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**KARKAEMYS ARABICUS, A NEW SIDE-NECKED TURTLE
(PLEURODIRA, BOTHREMYDIDAE) FROM THE UPPER CRETACEOUS
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IYAD S. ZALMOUT¹, HAKAM A. MUSTAFA², AND JEFFREY A. WILSON¹

Abstract—A new fossil vertebrate locality from Jordan has yielded the first diagnostic turtle from the Cretaceous of the northeastern Arabian Peninsula. This fossil provides new information about the history and paleobiogeographic distribution of the side-necked turtles (Pleurodira). *Karkaemys arabicus*, n. gen. et sp., is described from the Upper Cretaceous (uppermost Santonian) Wadi Umm Ghudran Formation of central Jordan. *Karkaemys* is known from a nearly complete skull, plastron, and partial hindlimb, and displays synapomorphies of Pleurodira that include the presence of a trochlear process on the pterygoid and fusion of the pubis and ischium to the plastron. Comparisons with other Cretaceous pleurodires indicate that *Karkaemys* is a bothremydid sharing close affinities to *Zolhafah bella* and *Bothremys cooki* from the Late Cretaceous of Egypt and of North America, respectively.

INTRODUCTION

Late Cretaceous paleolatitudinal and sea level changes produced marine carbonate deposits in basins on the northern margin of the Arabian Peninsula (Bender, 1968, 1974). These nearshore littoral deposits have preserved a wealth of selachian remains and fragmentary reptilian remains (Mustafa et al., 2002). The latter indicate the presence of both squamates (Mosasauridae) and archosaurs (Pterosauria, Crocodylomorpha, Dinosauria) but are too fragmentary to elucidate lower-level relationships, precluding detailed paleobiogeographic comparisons between the Arabian Peninsula and neighboring areas.

We report here on the first diagnostic and well preserved reptilian remains from Mesozoic rocks of Jordan (Fig. 1), which pertain to a new side-necked turtle (Pleurodira) that is represented by a nearly complete skull associated with a plastron, caudal vertebrae, partial pelvis, and partial hindlimb. Characteristics of the skull and plastron allow attribution of this new taxon to the pleurodire subgroup Bothremydidae. Below we provide a brief review of the fossil vertebrates of Jordan and the distribution of Mesozoic bothremydids to provide a context for description and interpretation of this new turtle.

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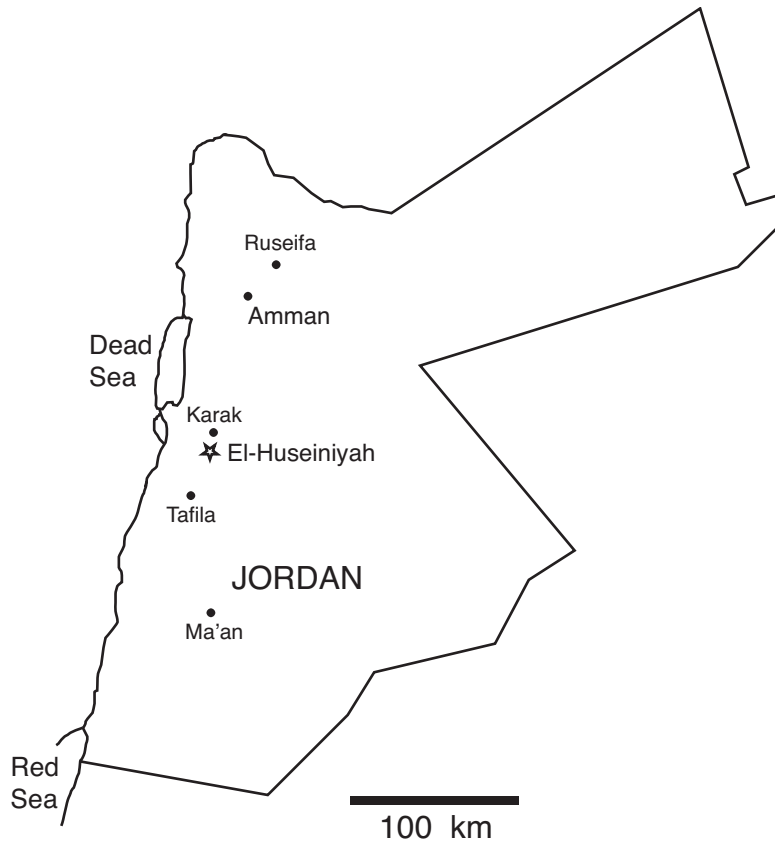


FIG. 1 — Map of Jordan showing the Huseiniyah locality (star), where the holotypic specimen of *Karkaemys arabicus* was collected.

Cretaceous Vertebrates of Jordan.— The record of the Cretaceous vertebrates of Jordan is dominated by selachians, many of which have been recovered from phosphatic beds of the Ruseifa area (Fig. 1). In addition to well-preserved teeth of sharks and rays, the Ruseifa area has occasionally produced tetrapod remains. These include mosasaurid teeth (Avnimelech, 1949) and remains of a large pterosaur (Arambourg, 1953). The mosasaurid material was not named, but Arambourg (1959) described the pterosaur as *Titanopteryx philadelphiae*, based on a supposed metacarpal that was later identified as a cervical vertebra (Lawson, 1975). *Arambourgiania* was later suggested as a replacement generic name for the preoccupied *Titanopteryx* (Nessov and Yarkov, 1989). Arambourg's original materials were long thought lost, but Martill et al. (1998) rediscovered and rescribed the holotype of *Arambourgiania*, and Frey and Martill (1996) described additional pterosaur material found at the same phosphate mine. Other indeterminate plesiosaur, mosasaur, and crocodylomorph teeth were also recorded from the Ruseifa mine (Signeux, 1959). Martill et al. (1996) described a limb bone fragment that, if correctly identified as an ornithomimid tibia, represents the only dinosaur remain described from Jordan. Mustafa and Zalmout (1999) and Bardet and Pereda-Suberbiola (2002:837) reviewed the marine reptile teeth from the Late Cretaceous phosphates of Jordan, concluding that they resemble teeth from the latest Cretaceous of Syria and are generally comparable to the marine reptile fauna of the southern margin of Mediterranean Tethys.

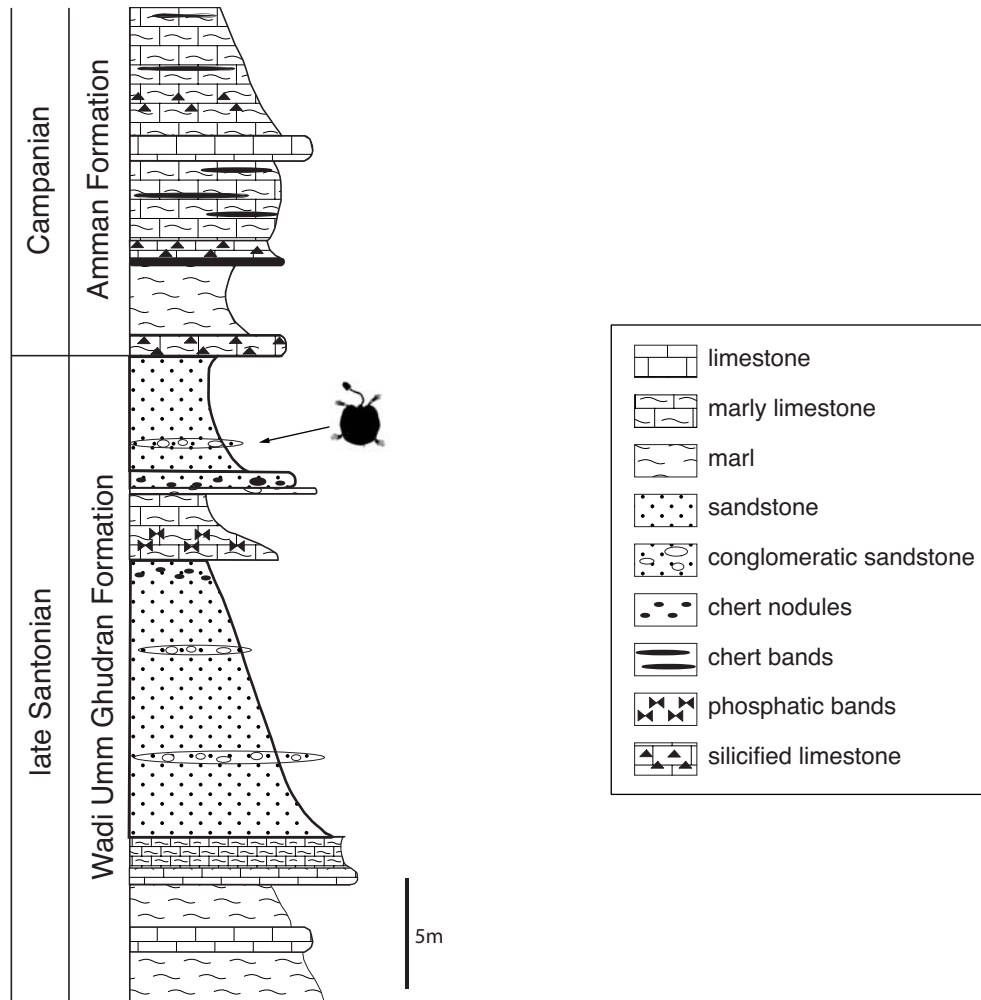


FIG. 2 — Stratigraphic section at the Huseiniyah locality. *Karkaemys arabicus* and other vertebrate remains were collected 3-4 m below the top of the Wadi Umm Ghudran Formation. The exact stratigraphic level is marked by the turtle icon (based on Meylan, 1996: fig. 1).

In addition to the Ruseifa phosphate mine, there are many new localities distributed in northern, central, and eastern Jordan that hold potential for yielding Cretaceous and early Tertiary fossil vertebrates (e.g., Mustafa and Zalmout, 1999, 2000a, 2000b; Cappetta et al., 2000; Mustafa, 2000; Zalmout, et al., 2000; Zalmout and Mustafa, 2001; Mustafa et al., 2002). The new side-necked turtle described here was excavated at one of these, the Huseiniyah locality, which is located 19 km south of Karak and about 105 km south of Amman (Fig. 1). The Huseiniyah locality is positioned stratigraphically at the top of the Wadi Umm Ghudran Formation (Mustafa et al., 2002), which caps the massive limestone of the Wadi Es Sir Formation (Parker, 1970) and reaches a thickness of 40 m in north and central Jordan (Fig. 2). The Wadi Umm Ghudran Formation contains vertebrate-bearing sandstones (Mustafa et al., 2002) that reach a thickness of 12 m but are less than 50 cm thick in some places. Similar sandstone bodies are also found in neighboring areas in southern Jordan (e.g., Tafila, Ma'an; Fig. 1). Koch (1968) interpreted the upper part of

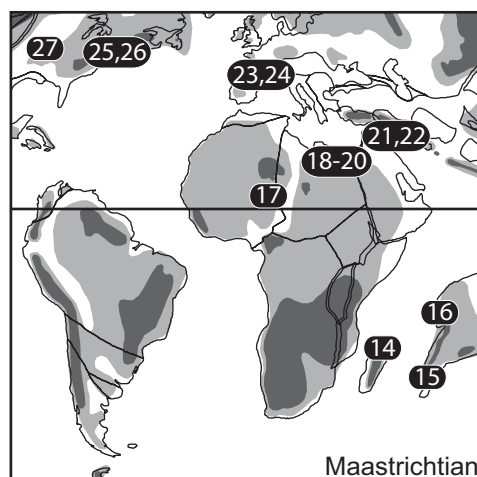
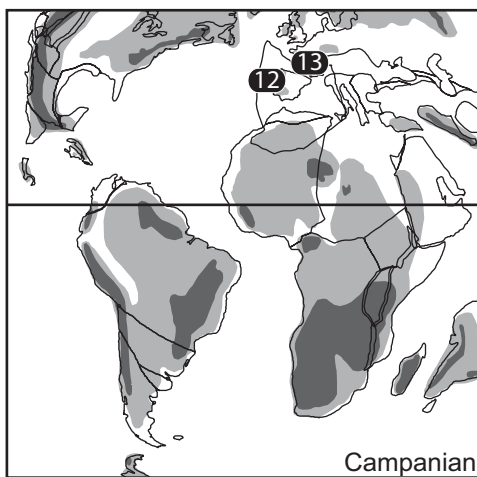
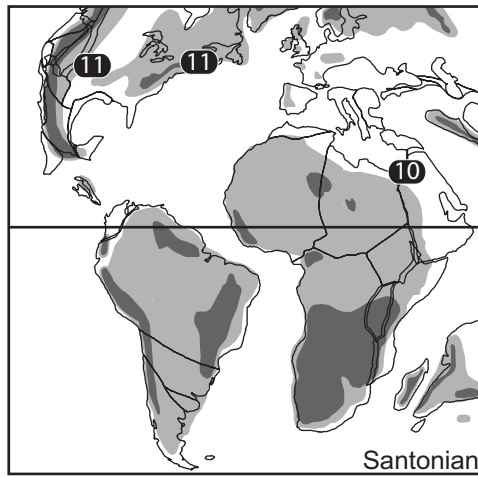
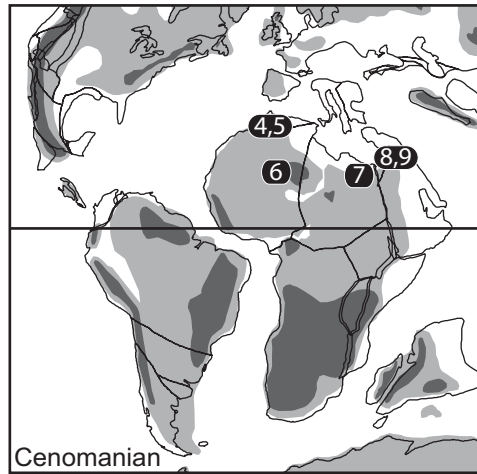
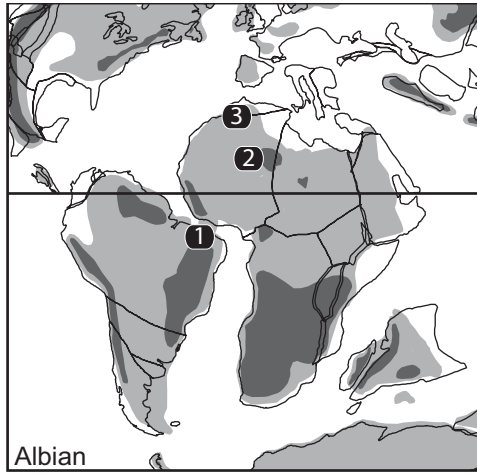
the Wadi Umm Ghudran Formation to be Santonian in age based on the presence of *Globotruncana concavata*.

Mesozoic bothremydids.—Living turtles include two main lineages, the “side-necked” Pleurodira and the “hidden-necked” Cryptodira, which retract their necks either horizontally or vertically, respectively (Gaffney, 1975b; Wood, 1984). Pleurodires are currently restricted to the southern continents (Australia, sub-Saharan Africa, South America, Madagascar, Seychelles), although they were more broadly distributed during the Mesozoic. The two pleurodire lineages, Chelidae and Pelomedusoides, diverged prior to the Early Cretaceous (Gaffney et al., 1991). Chelidae first appeared in the Late Cretaceous of Argentina (*Yaminuechelys gasparinii*; de la Fuente et al., 2001; *Prochelidella portezuelae*, and *Portezueloemys patagonica*, de la Fuente, 2003), and currently includes 40 species distributed amongst 10 genera (Iverson, 1992) that are restricted to South America and Australia. Pelomedusoides first appeared in the Early Cretaceous of Brazil (Lapparent de Broin, 2000; Gaffney et al., 2001) and currently includes 25 species in 5 genera that are widespread in Africa and South America (Iverson, 1992). There are three pelomedusoid lineages, Podocnemidae, Pelomedusidae, and Bothremydidae, the latter of which has been informally subdivided into the *Bothremys* group, *Nigeremys* group, and *Taphrosphys* group (Lapparent de Broin and Werner, 1998), terminology that we adopt here.

The eponymous bothremydid species, *Bothremys cooki*, was described by Leidy (1865) on the basis of a skull and lower jaw collected from Upper Cretaceous sediments of New Jersey, U.S.A (Fig. 3). Leidy (1856) also described as “*Platemys*” *sulcatus* shell fragments of the second New Jersey bothremydid (Hay, 1908; Gaffney, 1975a), which was later re-named *Taphrosphys* by Cope (1869). That same year, Matheron (1869) described from Upper Cretaceous horizons in southern France “*Pleurosternon*” *provinciale* (later referred to *Polysternon* by Portis 1882), which would become first bothremydid from Europe. Soon thereafter, Baur (1891:424) erected Bothremydidae to refer to the North American forms *Bothremys* and *Taphrosphys*, which share “vomer well developed; no free nasal bones, dentaries coossified, small mesoplastron present”. More recently discovered Laurasian bothremydids include taxa from Upper Cretaceous strata of France (*Elochelys perfecta*; Nopcsa, 1931; Laurent et al. 2002; *Foxemys mechinorum*; Tong et al., 1998) and Portugal (*Rosasia soutoi*; Carrington da Costa, 1940; Antunes and Broin, 1988).

Bothremydid discoveries increased in the second half of the twentieth century and these continue to the present, particularly on Gondwanan landmasses (Fig. 3). The earliest known bothremydids are found in the Albian of South America and Africa (Lapparent de Broin and Werner, 1998: table 4). One of the largest Cretaceous pleurodires, *Nigeremys gigantea*, as well as unnamed bothremydids, come from the Maastrichtian and Cenomanian of Niger, respectively (Bergounioux and Crouzel, 1968; Broin, 1977; Lapparent de Broin, 2000). Other Cretaceous African bothremydids

FIG. 3 — Paleogeographic configuration of the Cretaceous landmasses (after Scotese, 1997) and distribution of Cretaceous (Albian-Maastrichtian) bothremydid species. 1, *Cearachelys placidoi* (Albian, Brazil); 2, Bothremydidae indet. (Albian, Mali); 3, Bothremydidae indet. (Albian, Morocco); 4, *Galianemys emringeri* (Cenomanian, Morocco); 5, *Galianemys whitei* (Cenomanian, Morocco); 6, Bothremydidae indet. (Cenomanian, Niger); 7, *Apertotemporalis baharijensis* (Cenomanian, Egypt); 8, “*Podocnemis*” *parva* (Cenomanian, Israel); 9, “*Podocnemis*” *judea* (Cenomanian, Israel); 10, *Karkaemys arabicus* (Santonian, Jordan); 11, *Bothremys barberi* (Santonian, USA); 12, *Rosasia soutoi* (Campanian, Portugal); 13, *Polysternon provinciale* (Campanian, France); 14, Bothremydidae indet. (Maastrichtian, Madagascar); 15, *Kurmademys kallamedensis* (Maastrichtian, India); 16, *Sankuchemys sethnai* (Maastrichtian, India); 17, *Nigeremys gigantea* (Maastrichtian, Niger); 18, *Arenila krebsi* (Maastrichtian, Egypt); 19, *Zolhafah bella* (Maastrichtian, Egypt); 20, cf. *Taphrosphys sulcatus* (Maastrichtian, Egypt); 21, cf. *Taphrosphys sulcatus* (Maastrichtian, Syria); 22, cf. “*Nigeremys* group” (Maastrichtian, Syria); 23, *Elochelys convenarum* (Maastrichtian, France); 24, *Foxemys mechinorum* (Maastrichtian, France); 25, *Bothremys cooki* (Maastrichtian/?Paleocene, USA); 26, *Taphrosphys sulcatus* (Maastrichtian/?Paleocene, USA); 27, *Bothremys barberi* (Maastrichtian/?Campanian, USA).



include *Galianemys whitei* and *G. emringeri* from the Cenomanian Kem Kem Formation of southern Morocco (Gaffney et al., 2002), *Apertotemporalis baharijensis* from the Cenomanian Bahariya Formation of Egypt (Stromer, 1934), and *Zolhafah bella*, *Arenila krebsi*, and cf. *Taphrosphys* sp. from the Maastrichtian Ammonite Hill Member of the Dakhla Formation, Egypt (Lapparent de Broin and Werner, 1998). Across the Sinai Peninsula, Cretaceous sediments in the Levant have also produced bothremydids. Maastrichtian phosphatic deposits of Syria preserve shell fragments, postcranial elements, as well as lower jaws that have been attributed to *Taphrosphys* and to the *Nigeremys* Group (Bardet et al., 2000). Across the Jordan Valley, just 100 km west of the Karak area in Jordan, Cenomanian limestone quarries of 'Ein Yabrud, near Jerusalem have produced two pleurodires: "*Podocnemis*" *parva* (Haas, 1978a), and "*P.*" *judaea* (Haas, 1978b). Described from partially prepared, isolated shells, both species are now thought to be closely allied with *Bothremys* group turtles (Lapparent de Broin and Werner, 1998:189-191). We use quotation marks to denote the questionable attribution of these fossils to *Podocnemis*. Fossil bothremydids are also known from neighboring landmasses of Madagascar and India, but none is currently known from Australia or Antarctica. Late Cretaceous (Maastrichtian) sediments of Madagascar preserve a dentary fragment attributable to Bothremydidae (Gaffney and Forster, 2003). *Kurmademys kallamedensis* (Gaffney et al., 2001) and *Sankuchemys sethnai* (Gaffney et al., 2003), from the Late Cretaceous of southern and eastern India, respectively, represent the easternmost occurrence of Bothremydidae.

INSTITUTIONAL ABBREVIATIONS

UM — University of Michigan Museum of Paleontology, Ann Arbor
 YUP-HUS — Yarmouk University, Paleontological Collection (Huseiniyah), Irbid

SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus 1758
 PLEURODIRA Cope 1864
 PELOMEDUSOIDES Cope 1868
 BOTHREMYDIDAE Baur 1891

***Karkaemys arabicus*, new genus and species**

Figs. 4-7

Holotype.— YUP-HUS 100, a nearly complete skull lacking lower jaws, found in association with a plastron, caudal vertebrae, partial pelvis, and partial femur, tibia, and fibula. The skull preserves the premaxilla, maxilla, jugal, vomer, palatine, pterygoid, quadrate, basisphenoid, supraoccipital, exoccipital, opisthotic, and prootic; only fragments remain of the squamosal, prefrontal, parietal, and postorbital. Casts of the holotype specimens have been deposited in the University of Michigan Museum of Paleontology collection (UM 12406).

Type locality.— The holotype was discovered in Wadi Falqa, near El-Huseiniyah and El-Hashimiyah villages, in central Jordan (Fig. 1). This locality has been designated as "Huseiniyah" and has the coordinates (31° 00' 22" N, 35° 43' 52" E).

Formation, age, and distribution.— *Karkaemys arabicus* (YUP-HUS 100) was collected from the uppermost levels of a silicified quartz arenite bone-bearing bed at the top of the Wadi Umm Ghudran Formation, 3-4 meters below its contact with the overlying Campanian Amman Forma-

tion (Fig. 2). The Wadi Umm Ghudran Formation is made up of whitish soft chalk, chalky marl, marly limestone, interbedded hard fossiliferous limestone, and sandstone that occurs in large lenticular bodies that have uneven surfaces. The sandstone is a medium to coarse grained, yellow-reddish to brownish quartz arenite, which is usually soft and friable, but occasionally very hard due to silicification. The top of this sandstone member is capped by hard whitish-to-gray colored chert bands that mark the beginning of the Amman Formation (Fig. 2).

Koch (1968) reported that the upper part of the Wadi Umm Ghudran Formation is Santonian in age, based on the presence of *Globo truncana concavata*. Based on comparisons of fossil selachians, Mustafa et al. (2002) also assigned a Santonian age for the bone-bearing bed that produced *Karkaemys arabicus*. To date, *Karkaemys arabicus* has been recovered only from the Huseiniyah locality.

Diagnosis.— Autapomorphies diagnosing *Karkaemys* include a short, hourglass-shaped vomer that has broad contacts with the premaxilla and maxilla, a broad U-shaped palatal depression with correspondingly broad premaxillae, an elongate and anteromedially oriented pubic scar, and a comparatively small and rounded ischial scar. Other features unique to *Karkaemys* cannot be scored in closely related bothremydids such as *Zolhafah*, including relatively broad palatines that position the contact between the pterygoid and jugal on the lateral surface rather than the ventral surface of the skull, and the relatively large contribution of the jugal to the orbital margin. The skull of *Karkaemys* is amongst the largest Cretaceous bothremydids, but is smaller than those of the *Nigeremys* and *Arenila*.

Etymology.— *Karka* refers to the Aramaic name for the ancient capital of Moab (which is now known as Karak), where the holotype was discovered. The Aramaic root *krk*, means “to enclose” or “to circumference”, which refers literally to the walled city of Karak and can be applied figuratively to the turtle’s enclosure within its shell. The suffix *-emys* is Greek for turtle. The specific epithet refers to the Arabian Peninsula.

DESCRIPTION

The skull of *Karkaemys arabicus* has a well preserved palate, occiput, and partial quadrate. The skull roof is damaged, but remnants of most bones can be identified. The anterior end of the skull preserves a piece of the prefrontal and portions of both postorbitals. The jugal is preserved on the left side, the premaxilla is missing its anterior peak. The palate is well preserved, and all bones and foramina are in good condition except the labial ridge, which is incomplete. The occipital region is missing the squamosals. The plastron is well preserved and includes scars for the ventral pelvic bones, which were fused to it. A partial femur and tibia, as well as caudal vertebrae are present but damaged. Table 1 contains principal measurements of *Karkaemys arabicus*. Anatomical nomenclature follows that of Gaffney (1972, 1979).

General description of skull.— The skull is roughly triangular. Its width and length are almost equal, and its height is nearly one-third its length. The orbits face dorsally, and the external nares are large and triangular to trapezoidal. The palate is broad, with a well marked, arcuate triturating surface covering most of its anterior half (Fig. 6). Two conspicuous triturating pits are located on the lateral extremes of the triturating surface. Within the arch of the triturating surface is a large central depression that houses the internal nares, which are separated by the vomer. The otic region is enlarged and makes up most of the posterior portion of the skull. The occipital region is broad and low, and the foramen magnum is large and ovoid (Table 1).

Premaxilla.— Most of the right and left premaxillae are preserved; they lack only their anterior extremes, which form part of the labial ridge (Figs. 4A, C, D, F; 5A, C). The premaxillae are midline elements that contact the vomer posteriorly and the maxillae laterally.

In ventral view (Figs. 4A, D, 6), the premaxilla forms portions of both the lingual and labial ridges of the triturating surface. The premaxilla forms a large proportion of the lingual ridge, which is broad and U-shaped. Internal to this ridge, the premaxilla forms part of a large, central

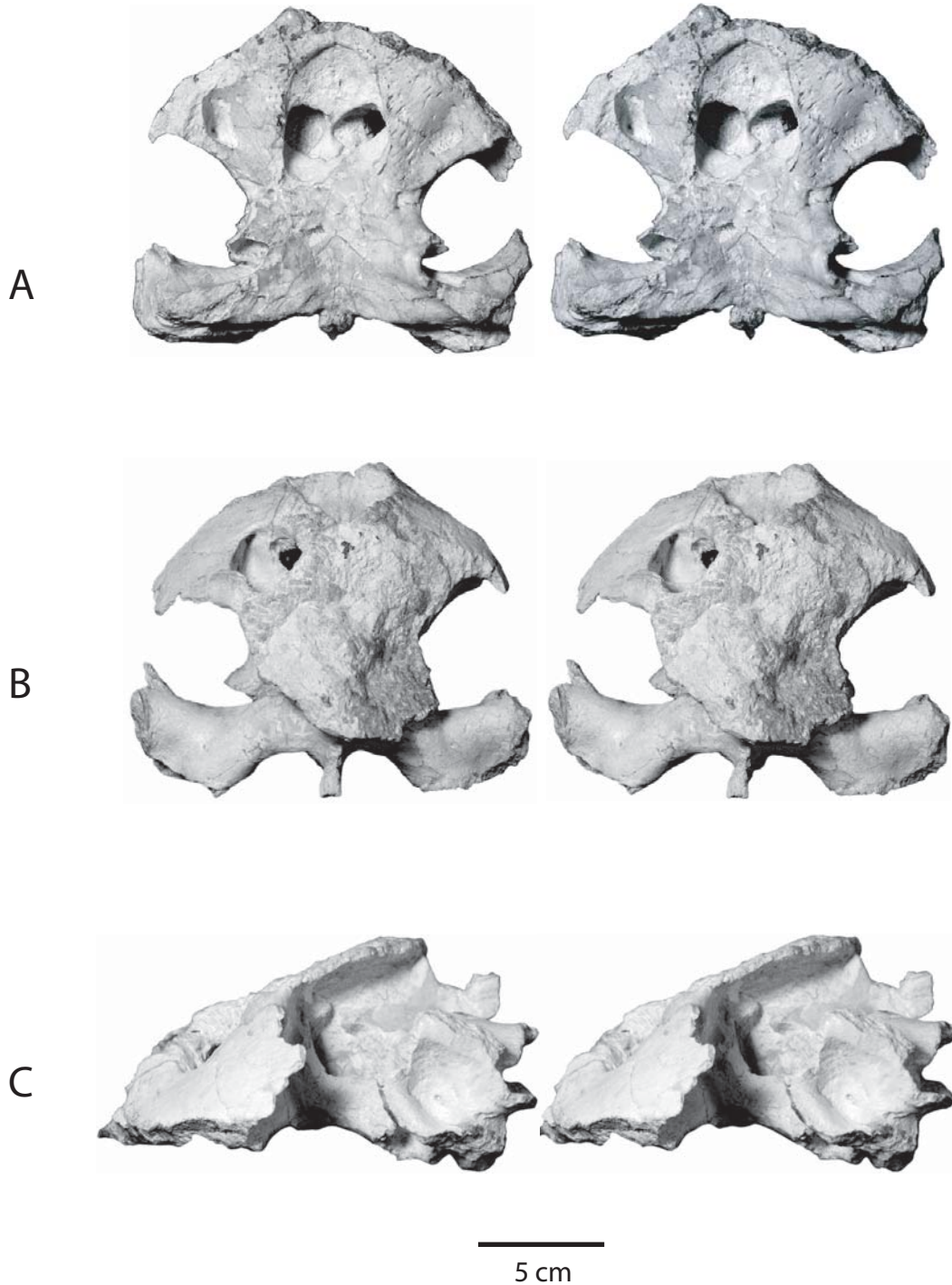
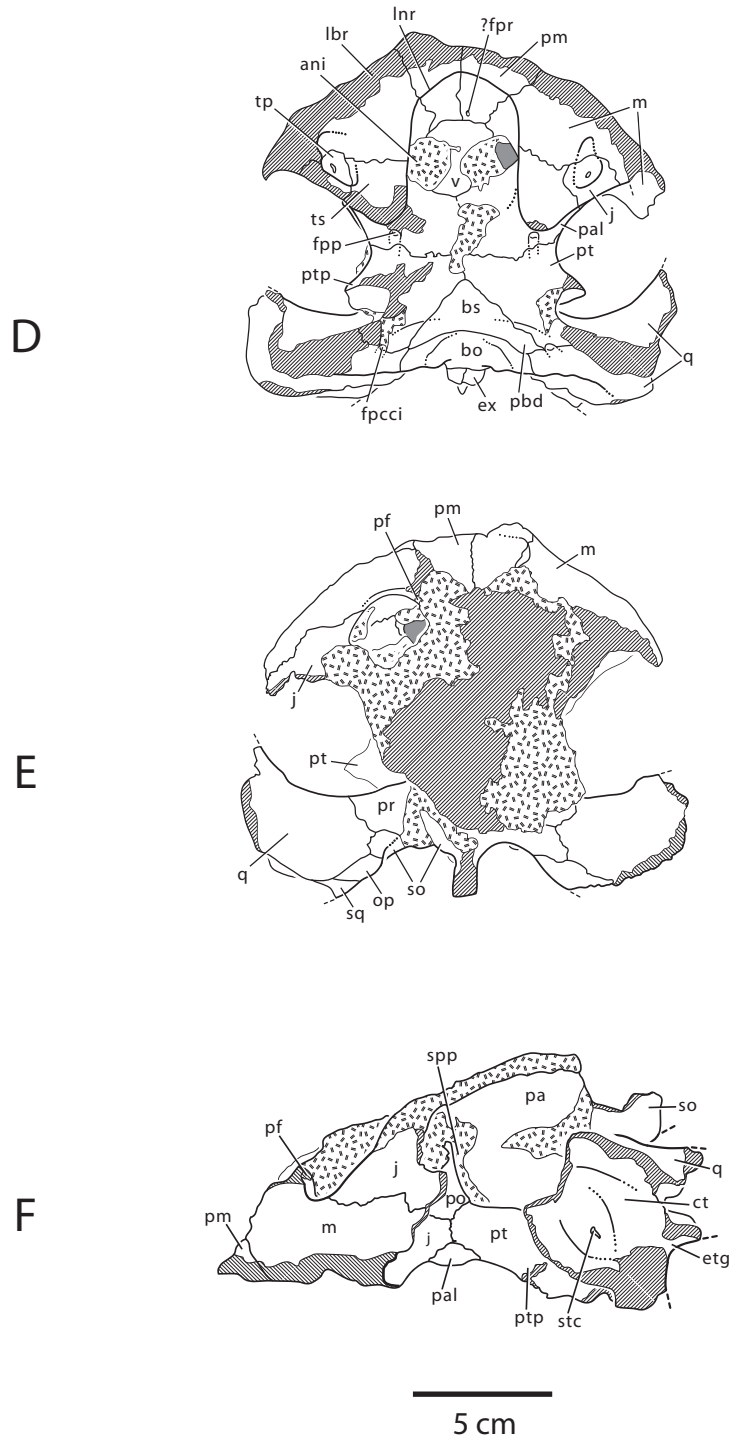


FIG. 4 — Holotypic skull of *Karakaemys arabicus* (YUP-HUS 100). Stereophotographs (A-C) and line drawings (D-F) in ventral (A, D), dorsal (B, E), and left lateral (C, F) views. Abbreviations: *ane*, apertura narium externa; *ani*, apertura narium interna; *bo*, basioccipital; *bs*, basisphenoid; *co*, condylus occipitalis; *ct*, cavum tympani; *etg*, eustachian tube groove; *ex*, exoccipital; *fjp*, foramen jugulare posterius; *fm*, foramen magnum; *fnh*, foramen nervi hypoglossi; *fp*, fenestra postotica; *fpcci*, foramen



posterior canalis carotici interni; *fpp*, foramen palatinum posterius; *fpr*, foramen praepalatinum; *j*, jugal; *lbr*, labial ridge; *lnr*, lingual ridge; *m*, maxilla; *o*, orbit; *op*, opisthotic; *pa*, parietal; *pal*, palatine; *pbd*, pterygoid basisphenoid depression; *pf*, prefrontal; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *pt*, pterygoid; *ptp*, processus trochlearis pterygoidei; *q*, quadrate; *so*, supraoccipital; *spp*, sulcus pterygo-palatinus; *sq*, squamosal; *stc*, stapedial canal; *tp*, triturating pit; *ts*, triturating surface; *v*, vomer.

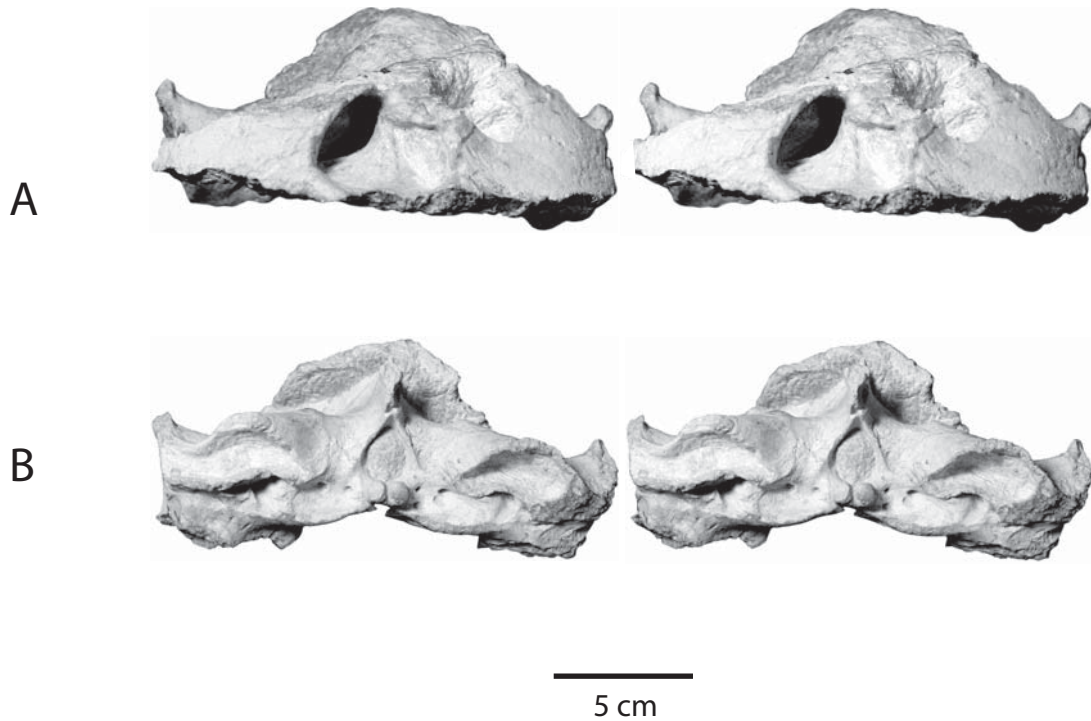


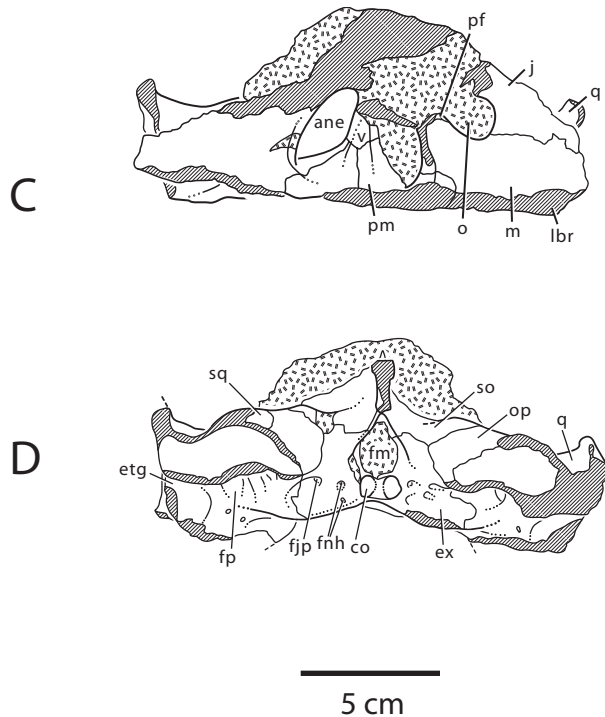
FIG. 5 — Holotypic skull of *Karkaemys arabicus* (YUP-HUS 100). Stereophotographs (A, B) and line drawings (C, D) in anterior (A, C) and posterior (B, D) views. Abbreviations as in Fig. 4.

depression that houses the internal nares. The premaxilla, however, does not contribute to the margin of these openings. The premaxillae contact one another on the midline at an elongate suture that terminates posteriorly at their transversely oriented contact with the vomer (Fig. 4A, D). There appears to be a small opening near this suture on the left premaxilla, but it is not present on the right side. Its relationship to a similarly-positioned foramen praepalatinum in *Bothremys cooki* (Gaffney and Zangerl, 1968) cannot be determined. Laterally, the premaxillae contact the maxillae at a suture that is also visible in the floor of the external nares.

Maxilla.— The maxillae are well preserved on both right and left sides, but neither completely preserves the labial ridge (Fig. 4A, D). The maxilla is one of the largest bones in the palate and makes up most of the triturating surface and the triturating pits, as well as a large portion of the labial ridge and a small part of the lingual ridge. The maxilla contacts the vomer and premaxilla medially, the palatine and jugal posteriorly, and the prefrontal near the margin of the orbit.

In ventral view, the maxilla is transversely broad and pierced by numerous pits that mark the position of the rhamphotheca (Fig. 6). The maxilla meets the premaxilla along an anterolaterally oriented suture that extends from the vomer to the lateral margin of the skull. The maxilla meets the palatine posteriorly along a transverse suture that extends from the internal naris to their mutual contact with the jugal. Lateral to the jugal is preserved a small portion of the maxilla that marks the lateral extreme of the skull. The maxilla forms the majority of the broad, curved labial ridge, which is incompletely preserved.

The maxilla forms much of the anteroventral portion of the orbital margin, as can be seen in anterior and dorsal views (Figs. 4B, E, 5A, C). Here, the maxilla contacts the prefrontal medially and the jugal dorsally. Medially, it reaches the margin of the external naris, which it shares with the premaxilla and the prefrontal.



Jugal.— The jugal is nearly completely preserved on both sides of the skull (Fig. 4A, D), with only a small portion of its contribution to the skull roof missing. The jugal is a complex element that contributes to the palate, skull roof, and orbit margin and is exposed in ventral, anterior, lateral, and dorsal views.

In ventral view (Figs. 4A, D, 6), the jugal forms part of the lateral margin of the palatal triturating surface, contacting the palatine posteromedially and the maxilla anteriorly. A prominent depression positioned level with the internal nares is present in the jugal of *Karkaemys* (Fig. 4A, D), as in *Bothremys cooki* (Gaffney and Zangerl, 1968). From the ventral surface of the skull, the jugal wraps dorsally to form part of the transversely oriented, vertical wall that bounds the adductor chamber anteriorly. Here, the jugal contacts the palatine, pterygoid, and postorbital (Fig. 4C, F). The jugal maintains its suture with the postorbital and maxilla anteriorly to form the lateral margin of the orbit and a part of the dermal shield of the skull. In anterior view, the jugal contacts the maxilla ventrally (Fig. 5A, C).

Prefrontal.— A very small fragment of the prefrontal is preserved in place on the anteromedial margin of the orbit (Fig. 4B, C, E, F). This piece of the prefrontal contacts the maxilla lateroventrally.

Parietal.— The parietal is poorly preserved, represented by a damaged portion of its median crest. No part of the parietal skull roof is preserved, and the degree of temporal emargination of the skull cannot be determined. On the left side, a relatively large fragment of the parietal is preserved (Fig. 4C, F). The parietal contacted the supraoccipital and likely the prootic and opisthotic, but the nature of this contact is not clear. A small process of the parietal extends ventrally to contact the pterygoid, as seen in lateral view.

Postorbital.— A fragment of the postorbital is preserved on the left side of the skull (Fig. 4C, F). This small piece is exposed in lateral view only and preserves contacts with three elements. It contacts the jugal anteroventrally, the pterygoid posteroventrally, and the parietal posterodorsally.

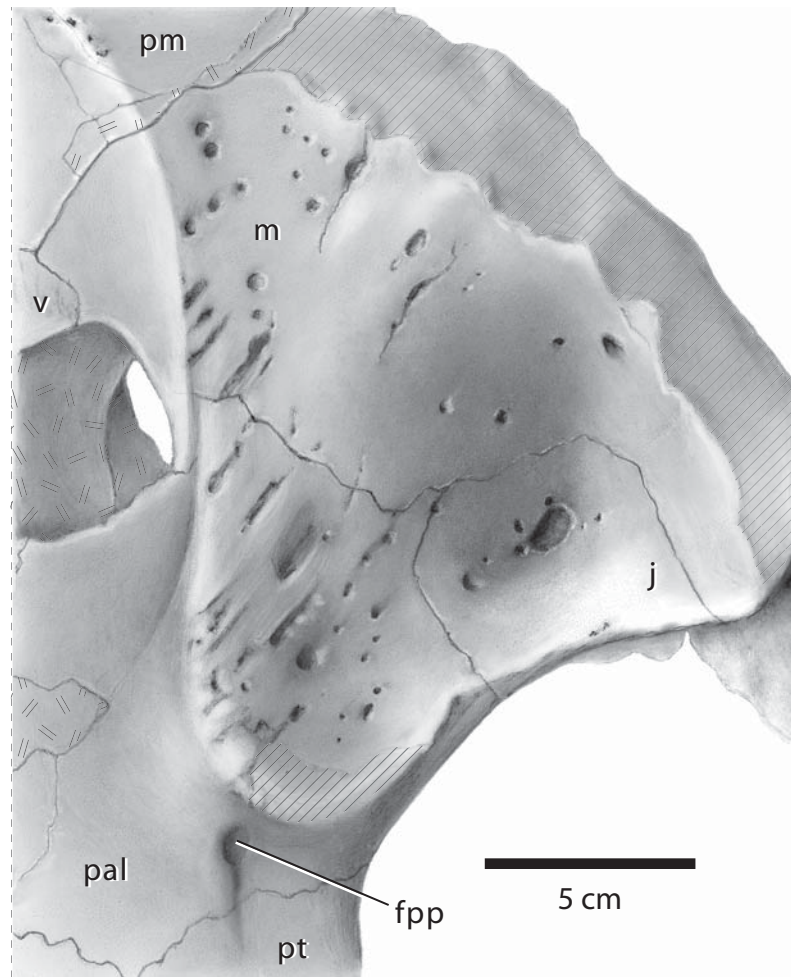


FIG. 6 — Holotypic skull of *Karkaemys arabicus* (YUP-HUS 100). Half-tone drawing of the triturating surface on ventral aspect of the left side of the palate. Abbreviations as in Fig. 4.

If complete, this element would have formed a portion of the skull roof and contributed to the margin of the orbit.

Squamosal.— A small fragment of the squamosal is preserved in place on the right side (Fig. 4B, E, 5B, D). Its contacts with the opisthotic and quadrate are preserved. If complete, the squamosal would have continued laterally to contact the quadrate and parietal.

Vomer.— The vomer is complete and well preserved. It is visible in ventral and anterior views (Fig. 4A, D, 5A, C). This median palatal element contacts both the premaxillae and maxillae anteriorly and the palatines posteriorly. The vomer probably contacted the prefrontal dorsally, but this contact cannot be observed in this specimen.

In ventral view, the vomer is hourglass shaped and slightly more expanded anteriorly than posteriorly. The vomer has a broad contact with the conjoined premaxillae and a narrower contact with the maxillae, with which it forms the anterior margin of the internal nares. The remainder of the margin of the internal nares is formed by the palatines, which have a narrow median contact with the vomer. The vomer is strongly arched dorsally such that in anterior view, it forms the dorsal portion of the median division of the external nares.

Palatine.— The palatine (Figs. 4A, C, D, F, 6) is a paired median element that contacts the midline just posterior to the vomers. The palatines extend the breadth of the mid-palate and are visible in ventral and lateral views. The palatines are completely preserved on both sides and their contacts to surrounding elements are well exposed. The palatine contacts the vomer and maxilla anteriorly, the jugal anteriorly and laterally, and the pterygoid posteriorly and laterally.

In ventral view, the palatines form the posteriormost portion of the triturating surface as well as the posterior portion of the median palatal depression. Several conspicuous foramina open in the palatine in the region of the triturating surface (Fig. 6). These likely carried vascular supply to the rhamphotheca (e.g., Gaffney, 1979). The palatine is approximately as long anteroposteriorly as it is broad transversely and has a small dorsal projection that wraps around the lateral margin of the palate. The postpalatine foramen opens near the palatine-ptyerygoid contact, just beyond the posterior margin of the triturating surface. It is completely enclosed by the palatines, but the posterior portion of its fossa surrounding extends onto the pterygoid. The palatine forms a portion of the floor of the orbit together with the maxilla and jugal.

Pterygoid.— The pterygoids are well preserved but incomplete laterally and slightly damaged near the midline (Fig. 4A, D). The pterygoid is a relatively large bone that forms much of the posterior portion of the palate as well as the trochlea for the pterygoideus musculature. Dorsal, ventral, medial, as well as lateral contacts and structures are visible.

In ventral view (Fig. 4A, D), the pterygoids meet each other at the midline along a suture that is considerably shorter than those of other fossil bothremydids. Anterior to their mutual contact, the pterygoids border the conjoined palatines along a suture that traverses the palate and wraps dorsally onto its lateral surface. Towards the lateral extreme, this suture passes through the posterior end of the fossa of the postpalatine foramen. The posterior portion of the pterygoids are separated from the midline by the apex of the basisphenoid, which extends anteriorly to the level of the adductor trochlea (Fig. 4A, D). The pterygoids contact the basisphenoid along its lateral face to its base, where they meet the quadrates. The pterygoids and quadrates share a short, concave-forward suture that is interrupted by the foramen posterius canalis carotici interni. This foramen is positioned within a shallow groove that can be identified as the pterygoid-basisphenoid depression, which probably represents the attachment site for adductor musculature (Gaffney, 1979). Lateral to this groove, the quadrate-ptyerygoid suture wraps onto the lateral surface of the skull. The pterygoid expands laterally to form the trochlea for the adductor musculature tendon, the processus trochlearis pterygoidei (Fig. 4). This structure is exposed laterally, ventrally and dorsally.

In lateral view (Fig. 4C, F), the pterygoid maintains a contact with the palatine that curves anteriorly. Where the pterygoid-palatine suture ends, the pterygoid rises vertically to contact the jugal and, further dorsally, the postorbital. Just posterior to the pterygoid-postorbital contact, a very narrow process of the parietal reaches the pterygoid. The dorsal margin of the pterygoid trochlea is free. Posterior to this, the pterygoid contacts the quadrate along a suture that arches medially. The pterygoid likely contacted the prootic, but their suture cannot be seen on either side of the skull.

Quadrate.— Both quadrates are preserved, including most portions of the ear region, but both articular condyles are missing. The quadrates have an extensive contact with the occiput and palate.

Dorsally (Fig. 4B, E), the quadrate contacts the prootic anteromedially, the opisthotic posteromedially, the supraoccipital medially, and the squamosal posteriorly and posteromedially. In ventral view (Fig. 4A, D), the quadrate is bordered by the pterygoid and basisphenoid anteromedially, and the basioccipital and exoccipital posteromedially. In occipital view, the quadrate encloses both fenestrae postotica, the posterior opening of the cavum acoustico-jugulare, and the incisura columellae auris (Fig. 5B, D). The foramina chorda tympani inferius and superius were not preserved. The wall between the quadrate and the pterygoid is damaged and has lost almost all details of the pterygoideus concavity. The foramina auditus canalis stapedio-temporalis is filled by sediment. Contacts between quadrates and quadratojugal, squamosal, and opisthotic are not clear because these three elements are partially or completely missing in lateral view.

TABLE 1 — Measurements (in millimeters) of *Karkaemys arabicus* (YUP-HUS 100). An asterisk (*) indicates measurement of an incomplete structure.

Skull length (along midline as preserved)	159.7
Skull width at both ends of the quadrate	171.0
Skull outer perimeter	508.0
Skull height (from the base of the condylus occipitalis to top of supraoccipital)	64.0
Skull Openings	
Orbital opening diameter (horizontal)	26.0
Apertura narium externus height at midline	30.3
Apertura narium externus width at the base	40.5
Apertura narium interna length (right)	21.4
Apertura narium interna width (right)	20.4
Foramen magnum maximum height	21.1
Foramen magnum maximum width	18.1
Palate	
Width of the palate across the foramina palatinum posterius	73.0
Distance between the two foramina palatinum posterius	50.7
Distance between left and right processus trochlearis pterygoidei	93.1
Distance between the two foramina posterius canalis carotici interni	63.6
Central depression length (along the midline)	64.8
Central depression maximum width	42.2
Central depression depth (measured at the front of the vomer)	16.2
Triturating pits depth	19.7
Distance between the two triturating pits	102.1
Occiput	
Condylus occipitalis width (left)	6.0
Condylus occipitalis width (right)	5.9
Condylus occipitalis height	9.1
Distance between the two condyli occipitales	1.5
Foramina nervi hypoglossi maximum diameter	2.0
Distance between the two foramina nervi hypoglossi (right)	3.1
Distance between the two foramina nervi hypoglossi (left)	2.9
Distance between foramina nervi hypoglossi on both sides across the condyli occipitales	23.8
Distance between the two foramina jugulare posterius (right)	4.8
Distance between the two foramina jugulare posterius (left)	4.5
Distance between the two across the condyli occipitales	41.9
Fenestra postotica height (right)	10.0
Fenestra postotica width (right)	5.5
Fenestra postotica height (left)	11.0
Fenestra postotica width (left)	8.2
Distance between the two fenestra postotica across the condyli occipitales	82.2
Exoccipital width across foramen magnum	39.6
Distance between contact point between supraoccipital, quadrate, and opisthotic on both sides	75.8
Distance between opisthotic and prootic	16.0
Plastron	
Plastron length*	530.0
Plastron width*	520.0
Anterior lobe length*	210.0
Anterior lobe width (at bridge)	290.0
Posterior lobe length	295.0

TABLE 1 — (continued)

Posterior lobe width	240.0
Bridge length	150.0
Hindlimb	
Femur breadth	15
Tibia breadth	17
Fibula breadth	10

The antrum postoticum is not preserved on either side. The eustachian tube lies in a shallow groove along the back of the quadrate, but not in a canal. The opening for the stapes, which is hosted by the cavum tympani, is completely enclosed by bone and separated from the eustachian tube. The precolumellar fossa is absent and the incisura columellae auris is enclosed by bone.

Basisphenoid.— The basisphenoid is complete, but only visible in ventral view. The basisphenoid is a triangular median element that contacts the paired pterygoids along the length of its lateral faces. The pterygoids meet one another at the apex of the basisphenoid (Fig. 4A, D). Along its base, the basisphenoid contacts the basioccipital at a slightly concave-backward suture that terminates prior to its posterolateral corner. A narrow projection of the quadrate contacts the basisphenoid at this corner. The basisphenoid does not participate in the margin of the posterior internal carotid foramen, which is completely enclosed by the pterygoid and quadrate.

Basioccipital.— The basioccipital is a broad median element that is exposed ventrally (Figs. 4A, D). The basioccipital contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipital dorsally.

In ventral view, the basisphenoid shares an elongate, transverse suture with the basisphenoid. Lateral to this contact, the basioccipital contacts the quadrate along a suture that wraps onto the occipital surface of the skull. In posterior view, the basioccipital-quadrate suture ends where these two elements meet the exoccipital. The basioccipital and exoccipital have a flat contact that extends medially to the occipital condyle, to which the basioccipital does not contribute.

Exoccipital.—The exoccipitals are completely preserved. The exoccipitals form much of the occiput, including the occipital condyle and the ventral and lateral margins of the foramen magnum (Fig. 4A, D). The exoccipital is bounded by the supraoccipital dorsally, opisthotic and quadrate laterally, and the basioccipital ventrally.

In posterior view (Fig. 5B, D), the exoccipitals bound nearly all of the foramen magnum, which is dorsoventrally elongate. Beneath the foramen magnum, they come together as two convexities to form the occipital condyle, which is much broader than it is tall dorsoventrally. Lateral to the occipital condyle, the exoccipital extends to contact the opisthotic and quadrate. Within this broad plate are housed paired openings for cranial nerve XII and the posterior jugular vein.

Supraoccipital.— The supraoccipital is nearly complete, lacking only a portion of its median crest, the crista supraoccipitalis (Fig. 4B, C, E, F). The supraoccipital forms the dorsal margin of the foramen magnum and is exposed in both posterior and dorsal views.

In posterior view (Fig. 5B, D), the supraoccipital contacts the exoccipital ventrally, the opisthotic, quadrate, and prootic laterally, and the parietal anteriorly. Its margin on the foramen magnum is raised into a low lip that continues dorsally as the crista supraoccipitalis. From its contact with the exoccipital on the margin of the foramen magnum, the supraoccipital extends laterally, contacting the opisthotic along a suture that extends onto the dorsal surface of the skull. Here, the supraoccipital reaches anteriorly, contacting the quadrate until their mutual contact with the prootic. The supraoccipital has an anterior contact with the parietal, but their suture is not preserved.

The supraoccipital is marked by two paramedian ridges that are visible in lateral and dorsal view. The two ridges form the dorsal edges of the foramen magnum as in other turtles, such as *Bothremys* and *Sankuchemys*.

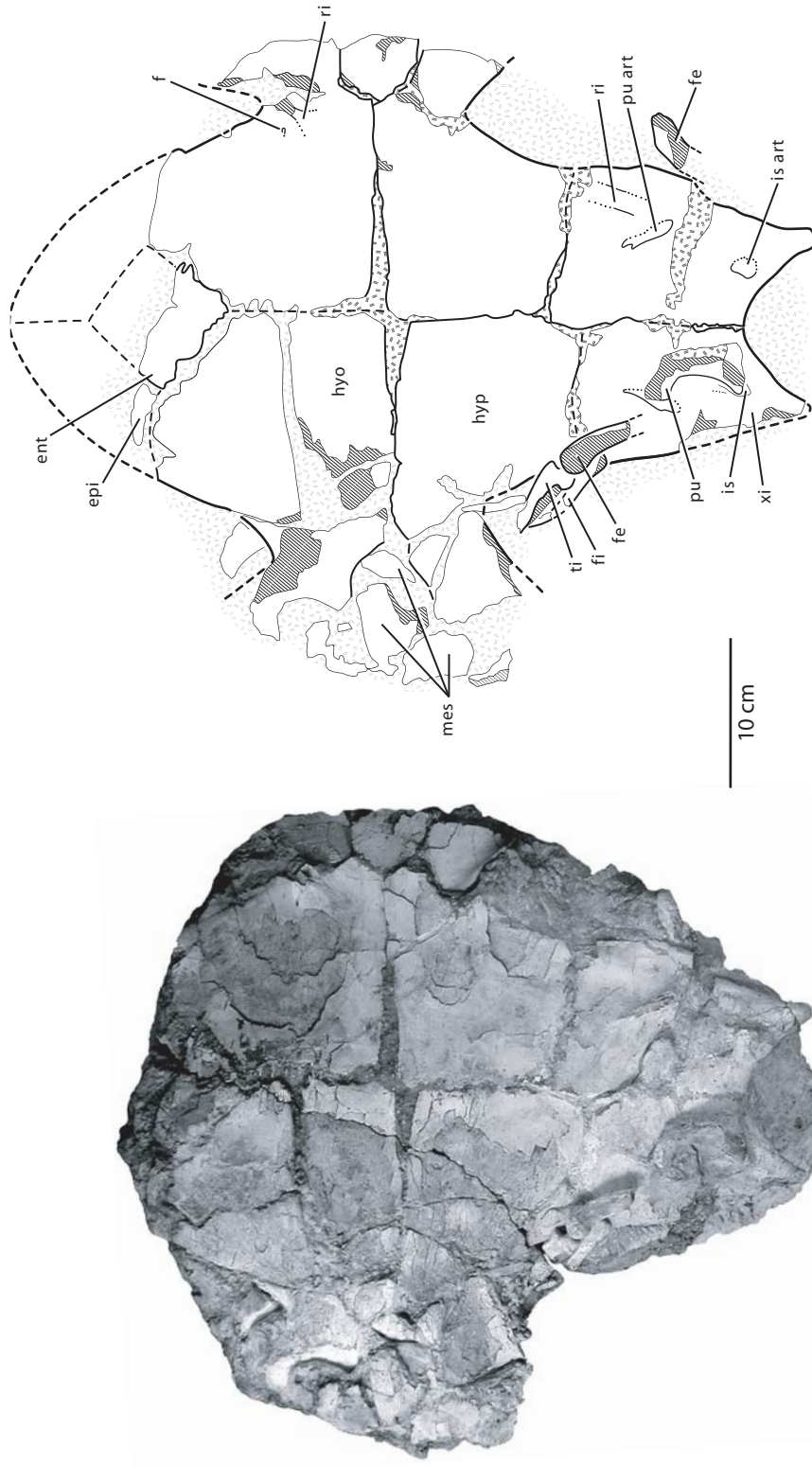


FIG. 7 — Holotypic plastron and postcranial elements of *Karkaemys arabicus* (YUP-HUS 100). Photograph and line drawing in internal view. Abbreviations: *ent*, entoplastron; *epi*, epiplastron; *mes*, mesoplastron; *hyo*, hyoplastron; *hyp*, hypoplastron; *f*, foramen; *fe*, femur; *fi*, fibula; *ti*, tibia; *ri*, ridge; *pu art*, pubic articulation; *is*, ischium; *is art*, ischial articulation; *xi*, xiphoplastron.

Opisthotic.—The right and left opisthotics are fairly well preserved, lacking only their posterolateral ends (Fig. 4B, E). The opisthotics form much of the otic region of the skull, contacting the exoccipital ventrolaterally, the quadrate dorsolaterally, the squamosal laterally, and the supraoccipital dorsomedially.

The opisthotic is a curved, strap-like element that wraps around the otic portion of the skull from the occiput onto its dorsal aspect. In posterior view (Fig. 5B, D), the opisthotic contacts the exoccipital along a short, oblique suture that is interrupted medially by the supraoccipital, which excludes it from the margin of the foramen magnum. From this contact, the opisthotic arches dorsolaterally to contact the quadrate on the dorsal face of the skull. The opisthotic maintains its contact with the supraoccipital throughout its length. The processus interfenestralis of the opisthotic is completely covered as in all other bothremydids and podocnemidids.

Prootic.—The prootic is nearly completely preserved on both sides, although some parts filled either with matrix or resin. The prootic covers the otic chamber anteriorly and contacts the posterior border of the pterygoid (Fig. 4B, E). The prootic meets the quadrate laterally and posterolaterally, the supraoccipital posterodorsally and posterolaterally, the parietal medially, and the pterygoid ventrally. The foramen stapedio-temporale opens anteriorly and cannot be seen in dorsal view. The cavum acoustico-jugulare is probably damaged.

Plastron.—The nearly complete plastron lacks only portions of the epiplastra and mesoplastra. Its exposed internal surface shows articulations between all plastron elements and the sutural surfaces for articulation of the two ventral pelvic elements, portions of which were preserved (Fig. 7). The external surface of the plastron is encased in matrix, so the presence of scale sulci could not be determined.

The plastron, as reconstructed, is longer anteroposteriorly than broad transversely (Table 1). Anterior and posterior emarginations of the lateral plastron define a bridge that contacted the carapace; this bridge is positioned closer to the anterior end of the plastron than to the posterior. A much smaller median notch emarginates the posterior extreme of the plastron. The plates comprising the plastron are articulated, and their boundaries are more or less distinct. Eleven major plates can be identified, five paired plates (epiplastra, mesoplastra, hyoplastra, hypoplastra, xiphiplastra) and a single median plate (entoplastron). The hyoplastra and hypoplastra are the largest elements and make up the middle, bridging portion of the plastron. They meet along a relatively straight, transversely oriented contact that is offset at the midline and interrupted at its lateral extremes by the mesoplastra, which are incomplete. The hyoplastron is slightly larger than the hypoplastron and bears a trace of a ridge that delimited the margin of the bridge. A large midline notch in the anterior margin of the hyoplastra forms a V-shaped articulation for the median entoplastron, which is partially preserved. The entoplastron is missing anterior and right lateral portions, but its breadth can be estimated from the preserved portion. It would have been bordered anteriorly by the epiplastra, of which only a small fragment is preserved on the left side. The xiphiplastra meet the hypoplastra along a transversely oriented but offset suture and form the posterior end of the plastron (Fig. 7). Each xiphiplastron tapers to a blunt tip posteriorly and is separated from its opposite by a broad notch. Roughened sutural surfaces for the pubis and ischium are preserved as distinct scars. The pubic scar is narrow, elongate, and oriented anteromedially (approximately 30° from midline). The ischial scar, in contrast, is small, rounded, and positioned near the posterior extreme of the xiphiplastron.

The plastron of *Karkaemys* is generally similar to that of other bothremydid turtles, but differs in the shape of the xiphiplastra and in the shape and position of the pelvic attachments. Although it is similar in size and most closely resembles *Bothremys barberi* (Gaffney and Zangerl, 1968:figs. 7, 8), the plastron of *Karkaemys* lacks the tab-like xiphiplastra, anteroposteriorly aligned pubic scar, and elongate ischial scar characteristic of *B. barberi*. Additionally, the xiphiplastral notch of *Karkaemys* is more angular than of *B. barberi*. The plastron of *Karkaemys* is almost three times larger than "*Podocnemis*" *parva* and "*P.*" *judaea* (Haas, 1978a, b), and it differs somewhat from the 'Ein Yabrud turtles in its relatively narrow, more elongate, and blunt-tipped xiphiplastra. Correspondingly, the xiphiplastral notch of *Karkaemys* is deeper and slightly more angular.

Caudal vertebrae.—Three fragmentary caudal vertebrae were preserved on the internal surface of the xiphiplastra. The vertebral centra are procoelous and approximately 25 mm long, but few other useful details can be observed.

Appendicular elements.—Fragments of the left pubis and ischium and part of the left hindlimb are visible on the dorsal (internal) surface of the posterior plastron (Fig. 7). The pelvic elements are poorly preserved and cannot be described in any detail. The partial hindlimb is quite damaged, but the distal end of the femur and proximal ends of the tibia and fibula are preserved in close to life position. The distal condyle of the femur and proximal condyle of the tibia are rounded, and their shafts are similar in breadth. The fibula is considerably smaller (Table 1).

PHYLOGENETIC RELATIONSHIPS

Relationships of fossil and recent Pleurodira have been examined by Gaffney (1975a, 1975b, 1977a, 1977b, 1979, 1982), Gaffney and Meylan (1988), Broin (1988), Gaffney et al. (1991, 2002), and Lapparent de Broin (2000). These phylogenetic analyses have identified synapomorphies of Pleurodira and its subgroups, which can be used to place *Karkaemys* in a phylogenetic framework.

Synapomorphies of Pleurodira preserved in *Karkaemys* include presence of a pterygoid trochlea (processus trochlearis pterygoidei) on the palate, a quadrate ventral process positioned below the cranioquadrate space, loss of the epipterygoid, a postpalatine foramen positioned behind the orbit, a sutural connection between carapace, plastron, and pelvis, and the presence of a mesoplastron. Other features, such as the absence of the nasals and a single, short interchoanal vomer suggest that *Karkaemys* is a pelomedusoid pleurodire.

Within Pelomedusoides, *Karkaemys* shows affinities to Bothremydidae, based on exclusion of the basioccipital from the occipital condyle, foramen stapedio-temporale facing anteriorly, and a basioccipital-basioccipital-quadrate contact. Amongst bothremydids, *Karkaemys* appears to share closer affinity with *Bothremys* group turtles (*Bothremys*, *Zolhafah*, *Rosasia*, *Foxemys*) than to *Nigeremys* group turtles (*Nigeremys*). *Karkaemys* has a relatively short, broad snout that bears well-developed triturating surfaces provided with conspicuous triturating pits. The posterior portion of the skull is abbreviated, and the occipital condyle is positioned near the level of the jaw articulation in ventral view. Like *Bothremys* and *Zolhafah*, the orbits of *Karkaemys* are dorsally facing, circular, and anteriorly positioned. *Karkaemys* and *Zolhafah* share a foreshortened snout in which the posterior margin of the external nares approaches the anterior margin of the orbits. Although the prefrontals were not preserved in *Karkaemys*, they were presumably short as they are in *Zolhafah*. Like *Zolhafah*, the external nares of *Karkaemys* appear to have been relatively large and dorsally exposed, in contrast to the condition in other *Bothremys* group turtles. The pterygoid does not participate in the triturating surface on the palate of *Karkaemys* or *Zolhafah*, which differentiates them from *Bothremys*. This feature may be symplesiomorphic, however, as it is shared by *Kurmademys* and *Rosasia*.

Autapomorphies diagnosing *Karkaemys* include a short, hourglass-shaped vomer that has broad contacts with the premaxilla and maxilla, a broad U-shaped palatal depression with correspondingly broad premaxillae, an elongate and anteromedially oriented pubic scar, and a comparatively small and rounded ischial scar. The lingual ridge surrounding the palatal depression appears to be thicker in *Karkaemys* than in other bothremydids, but this region is not completely preserved. The palatines are relatively broad in *Karkaemys*, positioning the contact between the pterygoid and jugal on the lateral surface of the skull rather than the ventral surface of the skull. The palatines appear to be broad in *Zolhafah* as well, but the position of the jugal-ptyerygoid contact is unknown. This feature may later be shown to characterize both genera. Likewise, the jugal appears to have a more extensive contribution to the orbital margin in *Karkaemys* than in other bothremydids, but the condition in *Zolhafah* is not known. The skull of *Karkaemys* is amongst the largest of the

Cretaceous *Bothremys* group turtles (*Bothremys*, *Zolhafah*, *Rosasia*, *Polysternon*, *Foxemys*, *Galianemys*, *Kurmademys*), but is smaller than those of the *Nigeremys* group as well as *Arenila krebsi*.

DISCUSSION

Fossil pleurodires attained a broad geographic distribution during the Late Cretaceous and early Tertiary, before terminal closure of the Tethyan Sea (Broin, 1988; Hirayama, 1997; Moody, 1997; Lapparent de Broin and Werner, 1998; Lapparent de Broin, 2000). Bothremydids, first recorded in the Early Cretaceous (Albian) of South America and North Africa, were numerous in Africa and the Arabian Peninsula during the Cenomanian. They are first recorded in North America and Europe in the Santonian and Campanian, respectively, and they attained their greatest diversity and broadest distribution during the Maastrichtian (Fig. 2). Although sampling effects cannot yet be discounted, as the record of bothremydids has dramatically improved even within the last decade, a few tentative paleobiogeographic conclusions may be drawn from their Cretaceous distribution.

First, one-half of all bothremydids (12 spp.) come from Africa and the Arabian Peninsula, which were contiguous during the Cretaceous. This high diversity is underscored by the fact that Africa has a poorer Cretaceous record than do South America, North America, Europe, and Asia. It is likely that the main diversification of bothremydids took place on Africa and the Arabian Peninsula, as suggested by Lapparent de Broin (2000).

Second, this pattern suggests that bothremydids originated on southern landmasses (South America, Africa/Arabian Peninsula) during the Early Cretaceous and later migrated to northern landmasses (North America, Europe) by the middle of the Late Cretaceous. The proximity of Africa and the Arabian Peninsula to Europe during the Cretaceous may account for the shared presence of bothremydids, as it may for closely related north African and European dinosaurs (e.g., spinosaurid theropods *Suchomimus*, *Spinosaurus*, and *Baryonyx*; rebbachisaurid sauropods *Nigersaurus*, *Rebbachisaurus*, *Histriasaurus*, and the Salas taxon; African and European *Valdosaurus*). Nonetheless, further investigation into the species-level relationships of bothremydids are required to corroborate this hypothesis.

Finally, although bothremydids first appear in Madagascar and India during the Maastrichtian, it is not yet known whether they were there previously, because pre-Maastrichtian Cretaceous sediments are not well-sampled on either landmass. Likewise, the complete absence of bothremydids from Antarctica and Australia does not constrain their geographic distribution because Cretaceous horizons are relatively poorly sampled on those landmasses. Better estimates of the spatial and temporal distribution of bothremydids await further investigation of Cretaceous vertebrate-bearing sediments. Although the bothremydid *Cearachelys* is present in the Albian of Brazil (Gaffney et al., 2001), bothremydids have not been recorded later in the Cretaceous of South America. Their presence in the Paleocene of Brazil and the Oligocene of Peru (Lapparent de Broin and Werner, 1998: table 3) can be attributed to either their undetected presence in intervening horizons or extinction followed by dispersal from some other landmass. At present, we cannot discriminate between these two explanations. In contrast, the absence of bothremydids from well-sampled Late Cretaceous and Tertiary sediments of Asia may not be artefactual and suggests they never reached there.

CONCLUSIONS

From the Santonian of Jordan, *Karkaemys arabicus* is the first diagnostic turtle from the Cretaceous of the Arabian Peninsula. *Karkaemys* lived in a nearshore or coastal environment, probably

on tidal sand waves or ribbons parallel to the coastline. These sandstone bodies, which have tabular cross-stratification, typical fining-upward sequences, well sorted quartz arenite, and rich marine vertebrate faunas (e.g., sharks, rays, mosasaurs), are diagnostic of a shallow clastic shelves on passive continental margins. *Karkaemys* provides new information about the history and paleobiogeographic distribution of the Gondwanan side-necked turtle subgroup Bothremydidae, which was common on southern landmasses during the Cretaceous. *Karkaemys arabicus* is most closely related to the Egyptian *Zolhafah bella* and more distantly related to the North American *Bothremys cooki*.

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