the Bahariya Oasis in the Western Desert of Egypt, approximately 320 km southwest of Cairo. *2*, Location of BDP 2001–13 in relation to Gebel el Dist and Bawiti. (Modified from Smith et al., 2001.)

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