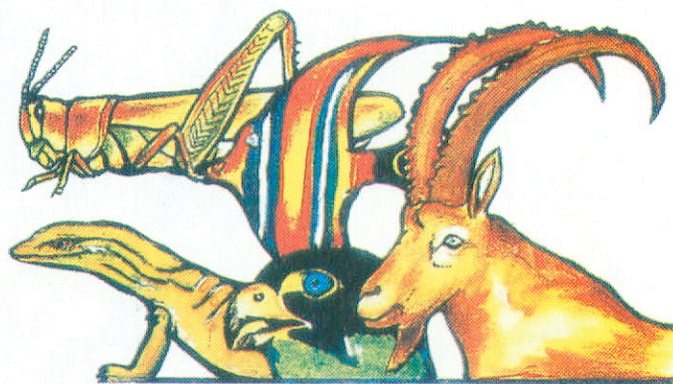


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**PRELIMINARY REVIEW OF THE FRESHWATER MUSSELS
(MOLLUSCA: BIVALVIA: UNIONOIDA) OF NORTHERN
AFRICA, WITH AN EMPHASIS ON THE NILE**

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ABSTRACT

The freshwater mussels (Mollusca: Bivalvia: Unionoidea) of Northern Africa, including the Nile Basin, have received a good deal of attention in recent decades, but published reviews/revisions are at odds with each other and with our own museum work. We undertook a preliminary reevaluation of the species of the region to provide a consistent baseline for future research efforts and to spark interest in the study of freshwater mussels among Egyptian zoologists. Twenty-nine species in four families are reported to occur in Northern Africa, of which 26 in three families in the Nile and Lake Turkana. The Nile is an area of overlap between the southern extent of the Palearctic fauna and the northern limit of the Afrotropical fauna. The traditional concept of the species *Chambardia wahlbergi* (Krauss, 1848) is herein regarded as four distinct lineages in the region: *Ch. wahlbergi hartmanni* (von Martens, 1866), *Ch. bourguignati* Bourguignat, 1885, *Ch. letourneuxi* Servain, 1890 and *Aspatharia marnoi* (Jickeli, 1874). We provide an annotated species list of all unionoid species in northern Africa, and Nile species are illustrated. Areas of future research potential are discussed.

INTRODUCTION

Freshwater mollusks of the bivalve order Unionoidea (also known as freshwater mussels or naiades) are conspicuous members of lentic and riverine habitats worldwide (Table 1). Although

estimates vary, the described global diversity for the group is estimated to be ca. 900 ± 50 species (Graf & Cummings, 2006b; Graf, in review). The "hot spots" of unionoid diversity are the large, stable river systems found in the

temperate climates of eastern North America and southeastern Asia (ca. 290 and 230 spp., respectively). In contrast, the African assemblage is relatively depauperate, with fewer than 90 species recognized in recent, continent-wide revisions (Haas, 1969; Mandahl-Barth, 1988; Daget, 1998). The Nile Basin (Fig. 1) has received special attention in the last three decades (e.g., Mothersill *et al.*, 1980; Bouchet & Danrigal, 1982; Adam, 1986, 1990; Van Damme, 1984; Abell *et al.*, 1995; Ibrahim *et al.*, 1999; Bogan, 2004). However, based upon both examination of specimens in major museum collections and a literature review, we have found the diversity estimates in those publications to be contradictory (to each other and to our own observations), and a preliminary reevaluation of the freshwater mussels of the Nile Basin is warranted. Our objective is to provide an illustrated checklist of the families, genera and species of the Nile and northern Africa in general, as well as a biogeographical context (*i.e.*, areas of endemism) to facilitate identification and to provide a consistent baseline for future research.

'Northern Africa' is here defined as the entire Nile Basin, including lake Victoria, Albert and Edward, the adjacent Lake Turkana Basin (Fig. 1), and the Mediterranean areas of Morocco

and Algeria. Only 150 years ago, the course and source of the Nile were unidentified (Burton, 1860). That river is now known to be the longest on Earth, running some 6,693 km from its headwaters in Uganda (5588 km from Lake Victoria) through Sudan and Egypt to the Nile Delta (Rosetta and Damietta branches) on the Mediterranean and draining roughly 2.8 million km². Its headwaters drain portions of Tanzania, Kenya, Burundi, Rwanda and the Democratic Republic of the Congo as well (Fig. 1). The main branches of the Nile are the White Nile (*Al-Neel al-Abyad*) fed by the central African Great Lakes (Victoria, Albert and Edward) and the Blue Nile (*Al-Neel al-Azraq*) flowing from Lake Tana in Ethiopia. Significant biogeographic features include a series of natural cataracts (*ganadel*) in the Upper Nile, the man-made Aswan high dam and Lake Nasser on the Egyptian-Sudanese border. The Nile Basin has been divided into a number of ecoregions based upon its freshwater fauna, though areas of endemism have generally been defined based upon fishes with little attention paid to mollusks (Thieme *et al.*, 2005).

The main aspects of the general biology and taxonomy of the Unionoida were recently reviewed by Bogan (2004). The principal reasons for studying the

Unionoida in Africa are because (1) they have been and continue to be neglected, and (2) they are biologically interesting. In the Nile and beyond, tropical malacology has historically focused on applied and medical aspects because of the hazardous prevalence of schistosomiasis and other gastropod-borne parasites (e.g., Kristensen *et al.*, 1999; DeJong *et al.*, 2001). We advocate a zoological (rather than medical) perspective to molluscan research, and the various taxa of the Unionoida provide interesting patterns applicable to studies of such topics as phylogeny (Graf, 2000; Graf & Cummings, 2006b), molecular evolution (Hoeh *et al.*, 2002; Walker *et al.*, 2006), life history variation (Haag & Staton, 2003), parasite-host interactions (Vaughn & Taylor, 2000), functional morphology (Watters, 1993), and biogeography (Banarescu, 1990). In other areas of the world, especially North America, freshwater mussels are also of special interest due to their imperiled status (Lydeard *et al.*, 2004; Strayer *et al.*, 2004), but the conservation status of the Nile fauna is not well understood (Bogan, 2004).

MATERIALS AND METHODS

We have recently set ourselves upon the revision of the freshwater mussels of the southern continents (*i.e.*, Australasia, India,

South America and Africa), and this preliminary reevaluation of the northern African species is based upon data gathered in that context. Specimens examined to-date are from 14 major collections in North America, Europe and Australia. Specimen images and label data were captured on-site and combined with published taxonomic literature as part of the MUSSEL Project Database (Graf & Cummings, 2006a; Graf, in review).

The recent revisions/reviews of Haas (1969), Van Damme (1984), Mandahl-Barth (1988), Daget (1998) and Ibrahim *et al.* (1999) provided the taxonomic hypotheses that served as the basis of our analyses of Nile freshwater mussels taxa, as well as those species in adjacent Algeria and Morocco and the rivers of the endorheic Lake Turkana Basin. Specimen images and locality records in the MUSSEL Project Database were used to test the range of conchological variation (no soft anatomy was available) and geographical distribution for taxa reported from the Nile Basin. Generic designations follow Daget (1998; except where noted) and family-level taxonomy is after Graf & Cummings (2006b; Table 1). Specimen records and complete synonymies are available under “*Mashrua Al-Mahar*” on the MUSSEL Project Web Site (<http://www.mussel-project.net/>).

RESULTS

As of February 2007, the MUSSEL Project Database contained 14,752 specimen records, including 3651 from Africa and 1355 from the Nile and Northern Africa.

Twenty-nine species of freshwater mussels are known from Northern Africa, 26 of which occur in the Nile and Turkana basins (see below). The remaining species are limited to Algeria and Morocco (in Africa). The Nile can be divided into three areas of endemism (Egypt, Upper Nile and the Great Lakes region) based upon freshwater mussel distributions (Table 2), and these roughly correspond to the ecoregions identified by Thieme *et al.* (2005). The area of highest endemism in the Nile Basin is the headwaters region associated with the Great Lakes (12 species, 71% endemic).

SPECIES ACCOUNTS

Superfamily UNIONOIDEA

Rafinesque, 1820

Family UNIONIDAE s.s.

Genus *Unio* Philipsson in Retzius, 1788

Unio mancus (Lamarck, 1819), (Fig. 2A) — Widely distributed in Mediterranean Europe, Northern Africa and the Levant (Haas, 1940; Falkner 1994; Falkner *et al.* 2001). Until recently, most authorities referred to this species under the name *Unio elongatulus* Pfeiffer, 1825 (Nagel *et al.*, 1998; Araujo *et*

al., 2005). *U. mancus durieui* Deshayes, 1847 has been applied to populations in Morocco and Algeria, and *U. mancus dembeae* Reeve, 1865 refers to those populations reported to occur in the White Nile, Blue Nile and Lake Tana. Fossils of *U. mancus dembeae* have been reported from the Omo (Turkana Basin) and the Faiyûm area in Egypt (Ibrahim *et al.*, 1999). A single recent lot (2 specimens) labeled “Egypte” in the Muséum National d’Histoire Naturelle in Paris has not been corroborated. *U. mancus* is the only Palearctic/European freshwater mussel species to occur in the Nile Basin.

Unio abyssinicus von Martens, 1866, (Fig. 2B) — Recent records substantiated by voucher specimens are known only from Lake Tana and the upper Blue Nile. Ibrahim *et al.* (1999) also listed two fossil forms from the lower Nile: *Unio willcocksii* Newton, 1899 and *U. fayumensis* Pilsbry & Bequaert, 1927. Egyptian researchers have occasionally referred to living specimens in the lower Nile (*e.g.*, Aboul-Dahab, 2002; Ramadan, 2003), but we are not certain of the validity of these reports.

Genus *Anodonta* Lamarck, 1799
Anodonta cygnea (Linnaeus, 1758), (Fig. 2C) — Widespread and common in western Eurasia,

including Northern Africa. Van Damme (1984) and Daget (1998) regarded *Anodonta anatina* (Linnaeus, 1758) as a distinct species, also in Algeria and Morocco. *Anodonta* is not known from the Nile Basin.

Genus *Potomida* Swainson, 1840

Potomida littoralis (Lamarck, 1801), (Fig. 2D) — Circum-Mediterranean in distribution, with the subspecies *P. littoralis fellmanni* (Deshayes, 1848) reported from Algeria and Morocco in northwestern Africa. *Potomida* is not known from the Nile Basin except for a single, corroborated specimen in the Muséum National d'Histoire Naturelle in Paris labeled "Abyssinie."

Genus *Coelatura* Conrad, 1853

Coelatura aegyptiaca (Cailliaud, 1827), (Fig. 3A) — Widespread, extending from the Nile Basin east through the Chad-Chari Basin and the Niger to Senegal. In the Nile, it occurs from the Delta up to the Great Lakes, including Lake Albert. *C. aegyptiaca* is an extremely variable taxon, and we predict that a thorough revision (e.g., applying molecular characters and a quantitative approach to morphological variation) will likely reveal the current concept to be a lumped species complex. What is unknown is the extent to which the observed variation is ecophenotypic, and deciphering conchological variation is a well-

known problem in freshwater malacology (Ortmann, 1920; Graf, 1998). Ibrahim *et al.* (1999) recognized fourteen "species" in Egypt corresponding to this complex. We suspect that that number is an over-estimate of the actual diversity — many of those species names were not treated as valid in the publication in which they were introduced (Pallary, 1924). We have seen specimens from Lake Turkana referred to this species in various collections.

Coelatura stagnorum

(Dautzenberg, 1890) — Does not occur in the Nile. Ibrahim *et al.* (1999; Bogan, 2004) listed "*Coelatura* [sic] (*Horusia*) *bourguignati* (Rochebrune, 1886)" as occurring in "Lower Egypt." That trivial name is preoccupied by *Unio bourguignati* Landrin, 1864, which is a junior synonym of *Coelatura aegyptiaca* (Mandahl-Barth, 1988). *Unio stagnorum* Dautzenberg, 1890 is the next available nomen for the species referred to by Rochebrune. However, *C. stagnorum* is otherwise known only from the lower Congo Basin (Graf & Cummings, 2006a: their figs. 26-27). Ibrahim *et al.*'s record was perhaps intended for Landrin's nominal species, which was figured by Pallary (1924: his Pl. 2, Figs. 19-21).

Coelatura bakeri (H. Adams, 1866), (Fig. 3B) — Previously

reported as endemic to Lake Albert (e.g., Mandahl-Barth, 1988; Daget, 1998; Scholz & Glaubrecht, 2004), but it is also known from Lake Edward (see next species).

Coelatura stuhlmanni (von Martens, 1897), (Fig. 3D) — Analogous to the case with *C. bakeri*, *C. stuhlmanni* has been claimed as endemic to Lake Edward, but it is also known from Lake Albert. It would seem that the taxonomy for these two species has incorrectly proceeded on strictly geographical bases: sculptured *Coelatura* from Albert were identified as *C. bakeri*, and those from Edward were called *C. stuhlmanni*.

Coelatura alluaudi (Dautzenberg, 1908), (Fig. 3E) — Endemic to Lake Victoria; rare. See comments under *C. cridlandi*.

Coelatura cridlandi Mandahl-Barth, 1954, (Fig. 3C) — Reported only from Lake Victoria. Mandahl-Barth (1988: 17) referred to *C. cridlandi* as, "The largest of the *Coelatura* [*sic*] species and the only one which cannot be confused with any other species." However, after examination of the available specimens (including the types) and a literature review, it is possible that this species is synonymous with *C. alluaudi*.

Coelatura hauttecoeuri (Bourguignat, 1883), (Fig. 3F) — Confined for the most part to Lake Victoria but also found down the Victoria Nile in Lake Kyoga. Like *C. aegyptiaca*, *C. hauttecoeuri* is a highly variable species and may be split into multiple lineages upon more rigorous scrutiny.

Coelatura rothschildi (Neuville & Anthony, 1906) — Known from fossils and subfossils in the endorheic Lake Turkana Basin.

Genus *Nitia* Pallary, 1924

Nitia teretiuscula (Philippi, 1847), (Fig. 4A) — Widespread; in the Nile Basin from the upper White Nile downstream to the Delta, and reported in West Africa from the Chad-Chari, Senegal, Volta and Niger basins. Specimens from the Chad-Chari Basin have been regarded as a distinct species, *N. mutelaeformis* (Germain, 1906) (Haas, 1969; Daget, 1998).

Nitia acuminata (H. Adams, 1866), (Fig. 4B) — Generally regarded as endemic to Lake Albert, although we have seen a single lot in the National Museum of Natural History, Washington from Ad Duwaym in Sudan.

Nitia monceti (Bourguignat, 1883), (Fig. 4C) — Endemic to Lake Victoria (but see the following).

Nitia chefneuxi (Neuville & Anthony, 1906) — Endemic to Lake Turkana; perhaps extinct. Mandahl-Barth (1988) regarded this taxon as conspecific with *N. moncei*.

Family MARGARITIFERIDAE
Henderson, 1929

Genus *Pseudunio* Haas, 1910

Pseudunio auricularia (Spengler, 1793), (Figure 2E.) — Distributed from the Iberian Peninsula South to Northwestern Africa. *P. auricularia* does not occur in the Nile and is the only margaritiferid found in Africa (D.G. Smith, 2001). The African populations have been referred to as *P. auricularia marocana* (Pallary, 1918).

Superfamily ETHERIOIDEA
Deshayes, 1830

Family ETHERIIDAE s.s.

Genus *Etheria* Lamarck, 1807

Etheria elliptica Lamarck, 1807, (Fig. 5) — Widespread; known from Angola and the upper Congo in Zambia through West Africa and the Nile, and Madagascar (Pilsbry & Bequaert, 1927: Map 6; Pain & Woodward, 1961). In the Nile, *E. elliptica* has historically been reported from Lake Victoria downstream to the Nile Delta, but it has not been found recently as far north as Egypt (Van Damme, 1984). Also found in the Turkana Basin.

Family IRIDINIDAE Swainson, 1840 (+ MUTELIDAE Gray, 1847)

Genus *Mutela* Scopoli, 1777

Mutela dubia (Gmelin, 1791), (Fig. 6A) — Widespread, with several recognized subspecies. *M. dubia dubia* occurs in West Africa, from Senegal to the Chad-Chari Basin. *M. d. garambae* Pilsbry & Bequaert, 1927 is known from the upper Congo Basin, adjacent to Lakes Albert and Edward. In the Nile, *M. d. nilotica* (Caillaud, 1823) occurs from the Great Lakes downstream to the Delta, and *M. d. emini* von Martens, 1897 is considered a Lake Albert endemic. These subspecies are poorly characterized and seem to be based more upon geography than morphology. We have seen a single lot reported from the Lake Turkana Basin referable to *M. dubia* in the Natural History Museum, London.

Ibrahim *et al.* (1999) treated *M. singularis* (Pallary, 1924) as an endemic species of the lower Nile in Egypt, but most other authorities have regarded that form as within the normal range of variation expressed by *M. dubia*.

Mutela rostrata (Rang, 1835), (Fig. 6B) — Widespread; known from West Africa east through the Nile Basin, from Lakes Albert and Edward north to the Nile Delta. The affinity of "*Mutela rostrata*" populations occurring throughout the northern Africa to those further south requires reevaluation (Graf &

Cummings, 2006a). A single lot of this species in the Academy of Natural Sciences of Philadelphia is recorded as being from Lake Turkana.

***Mutela bourguignati* Bourguignat, 1885**, (Fig. 6C) — Generally regarded as endemic to the Lake Victoria basin, as well as various localities along the Victoria Nile (but see the following).

***Mutela alluaudi* Germain, 1909**, (Fig. 6D) — Originally described from, and regarded as endemic to, Lake Albert, but we have also seen specimens from Lake Edward. *M. alluaudi* may be conspecific with the previous species. Both share conspicuous pseudotaxodont hinge dentition and a similar shell outline.

Genus *Aspatharia* Bourguignat, 1885

***Aspatharia chaiziana* (Rang, 1835)**, (Fig. 7A) — Widespread; from West Africa to the Nile Basin. In the Nile Basin, *A. chaiziana* is apparently restricted to the White Nile below the Great Lakes. We have only seen three lots of specimens in various collections attributed to the Lower Nile in Egypt.

The taxonomy of this *A. chaiziana* requires reevaluation. Until relatively recently, it was confounded with *Chambardia rubens* (Lamarck) (e.g., Leloup,

1950; Mandahl-Barth, 1968; Haas, 1969). Both are generally ovate in outline, with pink nacre, and both species are broadly sympatric in West Africa and the Nile. However, based upon soft-anatomical characters, specifically the degree of posterior mantle fusion, these two species belong to different genera (Daget, 1961, 1962). Conchologically, *A. chaiziana* can be recognized by its nearly parallel dorsal and ventral margins and its longer hinge line. There is a considerable gap between the umbos and the ligamental fossette, and the fossette often extends beyond the posterior pedal retractor scar. *Ch. rubens* is highly variable, but generally has a rounded ventral margin (especially in young specimens) and a shorter hinge line.

The concept of *A. chaiziana* applied here is that of Mandahl-Barth (1988; Van Damme, 1984), and it lumps *A. chaiziana* sensu stricto with five additional nominal species from West Africa recognized by Daget (1962, 1998). In the Nile, adult specimens are typically reniform, with a conspicuously concave ventral margin, and East African populations may warrant distinction from those in the West under the name *Aspatharia innesi* (Pallary, 1903).

Aspatharia marnoi (Jickeli, 1874), (Fig. 7C) — Confined to the upper Nile Basin.

Aspatharia marnoi has been treated as a synonym of *Chambardia wahlbergi hartmanni* in the Nile Basin (Van Damme, 1984; Mandahl-Barth, 1988; Daget, 1998; Ibrahim *et al.*, 1999). However, we have seen several specimens from the White Nile that are actually part of the widespread *Aspatharia pfeifferiana* Species Group, which includes *A. pfeifferiana* (Bernardi, 1860), *A. dahomeyensis* (Lea, 1859), *A. subreniformis* (Sowerby, 1867) and others (Graf & Cummings, 2006a). We have no first-hand experience with the type of *Spatha marnoi*, only Jickeli's plate (1874: his pl. 8, fig. 3). *Spathella fourtaui* Pallary, 1903 (his pl. 1, fig. 3) is also available for this species, and both may, with further study, be found to be conspecific with West African species of the *Aspatharia pfeifferiana* Species Group. *A. marnoi* is distinguished from *Ch. wahlbergi* by its slightly reniform outline, bluish nacre and longer hinge line.

Aspatharia divaricata (von Martens, 1897), (Fig. 7B) — We know this species only from the type specimen from Lake Victoria.

Genus *Chambardia* Servain, 1890
Chambardia rubens (Lamarck, 1819), (Fig. 8A) — Widespread; through West Africa and the Nile

Basin, from the White Nile downstream to the Nile Delta in Egypt. Nile populations are generally referred to *Ch. rubens arcuta* (Cailliaud, 1823) (later emended to *arcuata*), although our casual conchological observations have revealed little to distinguish it from *Ch. rubens rubens* in the West. See additional comments under *A. chaiziana*, above.

Chambardia trapezia (von Martens, 1897), (Fig. 8B) — In Lakes Victoria, Albert and Kyoga and the intervening Victoria Nile. Specimens from Lake Albert are treated as a separate subspecies, *Ch. trapezia ovoidea* (Mandahl-Barth, 1988).

Chambardia wahlbergi (Krauss, 1848), (Fig. 8C) — Widespread; from southern Africa, through eastern Africa to the Nile Basin. Numerous subspecies have traditionally been recognized throughout the continent: *Ch. wahlbergi wahlbergi* in southern Africa; *Ch. wahlbergi hartmanni* (von Martens, 1866) in the upper Nile, Great Lakes, Lake Turkana and coastal drainages in Kenya and Tanzania; *Ch. w. guillaini* (Récluz, 1850) in coastal Somalia; *Ch. w. tabula* (Sowerby, 1867) in West Africa; *Ch. w. welwitschi* (Morelet, 1868) in Angola; *Ch. w. bourguignati* (Bourguignat); and *Ch. w. letourneuxi* (Servain, 1890). *Ch. welwitschi* was elevated to species status by Graf & Cummings

(2006a), and the last two "subspecies" are here elevated to species level based upon their distinctive morphologies and broad-scale sympatry with *Ch. w. hartmanni* in the Nile and East Africa. The *Chambardia wahlbergi* Complex is in need of a continent-wide revision. It seems likely that the species-level diversity is currently under-estimated.

Chambardia bourguignati (Bourguignati, 1885), (Fig. 8D) — Poorly defined distribution in Tanzania including Lake Victoria, and perhaps East Africa well. *Ch. bourguignati* differs from *Ch. wahlbergi* in being less compressed and less elongate, with the umbos placed more centrally. *Ch. bourguignati* generally has white nacre. However, this taxon, as traditionally conceived is not well understood and may represent multiple lineages.

Chambardia letourneuxi (Servain, 1890), (Fig. 8E) — Endemic to the lower Nile in Egypt. It was recently listed as an extinct subspecies of *Ch. wahlbergi*, but we have identified a number of specimens mislabeled as "*Ch. rubens arcuta*." *Ch. letourneuxi* is distinguished by its heavier shell, white nacre and reniform outline.

DISCUSSION

The Nile River serves as a causeway connecting the southern extent of the Palearctic European and Southwest Asian freshwater mussel assemblage with that of the Sub-Saharan, Afrotropical (Table 2). Only a single Palearctic species, *Unio mancus*, reaches the Nile, but *U. abyssinicus* is a Nile endemic of an otherwise European genus. The other 22 species of the Nile belong to genera of western and central Africa, but the Nile freshwater mussel fauna is not homogeneous. Eight species (Table 2) are considered to be widespread, occurring widely in both the Nile and West Africa, and both *Chambardia wahlbergi hartmanni* and *Etheria elliptica* are found in East Africa as well. Among the 15 freshwater mussel species restricted to the Nile Basin, the taxa can be grouped according to three areas of endemism (Table 2): the headwaters area of the Great Lakes (17 spp., 12 endemic), the Upper Nile (11 spp., 2 endemic) and the lower Nile (i.e., Egypt; 8 spp., only 1 endemic). These patterns reflect the varied historical and contemporary influences on species diversity in those portions of the Nile Basin (Thieme *et al.*, 2005).

Lake Turkana (formerly Lake Rudolf) is an endorheic basin adjacent to Lake Victoria. The former, however, was, during the late Pleistocene and early Holocene,

part of the Upper Nile (Nyamweru, 1989). Today, the molluscan fauna is predictably depauperate, but over geologic time, the lake had a relatively richer assemblage of both gastropods and bivalves (Williamson, 1981, 1985). Van Damme (1984) considered the Recent freshwater mussel fauna of Lake Turkana to consist of a single species, *Nitia chefnuexi*. From Lake Turkana and the tributary Omo Basin, we have seen records in various collections of five additional Recent species (plus the fossil *Coelatura rothschildi*) (Table 2).

Our tally of the freshwater mussels of Northern Africa is most similar to that of Mandahl-Barth (1988). Van Damme (1984) and Daget (1998) regarded the African *Anodonta* populations to belong to two different species, *A. cygnea* and *A. anatina*, but otherwise those systems are similar as well. Our species list differs from all of those with regard to three species: we have elevated *Chambardia bourguignati* and *Ch. letourneuxi* to full species based upon their broad-scale sympatry with *Ch. wahlbergi hartmanni* and morphological distinctiveness, and we removed *A. marnoi* from the synonymy of *Ch. wahlbergi hartmanni* to the genus *Aspatharia*. We expect that a more comprehensive reevaluation of the Nile fauna will be able to reinstate additional species from synonymy, whereas others that are currently treated as valid will be revealed as

synonymous with other taxa. For example, *Coelatura aegyptiaca*, *Mutela dubia* and *Chambardia bourguignati* may each represent "lumped" aggregations of morphologically similar populations, and both *C. cridlandi* and *M. alluaudi* may be found to be conspecific with other species (see Species Accounts).

Having reviewed the current state of our knowledge of the freshwater mussel species in Northern Africa (with an emphasis on the Nile Basin), we would like to close this article with a brief discussion of some important problems and unanswered questions in freshwater malacology that might be addressed by further Nile research. Because Northern Africa is inhabited by 4 families of freshwater mussels (three in the Nile; Table 1), the components of the Nile assemblage have evolutionary ties to a wide range of taxa around the world. Research upon the mussels of Egypt (and indeed Africa in general) is of global importance to the freshwater malacological community.

Of foremost utility would be a modern, comprehensive revision of the Nile Basin malacofauna and the species-level relationships to mussels in the adjacent areas of Africa and the Palearctic and Indotropical regions. A number of continent-wide revisions of the African Unionoida are available (Flaas, 1969; Mandahl-Barth, 1988; Daget, 1998), but these generally

under-estimate Nile diversity. Van Damme's (1984) system for Northern Africa is generally similar to those of Mandahl-Barth and Daget. The bivalves of the Egyptian Nile were recently reviewed by Ibrahim *et al.* (1999), but that parochial work is inadequate for most rigorous, scientific purposes. In the absence of an accurate assessment of Nile species and genera, little can be deduced about the history of the freshwater mussel assemblage, and the generality of the results from other kinds of studies (e.g., physiology, life history, ecology, paleontology) can only be guessed — How can the biological importance of the freshwater mussel species of Northern Africa be considered if we don't even know what they are? We expect that such a comprehensive revision will require a complete reevaluation of museum material and fresh collections for molecular and anatomical analyses.

The study of the evolutionary patterns of the Unionoida suffers from a deficiency of basic life history and anatomical data. Freshwater mussels, among bivalves, are unique in their possession of both parental care and larval parasitism (reviewed by Kat, 1984 and Wächtler *et al.*, 2001), and variation in the structures associated with those functions have figured prominently in mussel systematics (Heard & Guckert,

1971; Graf & Ó Foighil, 2000; Graf & Cummings, 2006b). Malacological collections have historically relied upon post-larval shells, and the soft anatomical and larval characters of many species can only be inferred through conchological comparisons of adults. The larvae of the Iridinidae provide a perfect example. Iridinids are endemic to Africa (Table 1), and the family is hypothesized to possess a unique modification of the lasidium-type larva called an haustorium (Parodiz & Bonetto, 1963). However, as discussed by Graf & Cummings (2006b), haustoria are only known from a single species in Lake Victoria, *Mutela bourguignati* (Fryer, 1961; Wächtler *et al.*, 2001). Recently, Garo (2006) reported on the lasidium stage of *M. rostrata* in Egypt, but infection and metamorphosis were not observed; otherwise observations are missing for the other five genera and 36 species of the Iridinidae currently recognized (but see Kondo, 1984). For most species of the Nile, data on larval and adult anatomy are necessary to reevaluate their affinities to other species in Africa and other taxa around the world.

Only a single family, the Iridinidae, is endemic to Africa (Table 1). The other three families share inter-generic and inter-specific relationships with taxa outside of Africa. The Iridinidae is

most closely related to the Neotropical family, Mycetopodidae (Graf & Cummings, 2006b; but see Bonetto, 1963). Therefore, including Nile (and other African) species in global phylogenies of the Unionoidea can lend valuable insight on the last 200 million years of freshwater bivalve evolution. The families Unionidae and Etheriidae have especially contentious relationships since systematists have had to rely upon a dearth of accurate life history and anatomical data.

While it is easy to be overwhelmed by the magnitude of exactly how much we do not know about the freshwater mussels of the Nile (Bogan, 2004) and Northern Africa (Van Damme, 1984), we see this as an opportunity for students of malacology. The assemblage of freshwater mussels described herein is zoologically interesting and reasonably diverse. We hope that this brief article will encourage further research on these interesting mollusks.

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EXPLANATION OF FIGURES

Figure 1. Map of the Nile Basin, including Lake Turkana.

Figure 2. *Unio*, *Anodonta*, *Potomida* and *Pseudunio* known from Northern Africa. A *Unio mancus*. B *U. abyssinicus*. C *Anodonta cygnea*. D *Potomida littoralis*. E *Pseudunio auricularia*.

Figure 3. *Coelatura* from Northern Africa. A *Coelatura aegyptiaca*. B *C. bakeri*. C *C. cridlandi*. D *C. stuhlmanni*. E *C. alluaudi*. F *C. hauttecoeuri*.

Figure 4. *Nitia* of Northern Africa. A *Nitia teretiuscula*. B *N. acuminata*. C *N. monceti*.

Figure 5. *Etheria elliptica* from Northern Africa.

Figure 6. *Mutela* of Northern Africa. A *Mutela dubia*. B *M. rostrata*. C *M. bourguignati*. D *M. alluaudi*.

Figure 7. *Aspatharia* of Northern Africa. A *Aspatharia chaiziana*. B *A. divaricata*. C *A. marnoi*.

Figure 8. *Chambardia* of Northern Africa. A *Chambardia rubens*. B *Ch. trapezia*. C *Ch. wahlbergi*. D *Ch. bourguignati*. E *Ch. letourneuxi*.

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Preliminary review of the freshwater mussels
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with an emphasis on the Nile

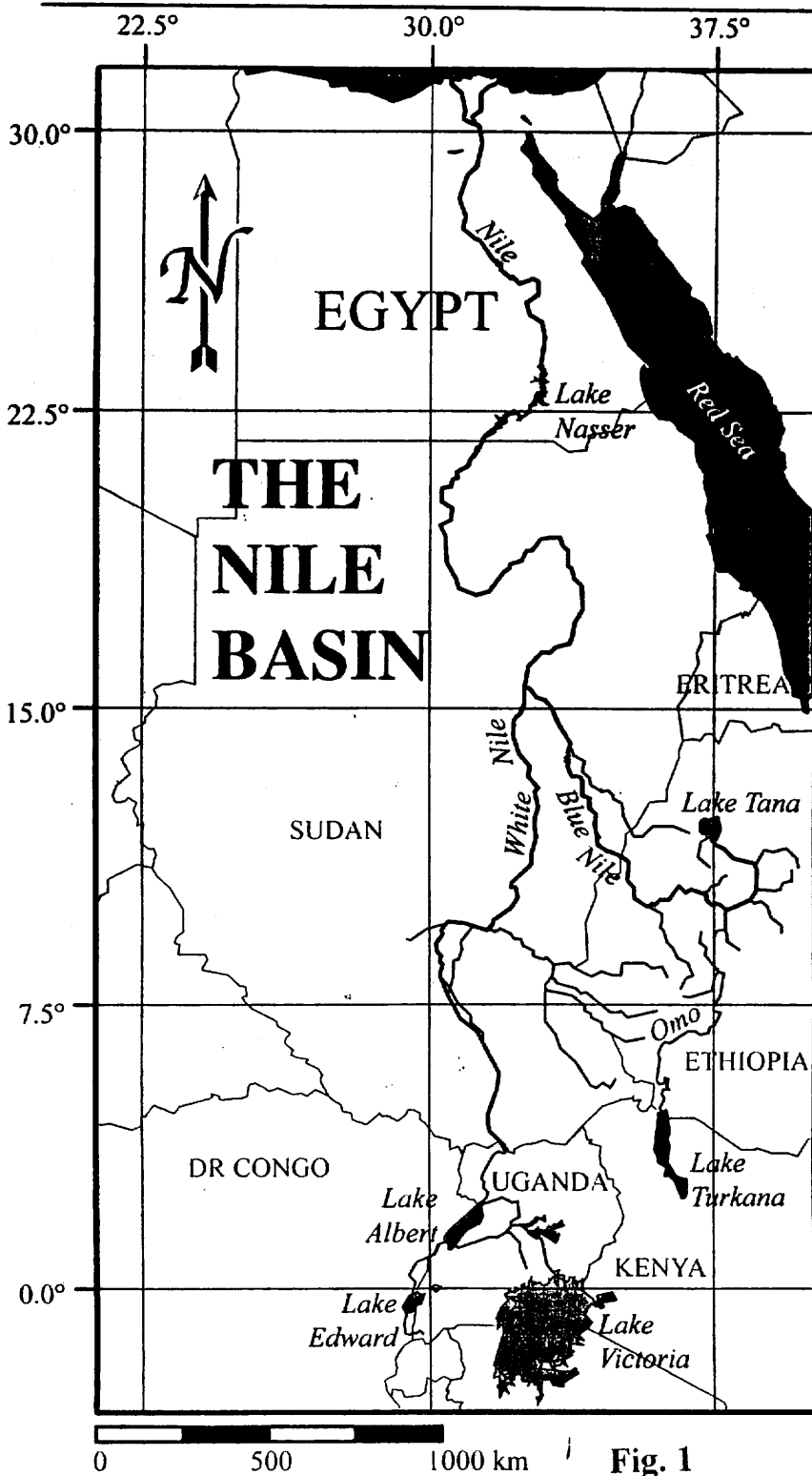
Table 1. The Classification and Global Distribution of the Unionoida. Classification follows Graf & Cummings (2006b). The families known from Northern Africa are shown in bold.

| Taxon | Distribution |
|--------------------------------|---|
| Phylum Mollusca | |
| Class Bivalvia | |
| Subclass Palaeoheterodonta | |
| Order Unionoida | |
| Superfamily Unionoidea | |
| Family Unionidae | Holarctic (including Mesoamerica), Africa, SE Asia, New Guinea |
| Family Margaritiferidae | Holarctic (including northern Africa), SE Asia |
| Superfamily Etherioidea | |
| Family Hyriidae | South America, Australasia |
| Family Etheriidae | South America, India and SE Asia |
| Family Mycetopodidae | South America |
| Family Iridinidae | Africa |

Table 2. Distribution of Freshwater Mussels (Unionoida) in Northern Africa. Species are arranged by their observed geographical patterns, discussed in the text. An X indicates presence, ? marks questionable records and F is for fossil records. Questionable and fossil records are excluded from column sums.

| Taxon | Egypt | Upper Nile | Great Lakes | Lake Turkana | Palaearctic | West Africa |
|------------------------------------|------------|------------|-------------|--------------|-------------|-------------|
| PALEARCTIC SPECIES | | | | | | |
| 1. <i>Unio mancus</i> | F? | X | | | X | |
| 2. <i>Anodonta cygnea</i> | | | | | X | |
| 3. <i>Potomida littoralis</i> | | ? | | | X | |
| 4. <i>Pseudunio auricularia</i> | | | | | X | |
| WIDESPREAD SPECIES | | | | | | |
| 5. <i>Coelatura aegyptiaca</i> | X | X | X | X | | X |
| 6. <i>Nitidulites teretiuscula</i> | X | X | | | | X |
| 7. <i>Mutela dubia</i> | X | X | X | X | | X |
| 8. <i>Mutela rostrata</i> | X | X | X | X | | X |
| 9. <i>Aspatharia chaiziana</i> | X | X | | | | X |
| 10. <i>Chambardia rubens</i> | X | X | | | | X |
| 11. <i>Chambardia wahlbergi</i> | | X | X | X | | X |
| 12. <i>Etheria elliptica</i> | X | X | X | X | | X |
| NILE ENDEMICS | | | | | | |
| 13. <i>Chambardia letourneuxi</i> | X | | | | | |
| 14. <i>Unio abyssinicus</i> | F? | X | | | | |
| 15. <i>Aspatharia marnoi</i> | | X | | | | |
| GREAT LAKES ENDEMICS | | | | | | |
| 16. <i>Coelatura bakeri</i> | | | X | | | |
| 17. <i>Coelatura stuhlmanni</i> | | | X | | | |
| 18. <i>Coelatura cridlandi</i> | | | X | | | |
| 19. <i>Coelatura alluaudi</i> | | | X | | | |
| 20. <i>Coelatura hauttecoeuri</i> | | | X | | | |
| 21. <i>Nitidulites acuminata</i> | | ? | X | | | |
| 22. <i>Nitidulites monceti</i> | | | X | | | |
| 23. <i>Mutela bourguignati</i> | | | X | | | |
| 24. <i>Mutela alluaudi</i> | | | X | | | |
| 25. <i>Aspatharia divaricata</i> | | | X | | | |
| 26. <i>Chambardia trapezia</i> | | | X | | | |
| 27. <i>Chambardia bourguignati</i> | | | X | | | |
| LAKE TURKANA ENDEMICS | | | | | | |
| 28. <i>Coelatura rothschildi</i> | | | | X | | |
| 29. <i>Nitidulites chefneuxi</i> | | | | X | | |
| TOTAL | 8 | 11 | 17 | 7 | 4 | 8 |
| Endemics | 1 | 2 | 12 | 2 | | |
| % Endemics | 13% | 18% | 71% | 29% | | |

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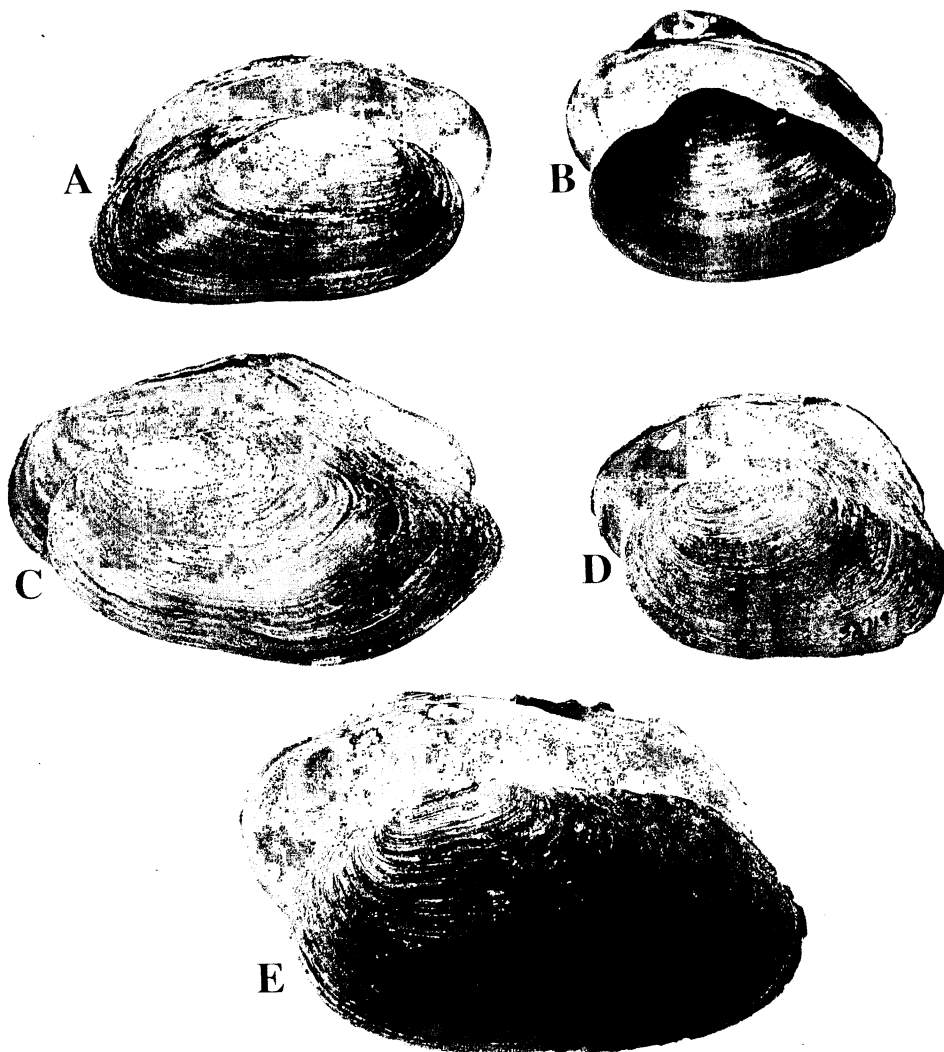


Fig. 2

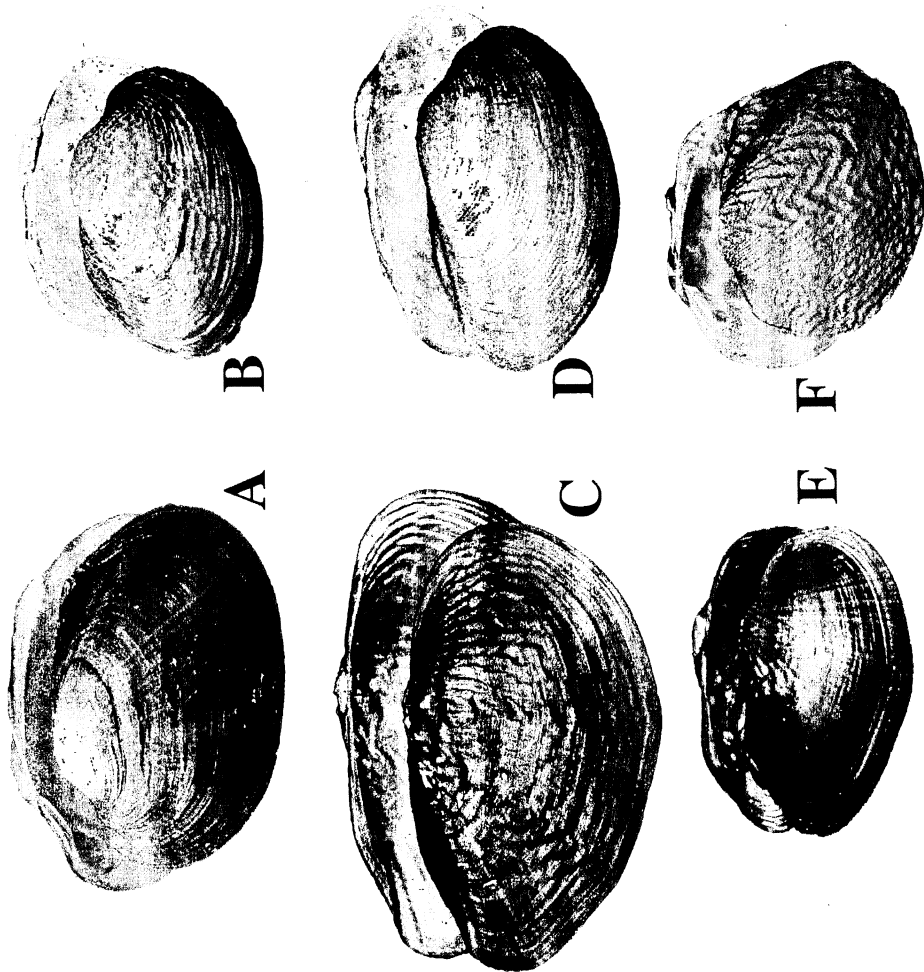


Fig. 3

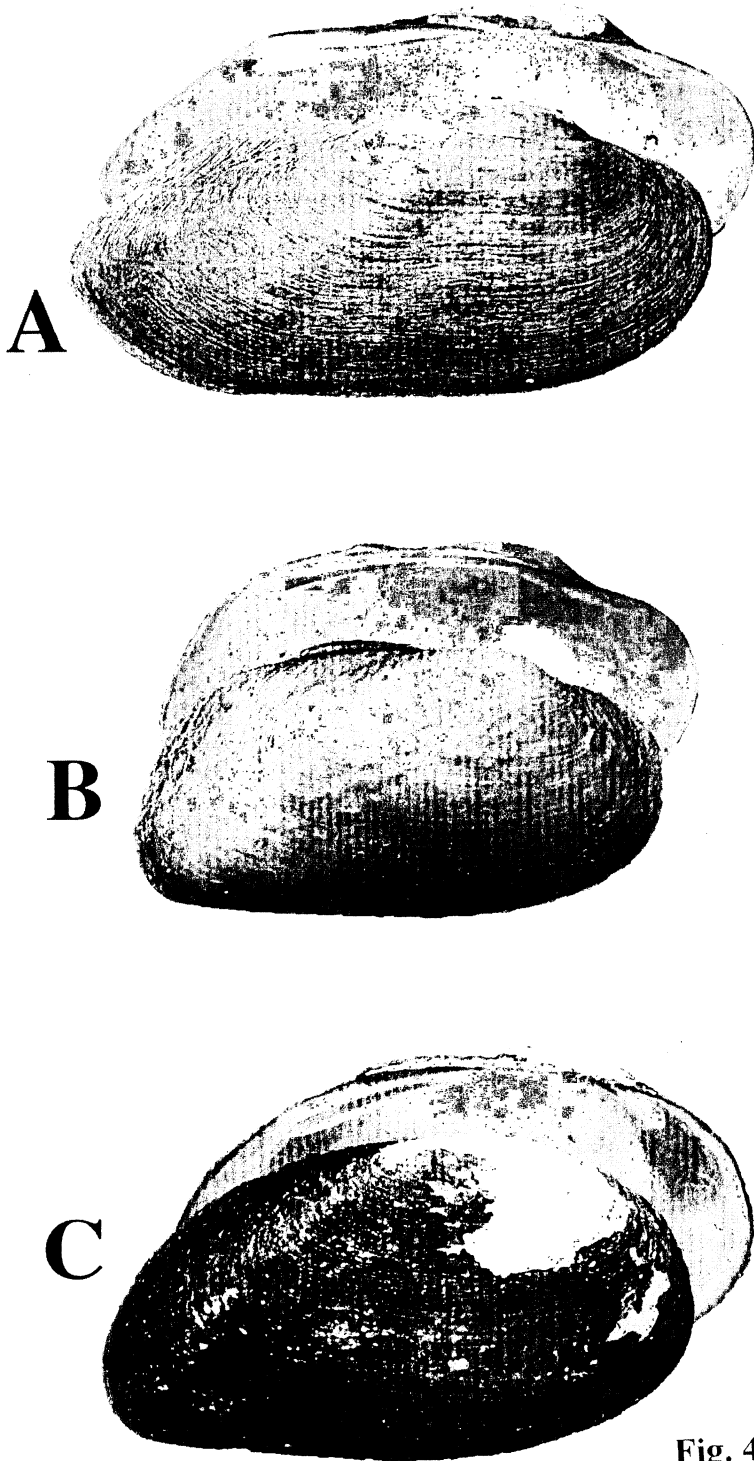


Fig. 4



Fig.5

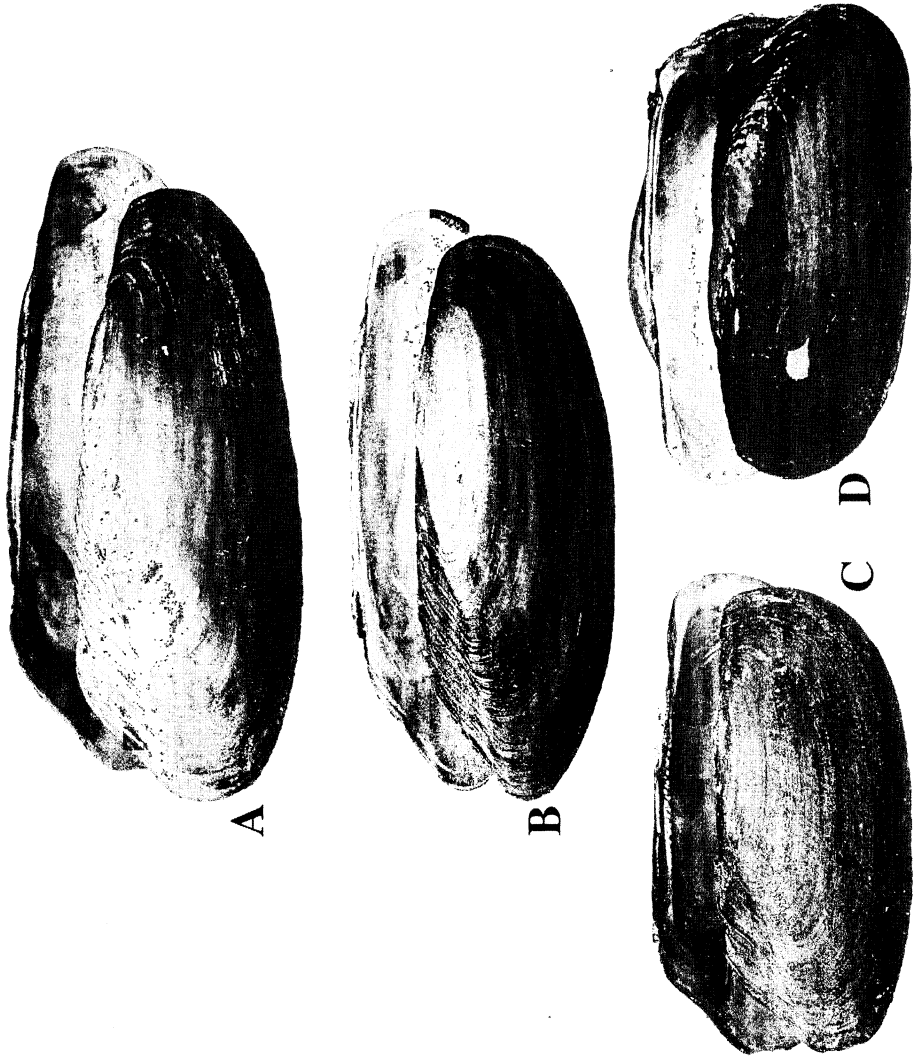


Fig. 6

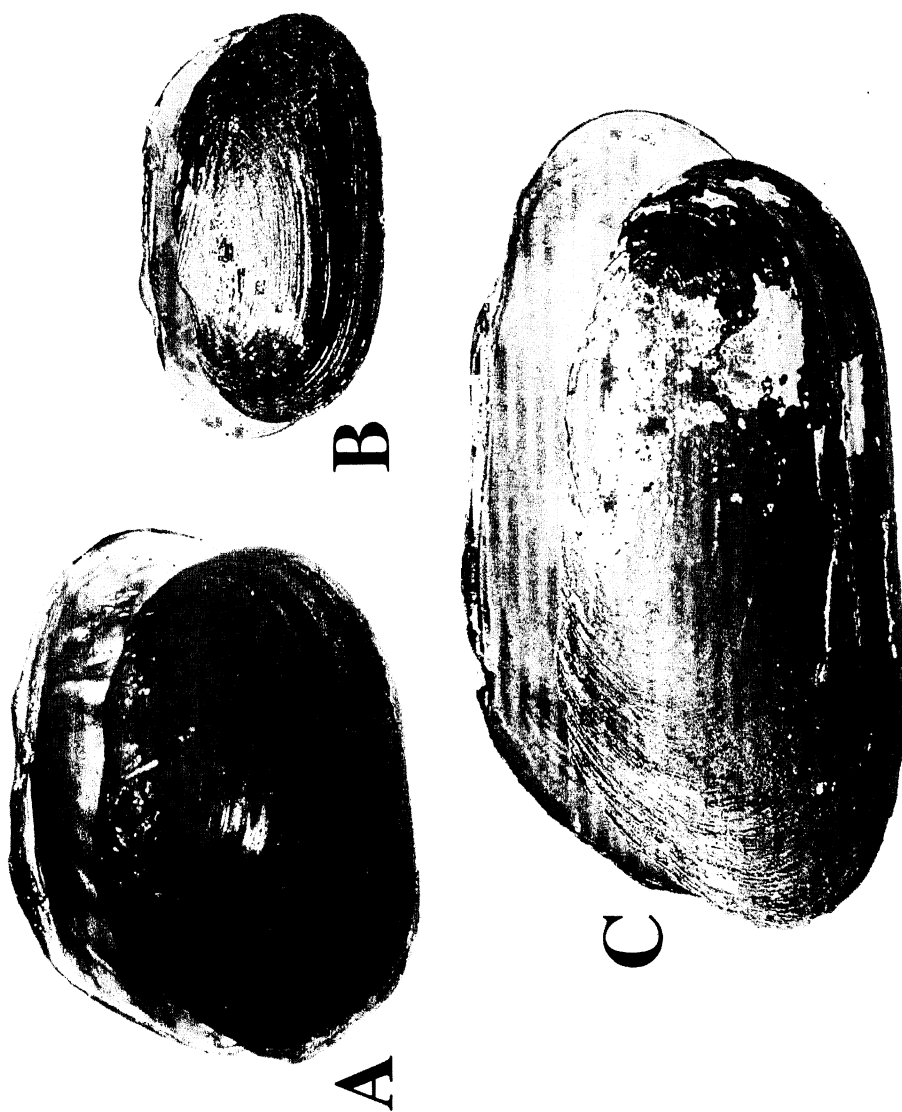


Fig. 7

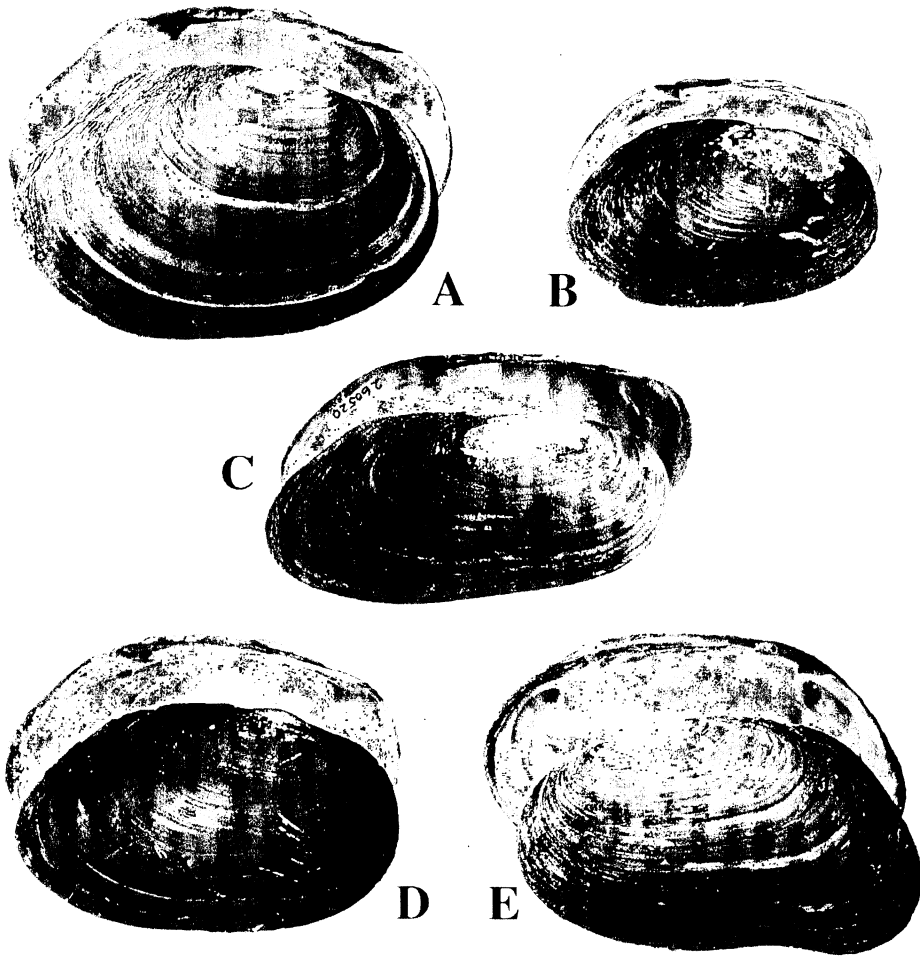


Fig. 8

عرض أولى لمحار الماء العذب (الرخويات : ذوات المصراعين : يونيونويدا) فى شمال إفريقيا وبخاصة فى نهر النيل

دانييل جراف^(١) - كيفن كومنجز^(٢)

(١) أكاديمية العلوم الطبية - فيلادلفيا ، بنسلفانيا - الولايات المتحدة الأمريكية
(٢) معهد إيلينوى للتاريخ الطبيعي - شامبين ، إيلينوى - الولايات المتحدة الأمريكية

نالنت محارات الماء العذب فى شمال إفريقيا ، بما فيها حوض النيل ، اهتماما كبيرا فى العقود الأخيرة ، ولكن المراجعات والتقارير المنشورة تتناقض مع بعضها ومع بحوثنا عن المجموعات المتحفية . ولقد أخذنا على عاتقنا أن نعيد تقييم أنواع المنطقة لتوفير قاعدة بيانات للجهود البحثية القادمة وإثارة الاهتمام بدراسة محار الماء العذب بين باحثى علم الحيوان المصريين .

وتشير الدراسة أن ٢٩ نوعا تضمها ٤ فصائل توجد فى شمال إفريقيا ، منها ٢٦ تضمها ٣ فصائل توجد فى نهر النيل وبحيرة توركانا . ونهر النيل هو منطقة تداخل بين الحد الجنوبى للفونا القطبية القديمة والحد الشمالى للفونا المدارية الإفريقية .

وفى هذه الدراسة يمثل النوع التقليدى شامبارديا والبيرجى (كراوس ، ١٨٤٨) أربعة أنواع محددة فى المنطقة : ش. والبيرجى هارتمانى (فون مانتز ، ١٨٦٦) ، ش. بورجونياتى (بورجونيات ، ١٨٨٥) ، ش. ليتورتكسى سيرفان ، ١٨٩٠ ، وآسباتاريا مارنوى (جيكيلى ، ١٨٧٤) . وقد أوردنا قائمة بكل الأنواع اليونيونويدية فى شمال إفريقيا مع أشكال الأنواع النيلية . وتمت مناقشة احتمالات البحوث التى يمكن أن تجرى فى المستقبل .

مجلة الجمعية المصرية - الألمانية لعلم الحيوان

علم الحيوان اللافقارى والطفيليات

