3.1

Fossil Crabs (Crustacea, Decapoda, Brachyura) from Lothagam

Joel W. Martin and Sandra Trautwein

Remains of fossil crabs attributable to the family Potamonautidae have been recovered from the Nawata Formation and the Apak Member of the Nachukui Formation. Their occurrence in the Lothagam sequence is consistent with the presence of a well-oxygenated riverine system. More precise identification requires access to features not normally preserved in fossil crab material.

Freshwater crabs are a tremendously diverse assemblage of true (brachyuran) crabs known from Central and South America, Africa (including Madagascar), Australasia, southern Europe, and south and Southeast Asia. There are an estimated 900 species in the group, making them one of the most diverse assemblages of crabs. Species are known from cold, rapidly flowing mountain streams, tropical rainforest floors (where they may even be semiterrestrial or arboreal), warm lowland ponds and paddies, and just about any other freshwater environment (Ng 1988; Rodríguez 1982, 1992; Cumberlidge 1991; Cumberlidge and Sachs 1989a, 1989b). Their diversity, range, and size make them important ecologically, economically, and medically (as vectors of some tropical diseases). Although they were originally thought to comprise a single family (Potamidae), the group was treated as 11 families in three superfamilies by Bott (1970a, 1970b) and Pretzmann (1972, 1973). In turn, Bott's and Pretzmann's work has been questioned by more recent workers who employ cladistic methodology that is based on new morphological and molecular sequence data (e.g., Guinot et al. 1997; Cumberlidge 1999; Sternberg and Cumberlidge 1999; Abele et al. 1999). The taxonomy and phylogeny of the group are actively being revised on the basis of some of these new data. In this contribution, we follow the admittedly conservative classification of Martin and Davis (2001), where the freshwater crabs are composed of one family (Trichodactylidae) in the otherwise marine superfamily Portunoidea, one family (Psuedothelphusidae) in its own superfamily Pseudothelphusoidea, and six Old World freshwater families. The Old World families are partitioned among the superfamilies Gecarcinucoidea (families Gecarcinucidae and Parathelphusidae) and Potamoidea (families Deckiniidae, Platythelphusidae, Potamidae, and Potamonautidae (table 3.1). Many formerly recognized families have been synonymized in recent years (see discussion in Martin and Davis 2001).

Details of the timing of the invasion of freshwater by these crabs remain unclear. Hypotheses range from 11 independent unrelated invasions of freshwater by different groups of marine crabs during the Late Cretaceous to lower Tertiary (e.g., Bott 1970a, 1970b; Pretzmann 1973), to two lower Tertiary invasions (one in the Americas that resulted in the Trichodactylidae and another one elsewhere that led to all other families from some widespread marine ancestor; see Sternberg et al. 1998), to a single, much older (~200 Ma) colonization of the freshwater habitat; this resulted in freshwater crab monophyly (e.g., Rodríguez 1986; Ng et al. 1995).

In Africa, only the superfamily Potamoidea is known. (The superfamily Pseudothelphusoidea is restricted to Central and South America, as is the family Trichodactylidae of the otherwise marine superfamily Portunoidea; the two families of the Gecarcinucoidea are restricted to the Indian subcontinent, Southeast Asia, and Australasia). Of the four currently recognized potamoid families (Martin and Davis 2001), the Platythelphusidae are restricted to Lake Tanganyika, and

the Potamidae are found in northwest Africa, southeastern Europe, and Asia (figure 3.1).

Thus, with some certainty we can say that the fossil crabs from Lothagam could only belong to one of two families: Potamonautidae (known only from sub-Saharan Africa plus the Nile in Egypt and from Madagascar) and Deckeniidae (known only from East Africa). Species identifications in these families often are based on the detailed structure of the male pleopods (among other features), such that even remarkably preserved fossils could not be identified further (that is, to the level of genus or species). We are assuming that all of the Lothagam fossils are members of the freshwater crab superfamily Potamoidea and that, based on the modern-day distribution of this family, they are probably members of the family Potamonautidae. The "almost complete lack of a fossil record for all groups of African freshwater crabs" (Sternberg and Cumberlidge 1999:493) makes comparisons with existing fossil material virtually impossible. In this report we give brief descriptions of fossil freshwater crabs from the Late Miocene hominid-bearing locality of Lothagam, Kenya, that were collected during the 1991 and 1992 field seasons. Catalog numbers for these specimens begin with the acronym KNMI-LT, which denotes invertebrate fossils from Lothagam in the collections of the National Museums of Kenya, Nairobi.

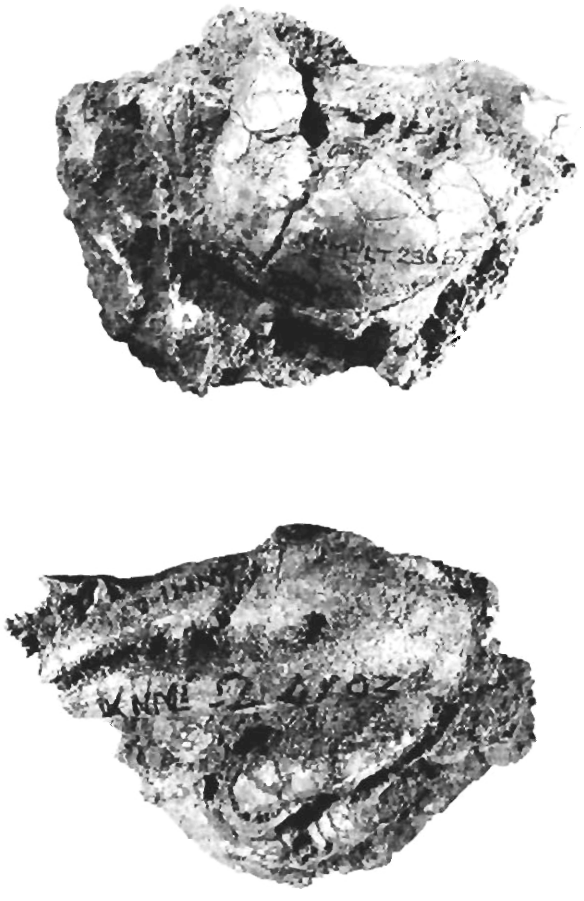

Figure 3.1 Two of the more complete fossil crab fragments from Lothagam. Top = KNMI-LT 23667, Upper Nawata, posterior two thirds of carapace, dorsal view, with carpus of right cheliped visible at upper right. Estimated size of entire crab is carapace width, 38.5 mm; carapace length (estimated because of incomplete frontal region), 33.1 mm. Bottom = KNMI-LT 24193, Lower Nawata, ventral view of different specimen with intact left cheliped (in outer view) and with portions of pereiopods two and three. Length of chela (base of propodus to tip of propodal finger), 28.4 mm; height (just proximal to articulation of dactylus and propodus), 11.5 mm.

Materials and Methods

We examined 32 specimens that represented parts of fossil crabs from Mio-Pliocene strata exposed at Lothagam. These samples derived from both members of the Nawata Formation and from the Apak Member of the Nachukui Formation; thus, they ranged in age from 4.2 to 7.4 Ma (McDougall and Feibel 1999). By far the majority of the specimens comprised extremities and midsections of the fingers of the chelipeds, including both dactylar and propodal finger pieces. Occasional larger specimens contained fragments of carapace, but none was complete enough to allow positive identification, even to the family level. Specimens selected for photography were lightly cleaned with a dry paintbrush. Observations and line illustrations were made with a Wild M5 APO stereomicroscope. Measurements were made with digital calipers and rounded to the nearest tenth of a millimeter.

Systematic Description

Superfamily Potamoidea

The superfamily Potamoidea contains four families, two of which—Deckiniidae and Potamonautidae—occur today in East Africa.

Family Potamonautidae

Most characters that serve to distinguish crabs of the family Deckiniidae from those of the family Potamonautidae involve details of the orbital margins and the fifth pereiopod dactylus (Sternberg and Cumberlidge 1999), features that are not preserved in any of the Lothagam fossils. The Deckiniidae contains only the genus *Deckenia*, which currently contains two species, *D. imitatrix* and *D. mitis* (Ng et al. 1995). The group is characterized by an "ovate carapace" caused by (or fa-

cilitating) greatly swollen branchial chambers, which "seems to be associated with terrestrial habits or life in stagnant, poorly oxygenated waters" (Ng et al. 1995:583). The few fragments of dorsal carapace (e.g., figure 3.1) revealed no signs of an expanded branchial region, and thus the genus *Deckinia* (and the family Deckiniidae) have been ruled out. Although we could not detect a clear epigastric crest or a postorbital crest that extends to the epibranchial tooth, both of which are reported to characterize species in the Potamonautidae (Sternberg and Cumberlidge 1999:505, 506), these regions of the carapace were very poorly preserved. By default, and assuming also that all fossilized pieces sent to us came from crabs with similar carapace structure, we have assigned all of the Lothagam fossils to the family Potamonautidae. Arguing against this placement is the fact that one chelipedal carpus was preserved (KNMI-LT 23667; figure 3.1, top), and it appeared to possess a single anteromedial spine, whereas potamonautids typically have two such spines (Sternberg and Cumberlidge 1999; Cumberlidge 1999).

Potamonautidae gen. and sp. indet.
(Figures 3.1, 3.2)

Lothagam Material

- *Lower Nawata:* 1, dactylus fragment; 24193, claw and part exoskeleton; 24194, claw and part exoskeleton; 24195, claw fragments; 24196, chela fragment; 24197, claw fragment; 25094, Rt. propodal finger; 25095, dactylus; 25100, claw fragment; 25101, chela fragment; 25102, chela fragments; 25415, exoskeleton and claw fragment; 25416, limb fragments.
- *Upper Nawata:* 23667, exoskeleton; 24188, claw fragment; 24190, claws; 24191, 2 claw fragments; 24192, chela fragment; 25087, claw fragment; 25088, claw fragments; 25089, exoskeleton; 25090, claw and exoskeleton fragments; 25091, claw; 25092, chela fragment; 25093, 3 claw fragments; 25096, chela fragments; 25097, propodal finger fragment; 25098, claw fragment; 25099, claw fragment; 25128, dactylus fragment.
- *Apak Member:* 24187, chela fragment; 24189, claw fragment.

KNMI-LT 23667 (figure 3.1, top) is a large specimen, consisting mostly of a badly fractured posterior two-thirds of carapace and part of the right cheliped. The carpus of the right cheliped is striking, with sharp anteromedial and smaller anterolateral spines. Greatest carapace width 38.5 mm; greatest carapace length (estimated because of deteriorated frontal region) 33.1 mm.

KNMI-LT 24187 comprises the middle portion of a chelipedal finger. Five teeth are visible, the middle being largest and approximately twice the height of the other four. Its curvature suggests this is the dactylus of the left chela or possibly the propodus of the right chela (less likely). Length 10.0 mm; greatest height (at basal tooth) 5.4 mm.

KNMI-LT 24188 consists of a small basal to three-fourths length of a left chela dactylus with six low, rounded teeth on the cutting surface. Length 9.9 mm; height 4.6 mm at base.

KNMI-LT 24189 is a small fragment of only the sclerotized portion (i.e., teeth and immediately adjacent area) of a right dactylus or left propodus. Nine teeth, of varying sizes, are visible along the cutting surface. Length 17.2 mm; greatest height (at approximate level of basalmost tooth) 3.5 mm.

KNMI-LT 24190 comprises the dactylus and most of the propodus of a right chela in "outer" view. Length 28.5 mm; height 12.3 mm.

KNMI-LT 24191 comprises two claw fragments. The larger (thicker) fragment (length 16.4 mm; greatest height 6.5 mm) appears to be the right propodal finger and bears a row of cutting teeth. These increase in size from 1 to 5; tooth 6 is small, tooth 7 is approximately equal to 5, and thereafter the teeth decrease in size toward the tip. The smaller (thinner) fragment (length 18.5 mm; height 5.1 mm) appears to be dactylar (slender, more curved), but this is not definite. Approximately eight teeth are visible on this fragment, the proximal four of which are larger than the distal four.

KNMI-LT 24192 (figure 3.2e) is a large (length 23.5 mm; height 7.9 mm at base), strongly curved dactylus of the right chela and is obviously from a crab that possessed a large "gape" when chela fingers were closed. The cutting surface has a row of three or four small, rounded teeth and has minute tubercles distal to the last tooth.

KNMI-LT 24193 (figure 3.1) represents an entire left chela, most of the cheliped, and the coxa of pereiopods 2 and (partial) 3. Part of the thoracic sternum is visible, showing cuticular punctae. Length of the entire chela (base of propodus to tip of propodal finger) 28.4 mm; estimated length of chela plus carpal segment 30.5 mm. Greatest height of chela (measured just proximal to point of articulation of dactylus) 11.5 mm.

KNMI-LT 24194 comprises parts of both fingers of the left chela; additionally, a small piece of the sternal plastron is visible. Length (of entire fossil) 16.8 mm; width of entire fossil 16.8 mm. Greatest length of chela fingers 13.5 mm; height of fingers (combined) 8.2 mm.

KNMI-LT 24195 contains 13 fragments of chelipedal fingers. Two of the fragments are quite large (length of largest 21.5 mm; height 9.9 mm measured from the bottom of the first tooth to the top of the finger).

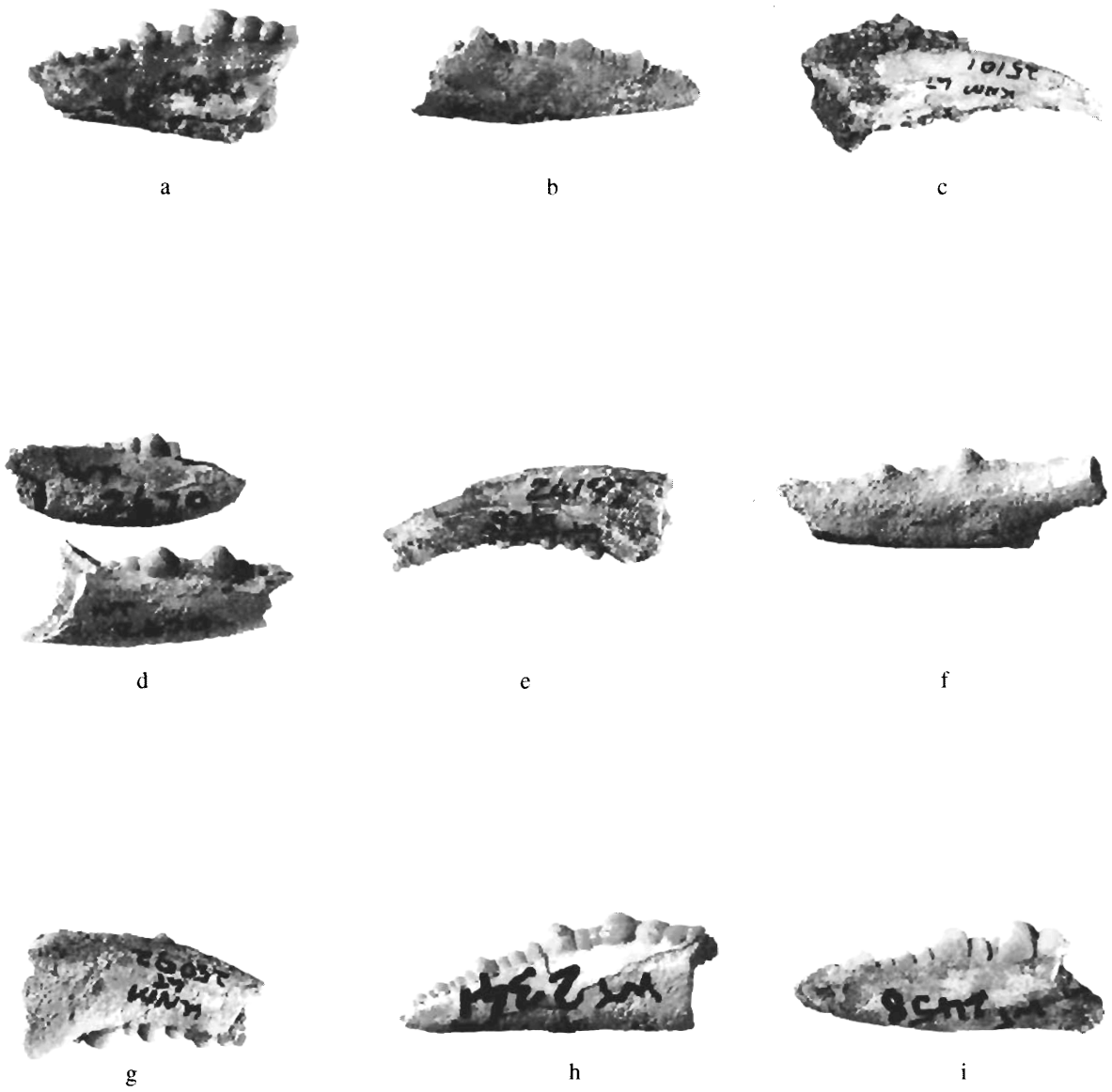

Figure 3.2 Photographs of representative fossil crab fragments from the Lower Nawata (a–d) and Upper Nawata (e–i). a = KNMI-LT 24196, length = 15.8 mm; b = KNMI-LT 25094, length = 23.2 mm; c = KNMI-LT 25101, length = 23.9 mm; d = KNMI-LT 25102 (two fragments), lengths = 19.7 mm and 17.2 mm; e = KNMI-LT 24192, length = 23.5 mm; f = KNMI-LT 25087, length = 18.0 mm; g = KNMI-LT 25092, length = 15.8 mm; h = KNMI-LT 25097, length = 13.3 mm; i = KNMI-LT 25099, length = 20.5 mm.

KNMI-LT 24196 (figure 3.2a) is a large piece of a chela tip (probably the propodal finger of the right chela), one of few that extends to almost the distal extremity. The cutting surface has 12 closely set teeth of varying sizes; teeth 4 and 7 (proximal to distal) are largest. Length 15.8 mm; height (at basalmost of two large teeth) 7.4 mm.

KNMI-LT 24197 is a minute tip of a claw with four or five low, well-worn teeth. Length 7.1 mm; height 3.0 mm.

KNMI-LT 25087 (figure 3.2f) probably represents a left dactylus. It consists of a long, thin claw fragment with two large teeth and one smaller one between them, also one small tooth distal to second large tooth. Length 18.0 mm; height 5.9 mm at basalmost large tooth.

KNMI-LT 25088 constitutes two fragments, both in poor condition. The larger (length 14.2 mm; height 3.5 mm at second basal tooth) consists of a row of eight teeth, sizes of which vary; teeth 2 and 4 (proximal to distal) are larger than the others. Smaller fragment length 11.2 mm; height at midpoint 3.4 mm.

KNMI-LT 25089 includes part of a fairly large female; the abdomen and part of the left chela propodus are fairly clear in ventral view. Greatest length of the

left chela 28.1 mm; greatest height 9.9 mm. There is also a partial right dactylus (length 18.0 mm; height 8.0 mm at base).

KNMI-LT 25090 includes six individual fragments of chelipeds. The matrix is extremely hard, and possibly for this reason the specimens appear glossy, much more so than in other samples. All specimens are badly fragmented; very little information can be gleaned from them. One notable specimen is a nearly entire claw in "outer view," with the manus ("hand" of the propodus) broken open and with tips of both fingers missing. Length of entire chela (fingers and imprint of propodus) 29.3 mm; height (measured just proximal to articulation with dactylus) 12.3 mm. Other pieces are mostly claw and leg fragments.

KNMI-LT 25091 constitutes an extremely large (length 25.4 mm; height 11.0 mm at base) dactylus of a right chela; most of the cutting surface is obscured by adhering calcareous matrix.

KNMI-LT 25092 (figure 3.2g) represents the proximal three-fourths of a right chela dactylus. A large basal tooth is followed distally by smaller, then larger, then smaller teeth. Eight teeth are visible along the cutting surface. Length 15.8 mm; height 8.7 mm at base.

KNMI-LT 25093 comprises three claw fragments. The largest fragment (length 18.7 mm; height 6.4 mm at base) is gently curving and bears 12 teeth on the cutting surface; the teeth are more or less alternate in size, medium to small. A second fragment constitutes a very small (length 10.1 mm; height 4.2 mm) claw tip, either left dactyl or right propodal finger; 13 teeth are present on the cutting surface, with teeth 4 and 6 larger and slightly more acute than the others. The third fragment comprises a midsection of a claw tip. Length 11.9 mm; height 6.5 mm.

KNMI-LT 25094 (figure 3.2b) is a large (length 23.2 mm; height 8.5 mm at base), heavy, well-formed right propodal fixed finger, entire nearly to the distal extremity. The entire row of teeth on the cutting surface is visible; teeth 5 and 9 (proximal to distal) are markedly larger and more acute than the others.

KNMI-LT 25095 is a thick, blunt finger, clearly the dactylus of a right chela, worn, with few details discernible. Length 18.0 mm; height 8.4 mm at base.

KNMI-LT 25096 comprises four small fragments. The largest (length 20.6 mm; height 8.8 mm at base) is probably a right chela dactylus. Another is the base of a chela dactylus.

KNMI-LT 25097 (figure 3.2h) is a small but remarkably clean fragment of a right propodal finger; it is fragile and hollow. Eighteen teeth are visible along the cutting surface; teeth 4 and 7 (proximal to distal) are larger than the others, some of which are minute, especially toward the tip. Length 13.3 mm; height 5.0 mm.

KNMI-LT 25098 is a thick basal portion of right chela dactylus. The basal tooth is large and is followed by seven or more teeth (extremity of finger missing) of alternating sizes. Length 13.2 mm; height at base 7.8 mm.

KNMI-LT 25099 (figure 3.2i) is a large piece of what appears to be the right propodal finger of an obviously sizeable crab (length 20.5 mm; height 7.4 mm at second basalmost tooth). Approximately ten teeth are visible along the cutting edge; the basal-most two teeth and teeth 5 and 9 (proximal to distal) rise above the others.

KNMI-LT 25100 represents the partial dactylus of a right chela with a large basal tooth plus eight small teeth; lots of adhering matrix. Length 20.2 mm; height 10.0 mm.

KNMI-LT 25101 (figure 3.2c) is a large (length 23.9 mm; height 9.5 mm at base), curving dactylus of a left chela (possibly the propodus of a right chela, but very delicate if so). Cutting surface with eight teeth, varying in size but mostly small.

KNMI-LT 25102 comprises two specimens. The larger is a dactylus of a left chela (length 19.7 mm; height 7.9 mm at most basal tooth) (figure 3.2d, lower photograph); there are two large teeth, with smaller teeth proximally and distally (not between them). The smaller specimen (length 17.2 mm; height 6.6 mm) (figure 3.2d, upper photograph) is a right dactylus or left propodal finger, with a cluster of three tightly opposed teeth, of which the center one is the largest.

KNMI-LT 25128 comprises a midsection of a right chela dactylus; the cutting surface has eight visible teeth. Length 11.5 mm; height 7.8 mm at base.

KNMI-LT 25415 comprises two specimens. The (larger) first specimen is a rare "whole crab" fossil, showing the underside (mostly) and partial upper surface of the carapace, plus part of one cheliped. Some sternal plates and sutures are visible, but it is difficult to enumerate these as the specimen is in very poor condition. Estimated size of the entire crab is 27.8 mm carapace width. The second specimen is a very thin (probably dactylar) chela finger with approximately seven low, worn teeth. Length 12.4 mm; height 3.9 mm at base.

KNMI-LT 25416 includes a nearly complete left chela and a large carpal segment (possibly from a different crab). Length of nearly complete chela 21.5 mm; height 7.8 mm. Other material includes small pieces of carapace and a partial right cheliped dactylus (length 15.1 mm; height 9.5 mm at base). There are also many unidentifiable fragments.

KNMI-LTI 1 appears to be a partial left chela dactylus; seven teeth are visible near the base of the cutting surface. Length 17.6 mm; height 10.9 mm at base.

Paleoenvironmental Interpretation

Had these fossils proven to be members of the East African family Deckiniidae, some speculation on habitat might have been warranted because the inflated carapace of deckiniids may reflect a low oxygen environment (Ng 1988; Ng et al. 1995). The fact that they are apparently members of the Potamonautidae reveals less information, as potamonautids are known from a much wider range of habitats, virtually throughout sub-Saharan Africa and including the Nile River in Egypt, eastern Africa, South Africa (e.g., Stewart 1997; Cumberlidge 1999), and parts of Madagascar. In general, however, potamonautids are commonly referred to as "river crabs" because of their propensity for these habitats. Thus, we may assume that the Lothagam fossil crabs are indicative of a relatively well-oxygenated riverine system. Virtually all freshwater crabs, including the African potamonautids, are opportunistic scavengers and predators, and thus the presence of these crabs in Lothagam furnishes little information about co-occurring species.

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References Cited

Abele, L. G., T. Spears, and N. Cumberlidge. 1999. Biogeography and phylogeny of freshwater crabs based on molecular evidence. In *Program and Abstracts, The Crustacean Society Summer Meeting*, p. 20. Lafayette, Louisiana, 26–30 May 1999.

Bott, R. 1970a. Betrachtungen über die Entwicklungsgeschichte und Verbreitung der Subwasser-Krabben nach der Sammlung des Naturhistorischen Museums in Genf/Schweiz. *Revue Suisse de Zoologie* 77:327–344.

Bott, R. 1970b. Die Subwasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte. Eine revision der Potamoidea und der Parathelphusoidea (Crustacea, Decapoda). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 526:1–338.

Cumberlidge, N. 1991. *Sudanonautes kagorensis*, a new species of fresh-water crab (Decapoda: Potamoidea: Potamonautidae) from Nigeria. *Canadian Journal of Zoology* 69: 1938–1944.

Cumberlidge, N. 1999. *The Freshwater Crabs of West Africa: Family Potamonautidae.* Faune et Flore Tropicales No. 35. Paris: Institut de Recherche pour le Développement.

Cumberlidge, N., and R. Sachs. 1989a. A key to the crabs of Liberian fresh waters. *Zeitschrift für Angewandte Zoologie* 76:221–229.

Cumberlidge, N., and R. Sachs. 1989b. Three new subspecies of the West African freshwater crab *Liberonautes latidactylus* (de Man, 1903) from Liberia, with notes on their ecology. *Zeitschrift für Angewandte Zoologie* 76:425–439.

Guinot, D., B. G. M. Jamieson, and C. C. Tudge. 1997. Ultrastructure and relationships of spermatozoa of the freshwater crabs *Potamon fluviatile* and *Potamon ibericum* (Crustacea, Decapoda, Potamidae). *Journal of Zoology* (London) 241: 229–244.

Martin, J. W., and G. E. Davis. 2001. *An Updated Classification of the Recent Crustacea.* Science Series No. 39. Los Angeles: Natural History Museum of Los Angeles County.

McDougall, I., and C. S. Feibel. 1999. Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift. *Journal of the Geological Society* (London) 156:731–745.

Ng, P. K. L. 1988. *The Freshwater Crabs of Peninsular Malaysia and Singapore.* Singapore: Department of Zoology, National University of Singapore, and Shing Lee Publishers.

Ng, P. K. L., Z. Stevcic, and G. Pretzmann. 1995. A revision of the family Deckiniidae Ortmann, 1897 (Crustacea: Decapoda: Brachyura: Potamoidea), with description of a new genus (Gecarcinucidae, Gecarcinucoidea) from the Seychelles, Indian Ocean. *Journal of Natural History* 29: 581–600.

Pretzmann, G. 1972. Die Pseudothelphusidae (Crustacea, Brachyura). *Zoologica* 42:1–182.

Pretzmann, G. 1973. Grundlagen und Ergebnisse der Systematik der Pseudothelphusidae. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 11:196–218.

Rodríguez, G. 1982. *Les crabes d'eau douces d'Amerique: Famille des Pseudothelphusidae.* Faune Tropicale 22. Paris: ORSTOM.

Rodríguez, G. 1986. Centers of radiation of fresh-water crabs in the neotropics. In R. H. Gore and K. L. Heck, eds., *Biogeography of the Crustacea*, pp. 51–67. Crustacean Issues 4. Rotterdam: Balkema.

Rodríguez, G. 1992. *The Freshwater Crabs of America: Family Trichodactylidae and Supplement to the Family Pseudothelphusidae.* Faune Tropicale 31. Paris: ORSTOM.

Sternberg, R. von, and N. Cumberlidge. 1999. A cladistic analysis of *Platythelphusa A.* Milne-Edwards, 1887, from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. *Journal of Natural History* 3:493–511.

Sternberg, R. von, N. Cumberlidge, and G. Rodríguez. 1998. On the marine sistergroups of the freshwater crabs (Crustacea: Decapoda). *Journal of Zoological Systematics and Evolutionary Research* 37:19–38.

Stewart, B. A. 1997. Morphological and genetic differentiation between populations of river crabs (Decapoda: Potamonautidae) from the Western Cape, South Africa, with a taxonomic revision of *Gecarcinautes brincki. Zoological Journal of the Linnean Society* 199:1–21.

TABLE 3.1 Classification of Freshwater Crabs[a] and Their Present-day Distribution

Subphylum Crustacea
Order Decapoda
Suborder Pleocyemata
Infraorder Brachyura
Section Eubrachyura[b]
Subsection Heterotremata

Family	Location
Superfamily Portunoidea[c]	
Family Trichodactylidae	Central and South America
Superfamily Pseudothelphusoidea	
Family Pseudothelphusidae	Central and South America
Superfamily Gecarcinucoidea	
Family Gecarcinucidae	Indian subcontinent and Southeast Asia
Family Parathelphusidae	Indian subcontinent, Southeast Asia, and Australasia
Superfamily Potamoidea	
Family Deckiniidae	East Africa
Family Platythelphusidae	Lake Tanganyika
Family Potamidae	Northwest Africa, southeast Europe, the Middle East, the Himalayas, Southeast Asia, and China
Family Potamonautidae	Subsaharan Africa (plus the Nile in Egypt) and Madagascar

[a] Contains a total of three subsections, 20 superfamilies, and 61 families (Martin and Davis 2001).

[b] Other families of brachyuran crabs have species that can or must live in freshwater (e.g., *Metapaulius depressus* in the Grapsidae, *Uca subcylindrica* in the Ocypodidae, and others) but that are not confused with the potamon-like crabs (the former "Family Potamida").

[c] Contains two other families of crabs restricted to marine or estuarine waters.