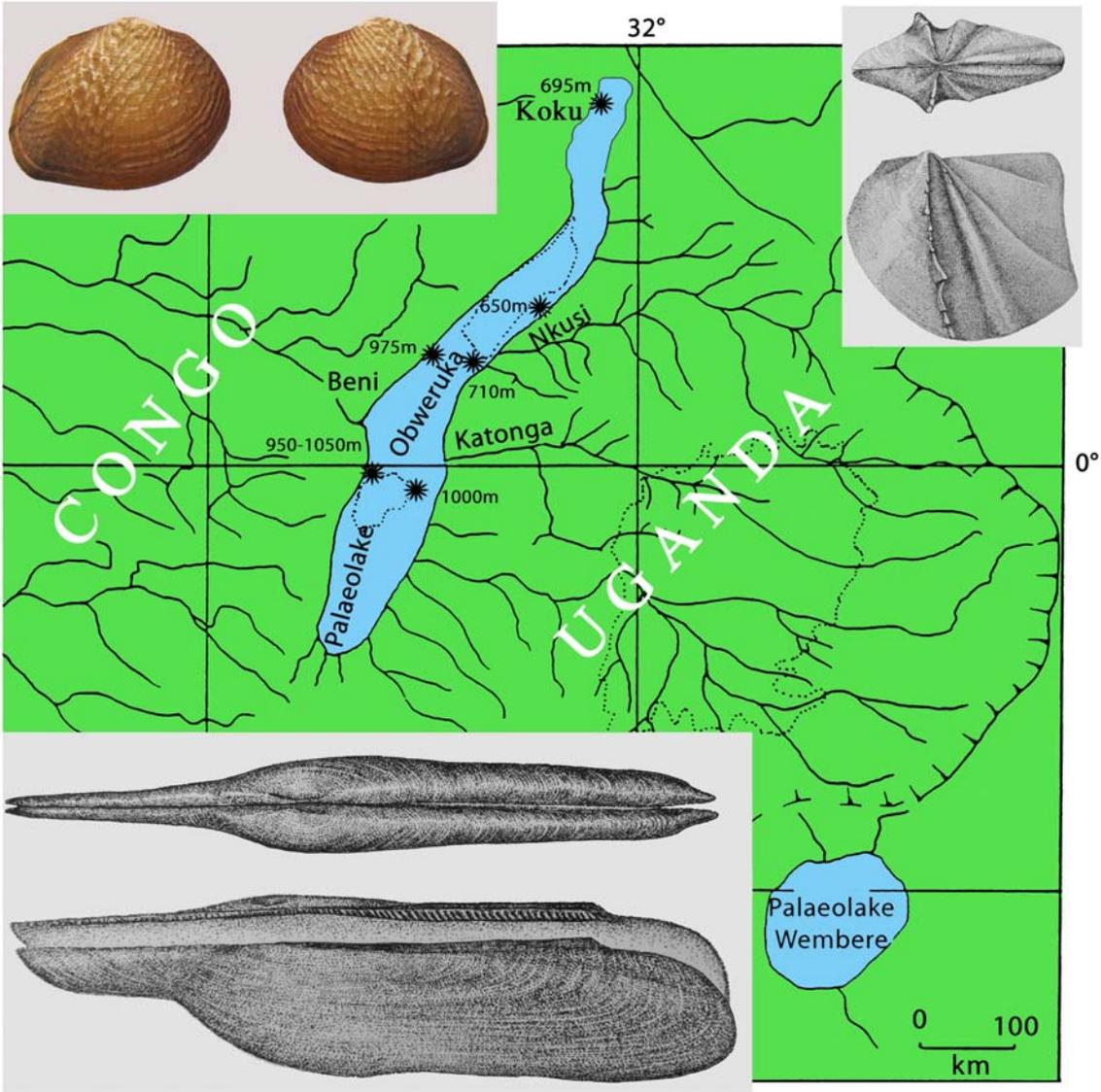


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The Late Cenozoic Bivalves of the Albertine Basin (Uganda-Congo)

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ABSTRACT

The Mio-Pliocene lacustrine deposits of the Albertine Basin span a period of 15 million years and contain the most complete and longest record of African freshwater bivalves known. Species of two aquatic environments occur: (1) fluvio-paludal species that had a wide range in the Palaeo-Congo Basin and (2) lacustrine species which were endemic to the long-lived Palaeolake Obweruka. This lake, that existed from ca 8 to 2 Ma, was in size and depth similar to present day Lake Tanganyika. As in other African Cenozoic fossil sites the Middle Miocene deposits only contain Etherioidea. In terminal Miocene and Pliocene times a significant number of Unionoid genera appear, some of which (e.g. *Coelatura*, *Nitia*) persist until today. While some genera are most likely Indotropical invaders, the origin of most of these unionids remains unknown. In Late Pliocene to Early Pleistocene times the Albertine fossil record shows that the African bivalve fauna was reaching its Modern configuration, most early unionid genera having become extinct and *Coelatura* being dominant, the Iridinidae genera *Pleiodon* and *Iridina* becoming relictual and the Asian *Corbicula* firmly established. The endemic lacustrine faunal component of the Albertine fossil bivalve record shows the same universal evolutionary pattern of freshwater bivalves by the absence of radiation. However, the Obweruka fauna is of particular interest because of the dramatic intensity of evolutionary change, resulting in morphological features such as spines, the presence of a sulcus or of a strongly elongated rostrum. These marked changes, which are relatively rare in naiads, occurred rapidly, geologically speaking. It is possible that the evolution of a marked tubular rostrum in the iridinid *Iridina adami* indicates chemosymbiosis.

Key words : Long-lived lake, Chemoautotrophic symbiosis, Convergence, Evolutionary escalation, Unionidae, Iridinidae, Neogene, Africa, Asian invaders.

INTRODUCTION

We refer to the papers on the Ampullariidae, Viviparidae and in particular the Thiaridae s.l. (Thiaridae + Paludomidae + Pachychilidae) of the Albertine Basin by Van Damme & Pickford (1995, 1999, 2003) for the geological and palaeolimnological contexts of the Albertine fossil molluscs. In this section we restrict the geological and stratigraphic context to a summary based on the content of these three papers.

The Albertine Trough or Basin (Uganda, Congo) is that part of the western branch of the Great African Rift in which recent Lakes Albert and Edward-George are situated, separated from each

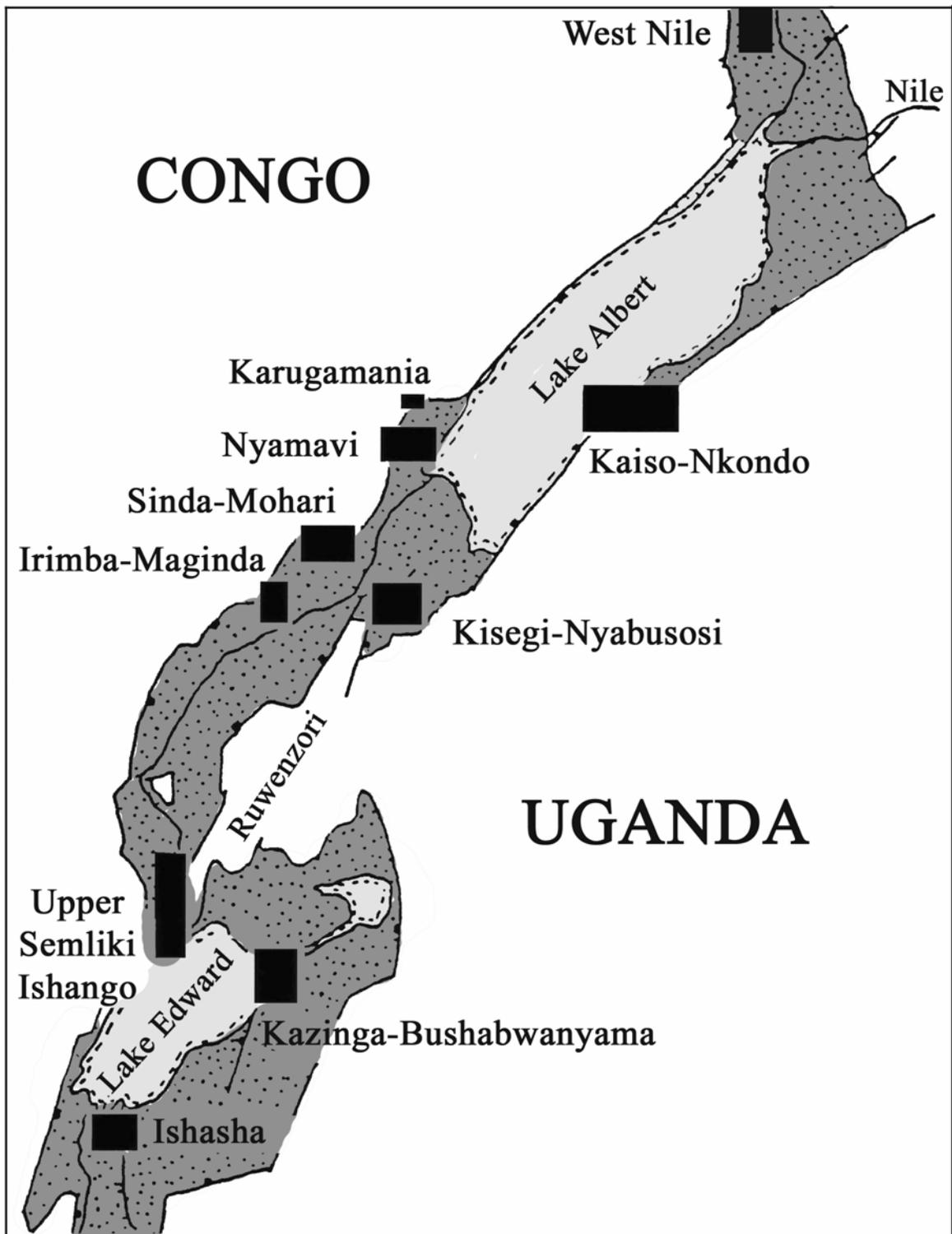


Figure 1. The Albertine Rift Valley (Uganda – Congo) with indication of the main fossiliferous areas. The dark stippled zone corresponds to sedimentary deposits, and approximates the outline of Palaeolake Obweruka during transgressive stages in the period from 7.5 to 2.5 Ma.

other by the Semliki Plains and the Ruwenzori Mountains. These lakes together with Lakes Victoria and Kyoga drain northwards into the Nile. This present day hydrographic and lacustrine configuration in central Africa is of geologically recent date and is radically different from the Early Pliocene network in the same area that was part of the Congo drainage (see Fig. 47).

The Albertine Basin contains a sedimentary infilling up to 6 km thick. In a few places within the rift (Fig. 1) extensive blocks of sediment have been left high above present day lake level by tectonic activity, and these are now undergoing erosion. Geological mapping of the various outcrops has resulted in the recognition of a more or less continuous sequence of strata ranging in age from Middle Miocene (*ca* 13 Ma) at the base to Modern at the top (Fig. 2).

The thicknesses of fully lacustrine deposits in the succession reveal that the palaeolakes in which the sediments accumulated were extremely long-lived. From *ca* 7.5 to 2.5 Ma Palaeolake Obweruka existed and for most of that period it drowned the entire Albertine Basin (17,000 km²) (Fig. 1). Although around 2.5 Ma this huge palaeolake was broken up by the Ruwenzori Horst into southern and northern basins, the lacustrine ecosystem persisted in the two smaller Palaeolakes Lusso and Kaiso for another 0.5 million years. Palaeolake Obweruka and its successors were not connected to the Nile but drained into the Congo via the Aruwimi.

After the disappearance of Palaeolakes Kaiso and Lusso near the beginning of the Pleistocene, the drainage system remained unchanged but for most of that epoch only rivers crossed the basin, with the occasional formation of shallow lakes or playas. It is only during Late Pleistocene times that Lakes Albert and Edward were formed and due to a northward tilting of the rift floor these lakes started to drain towards the North, becoming part of the Nile system. During the Glacial Maximum drought, Lakes Albert and Edward dried out. The Modern malacofauna thus consists of recent arrivals, partly from the north and partly from the inter-rift region. It bears no connection with the Obwerukan one.

The number of fossiliferous sites with bivalve fossils is considerably smaller than those with gastropods and only a few species are well represented. Preservation is usually excellent, all details being preserved on the black or red hematite fossils.

The distribution of the main fossiliferous areas discussed herein is given in Figure 1 and the age and stratigraphic relations of the sequences in Figure 2, while Table 1 summarizes the main environmental events in the Albertine Basin.

Table 1. The composition of the Late Cenozoic bivalve assemblages of the Albertine Basin and their stratigraphic, limnological and evolutionary context. The absolute ages are mainly based on mammalian biochronological inference (Pickford *et al.*, 1993). (F. – Formation; * : the molluscan bio-units or molluscan associations G0 to G6 (Gautier 0 - 6) are those discerned by Gautier (1970a) based on molluscan assemblages from all over the Albertine Basin. The associations L0 to LIII (Lusso 0 - III) were used by Williamson (1990) for molluscan assemblages in the Upper Semliki region, where only deposits younger than 4 Ma are exposed).

| Age (Ma) | Lithostratigraphic Units | | Bivalve Assemblage | Mollusc. Bio-unit | Aquatic ecosystem characteristics & Evolutionary events in the bivalve fauna |
|---------------------|-------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| | L. Albert Basin | L. Edward Basin & Upper Semliki | | | |
| 12.5 - 7.5 | Kisegi F. Kakara F. L. Oluka F. | Mohari F. | <i>Pleiodon tavernieri</i> , <i>Iridina moharensis</i> , <i>Iridina subelongata</i> , <i>Chambardia triangulata</i> , <i>Chambardia wissmanni</i> , <i>Etheria elliptica</i> , <i>Pisidium lepersonnei</i> | G0-G2 | Shallow intermittent lakes and braided river systems that are part of the PalaeoCongo. Fluvial catchment fauna in evolutionary stasis. Unionoidea represented by the families Iridinidae and Etheriidae only |
| 7.5 - 5.5 | U. Oluka F. L. Nkondo F. (Nkondo Member) | No deposits known. | <i>Pseudobovaria mwanyana</i> , <i>Gautieraia rugosa</i> , <i>Nkondonaia bisulcata</i> , <i>Coelatura cf stanleyvillensis</i> , <i>Nitia cf monceti</i> , <i>Iridina adami</i> , <i>Iridina lepersonnei</i> , <i>Iridina palaeospekii</i> , <i>Chambardia wissmanni</i> , <i>Etheria elliptica</i> . | G3a | Large deep meromictic to holomictic rift lake: Palaeolake Obweruka I. Appearance of a diverse fauna of Unionidae. In-lake evolution of a possibly chemosymbiotic morph in the Iridinidae (<i>Iridina adami</i>). |
| 5.5 - 5 | L. Nyaburogo F. U. Nkondo F. (Nyaweiga Member) | Base of the Lusso F. at Nyakasia Ravine | <i>Pseudobovaria mwanyana</i> , <i>Gautieraia rugosa</i> , <i>Coelatura cf stanleyvillensis</i> , <i>Coelatura scholzi</i> , <i>Nitia cf monceti</i> , <i>Iridina adami</i> , <i>Iridina lepersonnei</i> , <i>Iridina wasai</i> , <i>Iridina atrox</i> , <i>Chambardia wissmanni</i> , <i>Etheria elliptica</i> . | G3b L0* | Large deep holomictic to meromictic Palaeolake Obweruka I. Evolution of an ornate thalassoid species in the Iridinidae (<i>Iridina atrox</i>). |
| 5 - 4.5 | No deposits known. | Base Lusso F. at Nyakasia Ravine and between Kanyatsi and Kakungu. Kazinga Beds | <i>Pseudobovaria mwanyana</i> , <i>Iridina adami</i> , <i>Iridina lepersonnei</i> , <i>Iridina wasai</i> , <i>Iridina atrox</i> , <i>Chambardia wissmanni</i> , <i>Etheria elliptica</i> | G3c L0 | Onset of decrease in diversity ending with a severe extinction event due to an ecosystem crash. |
| 4.5 - 3.5 | Warwire F. U. Nyaburogo F. | Base of the Lusso F.? | <i>Pseudobovaria mwanyana</i> , <i>Nitia cf monceti</i> , <i>Obwerukanio pliocenica</i> , <i>Iridina lepersonnei</i> , <i>Etheria elliptica</i> | G4 L0? | Meromictic large and deep Palaeolake Obweruka II. Only one endemic naiad, <i>Iridina lepersonnei</i> (Iridinidae) still occurs in the lake. |
| 3.5 - 2.5 | Nyakabingo F. Kyeoro F. Nyamavi Beds Sinda Beds Irimba Beds | Lusso F. between + 35 m and the lowest ironstone at Lusso Point. Bushabwanyama Beds | <i>Pseudobovaria mwanyana</i> , <i>Pseudobovaria grandis</i> , <i>Pseudobovaria truncata</i> , <i>Coelatura cf hauttecoeuri</i> , <i>Nitia cf monceti</i> , <i>Iridina lepersonnei</i> , <i>Iridina williamsoni</i> , <i>Mutela nyamaviensis</i> , <i>Aspatharia pfeifferiana</i> , <i>Etheria elliptica</i> | G5a LI | Meromictic large and deep Palaeolake Obweruka II. Deep north and south basin possibly intermittently separated during low level stands by the rising Ruwenzori Horst. A new putative chemosymbiotic lineage (<i>Pseudobovaria truncata</i>) evolves from the endemic <i>Pseudobovaria grandis</i> . |
| 2.5 - 2 | Kaiso Village F. Hohwa Member Kaiso Village Member. | | <i>Pseudobovaria mwanyana</i> , <i>Pseudodiplodon hohwae</i> , <i>Coelatura cf hauttecoeuri</i> , <i>Iridina lepersonnei</i> , <i>Chambardia wissmanni</i> , <i>Etheria elliptica</i> , <i>Corbicula fluminalis</i> . | GX | Palaeolake Obweruka II definitely divided by the rising Ruwenzori Horst into two deep meromictic lakes: Palaeolake Kaiso and Palaeolake Lusso. Early Palaeolake Kaiso times: appearance of the enigmatic genus <i>Pseudodiplodon</i> . |
| | Kaiso Village F. Top of Kaiso Village Member. | | <i>Pseudobovaria mwanyana</i> , <i>Coelatura cf hauttecoeuri</i> , <i>Grafunio dagei</i> , <i>Iridina williamsoni</i> , <i>Chambardia wissmanni</i> , <i>Chambardia trapezia</i> , <i>Etheria elliptica</i> , <i>Corbicula fluminalis</i> | GX* | Terminal Palaeolake Kaiso times: increased sedimentation and gradual destabilisation of the holomictic lacustrine ecosystem. Subsequent extinction of all endemics and replacement by 'Nilotic' fauna |
| 2.5 - 2 | | Lusso F. between + 45 m and + 35 m from the base at Lusso Point. | <i>Pseudobovaria mwanyana</i> , <i>Pseudobovaria grandis</i> , <i>Pseudobovaria truncata</i> , <i>Pseudodiplodon sengae</i> , <i>Coelatura cf hauttecoeuri</i> , <i>Iridina williamsoni</i> , <i>Pteromutela cummingsi</i> , <i>Etheria elliptica</i> , <i>Corbicula fluminalis</i> . | G5b LII | Early Palaeolake Lusso times: persistence of the endemic taxa and appearance of invaders of unknown origin (<i>Pseudodiplodon</i>) and of 'Nilotic' origin |
| | | Lusso F. from + 45 m above the lowest ironstone at Lusso Point till the '3 Metre Ironstone' at the top. | <i>Pseudobovaria mwanyana</i> , <i>Pseudobovaria grandis</i> , <i>Coelatura cf hauttecoeuri</i> , <i>Etheria elliptica</i> , <i>Corbicula fluminalis</i> , <i>Eupera sp.</i> | G5c LIII | Terminal Palaeolake Lusso times: increased sedimentation and gradual destabilisation of the holomictic lacustrine ecosystem. Subsequent extinction of all endemics and replacement by 'Nilotic' fauna. |
| 2 - 1.5 | Nyabusosi F. | Semliki F. | <i>Pseudobovaria mwanyana</i> , <i>Mutela dubia</i> , <i>Etheria elliptica</i> , <i>Corbicula fluminalis</i> , <i>Eupera sp.</i> | G6 | Shallow unstable lakes and playas. Mainly fluvial environment. Ubiquitous 'Nilotic' fauna. |
| Modern | Recent beach deposits | | Modern Lake Albert Fauna: | Modern | Modern holomictic L. Albert. Fauna of 'Nilotic' origin with very weak endemism. |
| 6,000 y BP - Modern | | Holocene terraces & Modern beach deposits | Modern Lake Edward Fauna: | | Modern holomictic L. Edward. Fauna of 'Nilotic' origin with very weak endemism |

Biochronology of Albertine Rift Sediments

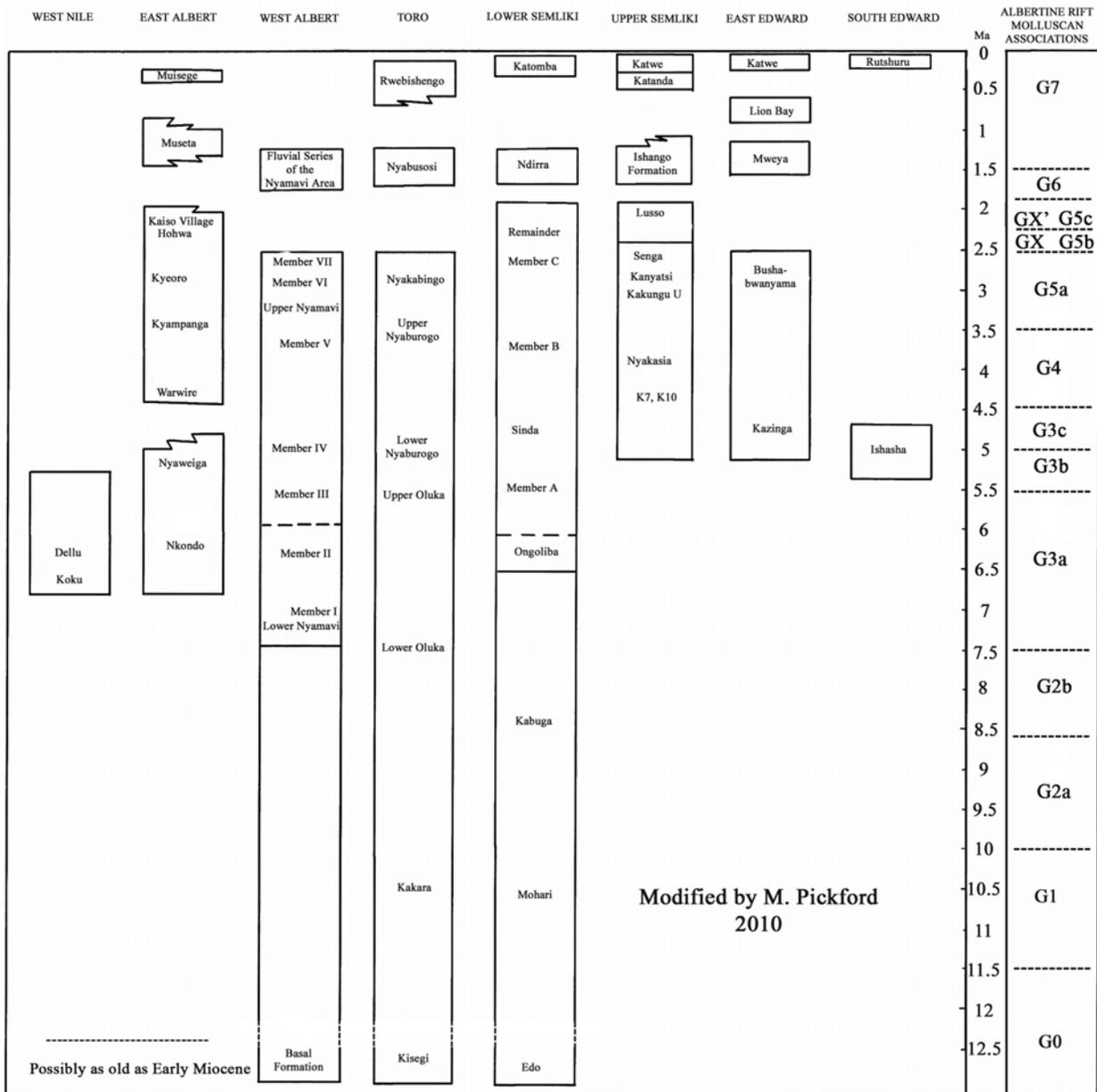


Figure 2. Biochronology of Albertine Rift sediments and molluscan associations (updated and extended from Van Damme & Pickford, 1999).

Table 2. Late Cenozoic bivalve fauna of the Albertine Basin. Geochronologic division according to Berggren *et al.*, (1995) (* - New genus, new species). (Abbreviations and symbols: ◆: present; Al = Modern Lake Albert; Ed = Modern Lake Edward).

| | GEOMORPHOLOGIC STAGES OF THE ALBERTINE PALAEOLAKES | | | | | | | | | | | | | |
|----------------------------------------------------|----------------------------------------------------|--------------|---------------------------------------------|----------------|---------------|---------------|-----------------------------------------|--------------|----------------------------------------------|---------------|-----------------------------------|----|----|----|
| | Pre-Obweruka Stage | | Obweruka Stage | | | | | | Post-Obweruka Stage | | | | | |
| | Shallow lakes or Kisegi Stage | | Mero-Holomictic L. Obweruka Nkondo Substage | | | NK-27 Event | Meromictic L. Obweruka Warwire Substage | | Mero- Holomictic L. Kaiso –L. Lusso Substage | | Unstable ‘Nilotic’ lakes Substage | | | |
| | Kisegi Times | Oluka Times | Nkondo Times | Nyaweiga Times | Kazinga Times | Warwire Times | Nyakabingo Times | Lusso Times | Kaiso Times | Semliki Times | Modern L. Albert & Edward | | | |
| Time span | 12 - 10 Ma | 10. - 7.5 Ma | 7.5 - 5.5 Ma | 5.5 - 5.0 Ma | 5.0 - 4.5 Ma | 4.5 - 3.5 Ma | 3.5 - 2.5 Ma | 2.5 - 2.0 Ma | 2.5 - 2.0 Ma | 2.0 - 1.5 Ma | 5 - 0 Ka | | | |
| Epoch | 11.2 | 11.2 | 5.2 | 5.2 | 3.6 | 3.6 | | | | 1.8 | 1.8 | 0 | | |
| | Middle | Late | | | Early | | Late | | | | | | | |
| | | Miocene | | | | | Pliocene | | | | Quaternary | | | |
| Molluscan Association | G0-G1 | G2 A+B | G3 A | G3 B | G3 C | G4 | G5 A | G5 B | G5 C | G X | G X' | G6 | Al | Ed |
| Bivalvia: Palaeoheterodonta | | | | | | | | | | | | | | |
| Unionidae | | | | | | | | | | | | | | |
| Genus <i>Pseudobovaria</i> | | | | | | | | | | | | | | |
| <i>Pseudobovaria mwayana</i> f. <i>fuchsi</i> | | | ◆ | ◆ | ◆ | | | | | | | | | |
| <i>Pseudobovaria mwayana</i> f. <i>typica</i> | | | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | | |
| <i>Pseudobovaria mwayana</i> f. <i>tuberculata</i> | | | | | | | | | ◆ | | | | | |
| <i>Pseudobovaria grandis</i> * | | | | | | | ◆ | ◆ | | | | | | |
| <i>Pseudobovaria truncata</i> * | | | | | | | ◆ | ◆ | | ◆ | | | | |
| Genus <i>Pseudodiplodon</i> | | | | | | | | | | | | | | |
| <i>Pseudodiplodon sengae</i> | | | | | | | | ◆ | | | | | | |
| <i>Pseudodiplodon hohwae</i> * | | | | | | | | | | ◆ | | | | |
| Genus <i>Grafunio</i> * | | | | | | | | | | | | | | |
| <i>Grafunio dageti</i> * | | | | | | | | | | | | ◆ | | |
| Genus <i>Gautieraia</i> * | | | | | | | | | | | | | | |
| <i>Gautieraia rugosa</i> * | | | ◆ | ◆ | | | | | | | | | | |
| Genus <i>Nkondonaia</i> * | | | | | | | | | | | | | | |
| <i>Nkondonaia bisulcata</i> * | | | ◆ | | | | | | | | | | | |
| Genus <i>Coelatura</i> | | | | | | | | | | | | | | |
| <i>Coelatura</i> cf. <i>stanleyvillensis</i> | | ◆ | ◆ | ◆ | | | | | | | | | | |
| <i>Coelatura</i> cf. <i>hauttecoeuri</i> | | | | | | | ◆ | ◆ | ◆ | ◆ | ◆ | | | |
| <i>Coelatura aegyptiaca</i> | | | | | | | | | | | | | ◆ | |
| <i>Coelatura bakeri</i> | | | | | | | | | | | | | ◆ | |
| <i>Coelatura stuhlmanni</i> | | | | | | | | | | | | | | ◆ |
| <i>Coelatura scholzi</i> * | | | | ◆ | | | | | | | | | | |
| Genus <i>Nitia</i> | | | | | | | | | | | | | | |
| <i>Nitia acuminata</i> | | | | | | | | | | | | | ◆ | |
| <i>Nitia</i> cf. <i>monceti</i> | | | ◆ | ◆ | | ◆ | ◆ | | | | | | | |
| Genus <i>Obwerukunio</i> * | | | | | | | | | | | | | | |
| <i>Obwerukunio pliocenica</i> * | | | | | | ◆ | | | | | | | | |
| Iridinidae | | | | | | | | | | | | | | |
| Genus <i>Pleiodon</i> | | | | | | | | | | | | | | |
| <i>Pleiodon tavernieri</i> | ◆ | | | | | | | | | | | | | |
| Genus <i>Iridina</i> | | | | | | | | | | | | | | |
| <i>Iridina moharensis</i> | ◆ | | | | | | | | | | | | | |
| <i>Iridina subelongata</i> | ◆ | ◆ | | | | | | | | | | | | |

| | | | | | | | | | | | | | | | | | |
|-----------------------------------|----------|----------|-----------|-----------|----------|----------|-----------|-----------|----------|----------|----------|----------|-----------|----------|---|---|---|
| <i>Iridina adami</i> | | | ◆ | ◆ | ◆ | | | | | | | | | | | | |
| <i>Iridina williamsoni</i> * | | | | | | | ◆ | ◆ | | | ◆ | | | | | | |
| <i>Iridina lepersonnei</i> | | | ◆ | ◆ | ◆ | ◆ | ◆ | | | | ◆ | | | | | | |
| <i>Iridina wasai</i> * | | | | ◆ | ◆ | | | | | | | | | | | | |
| <i>Iridina atrox</i> * | | | | ◆ | ◆ | | | | | | | | | | | | |
| <i>Iridina palaeospekii</i> * | | | | ◆ | | | | | | | | | | | | | |
| Genus <i>Mutela</i> | | | | | | | | | | | | | | | | | |
| <i>Mutela dubia</i> subsp. indet. | | | | | | | | | | | ◆ | ◆ | | | | ◆ | |
| <i>Mutela dubia emini</i> | | | | | | | | | | | | | | | | ◆ | |
| <i>Mutela alluaudi</i> | | | | | | | | | | | | | | | | ◆ | |
| <i>Mutela cf. alluaudi</i> | | | | | | | | | | | | ◆ | | | | | |
| <i>Mutela rostrata</i> | | | | | | | | | | | | | | | | ◆ | ◆ |
| ? <i>Mutela nyamaviensis</i> | | | | | | | ◆ | | | | | | | | | | |
| Genus <i>Pteromutela</i> | | | | | | | | | | | | | | | | | |
| <i>Pteromutela cummingsi</i> * | | | | | | | | ◆ | | | | | | | | | |
| Genus <i>Aspatharia</i> | | | | | | | | | | | | | | | | | |
| <i>Aspatharia pfeifferiana</i> | | | | | | | ◆ | | | | | | | | | | |
| Genus <i>Chambardia</i> | | | | | | | | | | | | | | | | | |
| <i>Chambardia triangulata</i> | ◆ | | | | | | | | | | | | | | | | |
| <i>Chambardia wissmanni</i> | | | | | | | ◆ | ◆ | ◆ | ◆ | ◆ | | | | | ◆ | |
| <i>Chambardia trapezia</i> | | | | | | | | | | | ◆ | | | | | | |
| Etheriidae | | | | | | | | | | | | | | | | | |
| Genus <i>Etheria</i> | | | | | | | | | | | | | | | | | |
| <i>Etheria elliptica</i> | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ |
| Bivalvia.:Heterodonta | | | | | | | | | | | | | | | | | |
| Corbiculidae | | | | | | | | | | | | | | | | | |
| Genus <i>Corbicula</i> | | | | | | | | | | | | | | | | | |
| <i>Corbicula fluminalis</i> | | | | | | | | ◆ | ◆ | | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ |
| Pisidiidae | | | | | | | | | | | | | | | | | |
| Genus <i>Eupera</i> | | | | | | | | | | | | | | | | | |
| <i>Eupera</i> sp. indet. | | | ◆ | | | | | | ◆ | | | ◆ | | | | | |
| <i>Eupera ferruginea</i> | | | | | | | | | | | | | | | | ◆ | |
| Genus <i>Sphaerium</i> | | | | | | | | | | | | | | | | | |
| <i>Sphaerium victoriae lacuum</i> | | | | | | | | | | | | | | | | ◆ | ◆ |
| <i>Sphaerium v. albertianum</i> | | | | | | | | | | | | | | | | ◆ | |
| <i>Sphaerium regularis</i> | | | | | | | | | | | | | | | | | ◆ |
| Genus <i>Pisidium</i> | | | | | | | | | | | | | | | | | |
| <i>Pisidium lepersonnei</i> | ◆ | | | | | | | | | | | | | | | | |
| <i>Pisidium pirothi</i> | | | | | | | | | | | | | | | | | ◆ |
| N bivalve species | 6 | 3 | 10 | 12 | 7 | 5 | 11 | 10 | 7 | 6 | 9 | 7 | 13 | 6 | | | |

In the present account all bivalve taxa that formerly occurred in the Albertine Basin are described in detail. The modern faunal list (see Table 2) is based on Van Damme & Van Bocxlaer (2009). For more detailed descriptions we refer to Mandahl-Barth (1988) and to Graf & Cummings (2007b).

In order to place the changes of the Albertine bivalve fauna through time into a broader context the main changes in the African bivalve fauna since the Cretaceous are briefly summarised.

The oldest known freshwater bivalve fossils on the African continent date from the Early/Middle Cretaceous (Aptian-Albian, ca. 112 Ma). The fossiliferous deposits belong to the Continental Intercalaire Series in particular to the Elrhaz Formation in the region of Gadoufaoua (Niger)

(Mongin & Lapparent, 1968). While palaeontological research in the area is ongoing (Serenio *et al.*, 2001, 2004; Brussatte & Sereno, 2006) it concentrates mainly on vertebrate remains. All malacological studies are based on old material from French expeditions in the 1950s-60s (Goumard, 1956; Lapparent & Mongin, 1959; Mongin, 1954, 1963, 1977; Mongin & Lapparent, 1968). Denise Mongin, who studied the bivalves, ranged them in existing or extinct genera that belong to the superfamily Unionoidea (Margaritiferidae + Unionidae). This arrangement was already questioned at the time because of lack of diagnostic evidence (Cox, 1969). It is also incompatible with the current general opinion that Unionoidea evolved in Laurasia and that the continents that were part of Gondwana were originally only inhabited by representatives of the superfamily Etherioidea (Etheriidae + Iridinidae + Mycetopodidae + Hyriidae).

The present authors restudied Mongin's material and reached the same conclusion as Cox (1969). Because the hinge is not visible in most of the fossils, their taxonomic affiliation to a specific superfamily, whose distinction is exclusively or mainly based on anatomical and larval characters, remains speculative. Some of the few Cretaceous specimens with discernible hinges may as well belong to the Hyriidae (e.g. *Cucumerunio*) as to the Unionidae. But there is no conclusive evidence of the presence of Hyriidae and we agree with Mongin that some specimens with extremely heavy cardinal and lateral teeth belong to the Margaritiferidae (*Margaritanopsis* Haas, 1910 according to Mongin). Dinosaur distribution patterns are indicative for a geographical connection between Africa and Iberia during Early/Middle Cretaceous times (Canudo *et al.*, 2009). The African bivalve fauna of that time also seems to be a mix from the two megacontinents. It should be stressed that it is striking that none of these Cretaceous bivalves with palaeoheterodont hinges bear any resemblance to Cenozoic African palaeoheterodonts.

The Early Tertiary African malacofauna is extremely poor in sharp contrast to the rich Middle Cretaceous one. The reason for the remarkable impoverishment remains speculative. Did they disappear during the K/T extinction event? A less dramatic cause may well be the uniformisation of aquatic environments due to the cyclic erosion and planation of the African continent. It is assumed that for long periods during ca 80 Ma, surface waters were ion poor and river basins restricted (see Burke & Gunnell, 2008).

Late Cretaceous bivalve fossils are known from the Nubian Sandstone Series in southern Egypt, in this region considered to span the period from the Late Cretaceous (Maastrichtian) to the Early Tertiary (Palaeocene) (Tantawy *et al.*, 2001).

The freshwater bivalves from these deposits have originally been identified respectively as *Pleiodon* or *Iridina*, *Mutela* (Iridinidae) and *Unio s.l.* (Unionidae) (Newton, 1909; Cox, 1955). The placement of the fossils in the first two genera seems in our opinion to be justified. The identification as *Unio* was not followed by Mongin (1963) who considered that Cox's *Unio jowikolensis* (with a distinct unionid hinge) belongs to *Coelatura* (Unionidae) and Newton's *Unio crossthaitei* belongs to *Aspatharia* (Iridinidae). Re-examination of the material leads us to conclude that *U. jowikolensis* is indeed a hinge-bearing unionoid which may belong to the Hyriidae (Etherioidea) or the Unionidae (Unionoidea) but certainly does not fall within the known morphological range of *Coelatura*. As to *Unio crossthaitei*, since the hinge is not fully visible, identification remains somewhat speculative.

Fossils from Niger are known from oolitic ferruginous deposits near Niamey that belong to the

Continental Terminal Series. In that region the deposits are probably of Eocene age (Miko, 1999; Obaje, 2009). The excellently preserved fossil bivalves, kindly placed at our disposal by Dr. Dominique Chardon, Université Paul Sabatier, Toulouse, belong to the genera *Pleiodon* and *Mutela* and to an unidentified subtrigonal and sulcate shell whose hinge is not visible.

At the onset of the Neogene, during Early and Middle Miocene times, although the fossil record is relatively detailed, only representatives of the superfamily Etherioidea have been found, namely *Pleiodon*, *Iridina*, *Chambardia* (Iridinidae) and *Etheria* (Etheriidae).

The striking poverty ends during Late Miocene times with the appearance in the East African deposits of the Albertine Basin (this paper) and the Tugen Hills (De Groeve, 2005) of several genera of medium sized bivalves, including the extinct *Pseudobovaria* and the extant *Coelatura* and *Nitia*, all belonging to the Unionidae.

It was only during Pliocene times that the African bivalve community started to reach its present configuration, with a dominance of unionids (*Coelatura* and *Pseudobovaria*) and corbiculids (*Corbicula*) contrasting with the previously exclusively etherioid fauna (*Pleiodon*, *Chambardia*, etc.).

The absence of unionids as well as such gastropod families as viviparids and thiarids in Early Cenozoic Africa has been noted by several authors (Van Damme & Pickford, 1999, 2003; Watters, 2001) and discussed in Van Damme & Van Bocxlaer (2009).

There are no indications for the occurrence of a marked ecological or climatological change during Miocene times that could explain this compositional shift but there is abundant evidence for the formation of intercontinental and intracontinental connections. During the Miocene the old African topography, consisting of a number of isolated endorheic basins was replaced by a more open system of extensive hydrographic systems such as the Palaeo-Congo and the Palaeo-Qena river that ran from Egypt west to the Atlantic Ocean. During the same period a good connection existed between Asia-Arabia and Africa prior to the opening of the Red Sea (see Van Damme & Van Bocxlaer, 2009 for discussion). These authors therefore concluded that a number of the unionid genera appearing in the fossil record are Asian invaders that reached Africa via Arabia and the Bab el Mandeb connection.

During Middle Pliocene to Early Pleistocene times the African bivalve community appears to have reached its present composition, with the invasion and subsequent dominance of the Asian clam *Corbicula*, the extinction of *Pseudobovaria* and the dominance shift in the Iridinidae from pseudotaxodont species (*Pleiodon*, *Iridina*) to edentulous ones (*Mutela*). Around the end of the Pliocene the biogeographic distribution pattern must also have resembled the present one.

A marked trend that can be noted in the African bivalve fossil record is one of reduction in size. While at the beginning of the Tertiary the average length was more than 10 cm (dominance of large Iridinidae), dimensions decrease during the Pliocene to ca 6 cm (dominance of *Coelatura* and *Pseudobovaria*) to decline further during the Pleistocene to ca 4 cm with *Corbicula* becoming overwhelmingly dominant. The success of smaller species is most likely linked with increasing climatological destabilisation, favouring small, short lived species that become rapidly fertile to the detriment of large, long-lived species that reach sexual maturity slowly.

FOSSIL BIVALVES OF THE ALBERTINE BASIN

Material and methods

This paper is based on the collections housed in the Museum of Central Africa at Tervuren (abbreviation: **MCA**), the Royal Belgian Institute of Natural Sciences, Brussels (**BNH**), the Natural History Museum, London (**NHM**), the Sedgwick Museum, Cambridge (**SMC**), the Research Unit Palaeontology of Ghent University, Ghent (**LPG**) and the Uganda Museum, Kampala (**UM**). The detailed stratigraphical/geographical context of the reference numbers cited in this paper have been published in various reports (Cox, 1926; Fuchs, 1936; de Heinzelin, 1955; Adam, 1957, 1959; Gautier, 1965, 1966, 1970a; Lepersonne, 1970, Williamson, 1990; Verniers & de Heinzelin, 1990; Pickford *et al.*, 1993; de Heinzelin & Verniers, 1996; Morris, 1996). Type localities of the species described as well as the numbers of the field samples and locations referred to in the text are indicated on detailed maps of the main collecting areas (Figs. 3-10). Locations of some of the species described by former authors could only be approximately indicated. In the specimen lists in Adam (1957, 1959) and Lepersonne (1970) references such as L. 37 or Lep. 53 refer to the number of the site used by Lepersonne in his field notes, Adam occasionally also used as additional reference the abbreviation 'de H., p. x' that stands for de Heinzelin (1955, p. x), The specimen numbers used for the Uganda Palaeontology Expedition material are comprised of three parts, e.g. specimen NK 503'93 consists of a two letter prefix representing the collecting region (Nkondo) followed by a catalogue number (503) and the year (1993). Precise collecting localities are provided for each specimen comprising a two letter prefix followed by the site number (e.g., NY 51 for Nyaburogo site 51) (see figures 3-10 for the location of sites). Following abbreviations for the Uganda collecting sites are used: HO = Hohwa region, KI = Kisege region, KN = Kazinga region, KS = Kaiso Village region, NK = Nkondo region, NY = Nyaburogo-Nyabusosi region (see figs. 4-6).

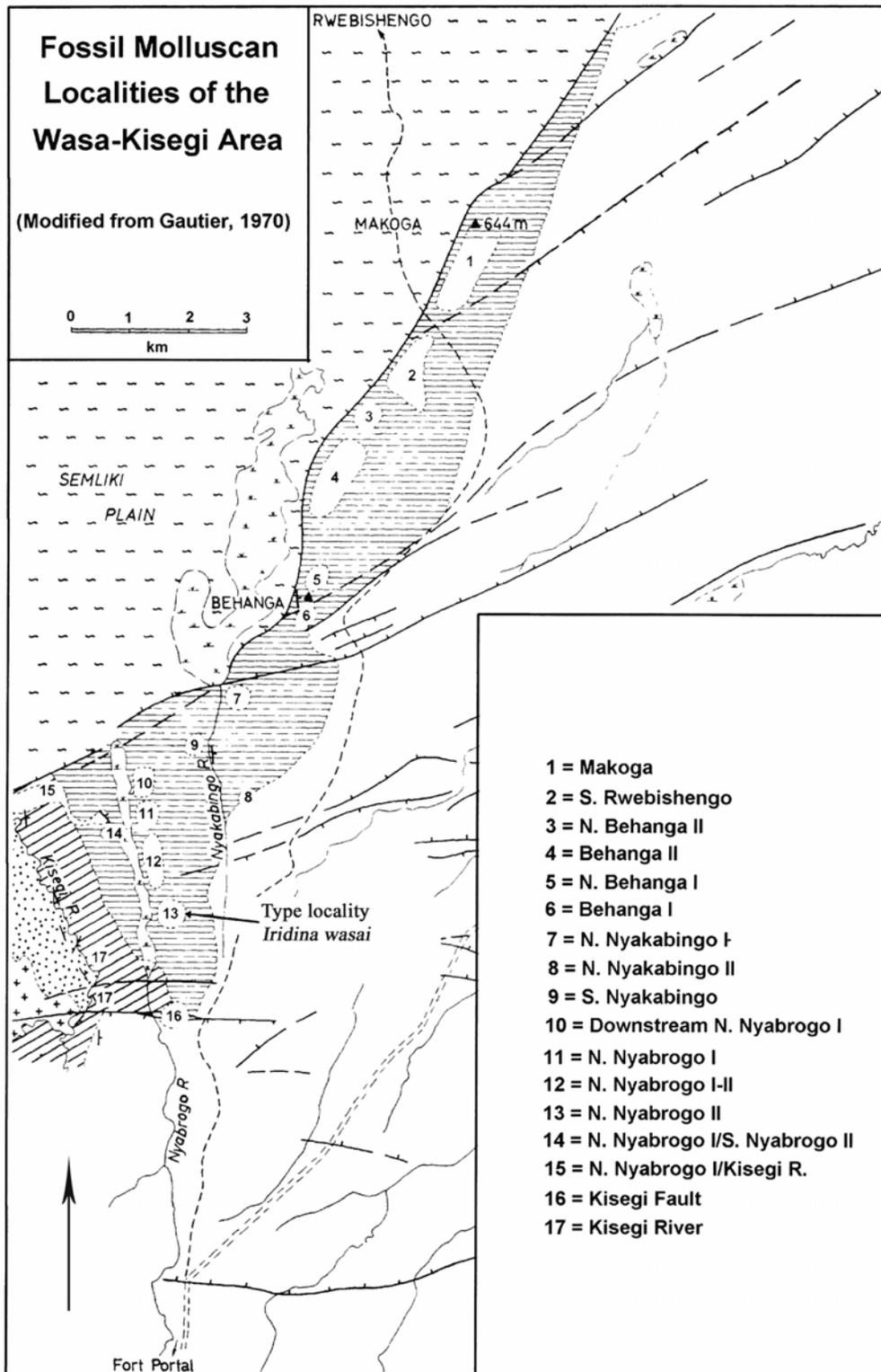


Figure 3. Wasa-Kisegi area, southwest of Lake Albert, Uganda: fossil molluscan localities (we have retained the original spellings as published by Gautier, 1970a : for updated spellings of place names refer to Fig. 4).

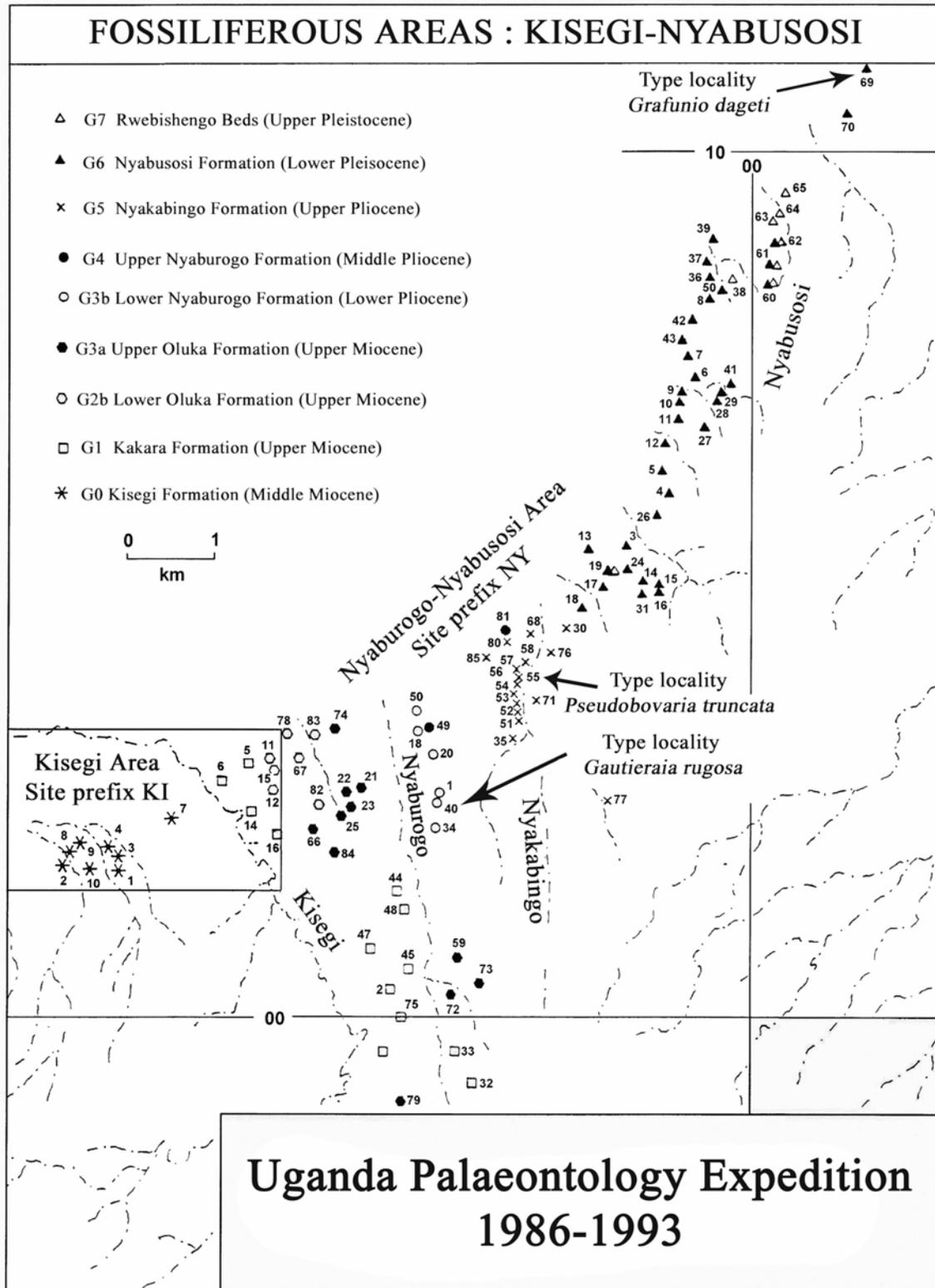


Figure 4. Kisegi-Nyabusosi area, Toro region, Uganda: fossil molluscan localities.

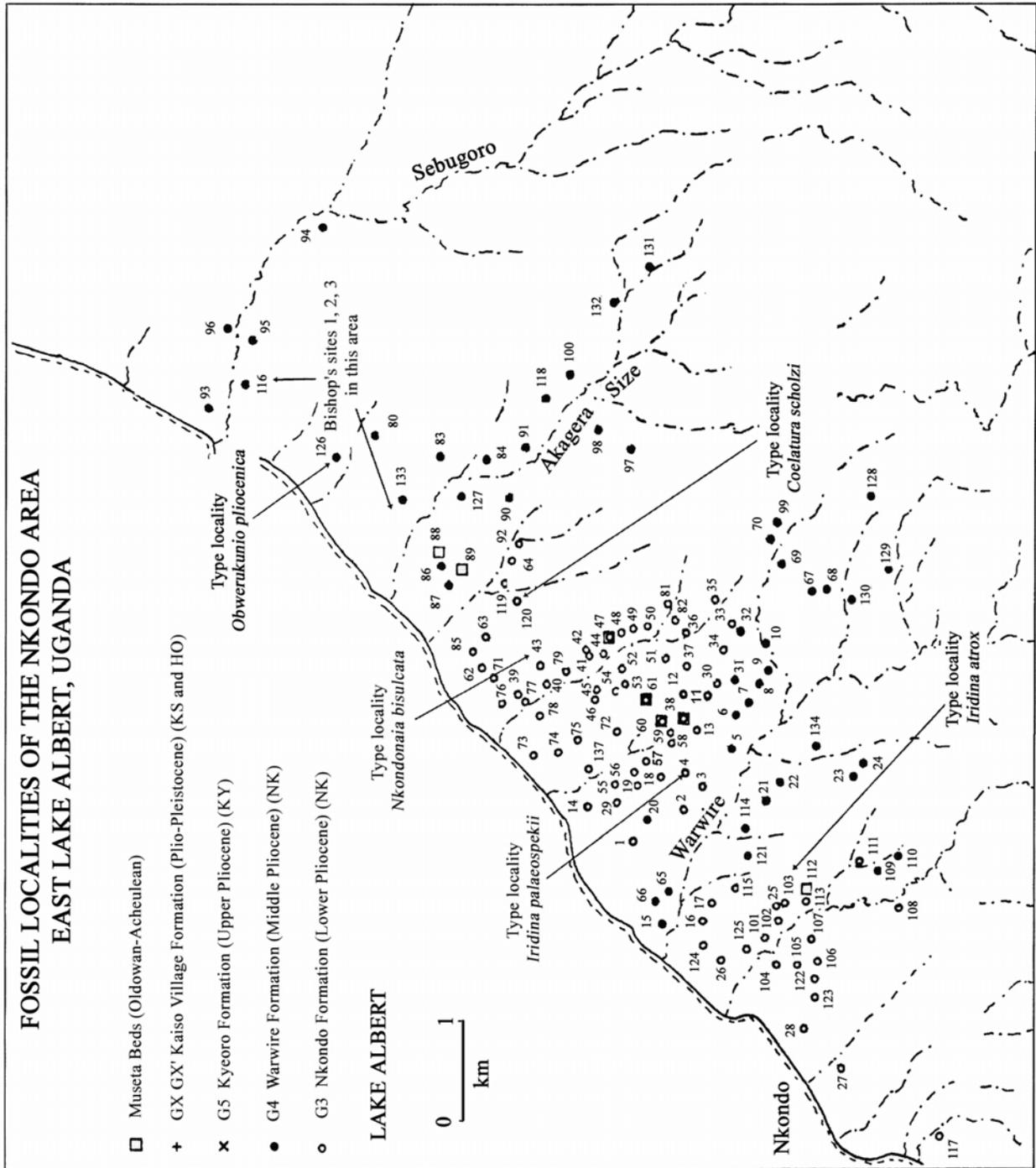


Figure 5. Nkondo area, eastern margin of Lake Albert, Uganda: fossil molluscan localities.

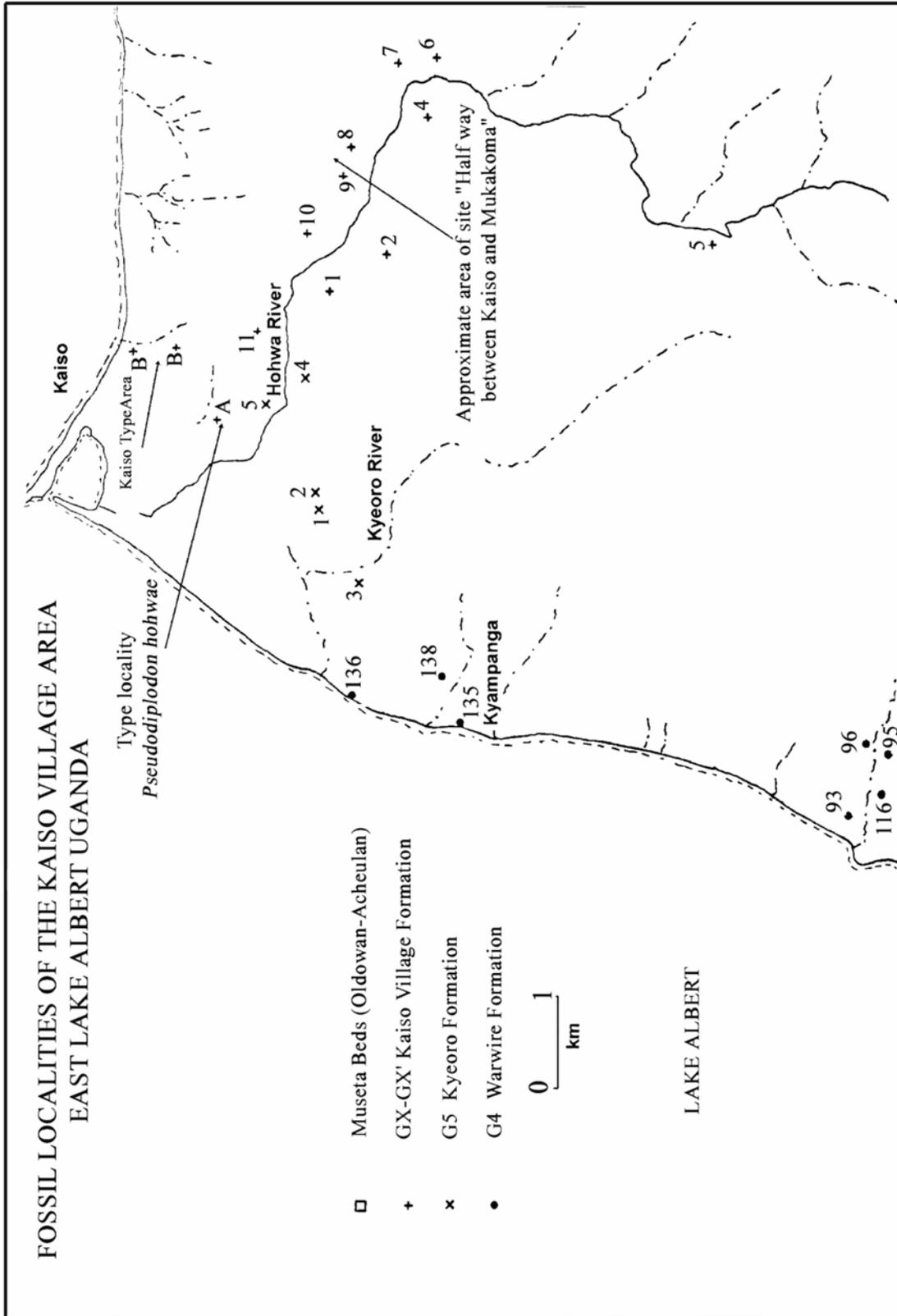


Figure 6. Kaiso Village area, eastern margin of Lake Albert, Uganda: fossil molluscan localities.

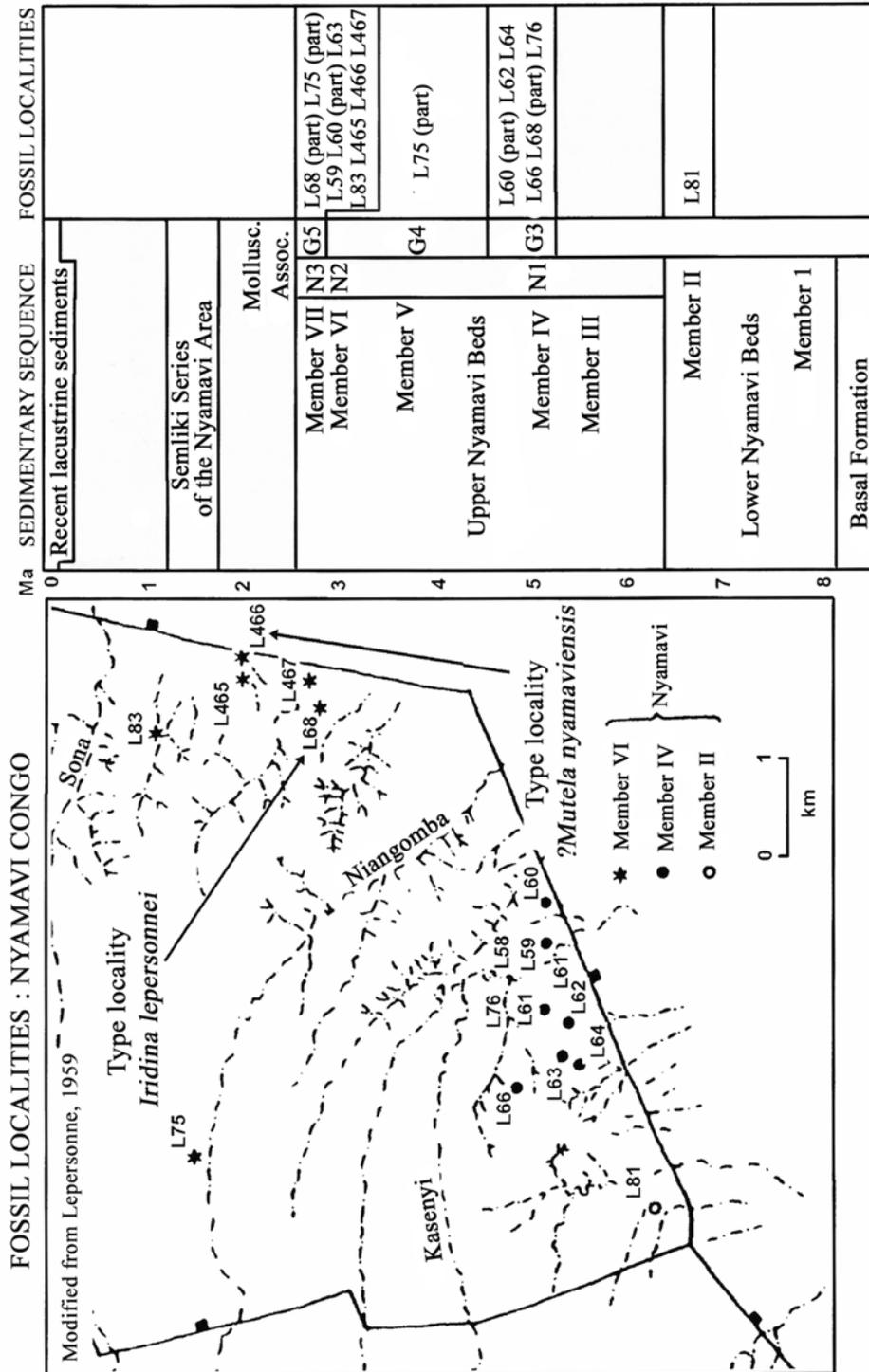


Figure 7. Nyamavi area, western margin of Lake Albert, Congo: fossil molluscan localities.

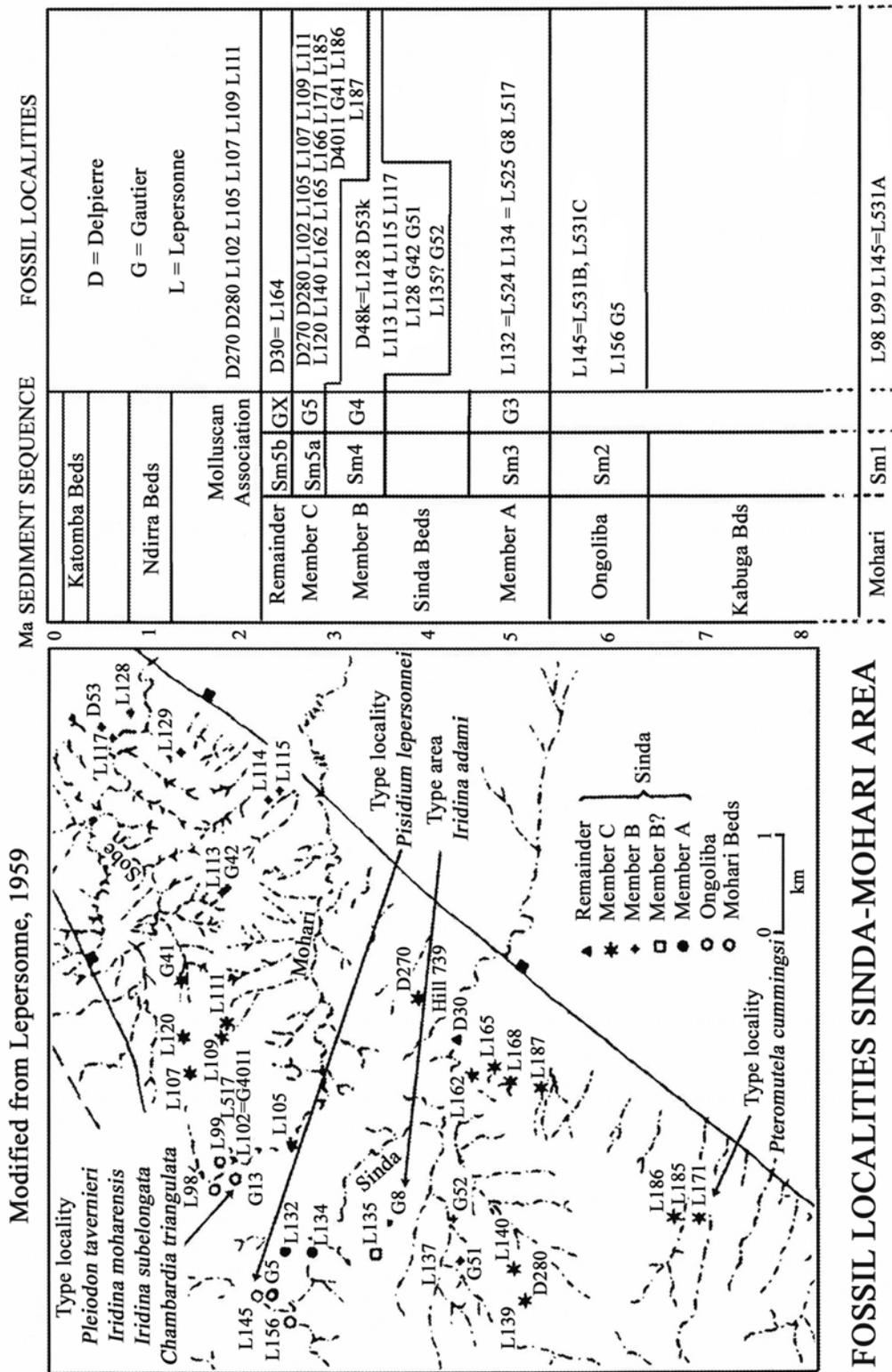


Figure 8. Sinda-Mohari area, western Semliki Plain, Congo: sedimentary sequence and fossil molluscan localities (modified from Lepersonne, 1959).

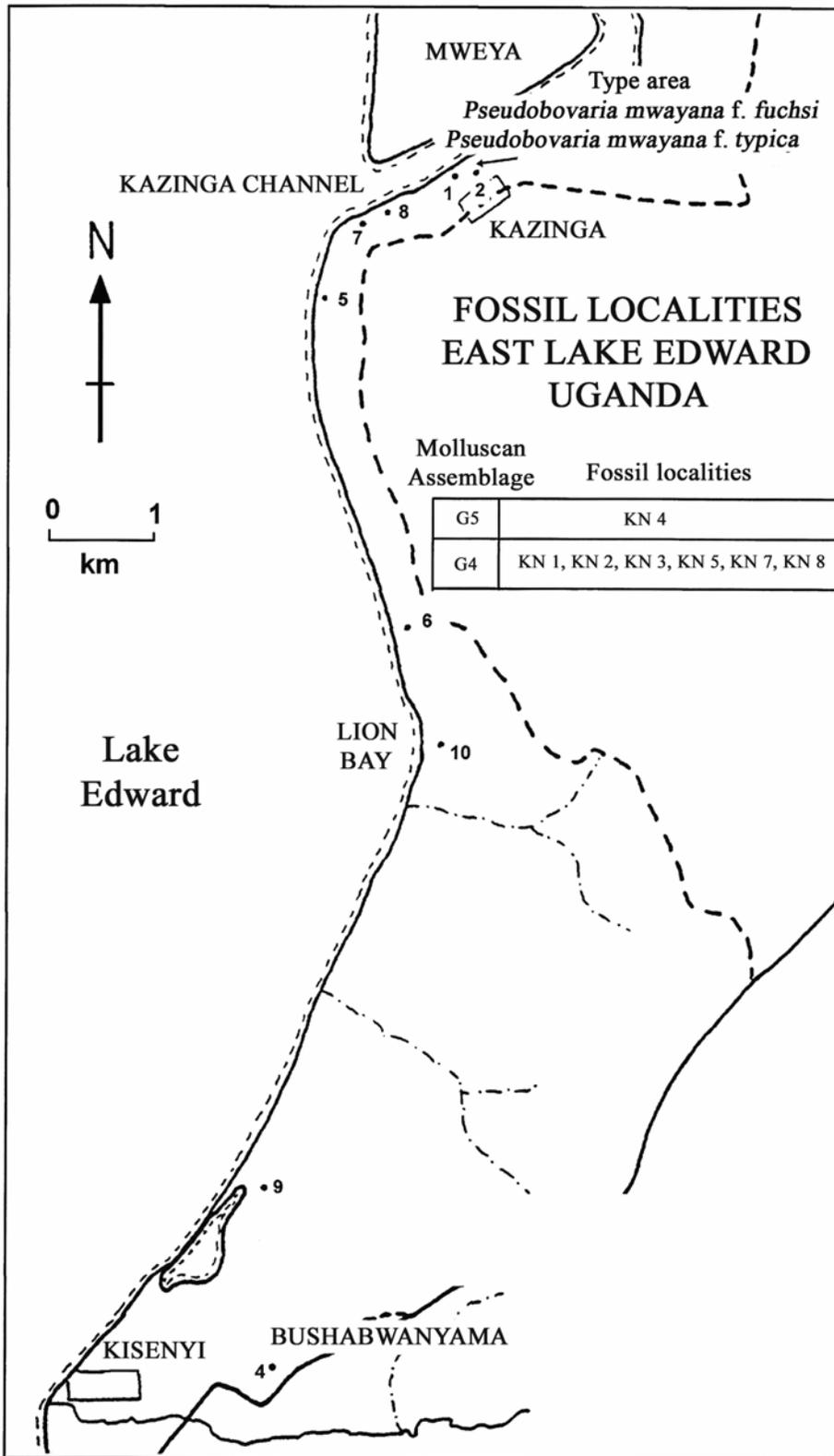


Figure 9. Kazinga-Bushabwanyama area, north-eastern margin of Lake Edward, Uganda: fossil molluscan localities.

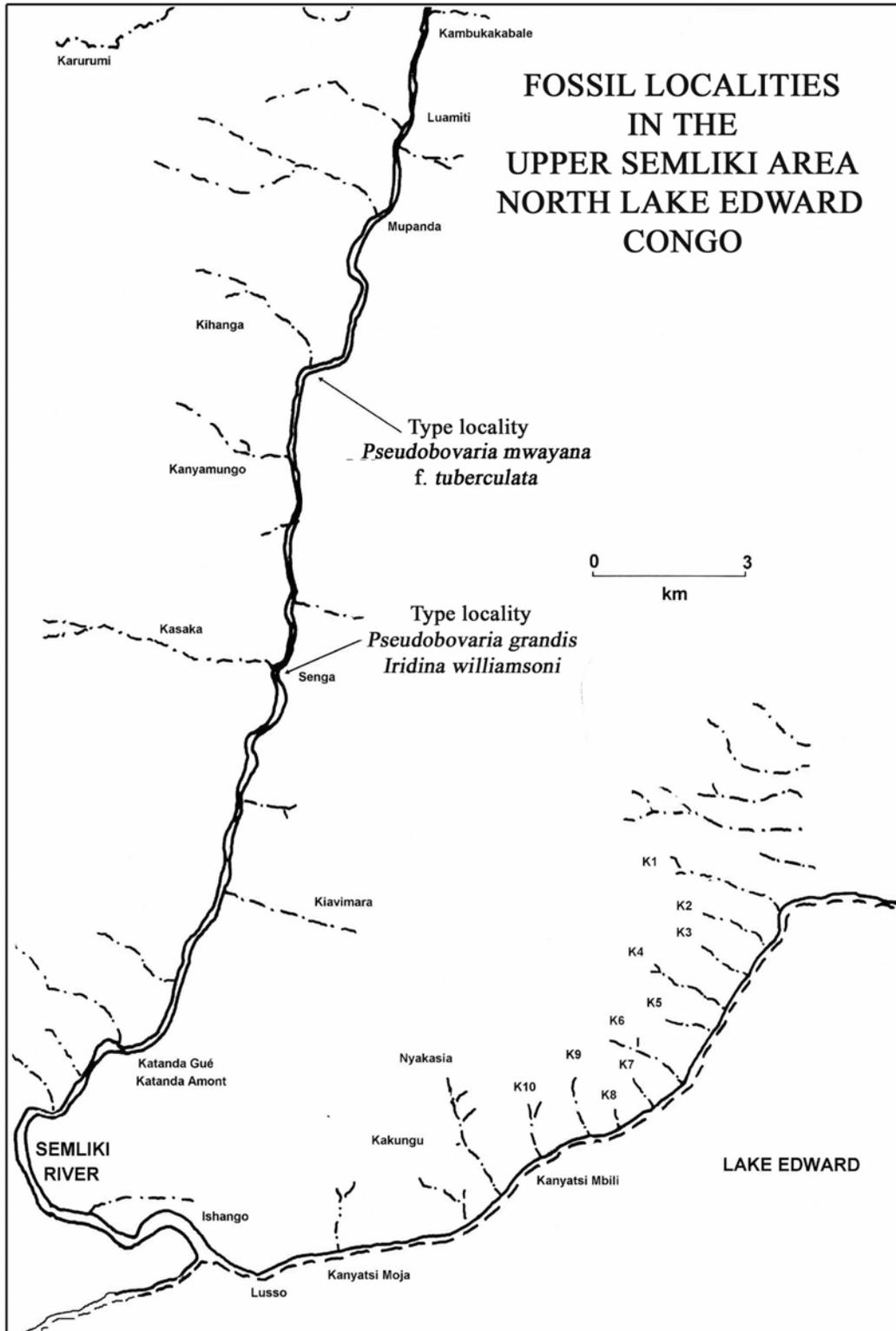


Figure 10. Upper Semliki-Ishango area, northern margin of Lake Edward, Congo: fossil molluscan localities.

The morphological characters of the shell are defined in Fig. 11. Measurements were taken as shown in Fig. 12. Drawings were made by camera lucida. Some drawings are composites, i.e. for the general outlines and main features a specific well preserved specimen is used, but details concerning ornamentation for example, may be filled in using other specimens. Morphometric analyses such as Fourier analysis were not applied for reason that fewer than half a dozen species are preserved by a statistically significant quantity of well preserved specimens. For example, although more than a hundred specimens of *Iridina adami* were collected there is only one specimen with a completely preserved rostrum. In addition, while trendy, such morphometric techniques can not make a distinction between ecophenotypic and genotypic based shell characters (Zieritz & Aldridge, 2009)

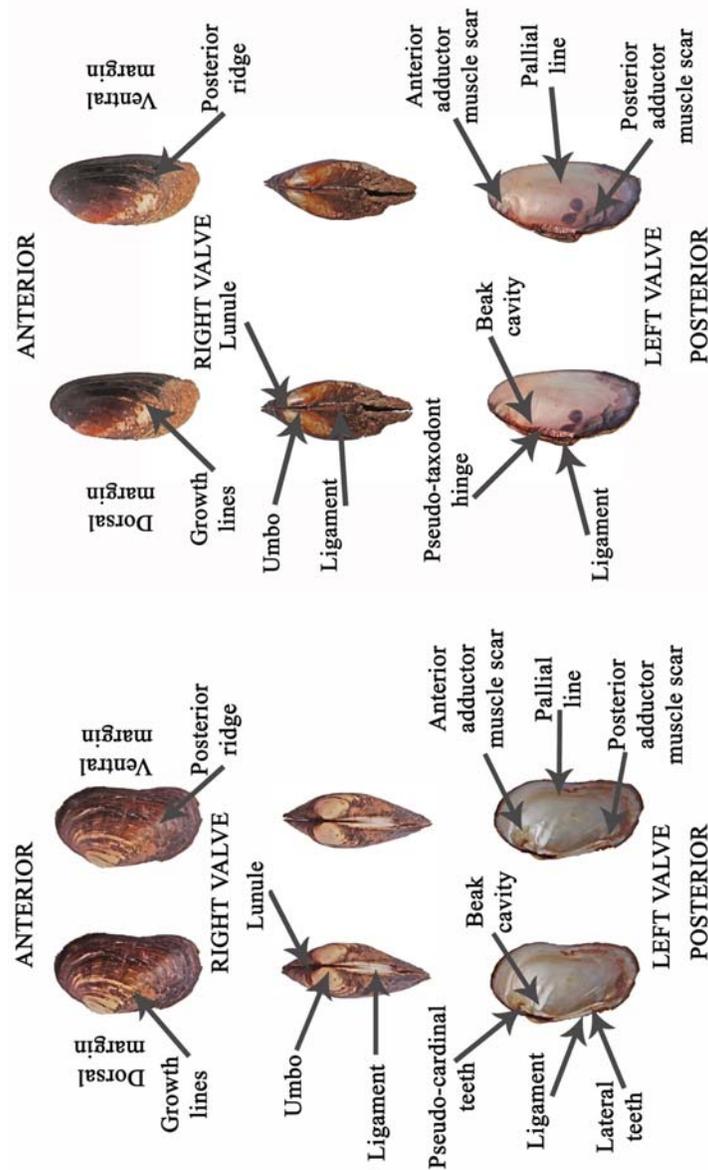


Figure 11. Morphological features of freshwater unionoid shells (left stereo images - *Psilunio littoralis*; right stereo images - *Iridina spekii*).

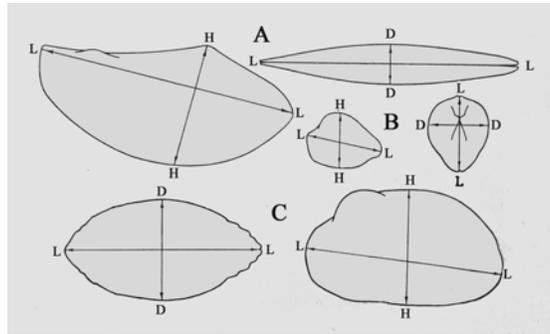


Figure 12. Contours of Tanganyikan shells showing the morphometric methodology used. LL = Length; HH= Height; DD = Diameter (modified from Leloup, 1950).

SYSTEMATIC PALAEOONTOLOGY

Class Bivalvia Linné, 1758 (Buonanni, 1681)

Subclass Heteroconchia Hertwig, 1895

Superorder Palaeoheterodonta Newell, 1965

Order Unionoida Stoliczka, 1871

In the last two decades interest from scientists and environmentalists in the large freshwater bivalves or naiads (Unionoida) has taken a quantum leap subsequent to the discovery that many species are extremely long-lived (more than 150 years) and highly sensitive to ecosystem stress. It has been established that of all groups of aquatic invertebrates freshwater bivalves are worldwide the most endangered. Particularly in industrialised countries a number of species has already been extirpated or is on the brink of extinction.

This interest has led to a re-examination and re-evaluation of naiad taxonomy not only of recent but also of fossil species, using morphological, molecular and larval diagnostic characters. Considering that unionoid taxonomy based on morphological characters is highly subjective due to lack of good diagnostic features and a high degree of homeoplasy, it was hoped that molecular investigations would provide an answer. Thus far, the results have been rather meagre for the African unionid genera. Consequently, all questions pertaining to their relationship with each other and with taxa from other continents remain largely unanswered.

Superfamily Unionoidea Fleming, 1828

The order Unionoida consists of the superfamilies Unionoidea (Unionidae + Margaritiferidae) and the Etherioidea (Etheriidae + Iridinidae + Mycetopodidae + Hyriidae). In spite of the large amount of molecular and morphological research on unionoid phylogeny major questions on superfamily- and family-level relationships still remain unsolved (Bogan, 2008; Bogan & Roe, 2008; Bogan & Hoeh, 2000; Giribet & Wheeler, 2002; Graf, 2000; Graf & Cummings 2006a, 2007a, 2010a, 2010b; Graf & Ó Foighil, 2000; Hoeh *et al.*, 2001, 2009; Lydeard *et al.*, 1996; Roe & Hoeh 2003). Some authors (Hoeh *et al.*, 2009) even question the validity of the present approach, claiming that hypotheses about relationships on higher-level may be strongly influenced by the methods used and hence should be considered weakly supported. Here the taxonomic view of Graf & Cummings (2006a) is followed that is a synthesis partly from earlier studies and partly from these authors' own phylogenetic research based on molecular markers 28S and COI and morphological characters.

Family Unionidae Fleming, 1828

At present Graf & Cummings (2007a) state that they are only able to distinguish two subfamilies within the Unionidae, namely the Unioninae and the Ambleminae while a considerable number of taxa (including all Modern Afrotropical genera) remain *incertae sedis* their affinities still uncertain. In absence of conclusive molecular or morphologically diagnostic evidence, these authors do not adhere (at the moment) to the classical differentiation of the unionids into a considerable number of subfamilies (e.g. Unioninae, Ambleminae, Lampsilinae, Anodontinae,

Coelaturinae, etc.) (Lydeard *et al.*, 1996). But these authors' view has recently been abandoned e.g., by Hoeh *et al.*, (2009) and by Bieler *et al.*, (2010) who do recognize the Coelaturinae as an endemic African subfamily.

In Africa the Modern bivalve fauna comprises thirteen unionid genera, following the taxonomic arrangement of Graf & Cummings (2009b), namely *Anodonta** Lamarck, 1799; *Brazzaea* Bourguignat, 1885; *Cafferia* Simpson, 1900; *Coelatura* Conrad, 1853; *Germainaia*** Graf & Cummings, 2009; *Grandidieria*, Bourguignat, 1885; *Mweruella* Haas, 1936; *Nitia* Pallary, 1924; *Nyassunio* Haas, 1936; *Prisodontopsis* Tomlin, 1928; *Pseudospatha* Simpson, 1900; *Psilunio** Stefanescu, 1896; and *Unio** Philipsson, 1788 (*: in Palaearctic Africa only; **: in Madagascar only). The genera *Anodonta*, *Unio* and *Cafferia* belong to the subfamily Unioninae (Graf & Cummings 2007a), while most of the other genera are placed in the subfamily Coelaturinae (Bieler *et al.*, 2010). The new genera here described will probably all remain *incertae sedis* at the subfamily level.

Genus *Pseudobovaria* Adam, 1957

Type species. *Unio* (*Grandidieria*) *abruptus* Fuchs, 1936 (*non* Say, 1831) p. 101, Pl. III, figs 6-8.

Diagnosis. Adam (1959) created this (extinct) African genus, giving the following diagnostic characters: '*Unionid genus with equivalve strongly inequilateral and obliquely triangular shells; hinge comprising the cardinal teeth 3a, 4a and 2a strongly cut up in fine lamellae, 3b, 2b and 4b in the shape of elongated lamellae, 5a and 1 rudimentary*'. The heavy pseudocardinalia are situated under the beaks.

This author nominated *Pseudobovaria mwayana* (Fuchs, 1936) (type locality: Kazinga, Uganda) as type species of the genus. Unfortunately he did not base his description of the characteristics of the hinge of the original specimens from the type locality but on a specimen from Senga (Congo) that is actually not a *mwayana* but a representative of a derived lacustrine form, *Pseudobovaria grandis* sp. nov. Thus the type description for the genus is an amalgam of two different species. In *Pseudobovaria* the thickness of the hinge and the size and form of the cardinals is highly variable and are probably partially ecophenotypic. Small, thin and non-lamellate cardinals are typical of the fluvial form, *forma fuchsi*. Large and broad cardinals, the original structure of which is broken up into a series of lamellae, are typical of lacustrine forms such as *Pseudobovaria grandis* (see Fig. 14). The hinge of *Pseudobovaria mwayana* *forma typica* (see Fig. 13a), a form that seems to have occurred not only in shallow lake habitats but also in fluvio-estuarine habitats, is intermediate between the two and is also variable. Mandahl-Barth (1988) described a similar range of variability in the genus *Coelatura*, e.g. thin hinges in the fluvial, thin shelled *Coelatura aegyptiaca* and thick lamellate hinges in the heavily shelled lacustrine *Coelatura nyassaensis*. This author considered it to be an important argument for disregarding hinge-size and complexity as significant diagnostic elements (contrary to the views of Haas, 1936, 1969a).

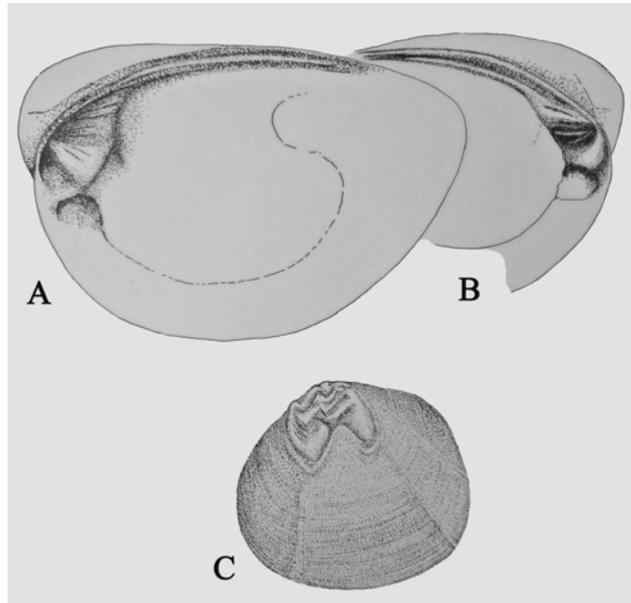


Figure 13. A-B) Hinge of *Pseudobovaria mwayana* (L = 13 mm) from the Turkana Basin (Site 'Gully North', Shungura Fm, Member H, *ca* 1.8 Ma); C) Juvenile shell of *Pseudobovaria mwayana* (NK 1178'89). (L = 3.5 mm).

The lengthy discourse by Adam (1957) on the hinge of *Pseudobovaria* should be simplified as follows: *hinge consisting of two large cardinals (2a and 4a) in the left valve, separated by a deep groove and a single cardinal (3a) in the right valve flanked on each side by a deep groove. Left valve with two laterals (or pseudocardinals) separated by a groove into which the single lateral of the right valve fits.* In lacustrine representatives of the genus the cardinals grow larger and are subdivided into a number of ridges or lamellae resembling tooth rows. To the above must be added that the umbonal sculpture on a young *Pseudobovaria* shell is limited to a few oblique ridges at the very top and a faint posterior ridge with minute tuberculi running from the beak towards the posterior end (Fig. 13b). In adult *Pseudobovaria* the shell is smooth and the umbonal ornamentation has eroded. The exception is *Pseudobovaria tuberculata*, where the embryonic sculpture has continued developing, resulting in an adult shell with two tuberculate ridges separated by a sulcus.

Pseudobovaria is not related to any of the other fossil or modern unionid genera known from Africa. The genus is as thick-shelled and shows an identical range of shell forms as the North American genus *Pleurobema* Rafinesque, 1819. The fluvial representative, i.e. *Pseudobovaria fuchsi*, is strikingly similar to *Pleurobema clava* (Lamarck, 1819) while *Pseudobovaria tuberculata* resembles *Pleurobema cordatum* (Rafinesque, 1820), etc. Adam (1957) already highlighted the similarities to the amblemine genus *Obovaria* Rafinesque, 1820. In our opinion there is little doubt that *Pseudobovaria* belongs to the group of unionids formerly vaguely referred to as 'Asian Ambleminae' which presently are placed in the subfamily Gonideinae (Bogan, A., pers. comm. 2010).

Since *Pseudobovaria* is unknown from any of the Early and Middle Miocene deposits in Africa but suddenly becomes widespread from the Terminal Miocene onward, it is assumed here that the

genus invaded from Asia during Late Miocene times. The oldest recorded representatives are from the Terminal Miocene Nkondo Member of the Nkondo Formation (*ca* 6.5 - 5.5 Ma) (Albertine Basin) and from deposits of Terminal Miocene-Early Pliocene age (*ca* 5.5 - 4.5 Ma) in the Afar, Ethiopia (unpublished material collected by Dr. T. White). Throughout the Pliocene and Early Pleistocene the genus is very abundant; often even being the dominant naiad, in the shell associations of the Albertine and Turkana Basins. *Pseudobovaria* was thus widely distributed in eastern and central Africa as far south as the Malawi Basin (Chiwondo Beds, unpublished material Research Unit Palaeontology, Ghent University).

The genus *Pseudobovaria* vanishes from the African fossil record between 1.5 and 1.2 Ma. The latest known records are from the Nyabusosi Fm (*ca* 1.5-1.2 Ma) (Albertine Basin) (this study) and from the Koobi Fora Fm, KBS Member (*ca* 1.5-1.3 Ma.) (Turkana Basin) (Van Damme, 1976). The cause of its extinction is unknown.

Species *Pseudobovaria mwayana* (Fuchs, 1936)

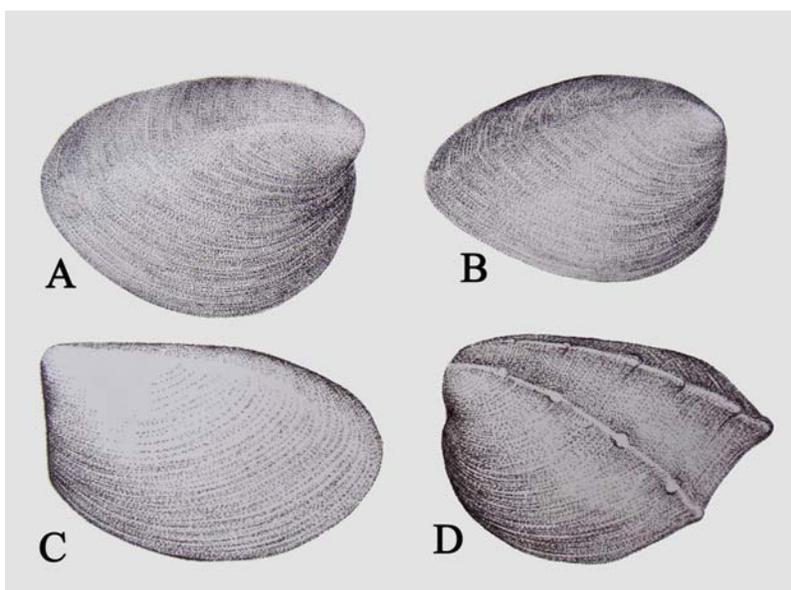


Figure 14. A) *Pseudobovaria mwayana* f. *typica* (NK 564'88 from Nkondo) (L = 34 mm); B) *Pseudobovaria mwayana* f. *fuchsi*, common shell morph from estuarine population (RG 16549 from Kazinga) (L = 29.5 mm), C) *Pseudobovaria mwayana* f. *fuchsi*, unusually elongated shell from fluvial population (NK 2555'89 from Nkondo) (L = 26 mm); D) *Pseudobovaria mwayana* f. *tuberculata*, Holotype (L = *ca* 23.5 mm).

Synonymy

(1) Formerly ranged under *Pseudobovaria fuchsi* Adam, 1957

Unio (*Grandidieria*) *abruptus* (Fuchs, 1936 (*non* Say, 1831), p. 101, Pl. III, figs 6-8).

Unio abruptus (Cahen, 1954, p. 342).

Unio abruptus (Adam, 1955, pp. 89, 90, 94, 97).

Pseudobovaria fuchsi (partim) (Adam, 1957, pp. 7, 8, 9, 125, 151, 156, Pl. VII, fig. 3).

(2) Formerly ranged under *Pseudobovaria mwayana* (Fuchs, 1936)

Unio (*Parreysia*) sp. nov. (Cox., 1926, p. 68, Pl. IX, fig. 4a-b).

?*Parreysia* sp. (Connolly, 1928, p. 206).

Unio (*Grandidieria*) *mwayanus* (Fuchs, 1936, p. 102, Pl. III, figs 13-15).

?*Unio parreysia* (Cahen, 1954, p. 342).

Pseudobovaria mwayana, (partim) (Adam, 1959, pp. 7, 122, 151, 156, Pl. VII, figs 1-2).

Pseudobovaria mwayana (partim) (Gautier, 1970a, pp. 104-107, Pl. III, fig. 22 a-b, Pl. IV, figs 1-8).

(3) Formerly ranged under *Pseudobovaria tuberculata* Adam, 1957

Unio tuberculé (Adam, 1955, pp. 36).

?*Pseudobovaria tuberculata* (Adam, 1957, pp. 8, 127, 151, 156, Pl. VII, fig. 4).

Material. *Pseudobovaria mwayana* forma *typica*: **BMNH**: L40263: 1 specimen (Kaiso, Cambridge Expedition); L 40264da: Kaiso, eastern shore of L. Albert (Wayland Exp.): 1 specimen. **SMC**: SM-D 4866: Kazinga (Fuchs Exp.): 1 valve; SM-D 4868: 1 valve (Fuchs Exp.). **UM**: NY 99'90 (NY 70): 2 specimens; NY 290'90 (NY 55): 2 specimens; NY 291'90 (NY 55): 1 specimen; NY 14'90 (NY 55): 1 specimen; NK 5'90 (NK 43): 1 specimen; NK 2441'89 (NK 135): 3 specimens; NK 429'89 (NK 106): 1 specimen; NK 564'88 (NK 87): several valves; NK 2236'89 (NK 120): 13 specimens; NK 171'89 (NK 36): 2 specimens; NK 263'89 (NK 115): 1 specimen; NK 769'89 (NK 115): 3 specimens; NK 1010'89 (NK 82): 1 specimen; NK 1003'89 (NK 32): 1 specimen; NK 830'89 (NK 125): 1 specimen; NK 635'89 (NK 62): 1 specimen; NK 498'89 (NK 122): 1 specimen; NK 117'88 (NK 82): 1 specimen; NK 67'88 (NK 43): 1 specimen; NK 305'88 (NK 84): 1 specimen; NK 65'88 (NK 43): 1 specimen; NK 851'88 (NK 115): 1 specimen; NK 28'88 (NK 39): 1 specimen; NK 806'88 (NK 115): 1 specimen; NK 75'88 (NK 42): 1 specimen; NK 75'88 (NK 42): 1 specimen; NK 72'88 (NK 43): 1 specimen; NK 836'88 (NK 93): 1 specimen; NK 114'88 (NK 81): 1 specimen; NK 625'88 (NK 104): 1 specimen; NK 847'88 (NK 115): 1 specimen; NK 188'88 (NK 85): 1 specimen; NK 467'88 (NK 74): 1 specimen; NK 113'89 (NK 126): 1 specimen; NK 200'88 (NK 84): 5 specimens; NK 564'88 (NK 97): several specimens and valves; KS 13'90 (KS B): 1 specimen; KS 39'89 (KS Village): 1 specimen; KN 10'88 (KN 2): 1 specimen; KN 88'88 (KN 6): 1 specimen; KN 35'88 (KN 5): 1 specimen; KN 162'88 (KN 7): 1 specimen; KN 203'88 (KN 6): 1 specimen; KN 213'88 (KN 9): 1 specimen; KN 164'88 (KN 7): 1 specimen; KN 1'88 (KN 1): 1 specimen; KN 89'88 (KN 6): 1 specimen. **MCA**: RG 16.755 & RG 16.553 (Wasa-Kisegi, Rwebishengo Site 2B): 16 fragmentary and 4 more complete molds; RG 16.638 (Kazinga, Site 1-2): 7 specimens; RG 16.640 (Kazinga, Site 3): fragmentary shells and fragments; RG 16.746 & RG 16.754 (Wasa-Kisegi, Makoga Site A.G.): about 15 molds in several pieces of ironstone; no reference number (Wasa-Kisegi, S. Rwebishengo Site W.B.): several cross sections in slag-like ironstone; RG 16.753 (Wasa-Kisegi, N. Behanga II Site 2 B): 3 specimens; RG 16.757 (Wasa-Kisegi, Behanga II Site 4): 1 mold; MC 907-908: Kazinga (Pitman-Fuchs Exp.): 2 valves. **LPG**: P 4694 (Kanyatsi Ravine, western slope, 937 m, G3c): 3 specimens; P 4695 (250 m N. of Kanyatsi excavation trench, G5b): 1 specimen; P 4710 (Nyakasia Ravine, western slope, 978 m, G3): 1 specimen.

Pseudobovaria mwayana forma *fuchsi*: **UM**: NK 2465'89 (NK 93): 4 specimens; NK 2555'89 (NK 115): 1 specimen 26 x 17 x 7.2; NK 2515'89 (NK 60): 1 specimen; NK 787'89 (NK 120): 6 specimens; NK 807'89 (NK 43): 1 specimen; NK 519 (NK 122): 1 specimen; NK 1072'89 (NK 48): 1 specimen; NK 304'89 (NK 119): 1 specimen; NK 273 (NK 115): 1 specimen; NK 187'88 (NK 85): 1 specimen; NK 473'88 (NK 85): 3 specimens; NK 200'88 (NK 84): 5 specimens; KN 12'88 (KN 2): 1 specimen. **MCA**: RG 16.688 (Kaiso, Site G): 3 calcareous specimens + fragment; RG 16.659 (Kaiso Site 1): 9 specimens; RG 16.659 (Kaiso, Site 2): 1

specimen; RG 16.686 (Kaiso, Site 3): 20 specimens; RG 16.688; RG 16.554 (Kaiso, Site G): one doubtful specimen and some molds in ironstone; RG 16.756 (Wasa-Kisegi, N. Behanga I Site 1 B): 1 specimen; RG 16.760 (Wasa-Kisegi, downstream N. Nyaburogo I Site 1): 1 specimen; RG 16.557 (Wasa-Kisegi, N. Nyaburogo I Site 2): 1 mold; RG 16.759 (Wasa-Kisegi, N. Nyaburogo I Site 3): 1 specimen; RG 16.645 (Kazinga, Site 4): one valve on ironstone and one very small juvenile specimen; RG 16.644, RG 16.555 (Kazinga, Site E): 1 fragment and 3 specimens; RG 16.643, RG 16.549 (Kazinga, Site Q): 20 specimens; RG 16.558 (Kazinga, Site D): 1 specimen on ironstone. RG 16.642 (Kazinga, Site 1-2): 9 specimens; RG 16.639 (Kazinga, Site A1): 15 specimens; RG 16.559 (Kazinga, Site A3): 1 specimen; MC 899-900 (Kazinga, Fuchs Expedition): 2 specimens. **BMNH**: RG 16.560 (Kazinga, Site C): 13 valves. **SMC**: SM-D 4848 (Kazinga): 1 specimen; SM-D 4849 (Kazinga): 1 valve; SM-D 4850 (Kazinga): 1 right valve (Fuchs Expedition material). **BNH**: (1) 65 to 80 m from the lake edge at Nyakasia Ravine (de H., p. 94 = L. 283-285, sample 641): several poorly preserved specimens (2) several outcrops east of Kanyatsi (de H., p. 90 = L. 282-283): 1 specimen. **LPG**: P 4709, Nyakasia Ravine, western slope, 987 m (G3c): 7 specimens; P4717, Nyakasia Ravine, eastern crest (G3c): 3 specimens.

Pseudobovaria mwayana forma *tuberculata*: **BNH**: Ford at Kihanga (de H., p. 36 = L. 318-319).

Pseudobovaria mwayana forma indet.: some material is too poorly preserved to warrant identification on the forma level. This is the case for Adam's (1957) material from the ravine east of Kanyatsi, the ford at Kihanga, the site '1000 m east of Ishango', the site '65 to 80 m from the lake border at Nyakasia Ravine', the site 'at the Semliki R. downstream of Katanda' and the site 'at the head of Nyakasia Ravine', as well as Gautier's (1970a) specimens from North Nyakabingo I and North Nyaburogo I (Wasa-Kisegi).

Distribution. *Pseudobovaria mwayana* f. *typica*: Upper Semliki - Ishango area, (L. Edward, Congo); Kazinga - Bushabwanyama area (L. Edward, Uganda); Nkondo area (L. Albert, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda); Wasa-Kisegi area (Lake Albert, Uganda), Kaiso Village-Hohwa area (Lake Albert, Uganda).

Pseudobovaria mwayana f. *fuchsi*: Upper Semliki - Ishango area, (L. Edward, Congo); Kazinga - Bushabwanyama area (L. Edward, Uganda); Nyaburogo - Nyabusosi area (L. Albert, Uganda); Nkondo area (L. Albert, Uganda), Wasa - Kisegi area (L. Albert, Uganda).

Pseudobovaria mwayana f. *tuberculata*: Sinda-Mohari area (Semliki Plain, Congo).

Description. The three species of *Pseudobovaria* created by Fuchs (1936) and Adam (1957), are here considered to be ecophenotypes belonging to a single polymorphic species. It is possible, even likely, that genetic differences did exist at some times but in our opinion this cannot be substantiated convincingly. In the Turkana Basin, for example, the only morphotype that is found in the estuarine deposits of the Shungura Formation is *Pseudobovaria mwayana* while in the typical lacustrine deposits of the Koobi Fora Formation, mainly or sometimes exclusively a form resembling *Pseudobovaria tuberculata* is recorded (Van Damme, 1976). However, since the different 'forms' are indicative of different ecological conditions and yield important environmental information, they are maintained here and the 3 original descriptions are given.

Pseudobovaria mwayana forma *typica*: the original description reads: 'Shell small, thick,

rounded; hinge line arcuate. Umbones high, situated anteriorly, curving forward and inward. Ornamentation of concentric growth lines only. Left valve, two long pseudo-cardinal teeth and deep posterior-lateral sockets. Right valve, one rather prominent triangular tooth and one very strong posterior lateral. Pallial line simple, anterior muscle-scars very deep, posterior scars unknown (Fuchs, 1936). To this must be added: the L/H ratio is 1.3-1.4, the umbo extends beyond the anterior margin, the ventral margin is strongly curved, the pseudo-cardinals are incised, the posterior scars are large but superficial and the pallial line is strongly curved posteriorly.

Pseudobovaria mwayana forma *fuchsi*: the original description reads: ‘Shell small, thick, rhomboid, inflated to a variable degree. Umbones prominent, boss-shaped, and situated on the anterior margin. Concentric striae on the surface. One very prominent divided tooth in the right valve, and one very long posterior lateral in each valve. Pallial line simple, anterior adductor scar very deep; posterior adductor unknown’ (Fuchs, 1936). To this can be added that the beak is situated anteriorly but either does not surpass or only slightly surpasses the anterior end, that the posterior dorsal margin is straight to evenly curved, the posterior end acuminate, the ventral margin strongly curved and the anterior side vertical and nearly straight. The hinge is typical and the posterior adductor scar is quite weak. Forma *fuchsi* specimens (Fig. 14b, c) differ from *Pseudobovaria mwayana* forma *typica* by having a smaller and thinner shell, a beak not extending beyond the anterior margin, a higher L/H ratio (the posterior part being longer), a smaller diameter, a more horizontal instead of downward slanting and curved posterior margin and a hinge with relatively weak teeth.

Pseudobovaria mwayana forma *tuberculata*: Adam did not give a detailed description. This form is similar to *mwayana* as to the general shape, size and hinge but differs from the typical form by its ornamentation consisting of two rows of tuberculi sometimes separated by a more or less marked sulcus running from the umbo to the posterior margin.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------------------------------------------------|---------|--------|----------|-----------------------------|
| <i>Pseudobovaria mwayana</i> f. <i>typica</i> | | | | |
| Holotype | c.18.0 | 13.8 | - | L 40263 |
| Nkondo NK 97 | 34.0 | 24.2 | 17.1 | NK 564’88 |
| Nkondo NK 97 | 27.2 | 20.5 | 15.7 | NK 564’88 |
| <i>Pseudobovaria mwayana</i> f. <i>fuchsi</i> | | | | |
| Lectotype | 26.0 | 17.0 | 9.0 | SM-D 4848 |
| Paratype | 21.7 | 13.0 | 11.5 | SM-D 4849 |
| Nkondo NK 115 | 20.3 | 16.0 | 12.8 | NK 2555’89 |
| <i>Pseudobovaria mwayana</i> f. <i>tuberculata</i> | | | | |
| Holotype | ca 23.5 | 16.0 | - | Adam (1957) Pl. VII, fig. 4 |

Type locality. *Pseudobovaria mwayana* f. *typica*: Kazinga, Mweya Peninsula, Lake Edward, Uganda (V. Fuchs *collevis*, Cambridge Exp., 1930-1931);

Pseudobovaria mwayana f. *fuchsi*: Adam (1957) failed to designate a holotype, the specimen described by Fuchs (1936) as *Unio abruptus* sp. n. ‘thin form’ (Fuchs, 1936, PL III, Fig 6) and registered in the Sedgwick Museum at Cambridge under reference SM-D 4848 is here

nominated as such. The type locality is Kazinga, L. Edward, Uganda (V. Fuchs *collevit*, Cambridge Exp. 1930-1931).

Pseudobovaria mwayana f. *tuberculata*: Kihanga Ford, Upper Semliki area, L. Edward, Congo (J. de Heinzelin *collevit*, Mission Jean de Heinzelin, 1950-52).

Stratigraphy and age. *Pseudobovaria mwayana* f. *typica*: Late Miocene to Early Pleistocene, Molluscan Associations G3a to G6. Nyaburogo, Nyakabingo, Nyabusosi, Nkondo, Warwire, Kyeoro, Kaiso, Lusso (LIII) and Semliki Formations and Kazinga Beds.

Pseudobovaria mwayana f. *fuchsi*: This form is restricted to deposits of Late Miocene to Early Pliocene age namely in the Nyaburogo, Nkondo and Warwire Formations and the Kazinga Beds and in the lower part of the Lusso Formation (Biozone L0, LI), Molluscan Associations G3a to G3c.

Pseudobovaria mwayana f. *tuberculata*: this form is restricted to the Upper Lusso Formation (LIII). Lower Pleistocene, Molluscan Association G5c.

Remarks. The morphological diversity observed in the Albertine *Pseudobovaria mwayana* shells is distinctly less than that observed in *Pseudobovaria mwayana* shells of similar age from the Turkana Basin.

These ecophenotypes represent 3 different aquatic habitats:

- The form described as *Pseudobovaria fuchsi* Adam, 1957 is of fluvial origin. The typical fluvial form (Fig. 14c) is strongly elongate somewhat reminiscent of a small *Nitia* with an eccentric beak. Such specimens are very rare since the Albertine deposits are exclusively lacustrine or estuarine. In the latter a *Pseudobovaria fuchsi* form (Fig 14b) occurs which is less elongate and stands morphologically closer to typical *Pseudobovaria mwayana*. The overlap with the estuarine-lacustrine *Pseudobovaria mwayana* morph is too great to consider *Pseudobovaria fuchsi* a distinct species, although it must be noted that typical *Pseudobovaria fuchsi* specimens are confined to the Lower Pliocene deposits, while in younger deposits only the typical *Pseudobovaria mwayana* morph persists.

- The typical estuarine-lacustrine, non-ornate *Pseudobovaria mwayana* form (Fig. 14a) seems to have been confined mainly to estuaries and shallow sandy lake margins. This is the most common morph in the Albertine deposits, ranging throughout the Pliocene and early Pleistocene.

- The ornate morph described as *Pseudobovaria tuberculata* Adam, 1957 (Fig. 14d) seems to indicate sandy-muddy to muddy bottoms in calm shallow environments. It is very rare in the Albertine deposits and is known only from the Upper Lusso Formation (Lower Pleistocene of Palaeolake Lusso). We agree with Williamson (1990) who considered this to be a form of *Pseudobovaria mwayana* and not a distinct species. Similar ornate *Pseudobovaria* shells are quite common in the Late Pliocene Koobi Fora Formation in the Turkana Basin. In these deposits shells with an almost central umbo and two rows of tuberculi are linked through all kinds of intermediates with typical unornamented *Pseudobovaria mwayana* shells with a strong eccentric umbo (Van Damme, 1976).

Concerning the molluscan associations of the Lower Semliki deposits, Williamson (1990) stated that he considered only the *Pseudobovaria* shells from the Semliki Formation (Site Katanda 3 and Katanda 13 of de Heinzelin & Verniers, 1996) to belong to *Pseudobovaria mwayana*, while those from the earlier levels were identified by him as a new species (*Pseudobovaria* nov. sp. A in Williamson, 1990). We agree with this view and the new species is here described as *Pseudobovaria grandis* nov. sp.

Species *Pseudobovaria grandis* nov.

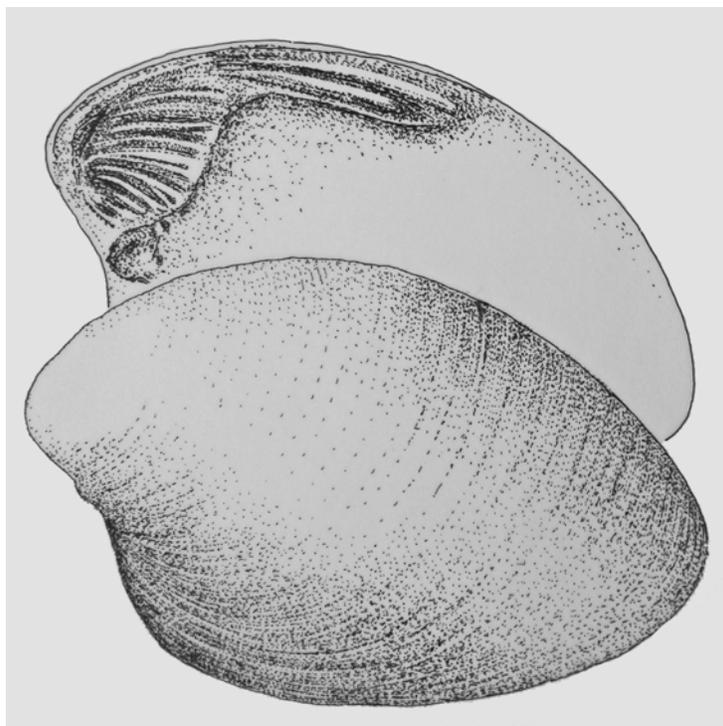


Figure 15. *Pseudobovaria grandis* sp. nov. Holotype (L = 42 mm).

Synonymy

Unio mwayanus (Adam, 1955, pp. 39, 96, 130).

Pseudobovaria mwayana (Adam, 1957, pp. 122-125, Pl. VII, fig. 1-2).

Pseudobovaria fuchsi (partim) (Adam, 1959, pp. 35-36, Pl. VII, fig. 2).

Material. **BNH:** Senga, Semliki R. in front of the Kasaka River, 1.0 to 3.6 m from the riverbank: many specimens (Adam, 1957). **MCA:** MC 2514 (Lep. 493: Nyamavi N° 83, right bank of the Suna): several specimens; MC2737 (Lep. 588: Irimba-Maginda N° 209, track from Bunabo to the Semliki): 3 large specimens intermediate between *Pseudobovaria grandis* and *Pseudobovaria truncata*.

Distribution. Lower Semliki, Lake Edward, Congo.

Description. ‘Shell equivalve, strongly inequilateral, obliquely triangular, umbones projected, passing beyond the anterior margin. Valves slightly concave anteriorly, flattened or slightly

convex posteriorly. The total diameter of the bivalve is about half the length; which slightly surpasses the width. The dorsal side is flattened, separated from the lateral sides by rounded angulations; not forming a well defined ridge. The ligament groove is narrow, elongated, with a length surpassing half the total dorsal length. Since the nymphae are not clearly visible, it is impossible to determine exactly the length of the ligament and of the sinus. Viewed laterally, the anterior margin that is distinctly concave below the umbones becomes brusquely convex in the basal part which gradually merges into the lower convex margin. The lunula is clearly defined, broadly ovate and so inflated as to be visible in profile. The surface is regularly striated with concentric lines and in addition shows a very fine radial striation.

The hinge presents principally the dental formula of the Unionidae $\frac{5^a, 3^a, 1, 3^b}{5^a, 2^a, 2^b, 4^b}$

In the Senga fossils the reduction of the width of the shell is still more marked than in *Unio littoralis* Lamarck. This can equally be said for the anterior shift of the umbones and for the thickening of the teeth of which the anterior teeth are even more directed backwards. This type of hinge is reminiscent of that of the genus *Obovaria* and in particular of *Obovaria retusa* Lamarck. The right valve shows the teeth 5^a , 3^a and 1 separated by two triangular grooves, together forming a whole divided into fine lamellae, spread out fan-like. Tooth 5^a is rudimentary, tooth 3^a is strongly developed and triangular while tooth 1 is very small. The ridge of the grooves is reflected, which makes these ridges look like additional lamellar teeth, as in *Obovaria retusa*. In the left valve the well-developed teeth 4^a and 2^a , separated by a deep groove, form a complex that is equally strongly laminate; 2^a is better developed than 4^b . The long pseudocardinals (or laterals) 2^b and 4^b are separated by a groove into which 3^a fits. In the interior of the valves the impressions of the adductor muscles are visible, the anterior being stronger than the posterior, which is quite faint. The impressions of the pedal muscles are indistinct, in particular those of the protractors, which cannot be separated from the impression of the anterior adductor. The impressions of the anterior retractors are situated on the interior side of the anterior cardinals, being more distinctly separated from the impressions of the anterior adductor than in *Obovaria*. ...The surface of the shell shows an ornamentation of dense concentric growth lines, crossed by fine radial striae barely visible to the naked eye, except in the centre of the basal region where they are somewhat more distinct.' (translated from Adam, 1957).

Dimensions (in mm).

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|------------------------------|
| Holotype | 42 | 36 | 22 | Adam (1957) Pl. VII, Fig. 1a |

Type locality. Senga, Semliki River in front of the Kasaka, Lake Edward, Congo (J. de Heinzelin *collevis*, Mission Jean de Heinzelin, 1950-52).

Stratigraphy and age. Lusso Formation (L II & III), Upper Pliocene, Molluscan Association G5a-b.

Etymology. Named after the large size of the shell.

Remarks. Adam (1957) considered the shells of *Pseudobovaria grandis*, as defined here, from Senga (Congo) to belong to *Pseudobovaria mwayana* f. *typica* Fuchs (1936). However, they differ markedly from *Pseudobovaria mwayana* f. *typica* shells by their size, which is 1.5 to 2

times larger and by their strongly elongated and lamellate cardinals. Williamson (1990) mentioned this species as *Pseudobovaria* sp. nov. A from the Lusso Formation (LII & LIII) from the sites Kanyavoghorwe 6, Chiribidi 6, Kishishio 2 and Senga 1 of de Heinzelin & Verniers (1996).

This morphotype is rare and has a very limited range in time and space. We consider *Pseudobovaria grandis* to be a lacustrine endemic form that evolved from a *Pseudobovaria mwayana* lineage and was restricted to the southern part of Palaeolake Obweruka during the final part of its existence and to the subsequent Palaeolake Lusso. During the terminal stage of that lake when its endemics were being replaced by widespread 'Nilotic' species, *Pseudobovaria grandis* also went extinct and the fluvio-estuarine *Pseudobovaria mwayana* reappeared in the lacustrine deposits.

Species *Pseudobovaria truncata* nov.

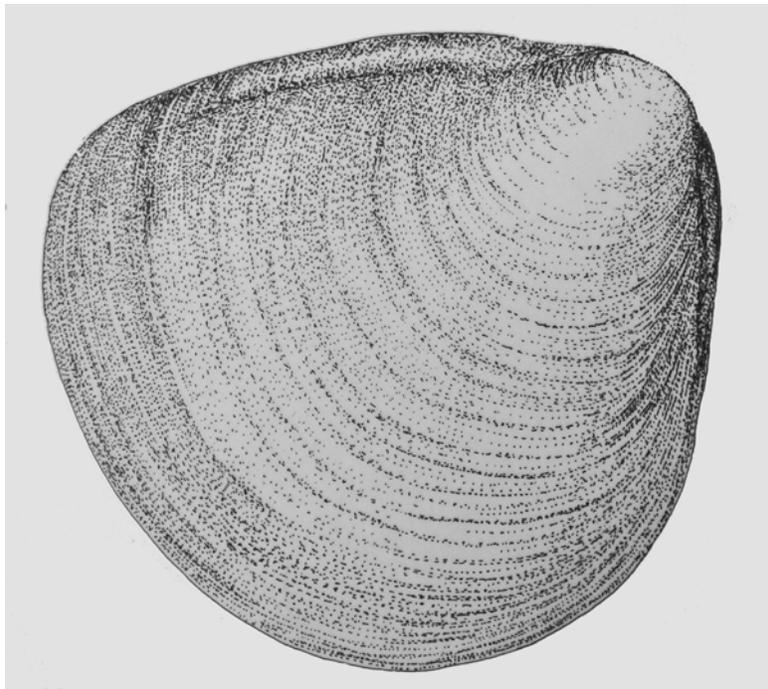


Figure 16. *Pseudobovaria truncata* sp. nov. Holotype (L = 34.0 mm).

Synonymy

Pseudobovaria fuchsi (partim) (Adam, 1957, p. 126, Pl.VII, fig. 3a-c).

Pseudobovaria fuchsi (partim) (Adam, 1959, pp. 35-36, Pl. VII, fig. 1).

Material. UM: NY 193'90 (NY 55): 1 valve (type); NY 14'90 (NY 55): 3 specimens. MCA: MC2765, Ravine east of Kanyatsi: 1 bivalve and a few poorly preserved specimens; MC 2460b (Lep. 483), Nyamavi N° 75, Nyangomba river: 1 specimen (pl. VII, fig. 1 in Adam, 1959).

Distribution. Upper Semliki - Ishango area, (L. Edward, Congo); Nyamavi area (L. Albert, Congo), Nyaburogo-Nyabusosi area (L. Albert, Uganda).

Description. Relatively large, inflated, solid, triangular unionid shell with a strongly eccentric, wide and inflated beak, curving forward. Posterior dorsal margin downward sloping and nearly straight, posterior end forming at the base a truncated angle with the ventral margin which is regularly curved. Anterior margin sloping nearly vertically downward, forming a truncated angle with the ventral margin. A blunt ridge runs from the posterior part of the beak to the basal posterior angle, a distinct sulcus is present above it. Of the hinge only the laterals are visible which are strongly curved, and part of the pseudocardinals which are so strongly developed that the part of the dorsal margin above them bulges. Ornamentation consisting of very fine growth lines only.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|-----------------|---------|--------|----------|--------------|
| Holotype | 34.0 | 33.3 | 22.0 | NY 193'90 |
| Paratype | ca 33.2 | 34.0 | 23.0 | NY 14'90 |
| Nyaburogo NY 84 | + 29.5 | 35.5 | - | NY 84'92 |

Type locality. Site NY 55 of Pickford *et al.*, (1993), Nyaburogo-Nyabusosi area, Toro District, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition, 1988-1993).

Stratigraphy and age. Nyakabingo Fm, Lusso Fm (LII or LIII), Nyamavi Beds Member V or VI. Terminal Pliocene to Early Pleistocene, Molluscan Association G5a-b & GX.

Etymology. Species named after the truncated shell morphology.

Remarks. *Pseudobovaria truncata* is known from a few specimens in the Nyakabingo and Nyamavi areas and the Upper Semliki region. The former deposits belong to the last part of the Palaeolake Obweruka sedimentary series, just prior to the division of this enormous lake into two smaller basins. The upper Semliki specimens may date from the same period (Lusso II) or from younger deposits (Lusso III), provided that the tentative stratigraphical correlation by Verniers & de Heinzelin (1990) is correct. In the latter case *Pseudobovaria truncata* would have persisted in Palaeolake Lusso, which we deem unlikely. The most puzzling aspect of this species is its general shape, as it is not evident how the shell was oriented in life. This species evolved from a *Pseudobovaria mwayana* or more likely a *Pseudobovaria grandis* strain in which the pedal muscle increased in size at the cost of the space occupied by the gills, causing a shift of the beak. In addition the shell became flatter and the height almost equals the length. Another evolutionary alteration is the presence of a sulcus. Kauffmann (1969) states that sulci and folds on infaunal bivalves normally reflect internal partitioning of the soft parts and development of interior supports for attachment of muscles, gills, or other organs. They may function externally to strengthen the shell and in some forms deep sulci terminate near the exhalant aperture and may function secondarily to channel currents passing over the shell into the exhalant area, ensuring dispersal of wastes.

The general shape of *Pseudobovaria truncata* indicates that it was an infaunal species, living erect and deeply buried in the substrate

Genus *Pseudodiplodon* Adam, 1957

Type species. *Pseudodiplodon sengae* Adam, 1957, pp. 7, 8, 128, 156, Pl. VIII, fig 1-3.

Diagnosis. The genus is distinct from any other African taxon by its rhomboidal and strongly flattened form, the strongly curved ventral margin and the robust hinge plate with a wide interdentum. As Adam (1957) stated (see below) the material from the Albertine Basin consists of only a single right valve in which the hinge is visible but eroded. This paratype appears to be lost. We therefore used *Pseudodiplodon* material from the Turkana Basin to complete the hinge description as follows:- Hinge broad and flattened with a faint ornamentation of parallel growth lines copying the ligamentary structure of a *Chambardia* (Iridinidae). The hinge of the left valve consists of an ovoid elevated pseudocardinal complex comprising five to seven teeth or lamellae, separated by grooves and situated nearly perpendicularly in relation to the dorsal margin. The highest part of this structure is a curved and long triangular lamella that runs parallel to the dorsal margin and is situated dorsally from the perpendicular teeth and is in its turn bordered dorsally by a small, slightly elevated bulge. This pseudocardinal complex is situated distinctly anteriorly to the beak. The two lateral teeth are delicate and weakly curved. They only occupy the lower posterior part of the hinge plate. The pseudocardinal complex and the pseudolaterals are widely separated by a broad and flat interdentum. The hinge of the right valve consists of a grooved impression into which the pseudocardinal complex of the left valve fits accompanied by a single delicate pseudolateral (Fig 17, B-C).

Occurrence. Late Pliocene Palaeolakes Lusso and Kaiso in the Albertine Basin (present study) and Late Pliocene Palaeolake Lokeridede in the Turkana Basin (Feibel, 1997; Van Bocxlaer & Van Damme, 2007). The genus appears synchronously in the two basins around ca. 2.6 Ma and rapidly vanishes (around 2.4 Ma).

Remarks. Adam (1957) stressing the likeness to the South American genus *Diplodon* Spix, 1827, placed *Pseudodiplodon* in the Mutelidae which in his time consisted of the Iridinidae + Hyriidae (McMichael & Hiscock, 1958). The Hyriidae are since considered to represent a distinct family in the Etherioidea (Parodiz & Bonetto, 1963). The possibility that Hyriidae may have persisted until recent times on the African continent, or more correctly on Madagascar, has been suggested by Graf & Cummings (2009a). *Pseudodiplodon* seemed to be the most likely candidate for a continental African hyriid, considering its taxonomic arrangement by Adam. In our opinion, *Diplodon* and *Pseudodiplodon* have no features in common except for the rhomboid shell shape that also is found e.g. in *Diplodon solisianus* (d'Orbigny, 1835). But *Pseudodiplodon* is much more flattened, it completely lacks ornamentation and the hinge is markedly different from that of *Diplodon*. The other hyriid genus with rhombiform representatives, the Australian *Westralunio* Iredale, 1934, has a fine delicate hinge. We do not feel that the evidence presented by Adam for ranging *Pseudodiplodon* in the Hyriidae is convincing; a rhomboid habitus also occurs in the Unionidae, e.g. in the modern Indotropical *Chamberlainia hainesiana* (Lea, 1856). While this unionid genus possesses a hinge resembling that of *Pseudodiplodon* (placement and form of the teeth) it attains a size 5 times that of *Pseudodiplodon*.

In his paper on punctuated equilibrium, Williamson (1981) considered that the *Pseudodiplodon* shells from his 'Suregei Isolate Fauna' were the result of a sudden and abrupt evolutionary change in a *Coelatura bakeri* lineage that occurred within Palaeolake Turkana. The derived

daughter lineage was, according to him, a new endemic *Coelatura* species. These Suregei shells are not the result of an in-lake evolution in *Coelatura* but are typical *Pseudodiplodon* shells (Van Bocxlaer *et al.*, 2008). They only differ from *Pseudodiplodon sengae* by their smaller size (maximal length *ca.* 37mm). This remarkable genus appears in the Turkana Basin during the same period that a West African gastropod ('Cameroon' *Potadoma*; Pachychilidae) and the Asian *Corbicula* invaded it (Williamson, 1985). The source of its origin (Indotropical or Afrotropical) thus remains unclear.

Species *Pseudodiplodon sengae* Adam, 1957

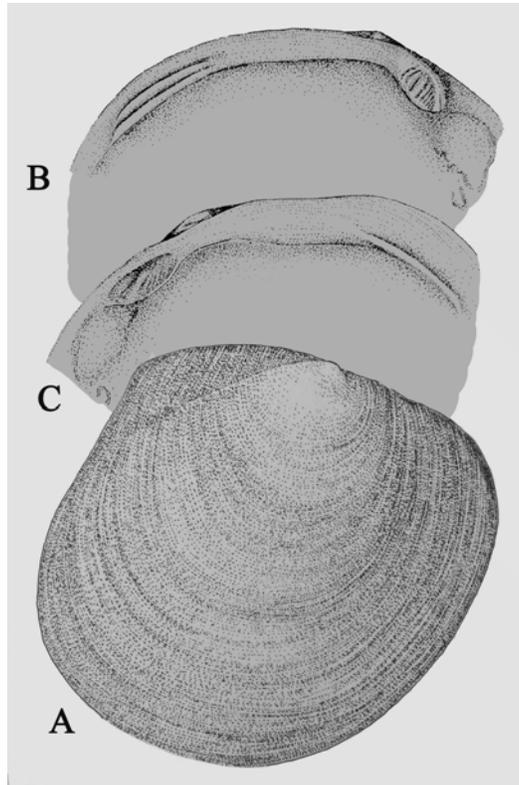


Figure 17. *Pseudodiplodon sengae* Adam, 1957. A) Holotype (L = 47.0 mm) from Senga, Congo, B) Left valve (L= 30 mm) and C) right valve (L= 29 mm) of *Pseudodiplodon cf. sengae* from the Turkana Basin (Koobi Fora, Koobi Fora Fm, Lower Burgi Member)

Synonymy

?*Diplodon* sp. (Adam, 1955, pp. 39, 40, 130).

Pseudodiplodon sengae Adam, 1957, pp. 7, 8, 128, 156, Pl. VIII, fig 1-3.

Pseudodiplodon sengae (Williamson, 1990, p. 136, fig 2).

Material. BNH: Senga, in front of the Kasaka River, 1.0 to 3.6 m above the Semliki river: a complete specimen (holotype) and a few poorly preserved valves; right bank of the Semliki River upstream of Senga: 2 poorly preserved valves (L. 315). **LPG:** P4696, 55 m north of Kanyatsi excavation trench (G5b): 1 fragment.

Distribution. Upper Semliki - Ishango area, (L. Edward, Congo).

Description. Adam's description of his new genus and species is inadequate: '*the shell consists of two equal valves and is almost equilateral, suborbicular or rhombiform, flattened and almost as high as wide. The test shows a fine concentric striation, more accentuated in the posterior part near the dorsal margin. The interior of the valves is poorly preserved. What remains of the hinge resembles that of the genus Diplodon*' (translated from Adam, 1957).

We therefore re-describe the type as follows: relatively large, thin shelled and extremely flattened rhomboid unionid shell. Length equal to the height, height more than 1.8 times the diameter. Surface of the shell flat, barely convex. Beaks are low, minute, and flat, with a sharp point and scarcely projecting above the hinge line. They are situated slightly anteriorly from the centre of the shell. The posterior margin is raised and almost straight, forming an angle of about 90° with the posterior end which in the upper half is slightly convex and in the lower part broadly rounded, passing into the equally strongly curved ventral margin. The anterior dorsal margin is about the same length as the posterior one and forms a blunt rounded angle with the ventral margin in the upper part of the shell's height. Ornamentation absent except for very fine and regular growth lines. Hinge of the type specimen not visible.

From the Albertine Basin only a single left valve (paratype A) with a visible hinge is known. It is poorly preserved but is identical to the abundant and well preserved valves from the Turkana Basin. We refer to their description under the diagnosis of the genus. The most remarkable features of *P. sengae* are its hinge and its extreme flatness, the diameter of a doublet not being in excess of 25 mm.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------|--------|--------|----------|------------------------------|
| Holotype | 47.0 | 45.2 | 24.3 | Adam (1957) Pl. VIII, Fig. 1 |
| Paratype A | 45.0 | 42.2 | - | Adam (1957) Pl. VIII, Fig. 2 |
| Paratype B | 48.8 | 45.4 | - | Adam (1957) Pl. VIII, Fig. 3 |

Type locality. Exposure at the Semliki River near Senga, Lower Semliki-Lake Edward, Congo (J. de Heinzelin *collevis*, Mission de Heinzelin, 1950-52).

Stratigraphy and age. Lusso Formation (LII). Late Pliocene, Molluscan Association G5b.

Remarks. Williamson (1990) recorded *Pseudodiplodon sengae* from other sites in the Senga region namely from Senga 5, 6, 13, 15 & 16 and also from Mupanda 4 of de Heinzelin & Verniers (1996). The internal molds (MC 2594; MC 2711) from Late Miocene deposits in the Sinda-Mohari region, referred to by Adam (1959, Pl. VII, figs 3 & 4) as *Pseudodiplodon sengae?*, probably pertain to *Chambardia triangulata*, a Middle Miocene species unknown to Adam. Of the material borrowed for study by Williamson, only the type was returned to the Museum of Central Africa after his death, the paratypes are still missing.

Species *Pseudodiplodon hohwae* nov.

Material. UM: KS 43'89 (Kaiso A): 1 specimen (type); HO 52'90 (HO 1): 1 specimen +

fragment.

Distribution. Kaiso Village-Hohwa area (Lake Albert, Uganda).

Description. Relatively large, moderately inflated and rather robust rhomboid-ovate unionid. Length equal to, or smaller than, the height which is about 2 to 3 times the diameter. Beak well-developed, broad and rounded, slightly protruding and excentric, being situated in the anterior third of the total length. Posterior margin straight and raised, with a broad curve joining the posterior end which is broadly rounded and most protruding at the base. Ventral margin evenly curved, forming a blunt angle with the sharply downward sloping, straight anterior margin. Growth lines very fine, almost incremental. Hinge unknown.

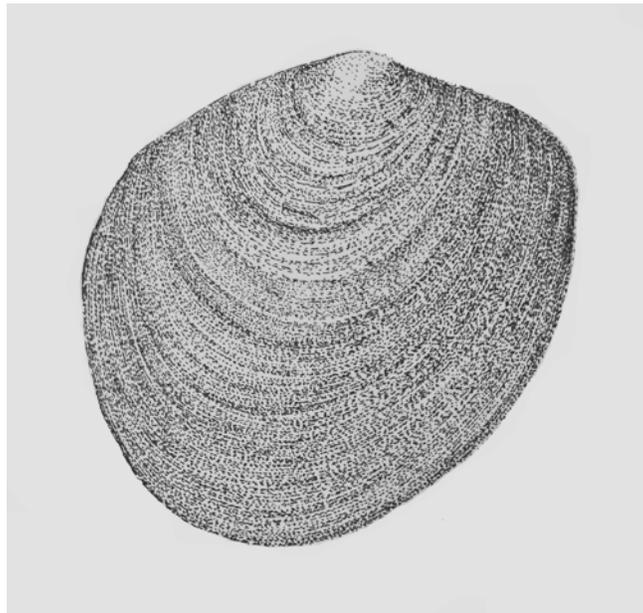


Figure 18. *Pseudodiplodon hohwae* sp. nov. (L = 38.5 mm).

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------|--------|--------|----------|--------------|
| Holotype | 38.5 | 36.8 | 20.4 | KS 43'89 |
| Hohwa HO 1 | 48.5 | 50.2 | 15.0 | HO 52'90 |

Type locality. Site Kaiso A of Pickford *et al.*, (1993), Kaiso Village, Lake Albert, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition, 1988-1993).

Stratigraphy and age. Kaiso Village Formation. Late Pliocene, Molluscan Association GX.

Etymology. Named after the Hohwa River (L. Albert, Uganda).

Remarks. Only 3 specimens of *Pseudodiplodon hohwae* have been recovered and the hinge plate is not visible, except for the upper part of the laterals. *Pseudodiplodon hohwae* is a peculiarly formed species that does not resemble any known African unionid except for the

contemporaneous *Pseudodiplodon sengae* and *Pseudodiplodon cf. sengae* from Pliocene deposits in the Turkana Basin. It differs however from these by its rounder shape, large, more excentric and broader beak and the smaller diameter. We therefore consider *Pseudodiplodon hohwae* to be a distinct endemic species that evolved in Palaeolake Kaiso from the widespread *Pseudodiplodon sengae*. We cannot exclude the possibility that it is a mere form of the latter but more material is needed to reach a definite conclusion.

Genus *Coelatura* Conrad, 1853

Type species. *Unio aegyptiaca* Cailliaud, 1827, p. 263, Pl. 61, figs. 6 & 7.

Diagnosis. Haas (see e.g. Haas, 1936, 1969a) rearranged the tropical African unionids in a number of genera and subgenera that, with the exception of *Prisodontopsis* Tomlin, 1928, were all lumped by Mandahl Barth (1988) into a single genus, *Coelatura*. But Daget (1998) re-established two of Haas' genera and elevated one of his subgenera to genus level (namely genus *Nyassunio* (Lea, 1864); genus *Nitia* Haas, 1936; subgenus *Mweruella* Haas, 1936) while Graf & Cummings (2007a, 2009a) in addition, revived the genus *Grandidieria* Bourguignat, 1885 and created a new genus *Germainia* Graf & Cummings, 2009a for the Malagasian *Coelatura geayi* (Germain, 1911). The problem resides in the fact that these rearrangements were only partial, the status of other *Coelatura*-like taxa considered by Haas as distinctive genera such as e.g. *Mesaфра* Haas, 1936, *Afroparresysia* Haas, 1936 or *Afroniaia* Haas, 1962 being ignored. Since neither Daget nor Graf & Cummings motivate their new arrangement on morphological or molecular grounds, the taxonomic diagnosis of *Coelatura* remains unresolved. In the present paper none of the above genera is discussed except for *Nitia*, which is here also considered as distinctive due to its morphological persistence since Early Pliocene times.

Occurrence. The genus *Coelatura* presently occurs all over tropical and subtropical Africa. It is absent from the temperate regions, i.e. northern Africa except the Nile and from most of southern Africa.

Fossil shells are widespread from the start of the Pliocene, the earliest being from the Oluka Formation (ca 5.5-5.0 Ma), Albertine Basin (this paper) and the Mabaget Formation (5.0-4.7 Ma), Tugen Hills, Kenya, (De Groeve, 2005).

Remarks. In literature predating 1990 the genus name is erroneously spelled as *Caelatura*, due to a confusion with a gastropod genus created in the same year (Rosenberg *et al.*, 1990).

The Cretaceous fossils placed by Mongin (1963) under *Caelatura* (*Caelatura jowikolensis* (Newton, 1909)) have been restudied by the present authors. The general habitus with the large anterior part, small, pointed beak and flattened shells as well as the hinge are unlike any *Coelatura*.

With the significant increase of African fossil sites it has become very difficult to explain the absence of *Coelatura* in pre-Pliocene deposits as being due to incompleteness of the fossil record. The likelihood that this genus and, for example, the related *Nitia*, are of 'recent' Asian origin as hypothesized by Kat (1987) and Hoeh *et al.*, (2001) is becoming highly plausible (Van Damme & Van Bocxlaer, 2009). This would imply that the African subfamily of the Coelaturinae Modell,

1942 would be closely related and descended from the tropical Asian Parreysiinae Henderson, 1935.

Species *Coelatura cf stanleyvillensis* (Pilsbry & Bequaert, 1927)

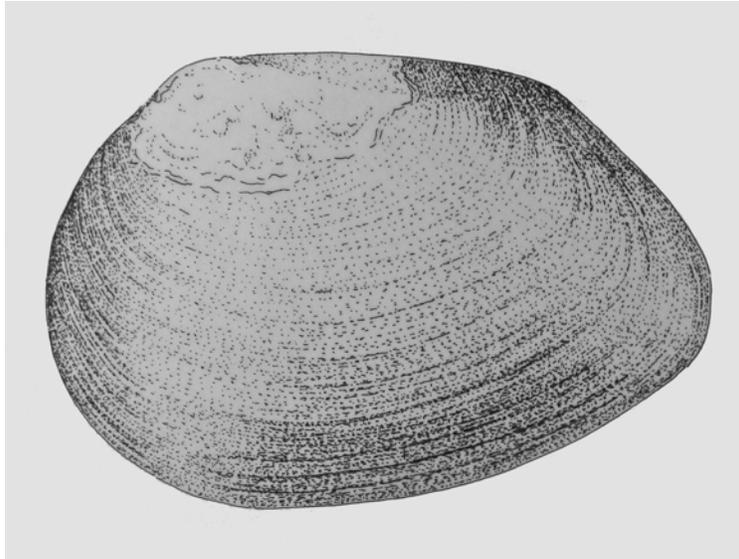


Figure 19. *Coelatura cf stanleyvillensis* (Pilsbry & Bequaert, 1927). Specimen NK 245'90 (L = 37.4 mm).

Type. *Coelatura stanleyvillensis* Pilsbry & Bequaert, 1927. *Terra typica*: Congo River at Kisangani (formerly Stanleyville), Congo.

Material. UM: KI 59'92 (KI 11): 5 specimens; KI 71'92 (KI 11): 8 specimens, one juvenile with chevrons; KI25'92 (KI 11): 1 specimen; KI 59'92 (KI 11): 2 internal molds; KI 96'92 (KI 15): 10 specimens; NY41'92 (NY 67) 1 broken specimen; NY69'92 (NY 83): 1 fragmentary specimen; NY 93'92 (NY 83): 5 specimens; NY 245'90 (NY 72): 1 specimen (fig 19); NY 89'92 (NY 67) 7 specimens; NY 93'92 (NY 83); 1 specimen.

Distribution. Nyaburogo-Nyabusosi area (L. Albert, Uganda); Kisege area (L. Albert, Uganda).

Description of the fossil material (*specimen NK 245'90*). Variable medium sized trapezoid and rather flat shell. Beak small and low, often corroded, barely protruding above the dorsal margin. Posterior dorsal margin long and straight or slightly curved and usually downward sloping, forming a distinct angle with the posterior end which is straight or slightly concave and forms a rounded angle with the weakly curved ventral margin. Anterior dorsal margin very short and downward sloping, forming a continuous regular curve with the dorsal margin and the anterior ventral margin. Greatest height beneath the beak. Ornamentation absent except for regular growth lines and chevrons on the beak, visible only in young specimens as the beak is corroded in adults. Hinge only partly visible, typically unionid and weakly developed (*Parreysia* hinge-type *sensu* Mandahl-Barth, 1988)

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|-----------------|--------|--------|----------|-----------------------------------|
| Holotype | 52.5 | 31.0 | 22.0 | Pilsbry & Bequaert (1927, p. 403) |
| Nyaburogo NY 72 | 37.5 | 28.0 | 17.2 | NY 245'98 |
| Nyaburogo NY 83 | 41.5 | 26.8 | 19.6 | NY 93'92 |
| Nyaburogo NY 83 | 34.5 | 26.4 | 18.4 | NY 69'92 |
| Kisegi KI 11 | 37.5 | 26.3 | 17.0 | KI 59'92 |
| Kisegi KI 11 | 44.4 | 29.2 | 21.3 | KI 59'92 |

Stratigraphy and age. Oluka Formation, Lower Nyaburogo Formation. Late Miocene - Early Pliocene. Molluscan Association G2b - G3.

Remarks. This species, although the most common *Coelatura* recovered from the Albertine Basin, shows no lacustrine adaptations and only about 30 specimens have been recovered from a limited number of sites at the eastern side, most with fragments of the river oyster *Etheria*. The species apparently lived in the lake's major tributaries and their estuaries and was occasionally transported into the lake.

The fossil specimens are variable in form but generally have a downward sloping posterior margin. The differences between these Albertine fossils and extant *Coelatura stanleyvillensis* are in our opinion too minor (the main distinction is the smaller size of the fossils) to warrant the creation of a new species. The taxonomic status of *Coelatura stanleyvillensis* needs to be further elucidated. We do not agree with Mandahl-Barth (1988), who considered *Coelatura stanleyvillensis* to be a form of *Coelatura gabonensis* (Kuster, 1862). According to Graf & Cummings (2007c) *Coelatura gabonensis* should be considered as a species complex of which a number of former synonyms have been already reinstated as valid species. We prefer for the moment to maintain *Coelatura stanleyvillensis* as a separate taxon, since it is not only morphologically quite distinct from typical *gabonensis* but there also exists a major geographical gap between the distribution ranges of the two taxa.

Species *Coelatura cf hauttecoeuri* (Bourguignat, 1883)

Type: *Unio hauttecoeuri* Bourguignat, 1883. *Terra typica:* Lake Victoria.

Synonymy of Albertine *Coelatura cf hauttecoeuri* material.

Caelatura sp. (partim) (Adam, 1955, pp. 42, 46, 93, 97).

Caelatura sp. (partim) (Adam, 1957, pp.117-118, Pl. VI, fig. 10, Pl. VII, fig. 5-6).

Caelatura ?bakeri (Adam, 1959, p.51, Pl. VI, fig. 4).

Caelatura bakeri (Williamson, 1990, p.136, Fig. 2).

Material. MCA: MC 2423: Nyamavi N° 68: 2 juvenile specimens; MC 2574, Mohari-Sinda, southern slope of the Pendre II: one complete specimen; RG 16546: Wasa-Kisegi. BNH: L312, downstream of Katanda: an internal mold; L288, ?Ravine K10, 80 to 100 m from L. Edward: an internal mold and a small bivalve.

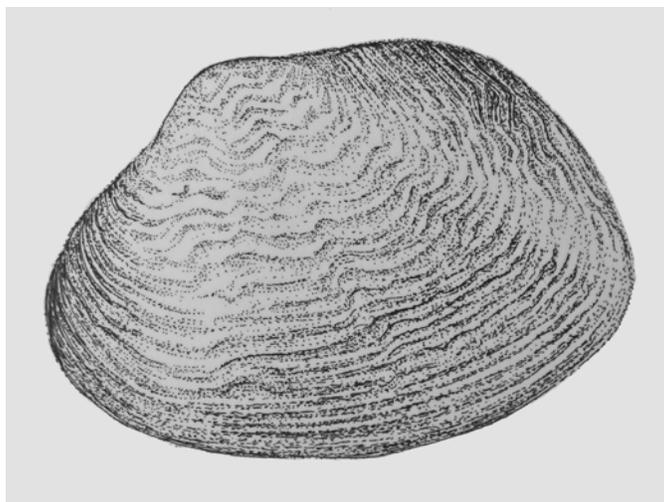


Figure 20. *Coelatura cf hauttecoeuri* (L = 26 mm) from Nyamavi N° 63 (MC 2574).

Distribution. Upper Semliki - Ishango area, (L. Edward, Congo); Sinda-Mohari area (Semliki Plain, Congo); Nyamavi area (L. Albert, Congo)

Description of fossil material (*specimen MC 2574*). Small to medium sized rectangular thin and rather flat shell with broad distinct beak slightly protruding above the dorsal margin. Dorsal posterior margin straight, slightly raised. Posterior end obliquely truncate, slightly produced, the margin weakly convex and with a blunt basal angle. Greatest length of the shell situated in the lower third. Ventral margin evenly and weakly curved. Posterior margin rather broad and regularly curved. Ornamentation consisting of chevrons on the beaks which grade into irregular wavy concentric ridges below the beaks that may cover the entire surface. Hinge weakly developed, of the *Parreysia* type.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|---------------------------|--------|--------|----------|--------------|
| Holotype (Modern) | 36 | 22 | 16 | L. Victoria |
| Nyamavi N° 63 | 26.0 | 18.2 | - | MC 2574 |
| Mupanda 1 | 30.0 | 24.0 | 12.5 | P 745 |
| Upper Semliki ?Ravine K10 | 28.9 | 24.4 | - | MC 2846 |
| Upper Semliki ?Ravine K10 | 19,7 | 14.0 | - | MC 2846 |

Stratigraphy and age. Lusso Formation (LII & LIII), Upper Nyamavi Formation VI, Sinda Beds, Member C. Late Pliocene- Early Pleistocene, Molluscan Association G5a-G5c and GX-X’.

Remarks. Previous authors have identified the *Coelatura* specimens from the Late Pliocene Albertine deposits, when ‘Nilotic’ invaders were entering the basin, as *Coelatura bakeri* (Adams, 1866), a species currently confined to Lake Albert. Although a small stunted form of modern *Coelatura bakeri* (30 x 19 x 15 mm) has been described from deeper water (60 feet) (Mandahl-Barth, 1954), *Coelatura bakeri* usually attains a length of 36 to 42 mm. The fossil specimens are from populations that lived in shallow water conditions and are much too small (< 30 mm length) to represent *Coelatura bakeri*. They are comparable in size, general form and sculpture to extant *Coelatura hauttecoeuri* and are thus referred with a *conferatur* as such. The extant *Coelatura*

hauttecoeuri is restricted to L. Victoria and the Victoria Nile, but it may be a Late Miocene relict that formerly had a wider range in East Africa, for this species has been recorded from the Early Pliocene Mabaget Formation in the Tugen Hills, Kenya, (De Groeve, 2005) and from virtually all lacustrine Late Pliocene-Pleistocene deposits in the Lake Turkana Basin, as *Coelatura rothschildi* Neuville & Anthony, 1906 (Van Damme, 1976). Mandahl-Barth (1988) stated that *Coelatura hauttecoeuri* is closely related to *Coelatura bakeri* from Lake Albert. At present, the discussion on relationships between the *Coelatura hauttecoeuri-bakeri-rothschildi-stuhlmanni* group remains unresolved. All these species do have a chevron ornamentation on the juvenile shell, in contrast to e.g., *Coelatura aegyptiaca*, whose apical ornamentation consist of two rows of tuberculi. Ongoing research (Zieritz, in prep.) indicates that juvenile unionids (less than 4 mm) are interstitial deposit feeders and that such microsculpture, widely used for species identification, may play an important role in locomotion and orientation in interstitial space. Possibly molecular research may show significant differences between the above mentioned species but it may also be that they represent geographical races.

Williamson (1990) recorded *Caelatura bakeri* from deposits ranging through most of the Lusso Formation, from the sites Katanda 3, 12 & 13, Senga 1, 5, 6, 13, 15 & 16, Kanyavoghorwe 6, Tshibiridi 7, Kishishio 2 and Mupanda 4 of Verniers & de Heinzelin (1990). We do not agree with this identification because extant *Coelatura bakeri* usually reaches a length of *ca* 40 mm and has ornamentation that is usually confined to the upper part of the shell. The rarity of the fossil specimens suggests that the species lived in the fringe habitats of late Palaeolake Obweruka and Palaeolakes Kaiso and Lusso but not in the lakes proper.

The internal molds ranged with a query under *Coelatura bakeri* by Adam (1957) from sites L. 317, L. 284 and L. 277 and from South Rwebishengo 2A by Gautier (1970a) are omitted because of the purely speculative nature of these identifications.

Species *Coelatura scholzi* nov.

Material. UM: NK 2238'89 (NK 120). 2 specimens.

Distribution. Nkondo area (L. Albert, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda).

Description. Small, thin shelled, inequilateral and globose unionid. Length about 1.2 times the height, height about 1.4 times the diameter. Beak swollen, broad and protruding, situated past the first third of the total length. Posterior dorsal margin short and slightly to strongly downward sloping. Posterior end truncated and with a wide angular curve passing into the strongly curved ventral margin. Anterior end short and regularly curved. Ornamentation consisting of very fine regular growth lines. Hinge only partially visible, of the unionid type.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|--------------|--------------|
| Holotype | 31.3 | 25.0 | <i>ca</i> 18 | NK 2238'89 |
| Paratype | 24.1 | 21.8 | <i>ca</i> 15 | NK 2238'89 |

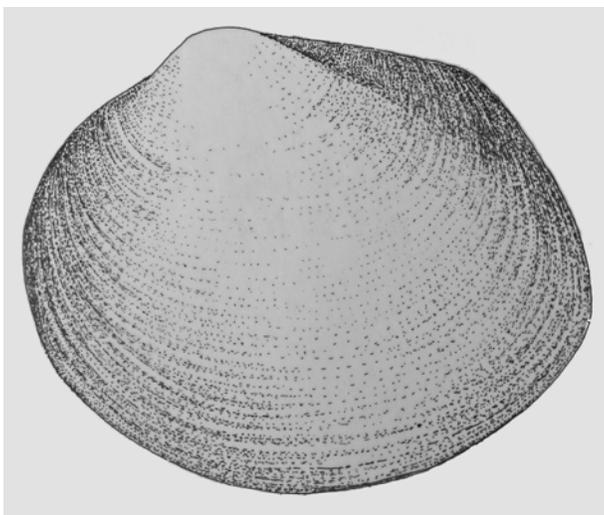


Figure 21. *Coelatura scholzi* sp. nov. Holotype (L = 31.3 mm).

Type locality. Site NK 120 of Pickford *et al.*, (1993), Nkondo area, L. Albert, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition, 1988 – 1993).

Stratigraphy and age. Nyaweiga Member of the Nkondo Formation. Terminal Miocene - Lower Pliocene, Molluscan Association G3b.

Etymology. Named after Dr. Henning Scholz for his contributions to African freshwater malacology.

Remarks. No relationship of this small, thin shelled and globular *Coelatura* species could be established with other recent and fossil representatives of the genus. It resembles somewhat *Nyassunio ujijensis* (Crosse, 1881) from the Malagarasi estuary (L. Tanganyika) but differs in too many aspects to be identified as such. *Coelatura scholzi* is probably a fluvial species accidentally carried into Palaeolake Obweruka.

Genus *Grafunio* nov.

Type species. *Grafunio dageti* ibi, fig. 22, specimen NY 84'90 from site Nyaburogo 69 (NY 69).

Diagnosis. See description of the species. The genus is highly distinctive from any other African or Eurasian unionid taxon by its extremely globose form and its very broad umbo. It belongs in our opinion to the Unionidae, considering its size, absence of umbonal ornamentation and marked globosity, but the relationship with African genera such as *Coelatura* is far from evident.

Etymology. Named in honour after Professor Dan Graf (University of Alabama) for his important contribution to the knowledge of freshwater bivalves in general and the African ones in particular.

Occurrence. Only known from an Early Pleistocene site in the Albertine Rift (Uganda).

Remarks. This peculiar and distinctive taxon morphologically resembles somewhat the extant *Afroparreysia* Frierson, 1913 from the Nyang River in Cameroon. But representatives of this poorly known (extinct?) genus - that is considered by Mandahl-Barth, 1988 and other authors to be a synonym of *Coelatura* - have a coarse wavy ornamentation extending over most of the shell, a non extruding umbo and a less globose shell.

Species *Grafunio dagei* nov.

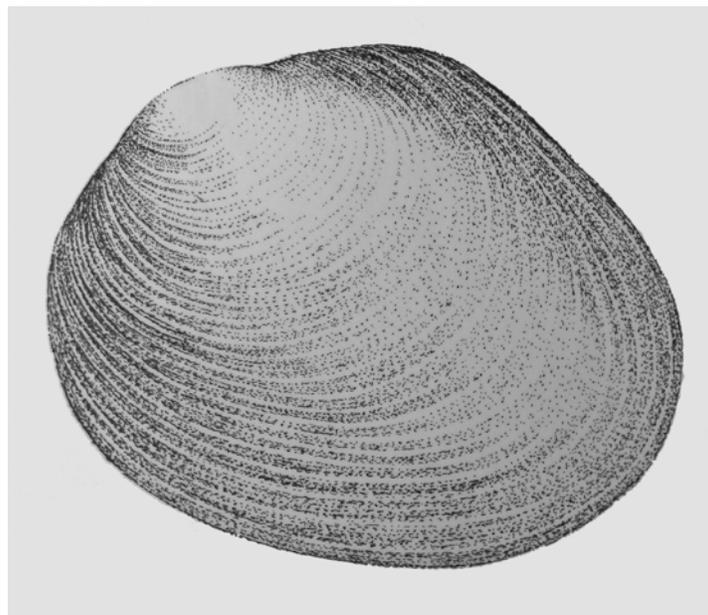


Figure 22. *Grafunio dagei* gen. nov. sp. nov. Holotype (L = 32.1 mm).

Material. UM: NY84'90 (NY 69): 1 specimen; NY 84'92 (NY 84): ?doublet.

Distribution. Nyaburogo-Nyabusosi area (L. Albert, Uganda).

Description. Extremely globose and strongly inequilateral ovate naiad. Length about 1.2 times the height, height about 1.25 times the diameter. Beak very broad, rounded, strongly inflated and excentric, slightly projecting above the dorsal margin. Posterior dorsal margin straight and short, gradually curving into the evenly curved and blunt posterior end. Ventral margin weakly curved passing via a blunt angle into the short, gently sloping straight dorsal anterior margin. Ornamentation absent except for regular growth lines. Hinge of the unionid type, only the curved short laterals are visible.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|-----------------|--------|--------|----------|--------------|
| Holotype NY 69 | 32.1 | 28.3 | 22.5 | NY 84'90 |
| Nyaburogo NY 84 | 36.5 | 31.0 | ca 28.0 | NY 84'92 |

Type locality. Site NY 69 of Pickford *et al.*, (1993), west of the Nyaburogo River, Toro Region, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition, 1988-1993)

Stratigraphy

and age. Nyakabingo Formation, Makondo or Behanga Member, Early Pleistocene, Molluscan Association G6.

Etymology. In honor of Dr. Jean Daget (ORSTOM) for his studies on African bivalves.

Remarks. This peculiar and distinctive species morphologically resembles the extant *Afroparreysia nyangensis* (Frierson, 1913) from the Nyang River in Cameroon (see comments under the genus). Only a single specimen of the fluvial *Grafunio dageti* was recovered from the Albertine basin.

Genus *Gautieraia* nov.

Type species. *Gautieraia rugosa* ibi, fig. 23, specimen from sample NY 331'90 at site Nyaburogo 40 (NY 40), Uganda.

Diagnosis. See description of the species. This is the only known African taxon in which such characters as a large central umbo and a wide central sulcus usually flanked by tuberculate ridges are combined.

Etymology. Named in honour of Professor emeritus Dr Achilles Gautier for his studies on Albertine molluscan biostratigraphy.

Occurrence. Late Miocene-Early Pliocene lacustrine deposits in the Albertine Basin (Uganda-Congo).

Remarks. The genus belongs in our opinion to the Unionidae, considering the size and the type of ornamentation absent in hyriids. In size and general form, *Gautieraia* resembles somewhat the Asian *Schistodesmus spinosus* Simpson, 1900, but in our opinion there is no relationship between them.

Species *Gautieraia rugosa* nov.

Diagnosis. See description.

Synonymy

? *Iridina* sp. A (Gautier, 1965, p. 140, Pl. V, Fig. 3 & 6).

Caelatura ?*bakeri* (Gautier, 1965, p. 135, Pl. III, Fig. 6).

Material. UM: NK 771'89 (NK 115): 1 specimen; NK 370'91 or 570 or 670 (NK): 1 fragmentary specimen; NK 699'89 (NK 106): 1 specimen; NK 810'89 (NK 124): 1 specimen; NK 759'88 (NK 35): 1 specimen; NK 956'89 (NK 36): 1 specimen; NK 1003'89 (NK 32): 1 specimen; NK 829'89 (NK 125): 1 specimen; NK 1392'89 (NK 100): 1 specimen; NY 331'90 (NY 40): 1 specimen. **MCA:** Sinda Mohari Site 8 (Sinda Beds): 3 specimens identified as *C* ?*bakeri* (S 8) and as ?*Iridina* sp. A (S 8/40I) by Gautier (1965).



Figure 23. *Gautieraia rugosa* sp. nov. Holotype (L = 25.0 mm).

Distribution. Sinda-Mohari area (Semliki Plain, Congo); Nkondo area (L. Albert, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda).

Description. Solid, trapezoidal, globose, strongly inequilateral shell. Beak strongly developed, broad, prominent and nearly central. Posterior and anterior dorsal margin of nearly equal length and slightly downward sloping, in the upper part forming a distinct angle with the posterior and anterior ends. Ventral margin strongly incurved in the central part, rising straight upwards posteriorly and forming a blunt angle with the anterior end. Ornamentation highly variable, varying from thick bulging irregular wrinkles in the central part of the shell to two vertical irregular ridges or folds accentuated by nodular growths running in an inverted V-shape from beak to ventral margin, with both ridges separated by a markedly concave central sulcus. In some specimens (NK 771'89) the vertical ornamentation is barely developed consisting of a single weak ridge and a few tuberculi on the beaks. Shell covered with regular concentric plicatulate growth lines. Hinge only partly visible and resembling the general unionid type.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|---------------------|--------|--------|----------|-----------------------------------------|
| Holotype | 25.0 | 23.0 | ca 15.0 | NY 331'90 |
| Nkondo Site 115 | 29.0 | 26.0 | 21.2 | NK 771'89 |
| Sinda Beds, Site 8 | 24.4 | 19.0 | 11.4 | <i>Caelatura ?bakeri</i> Gautier (1965) |
| Sinda Beds, S 8/40I | 20.4 | 21.0 | 16.5 | ? <i>Iridina</i> sp. A, Gautier (1965) |

Type locality. Site NY 40 of Pickford *et al.*, (1993), Nyaburogo area, Lake Albert, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition, 1988-1993).

Stratigraphy and age. Nkondo Formation; Upper Oluka Formation and Member A of the Sinda Beds. Late Miocene-Early Pliocene, Molluscan Association G3a-b.

Etymology. Named after the two median nodular folds.

Remarks. This highly characteristic species appears to have lived in Palaeolake Obweruka during the early stage of its existence. It became extinct during or even before the NK-27 Event. Gautier (1965) stated that he discerned fine tuberculi on part of a specimen's hinge and therefore with some hesitation placed it in the genus *Iridina* (Gautier's ?*Iridina* sp. A). We studied Gautier's broken specimen and it appears on closer inspection that the 'tuberculi' are broken oolitic pellets adhering to the shell. In some specimens parts of lateral teeth are visible posteriorly and one partly negative impression of large pseudocardinals on the anterior part, distinctly placing this species in the Unionidae and not in the Iridinidae.

Ornamentation in infaunal bivalves often has a double function, namely better fixation in the sediment and protection against predation. Marked ornamentation such as spines are found as a rule in infaunal species that bury superficially and are thus more susceptible to displacement by storms and attacks by predators (Vermeij, 1993). The large diameter of *Gautieraia rugosa* in combination with the ornamentation that impedes swift burying also suggests that it lived close to the surface.

Genus *Nkondonaia* gen. nov.

Type species. *Nkondonaia bisulcata*, ibi, Specimen from sample NK 801'89 at site Nkondo 43 (NK 43) (Uganda) (Fig. 24).

Diagnosis. See description of the species. This is the smallest and flattest African unionid known, highly distinctive by the double centrally situated sulcus and the posterior wing. There are no fossil and recent African or Eurasian taxa that resemble it.

Etymology. Named after the type locality Nkondo (L. Albert, Uganda).

Occurrence. Only known from Late Miocene deposits in the Nkondo area (Albertine Rift, Uganda).

Remarks. This taxon is enigmatic. It may be have evolved from the genus *Gautieraia*, that also is sulcate, but there are no intermediates between this robust and rather globose taxon and the tiny, fragile and flattened *Nkondonaia*.

Species *Nkondonaia bisulcata* nov.

Holotype. Specimen from sample NK 801'89 at site Nkondo 43 (NK 43) (Uganda) Fig. 24.

Material. UM: NK 801'89 (NK 43): ca 30 specimens (type); NK 670'89 (NK 43): 1 specimen; NK 2516'89 (NK 60): 1 specimen; NK 576'89 (NK 122): 1 specimen; NK 830'89 (NK 125): 1 specimen; NK 847'89 (NK 115): 1 specimen; NK 2238'89 (NK 120): 1 specimen; NK 679'89 (NK 76): 1 specimen; NK 2274'89 (NK 120): 3 specimens; NK 1075'89 (NK 48): 1 specimen; NK 500'89 (NK 122): 1 specimen; NK 846'89 (NK 47): 6 specimens; NK 802'89 (NK 42): 20 specimens; NK 510'89 (NK 122): 1 specimen.

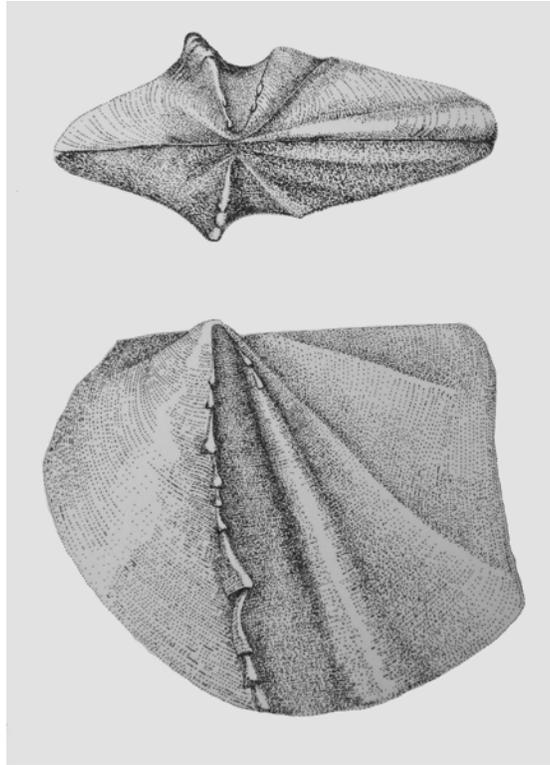


Figure 24. *Nkondonaia bisculcata* gen. nov. sp. nov. Holotype (L = 18.5 mm).

Distribution. Nkondo area (L. Albert, Uganda).

Description. Small, thin, rhomboid and flattened unionid. Beaks small and prominent, situated at about the anterior third of the total length. Shell with well-developed posterior dorsal wing. Posterior margin raised and straight near the beak forming at the posterior end a right angle with the slightly convex part of the posterior wing, which is separated from the rest of the shell by a posterior ridge running from the beak to the basal posterior point which forms a distinct angle with the ventral margin. Ventral margin convex, regularly and strongly curving, forming a sharp angle with the very short downward sloping anterior margin. The two nodular ridges on the beaks extend downwards, thickening and increasing in height while descending towards the basal margin, the anterior ridge bears a row of increasingly longer flanges or laterally spines, while the posterior one only bears spines or tuberculi in the umbonal region. The shell between the diverging ridges is strongly indented. Hinge only partially visible, apparently weakly developed with small simple pseudocardinals.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|--------------|
| Holotype | 18.5 | 16.2 | 6.8 | NK 801'89 |
| Paratype | 19.5 | 15.0 | 9.2 | NK 801'89 |
| Paratype | 21.0 | 18.8 | - | NK 670'89 |
| NK 46 | 22.0 | 18.8 | 10.5 | NK 846'89 |
| NK 48 | + 18 | 17.4 | 11.6 | NK 1075'89 |

Type locality. Site NK 43 of Pickford *et al.*, (1993), Nkondo area, Lake Albert, Uganda (M.

Pickford *collevis*, Uganda Palaeontology Expedition, 1988-1993).

Stratigraphy and age. Nkondo Formation. Late Miocene, Molluscan Association, G3a.

Etymology. Named because of the presence of two sulci.

Remarks. The origin of the minute *Nkondonaia bisulcata* is problematic. It may possibly be considered a miniaturized endemic lacustrine derivative from *Gautieraia rugosa* from which it differs by its diminutive size, its thin, strongly flattened shell, the posterior wing and the marked ornamentation. The differences are so significant that we prefer to consider *Nkondonaia* as a distinct genus with an unknown ancestor. The thin, flat shape and the rather brittle spines are indicative of a low wave energy environment such as a soft muddy substrate in calm water. Since the taphocoenosis in which *Nkondonaia bisulcata* occurs also contains *Lanistes* shells with parasitic fly eggs, chironomid cocoons, cichlid nests and freshwater crabs and their burrows, it must be assumed that the species lived in muddy-clayey bottoms in shallow waters such as protected bays. Due to the small dimensions of the anterior part and the small diameter of the shell, the pedal muscle must have been weakly developed, but the flag-like posterior side is suggestive of the presence of an elongated siphon. The species may have lived relatively deeply buried (1 to 2 times the shell's length) in the sediment. In dorsal view the shell shows a striking convergence with the fossil *Unio (Sculptunio) bituberculosis trigonoides* Lindholm from SW Siberia (Haas, 1969b). The spiniform extensions are interpreted as a defence against predators as well as for providing better anchorage in the sediment. The occurrence of *Nkondonaia bisulcata* is very restricted in time, as it was only found at a few sites of Late Miocene age in the Nkondo area and at Dells, West Nile (see appendix 2). But this scarcity could be correlated with its fragility. Like the other ornamented bivalves and gastropods of the early Palaeolake Obweruka *Nkondonaia bisulcata* did not survive the cataclysmic NK-27 Extinction Event around 4.5 My.

Genus *Nitia* Pallary, 1924

Type species. *Unio teresciusculus* Philippi, 1847, p. 45, pl. 3, fig. 3. Type locality: White Nile.

Diagnosis. Shell elongated digitiform, thin. Hinge thin, cardinals compressed. Umbo distinct but not or little extruding. The sculpture consists of pointed, elongated, narrow chevrons occurring in a distinctly concentric pattern (Haas, 1969a).

Occurrence. Widely distributed in Africa north of the equator in the Nile drainage except the Blue Nile, Chad Basin and Senegal River. Known as fossil since the Late Miocene of the Albertine Basin (this study) and the Early Pliocene of the Turkana basin (Van Damme, 1976).

Remarks. The elongated *Nitia* morphotype has existed in Africa for about 6 million years, clearly proving the characters of the genus to be distinctive.

Species *Nitia cf monceti* (Bourguignat, 1883)

Type. *Unio monceti* Bourguignat, 1883. *Terra typica*: Lake Victoria.

Synonymy (of Plio-Pleistocene material from the Albertine Basin only).

Caelatura sp. (partim) (Adam, 1955, pp. 42, 46, 93, 97).

Caelatura sp. (partim) (Adam, 1957, pp. 118).

Caelatura acuminata (Adam, 1959, p.50-51, Pl. VI, fig. 6).

Material. **BNH:** L288, Ravine K 10, 80 to 100 m from Lake Edward: 2 internal molds of elongated specimens; L284, head of Nyakasia Ravine: a poorly preserved specimen. **MCA:** MC 2325, Nyamavi N° 63, hill to the east of the Kaheri: 4 doubtful internal molds. **UM:** NK 539'88 (NK 38), 1 specimen; NK 323'89 (NK 13), 3 juvenile specimens, NK 534'98 (NK 38). 1 specimen, NY 95'92 (NY 83): 1 specimen.



Figure 25. *Nitia cf monceti* (L = 36 mm), specimen NK 534'98 from Nkondo.

Distribution. Upper Semliki - Ishango area, (L. Edward, Congo); Nyamavi area (L. Albert, Congo); Nkondo area (L. Albert, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda).

Description of fossil material (*specimen NK 534'98*). Shell strongly elongated and inequilateral. Length twice the height, height about 1.3 times the diameter, beak small, not projecting above the dorsal margin and situated in the anterior quarter of the total length. Posterior margin straight, posterior end elongated and obliquely truncated, produced into a rounded point near the basal margin. Ventral margin parallel to the dorsal margin, incurved. Anterior end regularly rounded. Ornamentation confined to a few irregular wavy folds on the beaks.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|-----------------------|--------|--------|----------|----------------------|
| Holotype (Modern) | 22 | 10 | 8 | L. Victoria |
| Large Modern specimen | 38 | 16 | 11.5 | Mandahl-Barth (1988) |
| Nkondo NK 38 | 36.0 | 18.0 | 14.2 | NK 534'98 |
| Nyaburogo NY 83 | 36.3 | 19.0 | 13.6 | NY 95'92 |

Stratigraphy and age. Lusso Formation (LII & LIII), Nyamavi Beds, Nkondo Formation, Nyaweiga Fm. Late Miocene – Late Pliocene, Molluscan association G3-G5.

Remarks. Adam (1959) identified the *Nitia* specimens at his disposal as *Nitia acuminata* (Adams, 1866), an extant endemic in L. Albert. *Nitia acuminata* has a greater height than *Nitia* cf *monceti*, a distinct chevron ornamentation and a straight, instead of an incurved ventral margin. The fossil specimens are identical in characteristics, shape and dimensions to large extant *Nitia monceti* (see dimensions in Table). Scholz & Glaubrecht (2004) point out that the shell morphology of extant populations of *Nitia monceti* remains very consistent over the range of occurrence of the species and that this is really unique among the African unionids. The fossil record confirms this morphological stasis that has endured for several million years.

Genus *Obwerukunio* nov.

Type species. *Obwerukunio pliocenica*, ibi, Fig.26. Specimen from site Nkondo 126 (NK 126), Lake Albert, Uganda.

Diagnosis. As for the species.

Occurrence. Only known from early Pliocene deposits in the Nkondo area, Lake Albert, Uganda.

Etymology. The genus is named after Palaeolake Obweruka, in the deposits of which it was found.

Remarks. The genus resembles in size and outline specimens of the monotypic genus *Grandidieria* Bourguignat, 1885, that occurs in Lake Tanganyika. It differs by the flattened shell and the maleate ornamentation. The possibility that *Grandidieria* is derived from *Obwerukunio* cannot be excluded.

Species *Obwerukunio pliocenica* nov.

Holotype. UM: NK 1113'89 (NK 126): 1 specimen.

Diagnosis. See description.

Distribution. Nkondo area (L. Albert, Uganda).

Description. Medium sized, quadrangular, thin shell, with the middle part of the shell flattened instead of curved. Length about 1.1 times the height, height about 2 times the diameter. The narrow beak, situated in the first quarter of the total length, barely extends beyond the dorsal margin. The dorsal posterior and anterior margins are short, virtually straight and slightly downward sloping. Posterior and anterior ends are concave forming a blunt angle with the dorsal margin. The convex ventral margin forms an obtuse angle with the posterior margin at the base of the shell and curves via a very blunt angulation into the anterior end. The ornamentation consists of very fine growth lines and a fine malleated sculpture in the central upper part of the shell. The hinge is not visible. Ligament short.

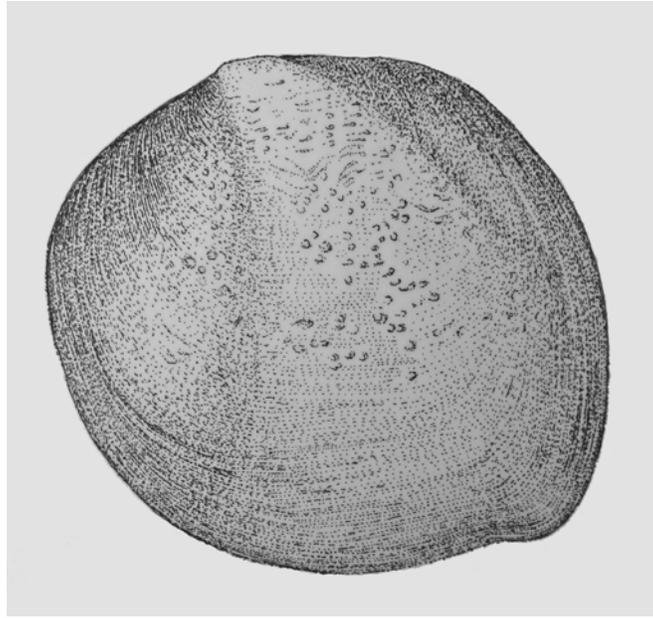


Figure 26. *Obwerukunio pliocenica* gen. nov. sp. nov. Holotype (L = 27.0 mm).

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|--------------|
| Holotype | 27.0 | 25.0 | 12.3 | NK 1113'89 |

Type locality. Site NK 126 of Pickford *et al.*, (1993), Nkondo area, L. Albert, Uganda (M. Pickford *collevis*, Uganda Palaeontology expedition, 1988-93).

Stratigraphy and age. Warwire Formation, Early Pliocene, Molluscan Association G4.

Etymology. Named after the Pliocene Epoch.

Remarks. In general shape and ornamentation the fossil shell resembles some shell types of extant *Grandidieria burtoni* from Lake Tanganyika, namely *Grandidieria cyrenopsis* Bourguignat, 1888 (see figure 30 E in Leloup, 1950) and the specimen of *Grandidieria rotundata* Bourguignat, 1885 figured by Mandahl-Barth (1988, p. 49, fig. 75). But the length/height ratio of extant *Grandidieria burtoni* shells is always in excess of 1.2 and usually > 1.3 (Leloup, 1950) while that of the fossil specimen is less than 1.1. In addition there is a marked difference in ornamentation.

It is tempting to consider *Obwerukunio pliocenica* as the fluvial ancestor of the lacustrine *Grandidieria burtoni*. But more material of *Obwerukunio* is needed to support such a hypothesis and we therefore prefer to consider the latter to be a distinct genus. In addition, it is possible that recent *Grandidieria* may prove to be paraphyletic.

The extreme scarcity of *Obwerukunio pliocenica* in the Albertine deposits suggests that it did not live in Palaeolake Obweruka itself but in a tributary or its estuarine fan.

Superfamily Etherioidea Deshayes, 1830
Family Iridinidae Swainson, 1840 (= African Mutelidae auctores)

The family Mutelidae H. & A. Adams, 1858, originally comprised a number of South American, Australian and African genera which were divided into two subfamilies, the Mutelinae, containing the taxa with a *lasidium*-type larva (= *haustorium*, auctores) and the Hyriinae, with a *glochidium* larva. Valid arguments have recently been presented (see Cummings & Bogan, 2006; Graf & Cummings, 2006a, b, 2007a) to consider the Hyriidae (S. America and Australia) as a separate family. Since the name Mutelidae is no longer valid, the African genera with a *lasidium* are now placed in the Iridinidae.

At the generic level we follow, for the most part, Daget (1998) who distinguished six genera, namely *Aspatharia*, *Chambardia* (= *Spathopsis*, auctores), *Moncetia*, *Mutela*, *Chelidonopsis* and *Pleiodon*. The African taxa lumped under *Mutela* by Mandahl-Barth (1988) should, according to Daget (1998) and Graf & Cummings (2009b), be divided into 3 genera, *Mutela*, *Chelidonopsis* and *Pleiodon*. We agree about the validity of this division but on the basis of overwhelming fossil evidence we feel obliged to make an additional one. The fossil iridinids in the Albertine Basin (this paper) and the Turkana Basin (Van Bocxlaer & Van Damme, 2009) show an overwhelming dominance of species with a pseudotaxodont hinge that is restricted to or only well developed on the posterior part of the hinge. We thus feel obliged to make a difference between (1) iridinids with a pseudotaxodont hinge that is well developed on both sides of the umbo + a centrally situated beak (genus *Pleiodon*) (Fig. 27b), (2) iridinids with a pseudotaxodont hinge only developed on the posterior part of the hinge plate although sometimes reduced to an edentulous broad and flat ridge + a strongly excentrically placed beak (genus *Iridina*) (Fig. 27a) and (3) iridinids with a small, sharp hinge plate without teeth or at the most some secondary tubercular growths in old specimens + a strongly excentrically placed beak (genera *Mutela* and *Pteromutela*). We do agree with Graf & Cummings (2006b) that there may be other groups within *Mutela* that deserve generic status, but this is a matter that falls beyond the present paper.

The distinction between hinge type (2) and type (3) poses no problem in pre-Pleistocene fossil material but it does in modern shells. True *Iridina*, according to the description here given, are only found recently in L. Tanganyika (*Iridina spekii*) and western Africa (*Iridina exotica*, etc.).

In western Africa due to a mix up between the original pseudotaxodont type specimen of *Iridina exotica* and a nearly edentulous shell of *Mutela dubia*, the genus *Iridina* has been considered for quite some time to be synonymous with *Mutela* (for a detailed discussion, see Van Bocxlaer & Van Damme, 2009).

There is no doubt that edentulous iridinids as well as pseudotaxodont ones did co-occur in Africa since the beginning of the Tertiary (this paper). Molecular studies place the Iridinidae as the sister group to the edentulous Mycetopodidae (Graf & Cummings, 2006a, b, 2007a). The occurrence of typical *Pleiodon* in Cretaceous deposits in S. America indicates that the branching into edentate and pseudotaxodont morphs is ancient and took place before the break-up of western Gondwana. This implies that Mycetopodidae and Iridinidae co-existed during part of the Mesozoic. The break-up of western Gondwana may have precipitated their divergence as suggested by Graf & Cummings, (2007a). In any case, the presence of a (pseudo)taxodont hinge definitely is an ancient trait in the Iridinidae going back to the Mesozoic. Considering the extreme tendency for

convergence within unionoids, its occurrence restricted to the Iridinidae represents an interesting exception to the rule.

In Africa, apparently during most of the Tertiary the pseudotaxodont group of Iridinidae clearly dominated over the edentulous group (*Mutela*, *Aspatharia*, *Chambardia*...). The African fossil record provides evidence that the present day *Mutela* may be polyphyletic or paraphyletic, namely consisting partly of 'true' edentate *Mutela* species that trace this character far back in time and partly of representatives of *Iridina* species with weakly developed teeth whose hinge secondarily became edentulous. The present day *Mutela bourguignati* from Lake Victoria may be such a case of hinge reduction.

The dichotomous identification key for the shell characteristics of the Iridinidae adopted here is as follows:-

- | | | |
|----|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------|
| 1. | (a) Hinge plate terminating posteriorly in a large, sharply triangular sinulus | 2 |
| | (b) Hinge plate not terminating posteriorly in a large, sharply triangular sinulus | 4 |
| 2. | (a) Weak tooth below the beak of the left valve and corresponding to an indentation on the right valve, endemic to L. Tanganyika | <i>Moncetia</i> |
| | (b) Anodont hinge | 3 |
| 3. | (a) Umbonal sculpture consisting of parallel, broadly V-shaped ridges | <i>Aspatharia</i> |
| | (b) Umbonal sculpture consisting of concentric ridges | <i>Chambardia</i> |
| 4. | (a) Hinge plate narrow to moderately developed and toothless or with irregular ovate small tuberculi not separated by distinct indentations | 5 |
| | (b) Hinge plate broad and with a row of vertical thick folds (teeth) separated by deep indentations | 6 |
| 5. | (a) Anterior and posterior side of the shell with carinated ridges | <i>Chelidonopsis</i> |
| | (b) Anterior side of the shell without a ridge, posterior side smooth or carinated | 7 |
| 6. | (a) Shell strongly inequilateral and elongate, beak situated in the anterior 1/4 of the total length, well-developed more or less straight teeth on the posterior part only | <i>Iridina</i> |
| | (b) Shell weakly inequilateral and ovate, beak situated in the anterior 1/3 of the total length to virtually centrally. Well-developed curved teeth on both sides of the beak | <i>Pleiodon</i> |
| 7. | (a) shell without a posterior wing | <i>Mutela</i> |
| | (b) shell with a posterior wing | <i>Pteromutela</i> |

Genus *Pleiodon* Conrad, 1834

Type species. *Pleiodon macmurtriei*, Conrad, 1834, p. 113 (= *Iridina ovata* Swainson). Type locality unknown.

Diagnosis. Shell ovoid, hinge plate and teeth strongly developed (Haas, 1969a).

Occurrence. Recently cited from western Africa from Senegal to Sierra Leone but, except for one locality in Sierra Leone, all records are pre-1950. As fossil known in African deposits since the early Tertiary.

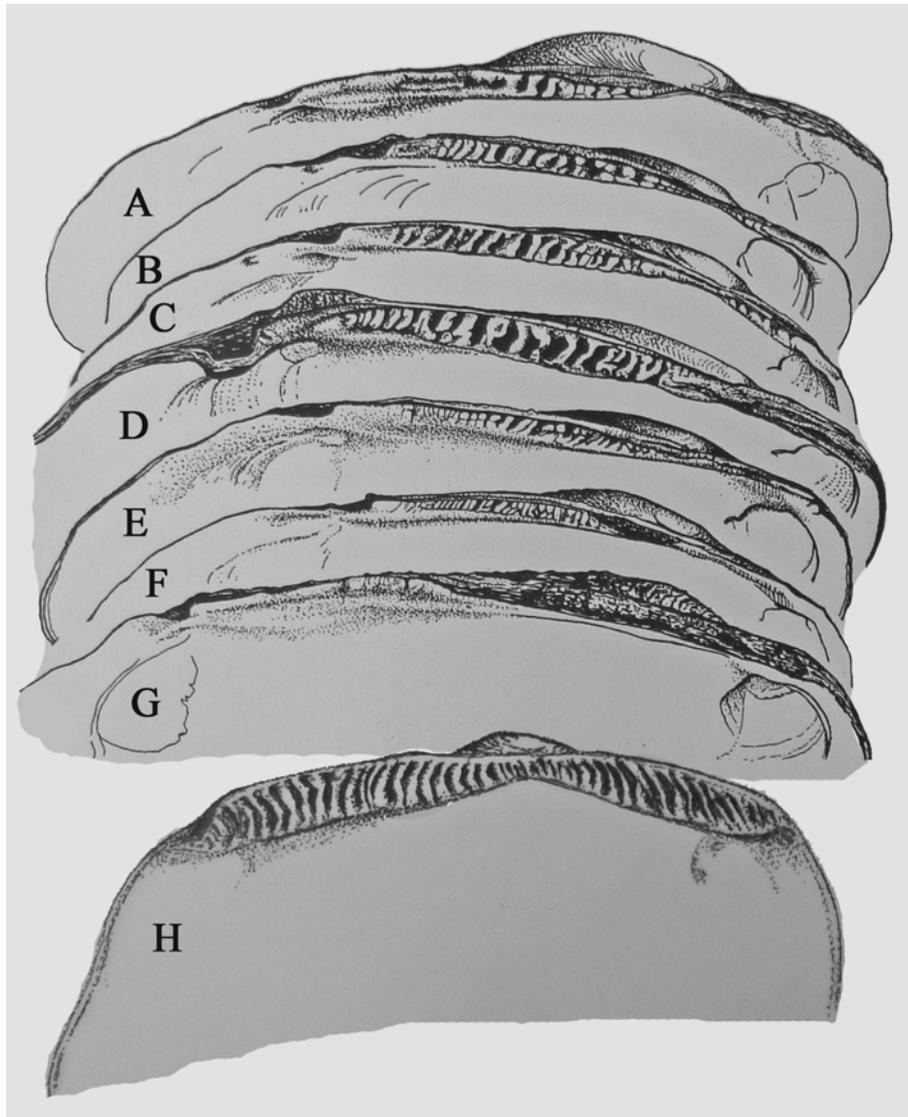


Figure 27. Hinge plates of A-G) *Iridina (Iridina spekii)* with the strongly excentric beak and showing the variation in hinge dentition, well-developed teeth are present only on the posterior part of the hinge and H) *Pleiodon (Pleiodon ovatus)* with the more centrally situated beak and well-developed teeth on both the posterior and anterior part of the hinge (Fig. 27a from Leloup, 1950; 27b after a photograph in Graf, 2000).

Remarks. In our opinion (see revised taxonomic key), at present, only *Pleiodon ovatus* (Swainson, 1823) and the dubious *Pleiodon waterstoni*, Pain & Woodward, 1964, belong to this

genus. The specimens collected by Nagel (1991) in Sierra Leone may represent a third, as yet undescribed species.

The genus *Pleiodon sensu stricto* appears to be very old and seems to have already existed in western Gondwana. *Pleiodon priscus* described by von Ihering (1912, p. 489-90, Pl. XLII, figs 20-23) from ‘Upper Cretaceous or Early Cenozoic deposits ‘near Itambe’ in São Paulo, Brazil, appears indeed also to belong to the genus. This shell (see Fig. 28b) possesses an almost centrally situated beak and a broad hinge with well-developed teeth on the posterior and anterior side. It must be added that von Ihering’s reconstruction drawing of the outer part of the shell (von Ihering, 1912, Plate XLII, Fig 20) is incorrect as to the curve of the growth lines which are represented as almost straight in the central part. When drawn correctly the real shell must have been more ovate than elongate (estimated height *ca* 65 mm instead of *ca* 44.8 mm) (Fig. 28b), resembling a large *Pleiodon tavernieri*. The Brazilian fossil may come from deposits belonging to the Adamantina Formation (Bauru Group), which according to recent authors (Suárez, 1999) is considered to be of Late Cretaceous (Cenomanian-Santonian) age.

The only other known *Pleiodon* ever described from the Americas is *Pleiodon* sp. from the Late Cretaceous (Maastrichtian) Hell Creek Formation of Montana (Morris & Williamson, 1988). When better material became available it transpired that this identification was erroneous since what these authors considered to be hinge teeth appear to be raised lamellar folds on the ligament platform and not part of the hinge. Apparently this taxon would have lived with the valves open (Hartman, 2001).

In Africa, *Pleiodon* is known from Late Cretaceous – Early Tertiary Nubian Sandstone deposits in Aswan, Egypt (*Iridina* sp. Cox, 1955), undescribed Early Tertiary material from the Continental Terminal of Niger, Miocene deposits in Kenya and Uganda (see under *Pleiodon tavernieri*) and in Pliocene-Lower Pleistocene deposits of the Turkana Basin (*Pleiodon bentoni* Van Bocxlaer & Van Damme, 2009).

Species *Pleiodon tavernieri* (Gautier, 1965)

Synonymy

Iridina tavernieri (Gautier, 1965, pp. 138 - 140, Pl. IV, figs 5 & 7; Pl. V, figs 1, 2, 4, 5, 7).

Pleiodon tavernieri (Gautier, 1970a, p. 123, Pl. V, fig 7).

Pleiodon (Pleiodon) tavernieri (Gautier & Van Damme, 1973, p., Pl. I, figs. 12-14).

Material. **MCA:** RG 11795, Sinda-Mohari, Site 13: *ca* 100 specimens & RG 11789: 4 fragments; RG 16574: Wasa-Kisegi, N. Nyaburogo I/Kisegi River Site 3: one poorly preserved mold; RG 11789: 4 fragments in the Lepersonne collection, **LPG:** P 2191: Sinda Mohari, Site 13: 2 specimens and 9 single valves, **UM:** KI 23’92 (KI 9): 2 specimens.

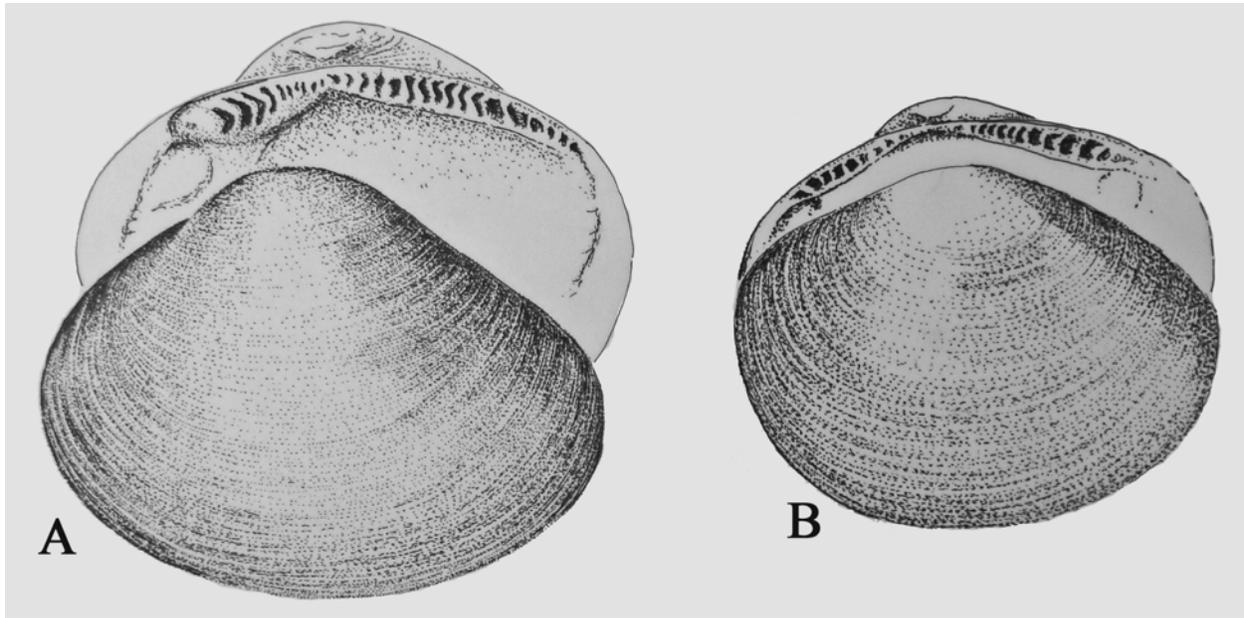


Figure 28. A) *Pleiodon tavernieri* (Gautier, 1965) (L = 32.1 mm). Holotype; B) *Pleiodon priscus* von Ihering, 1912 (L = ca 74.5 mm) (reconstruction based on the type).

Distribution. Kisegi area (Toro Region, Uganda); Sinda-Mohari area (Semliki Plain, Congo).

Description. ‘*Equivalve almost equilateral bivalve with height about two thirds of the length, diameter somewhat more than two thirds of the height. Umbones prosogyre and projecting far above the dorsal margin. General shape trigonal; anterior basal end elliptical; ventral margin slightly curved, posterior basal end with a rounded point; external strongly developed postumbonal ligament; regular growth lines crossed by radial striae, causing faint tuberculi on the crossings; umbonal region sometimes corroded. The hinge plate forms a blunt angle and is narrowed under the beaks. The hinge is pliodontiform*’ (Gautier, 1965).

To this may be added that this species is small (L = 17.6 mm, H = 11.7 mm) and that the length of the posterior side exceeds only 1.25 times that of the anterior side. The nearly centrally placed prosogyre beak is broad and rounded; both dorsal margins are strongly sloping, anterior margin evenly rounded, posterior margin bluntly angular, ventral margin evenly and strongly curved. Hinge plate very thick with ca 11 V-shaped well-developed teeth on the posterior side and ca 7 similar teeth on the anterior part. No shell ornamentation except for regular growth lines. We failed to observe the tuberculi mentioned by Gautier.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------|--------|--------|----------|--------------|
| Holotype | 32.1 | 22.0 | 13.6 | RG 11783 |
| Paratype A | 28.6 | 18.2 | 11.6 | RG 11784 |
| Paratype B | 24.4 | 17.4 | 11.6 | RG 11785 |

Type locality. Site 13 of Gautier (1965), Sinda Mohari, L. Albert, Congo (A Gautier *collevis*, Ganda Congo Mission, 1965).

Stratigraphy and age. Mohari Formation, Kisegi Formation, Middle Miocene, Molluscan Association G0 – G1.

Remarks. The triangular *Pleiodon* specimens recorded from the Early Miocene of Rusinga Island respectively as ‘*Genus novum?*’ (Verdcourt, 1963 p. 31-32) and the undescribed Rusinga specimens in the British Museum labelled *Iridina (Pliodon) miovata* (manuscript name) (see Gautier, 1965, p. 139) only differ from the Albertine specimens by their somewhat larger size and are conspecific with the Mohari material. The species is also recorded from the Middle Miocene Ngorora Fm. (12 – 10.5 Ma) (Tugen Hills, Kenya) (De Groeve, 2005). *Pleiodon tavernieri* is a pre-rift lake species that was widespread in fluvio-paludal biotopes before it became extinct prior to the Late Miocene. The Early Tertiary specimens from the Continental Terminal of Niger probably also have to be identified as *Pleiodon tavernieri* differing from the Miocene fossils only by their larger size (L = 80 mm).

The central location of the beak in *Pleiodon tavernieri* as a result of the short posterior side implies that a life position in which the animal was buried obliquely in the sediment along an anterior-posterior axis (e.g. *Mutela*) is not evident. It was probably a truly infaunal species, i.e. completely buried in the sediment with only the siphons sticking out. A lack of a pallial sinus indicates that these siphons were not significantly elongated. The combination of large diameter of the shell with a low L/H ratio (<1.5 in *Pleiodon tavernieri*) typifies infaunal species that bury superficially, e.g. *Cardium* species.

Genus *Iridina* Lamarck, 1819

Type species. *Iridina exotica*, Lamarck, 1819, p. 89. Type locality unknown.

Diagnosis. Shell elongate, hinge plate with a protrusion in the left valve below the umbo, with many small teeth over the entire length (description of the subgenus *Iridina* by Haas (1969)). We refer to the diagnostic key for additional information.

Occurrence. Recently cited from western Africa and Chad but detailed distribution unknown, also in Lake Tanganyika where it is often referred to under the genus name *Cameronia* Bourguignat, 1885. Fossils are known in African deposits since the Late Cretaceous- Early Tertiary, namely from the Nubian Sandstones in Egypt (*Iridina aswanensis* Cox, 1955) and from Continental Terminal deposits in Niger (undescribed material). The genus is dominant in the Miocene to Lower Pleistocene deposits in the Albertine Basin (this paper), the Turkana Basin (Van Bocxlaer & Van Damme, 2009), and is also known from Rusinga Island (Verdcourt, 1963; Pickford, 1998) and the Tugen Hills (De Groeve, 2005).

Remarks. Some species, such as *Iridina adami* or *Iridina lepersonnei* have a well developed posterior pseudotaxodont hinge with regular teeth. Other species such as *Iridina subelongata* have a more irregular tooth pattern which tends to become increasingly reduced over time (e.g. *Iridina subelongata* specimens from the Middle Miocene Mohari Fm in the Albertine Basin compared to Early Pleistocene specimens from Early Pleistocene deposits in the Turkana Basin (Van Bocxlaer & Van Damme, 2009)).

Species *Iridina moharensis* Gautier, 1965

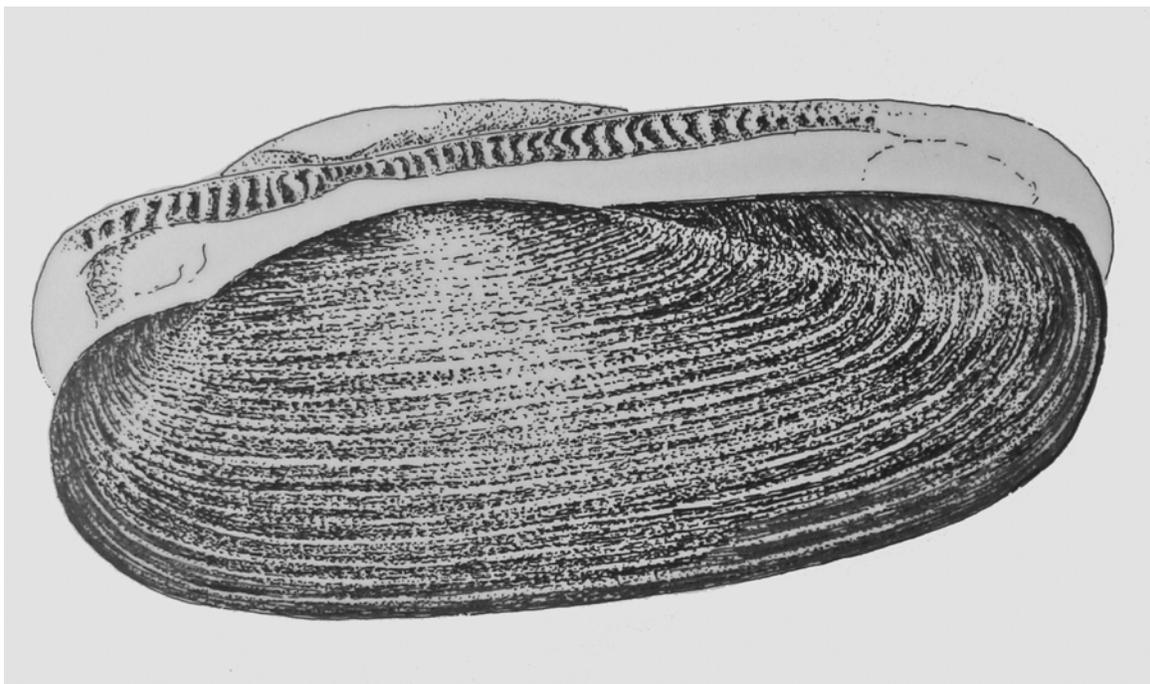


Figure 29. *Iridina moharensis* Gautier, 1965 (L = 52.7 mm). Holotype.

Synonymy

Mutela cf *rostrata* (partim) (Adam, 1959, p. 60, Pl. IX, fig 2).

Iridina (*Pliodon*) *moharensis* (Gautier, 1965, pp. 144-145, Pl. VI, figs 5-7).

Pleiodon (*Pleiodon*) *moharensis* (partim) (Gautier & Van Damme, 1973, pp. 50-51, Pl. I, fig 15).

Material. MCA: MC 2635, L531b: Mohari-Sinda N° 145, cliff north of the Sinda river: several fragments identified by Adam (1959) as *Mutela* cf *rostrata*; MC 2657, L531c: Mohari-Sinda N° 145-156: cliffs north of Sinda: identified by Adam as young specimens of *Mutela* cf *rostrata*; RG 11797 (Sinda Mohari, Site 13): 45 complete valves and 80 fragments; RG 11804 (Sinda Mohari, Site 5): 9 molds and about 95 fragments; RG 11796 (Sinda Mohari, Site 43): about 20 fragments.

Distribution. Early Miocene deposits of Rusinga Island (Kenya), Middle Miocene deposits of Sinda-Mohari area (Semliki Plain, Congo), Upper Miocene deposits of the Tugen Hills (Kenya).

Description. ‘Oblong equivalve, strongly inequilateral shell; height about 1/3 of the length, thickness about 2/3 of the height. Ventral and dorsal margins are nearly parallel. The umbones are very low and prosogyre, situated at 1/3 of the total length from the anterior end. The subelliptical anterior end meets the dorsal margin at a blunt angle. The posterior end is subangular, with a rounded point at 2/3 of the total height. The hinge plate is slightly curved and shows a typical pliodontiform hinge, of which the fine pre-umbonal teeth are as well-developed as the coarse postumbonal teeth. The hinge plate is narrowed under the beaks. The growth lines are rather coarse’ (Gautier, 1965, p. 145).

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|--------------|
| Holotype | 52.7 | 20.0 | 15.0 | RG 11797 |
| Paratype | 45.0 | 14.6 | 10.0 | RG 11800 |

Type locality. Site 13 of Gautier (1965), Sinda-Mohari, Semliki Plain, Congo (A. Gautier *collevis*, Ganda Congo Expedition, 1960).

Stratigraphy and age. Mohari Formation, Middle Miocene, Molluscan Association G1.

Remarks. *Iridina moharensis* is a species that was widespread and common in shallow lakes and floodplains during the Miocene. It has been found in Early Miocene deposits of Rusinga Island, Kenya (*Mutela* sp. in Verdcourt 1963, pp. 30-31, fig. 62 and *Iridina* sp., ibidem, p. 31, fig. 63), in the Upper Miocene Lukeino Fm. (6.0-5.7 Ma) (Tugen Hills, Kenya). Here the species reaches a size of ca 120 mm (De Groeve, 2005). The youngest known occurrence is from the Mabaget Fm. (5.0-4.7 Ma) (Tugen Hills, Kenya) (De Groeve, 2005). Gautier & Van Damme (1973) incorrectly lumped *Iridina moharensis* with *Iridina subelongata* (see below). There can be little doubt that *Iridina moharensis* is the ancestral lineage from which the lacustrine *Iridina adami*, endemic to Palaeolake Obweruka, evolved.

Synonymy

Iridina (Pliodon) subelongata (Gautier, 1965, 146-147, Pl. VII, fig. 7-8; Pl. VIII, fig. 3).

Iridina (Pliodon) sp. B (Gautier, 1965, pp. 143, Pl. VII, fig. 3).

Pleiodon (Pleiodon) moharensis (partim) (Gautier & Van Damme, 1973, pp. 50-51, Pl. I, fig. 16).

Species *Iridina subelongata* Gautier, 1965

Material. UM: KI 23'92 (KI 9): 5 specimens; KI 85'92 (KI 6): 3 internal molds in block of sandstone; KI 23'92 (KI 9): 7 fragmentary specimens; KI 86'92 (KI 4): 5 specimens; KI 30'91 (KI 5): 5 doublets in haematite; KI 34'92 (KI 4): 4 specimens; KI 83'92 (KI 6): 6 specimens; KI 99'92 (KI 6): 1 specimen; KI 16'91 (KI 4): 6 specimens; KI 45'92 (KI 5): 6 specimens; KI 51'92 (KI 12): 1 specimen; KI 84'92 (KI 6): 1 specimen; NY 16'92 (NY 74): 2 specimens + 1 fragment; NY 148'90 (NY 1): 2 fragmentary specimens; NY 97'90 (NY 70): 1 specimen. MCA: RG 11801: 1 left valve (type) and some fragments. LPG: P 2191b: Sinda Mohari, Site 13: 8 single valves; P2191c: Sinda Mohari, Site 5: 2 molds and a fragment (*Iridina* sp. B of Gautier, 1965).

Distribution. Middle Miocene deposits in the Sinda-Mohari area and Irimba-Maginda area (Semliki Plain, Congo), as well as in the Kisegi area (Toro region, Uganda) and Nyaburogo-Nyabusosi area (L. Albert, Uganda); Middle Miocene deposits in the Tugen Hills (Kenya) and in several areas in the Turkana Basin ranging from Early Pliocene to Early Pleistocene.

Description. 'Equivalve, inequilateral bivalve; general shape trigonal with gently curved ventral margin, passing gradually into the slightly angular subelliptical anterior margin. The posterior margin descends vertically from the hinge line to about midway the height where it passes into the curve of the ventral margin. Prosogyre umbones, rather highly projecting above the dorsal margin at about 1/3 of the length. Pliodontiform hinge on a hinge plate, narrowed under the

beaks.' (Gautier, 1965).

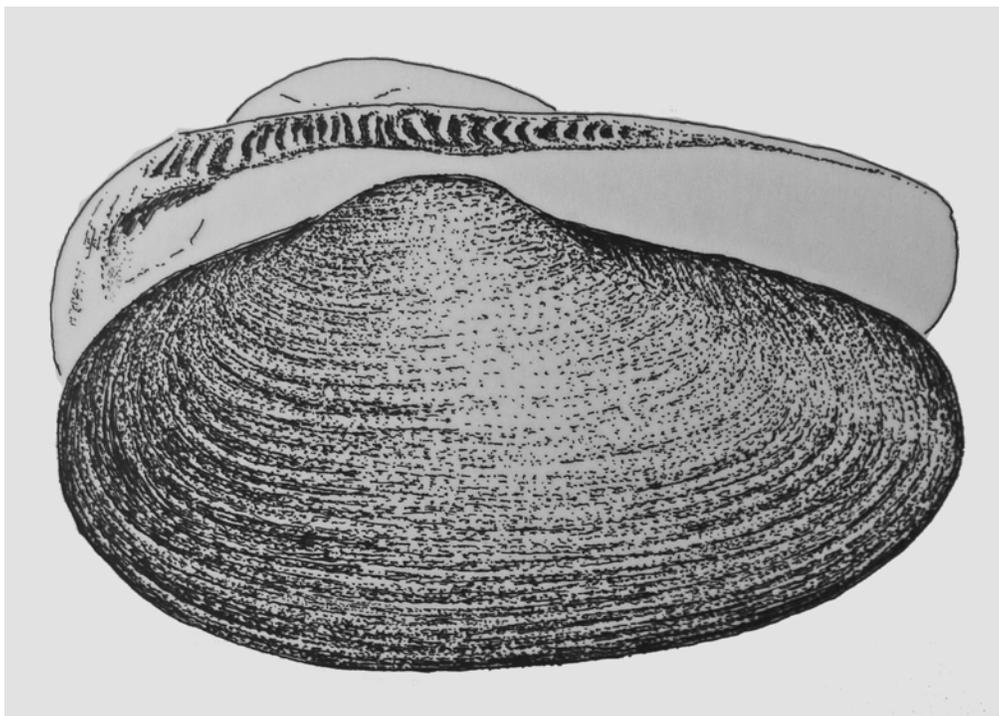


Figure 30. *Iridina subelongata* Gautier, 1965 (L = 32 mm). Holotype.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|--------------|--------|--------|----------|--------------|
| Holotype | 32 | 15 | 12 | RG 11801 |
| Kisegi KI 19 | 76 | 41 | 34 | KI 23'92 |
| Kisegi KI 19 | + 68 | 40 | 29 | KI 23'92 |
| Kisegi KI 19 | 72 | 34 | 33 | KI 23'92 |

Type locality. Site 13 of Gautier (1965), Sinda-Mohari, Semliki Plain, Congo (A. Gautier *collevis*, Ganda Congo Mission, 1960).

Stratigraphy and age in the Albertine Basin. Mohari Formation, Kisegi Formation, Oluka Formation. Middle Miocene, Molluscan Association G0-G2.

Remarks. This species lived in the shallow lakes that existed in the nascent rift. The type and paratypes from the Mohari Formation represent a dwarfed form, the specimens from other Albertine deposits being considerably larger (see table). *Iridina subelongata* also occurs in the Middle Miocene Ngorora Fm (Tugen Hills, Kenya) (De Groeve, 2005) and in several Early Pliocene to Early Pleistocene assemblages in the Turkana Basin (described by Van Damme (1976) as *Pleiodon browni* (*nomen nudum*), (Van Bocxlaer & Van Damme, 2009). The long persistence through time of this morph indicates that *Iridina subelongata* must be considered a distinct species and not a form of *Iridina moharensis* as Gautier & Van Damme (1973) stated. *Iridina subelongata* may have been the ancestral lineage from which the lacustrine *Iridina lepersonnei* evolved in Palaeolake Obweruka.

Species *Iridina adami* Gautier, 1965

Synonymy

Mutela (Mutelina) sp. (Cox, 1926, p. 69, Pl. IX, fig. 3a,b).

Mutela sp. (Connolly, 1928, p. 206).

Mutela sp. (Adam, 1957, p. 135).

Mutela cf *rostrata* (partim) (Adam, 1959, p. 60).

Iridina lepersonnei (partim) (Adam, 1959, pp. 63-66).

Iridina (Pliodon) moharensis (partim) (Gautier, 1965, pp. 144-446).

Iridina (Pliodon) adami (partim) (Gautier, 1965, pp. 147 – 149, Pl. VIII, figs. 1-2, 4, 6 & 7).

Pliodon adami (partim) (Gautier, 1970a, pp. 128-130, Pl. VI, fig. 9; Pl. VII, fig. 1-4).

Pleiodon moharensis (Musisi, 1991, p. 205).

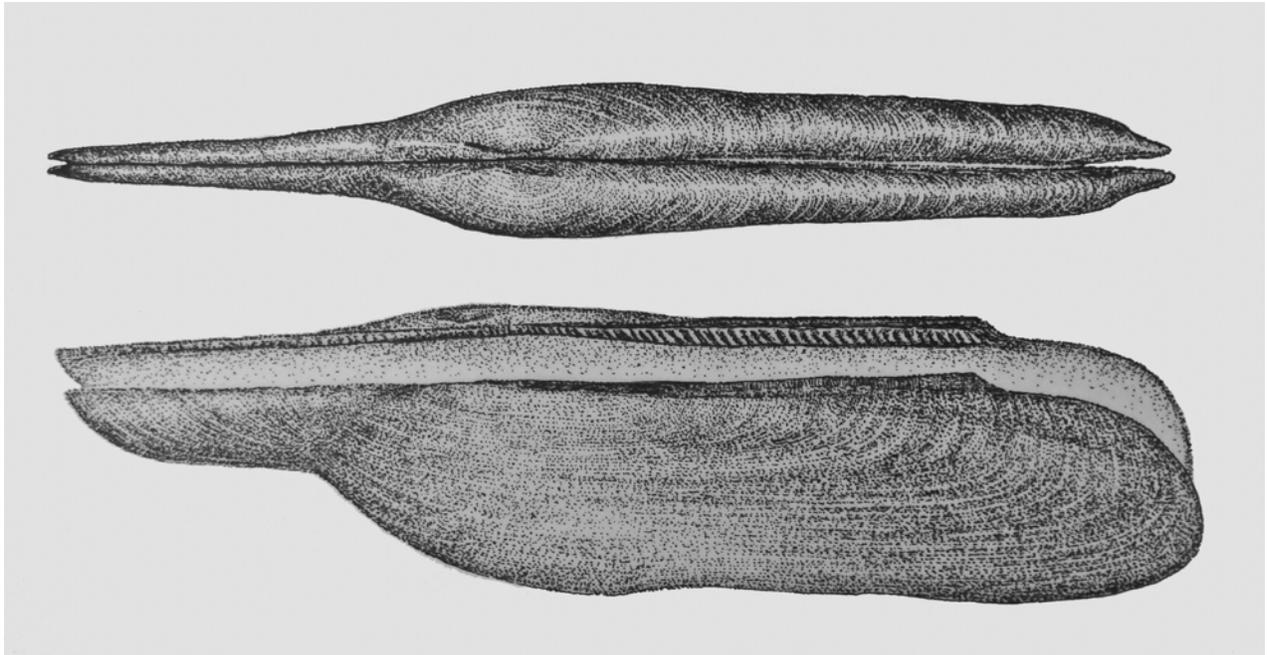


Figure 31. *Iridina adami* Gautier, 1965. Holotype with anterior end reconstructed (L = ca 155 mm).

Material. UM: NY 331'90 (NY 40): 1 specimen; NY 166'90 (NY 32): 1 specimen; NY 302'90 (NY 40): 2 specimens; NY 31'90 (NY 40): 5 specimens; NY 28'90 (NY 40): 1 specimen; NY 6'90 (NY 48): 3 specimens; NY 164'87 (NY 40): 1 specimen; NK 1207'89 (NK 4): 2 specimens; NK 2378'89 (NK 48): 1 specimen; NK 77'89 (NK 54): 2 specimens; NK 92'89 (NK 78): 1 specimen; NK 848'89 (NK 47): 7 specimens; NK 146'89 (NK 117): 1 specimen; NK 888'89 (NK 19): 7 specimens; NK 450'89 (NK 106): 1 specimen; NK 397'89 (NK 103): 1 specimen; NK 500'89 (NK 122): 2 specimens; NK 556'89 (NK 123): 2 specimens; NK 852'89 (NK 73): 1 specimen; NK 19'89 (NK 47): 1 specimen; NK 869'89 (NK 19): 1 specimen; NK 465'89 (NK 106): 1 specimen; NK 900'89 (NK 28): 1 specimen; NK 1100'89 (NK 122): 1 specimen; NK 812'88 (NK 43): 1 specimen; NK 31'88 (NK 77): 1 specimen; NK 690'88 (NK 111): 1 specimen; NK 447'88 (NK 44): 1 specimen; NK 13'88 (NK 76): 1 specimen; NK 229'88 (NK 1):

1 specimen; NK 633'88 (NK 106): 1 specimen; NK 804'88 (NK 115): 1 specimen; NK 482'88 (NK 49): 1 specimen; NK 83'88 (NK 41): 1 specimen; NK 188'88 (NK 85): 1 specimen; NK 848'89 (NK 47): 1 specimen; NK 2237'89 (NK 85): 1 specimen; NK 2237'89 (NK 120): 1 specimen; NK 1112'89 (NK 126): 1 specimen; NK 1250'89 (NK 52): 1 specimen; NK 272'89 (NK 115): 1 specimen; NK 69'89 (NK 41): 1 specimen; NK 637'89 (NK 62): 1 specimen; NK 718'89 (NK 115): 1 specimen; NK 607'89 (NK 71): ?1 specimen; NK768'89 (NK 115): 1 specimen; NK 305'89 (NK 119): 1 specimen; NK 190'89 (NK 90): 1 specimen; NK 832'89 (NK 125): 1 specimen; NK 288'89 (NK 120): 1 specimen; NK 679'89 (NK 76): 1 specimen; KN 162'88: 1 specimen (KN 7); KN 20'88 (KN 4): 1 specimen; KN 212'88 (KN 9): 1 specimen; KN 202'88 (KN 8): 1 specimen; KN 165'88 (KN 7): 1 specimen; KN 36'88 (KN 5): 1 specimen. **MCA:** RG 16.700 (Kaiso, Site surface between E and F): 2 fragments; RG 163699 ('Kaiso', Site 1): 1 internal mold; RG 16.697 ('Kaiso', Site 3): 1 fragment; RG 16.698 ('Kaiso', Site 1): 2 fragments; RG 16788 (Wasa-Kisegi, downstream N. Nyaburogo I Site 1): 6 fragments; RG 16.783, RG 16.593 (Wasa-Kisegi, N. Nyaburogo I Site 2): 26 specimens and fragments; RG 16.784, RG 16.692 (Wasa-Kisegi, N. Nyaburogo I Site 3): 26 fragments; RG 16.787, RG 16.591 (Wasa-Kisegi, N. Nyaburogo I/S. Nyaburogo II Site 3): 7 fragments; RG 16.785 (Wasa-Kisegi, N. Nyaburogo I/II Site 1): 8 fragments; RG 16.786 (Wasa-Kisegi, N. Nyaburogo I/II Site 2): 2 fragments, probably washed down from the upper site 1; RG 16.590, RG 16.789 (Wasa-Kisegi, Kisegi Fault Site 2): 1 specimen, 3 typical fragments; RG 16.589 (Kazinga Site A 3): 1 fragmentary specimen, no reference N° (Sinda Mohari, Site 8 of Gautier, 1965): 18 well preserved specimens and about 100 fragments; no reference N° (Sinda Mohari, Site 40I of Gautier, 1965); no reference N° (Sinda Mohari, Site 43 of Gautier, 1965): as *Iridina moharensis*; MC 2322, Lep 472: Nyamavi N° 60, western side of the 5th river west of Nyamavi camp: 2 fragments identified as *Mutela cf rostrata* by Adam (1959); Coll I.P.N.C.B.: uphill of the Mohari towards Kalunda about halfway to the top (de Heinzelin, 1957,401). **LPG:** P347: ca 5 fragmentary specimens collected by Dr. J. Musisi in 1989 at the type locality of the Kamahe Formation, i.e. in a gully along the northern bank of the Kamahe River, ca 600 m. upstream from its confluence with the Ntabagwe River (Kisegi District, Uganda) (Musisi, 1991).

Distribution. Upper Semliki - Ishango area, (L. Edward, Congo); Kazinga - Bushabwanyama area (L. Edward, Uganda); Kisegi area (Toro region, Uganda); Sinda-Mohari area (Semliki Plain, Congo); Nkondo area (L. Albert, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda);

Description. 'Equivalve, strongly inequilateral shell; height somewhat less than one third of the length; thickness about two thirds of the height; dorsal and ventral margin somewhat divergent; the ventral margin shows a faint incurvation in the middle; the prosogyre umbones are low and situated at about 1/8 of the total length; posterior margin oblique, meeting the posterior ventral margin in a rounded point; anterior end with an elongate point of which the anterior termination is unknown; the hinge is pliodontiform with fine but distinct pre-umbonal and coarser post-umbonal teeth' (Gautier, 1965).

To this must be added the following: 'shell very thin and fragile, the anterior tubular 'spine' makes up about 1/3 of the total length, it is ovate in cross section with a height of ca 8 mm and a width of ca 5 mm near the end, which is slightly gaping; the posterior end is strongly gaping; the ornamentation consists of fine growth lines with sometimes fine radiating striae on the anterior part and the teeth are small, numerous but very regular posteriorly and irregular and weakly developed to virtually absent anteriorly (see Fig. 31)

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------------|--------------------------|--------|----------|----------------------------|
| Holotype | ca 155 | + 35 | 20 | MCA Gautier PLVIII, fig. 4 |
| Paratype | + 105 (spine broken off) | + 27 | + 17 | MCA Gautier PLVIII, fig. 6 |
| Paratype | + 97 (spine broken off) | 24 | 14 | MCA Gautier PLVIII, fig. 7 |
| N. Nyaburogo I/2 | + 110 (spine broken off) | 35 | 20 | MCA RG 16593 |
| Nkondo NK 4 | + 135 (spine broken off) | 30 | 22 | UM NK 1207'89 |

Type locality. Sinda, Gautier's Site 8 (Sinda-Mohari, Semliki Plain, Congo) (A. Gautier *collevis*, Ganda-Congo Expedition, 1960).

Stratigraphy and age. Nkondo Formation; Nyamavi Beds, Member IV; Lower Nyaburogo Formation, Upper Oluka Formation (?); Sinda Beds, Member A; Kazinga Formation; Kamahe Formation; Base Lusso Formation at Nyakasia. Molluscan association G3a to G3c, Upper Miocene (7.5 Ma) until Early Pliocene (4.5 Ma). Recently it collected at Dellu (West Nile, Uganda) in the most northern part of the Albertine Basin (see appendix 2).

Remarks. Albertine iridiniid material is generally poorly preserved and fragmentary. Gautier (1965, 1970a), although admitting that identification at the species level was impossible, ranged all unidentifiable fragments of more or less elongated iridiniids under *Iridina adami*. This resulted in a puzzling biozonation, namely a first occurrence of *Iridina adami* in the early deposits (Association G3, 6-4.5 Ma) and a second reappearance during the terminal Lusso-Kaiso stage (Molluscan Association G5b-c and GX-X', ca 2 Ma), together with a modern 'Nilotic' fauna.

The stratigraphically solidly calibrated *Iridina adami* material (this study), collected by the Uganda Palaeontology Expedition, is strictly confined to Molluscan Association G3 (Nkondo Stage of Palaeolake Obweruka). We failed to find *Iridina adami* in younger deposits in the north along the Ugandan side (Palaeolake Kaiso). Gautier's (1970a) record of the species in the Kaiso area (Kaiso sites 1, 2, 3 and L) are not from the Kaiso Village-Hohwa River region, in which only Late Pliocene deposits crop out, but from the region 10 to 20 km south between the Sebugoro River and Nyaweiga Village where Late Miocene and Early Pliocene deposits occur. Some of Cox's (1926) material (e.g. his *Mutelina* sp.) also appears to have been collected there. Williamson (1990) came to the same conclusion that the elongated bivalves from the younger deposits in the south on the Congo side (Palaeolake Lusso) identified as *Iridina adami* belong to different species (Williamson's *Pleiodon* sp. nov. A), here described as *Iridina williamsoni* sp. nov. The particularly shaped *Iridina adami* not only has a clearly defined time range but it seems to have been restricted to a particular habitat, namely fine organic-rich muds. From the very beginning of the palaeontological investigation of the Albertine Basin it was noted that the sequence of units showed a cyclic sedimentation pattern. de Heinzelin & Verniers (1996) state that a fully cyclothemic unit of ca 2 m would successively be composed from bottom to top of clay (possibly spongolite), clay-silt, silt, sand, limonitic sand (possibly with shell beds), pseudo-oolitic ironstone, conglomerate of rolled bones and finally of fine to medium gravels. It is now generally accepted that this reflects sedimentary changes due to the uplift of a part of the basin's edge from deep to increasingly shallow waters (Pickford *et al.*, 1993; de Heinzelin & Verniers, 1996). The (usually spongolite) blue-gray clays accumulated in reduced, hypoxic to anaerobic conditions (de Heinzelin & Verniers, 1996), hence at a depth below or around the mixolimnion.

Gautier (1965, 1970a) and Pickford *et al.*, (1993) state that the only mollusc found *in situ* in these reduced deep water clays is *Iridina adami*.

On the basis of the revised evidence it can now be safely demonstrated that *Iridina adami* was an Obwerukan endemic species that was confined (1) in time to the Nkondo Stage of Palaeolake Obweruka, i.e. the period prior to the NK-27 Event and (2) in space to the deep hypoxic carbonate-enriched muddy bottoms.

Though the origin of this strongly elongated species seems relatively certain - it evolved from the already elongated *Iridina moharensis* - the function of the anterior elongation, unique among freshwater bivalves, remains unclear. Gautier (1965, 1966), taking into account the fact that *Iridina adami* was the only mollusc stratigraphically correlated with the fine reduced clays, hypothesized that the elongation functioned as a kind of lever, preventing the animal from sinking and suffocating in the oozy mud. During the early investigations, the cyclothemic units were interpreted as layers deposited in shallow lakes. According to Gautier (1966), the oozy organic mud layer represented the end stage of a shallow lake's existence when it was turning into a bog clogged with organic black ooze (cf Modern L. Mweru). This type of habitat was each time colonized by *Iridina adami*.

Since then it has generally been accepted that the spongolite clay layers in the Albertine depositional sequences were formed at great depths (Pickford *et al.*, 1993; de Heinzelin & Verniers, 1996). Fluid organic 'abyssal' muds, which occur mainly in stratified lakes, indeed necessitate shell adaptations that increase buoyancy, such as strongly inflated and light shells (Kauffman, 1969). The thin and strongly elongated shells of *Iridina adami*, without the additional anterior elongation, provide in our opinion, sufficient stabilization to keep the animal from sinking. But the major puzzle provided by the presence of the narrow anterior elongation pertained to the use of the foot. From the shell's developmental growth it can be deduced that the elongation remains weak and the height of the elongated part stays about equal to the total height until the animal reaches a length of *ca* 50-60 mm. Subsequently however the development rate starts to change with a rapid elongation both of the posterior and anterior part, the latter however only increasing significantly in length but not any more in height. This leaves two possibilities in regard to the foot's anatomy:

- (1) the pedal muscle remained about the same size diameter as in the juvenile shell of *ca* 50 mm and continued to develop into the tubular extension as a worm-like appendage.
- (2) the pedal muscle developed further in width, implying that it could not use the tubular extension which would break when the foot muscle would suddenly contract or extend. This second possibility also implies that the anterior shell extension would be empty and thus would become filled with mud since the anterior end is gaping.

In his study on aberrations in bivalve evolution related to photo- and chemosymbiosis (Seilacher, 1990) was the first to point out that such anteriorly elongated freshwater bivalves as the African *Iridina adami* and the Asian *Arconaia lanceolata* were likely candidates for a chemosymbiotic lifestyle (as well as such genera as *Solenaia* with gaping shells and an unretractable foot). This hypothesis was further developed by Savazzi & Peiyi (1992) and Ghilardi & Simões (2002) used it to explain the presence of the sulcus in *Anhemia* spp. from Permian deposits in Brazil.

Seilacher's hypothesis concerning *Iridina adami* seems to be corroborated by the fact that this species is found *in situ* only in deep water clays.

Recent research on marine thyasirid bivalves, living in chemoautotrophic symbiosis (Dufour & Felbeck, 2003) has demonstrated that these animals that are found in organic rich muds under hypoxic conditions, are able to extend their tentacle-like foot (diameter = 2 mm) to a length 30 times the contracted length. With this tentacle-like structure the food source, i.e. pockets of sulphides, are chemotactically traced. When the pedal muscle is retracted, symbiotic bacteria are carried into the shell to the gills. The extreme extension of the foot in thyasirids is, according to the authors, likely to have a hydrostatic component with haemolymph being pumped by the heart from the body mass into the foot. A significant lengthening is only possible if the diameter of the foot remains constant or is reduced (Dufour & Felbeck, 2003). In the case of *Iridina adami* the tubular elongation of the anterior part may thus have functioned as a means to reduce the foot's diameter, when squeezed through the funnel.

The notion of chemosymbiosis in *Iridina adami*, or for that matter other freshwater bivalves, must remain hypothetical till proven by chemical/microbiological analysis. Specimens of *I. adami* were sent by the authors for analysis for traces of sulfur. The tests were negative though this may be due to replacement of elements during fossilization (Van Rensbergen, pers. comm., 2007).

Species *Iridina williamsoni* nov.

Synonymy

Iridina ? *exotica* (Adam, 1955, p. 39).

Iridina ? *exotica* (Adam, 1957, p. 136, Pl. VII, Fig. 10).

Mutela sp. (Adam, 1957, pp. 133-134, Pl. VIII, fig. 4).

Mutela cf *rostrata* (partim) (Adam, 1959, pp. 60-61, Pl. IX, fig. 1).

Iridina lepersonnei (partim) (Adam, 1959, pp. 63-66).

Iridina (Pliodon?) moharensis (partim) (Gautier, 1965, pp. 144-446).

Iridina (Pliodon) adami (partim) (Gautier, 1965, pp. 147 – 149).

Pliodon adami (partim) (Gautier, 1970a, pp. 128 – 130).

Pleiodon sp. A (Williamson, 1990, pp. 131-132, text Table 2).

Material. MCA: RG 16.608 (Bushabwanyama, site W.B. 2): 5 fragments; RG 16.609 (Bushabwanyama Site A/6): 3 fragments; Senga, facing mouth of the Kasaka river, 1.0 m to 3.6 m: numerous poorly preserved specimens; L. 317: 1000 m downstream from Senga, right bank: strongly elongated fragments; L. 132: upstream from the mouth of the Kasaka river, left bank: one fragment; L 312: downstream from Katanda, right bank: elongated fragments; L. 279: Ravine east of Kanyatsi: one fragment; L. 273 & 302: 1 to 1.5 km east of Ishango, between 30 and 60 m above lake level: fragments of a large strongly elongated specimen with almost parallel upper and lower margins; Sinda-Mohari, Site 7: one broken specimen in ironstone; MC 2621, Lep. 528.: Mohari-Sinda N° 140 between Munene II and III: one doubtful specimen (Member B); MC 2695c, N°555 (site L. 186): Mohari-Sinda, between Sinda and Ndira: 1 large doubtful specimen; MC 2418, Nyamavi N° 68 (Lep. 464): two strongly elongated fragments with small teeth. Possibly also at Gautier's Site E and Site between E-F at 'Kaiso'; MC 2322, Lep. 472: Nyamavi N° 60, western side of the 5th river west of Nyamavi camp: 2 fragments.

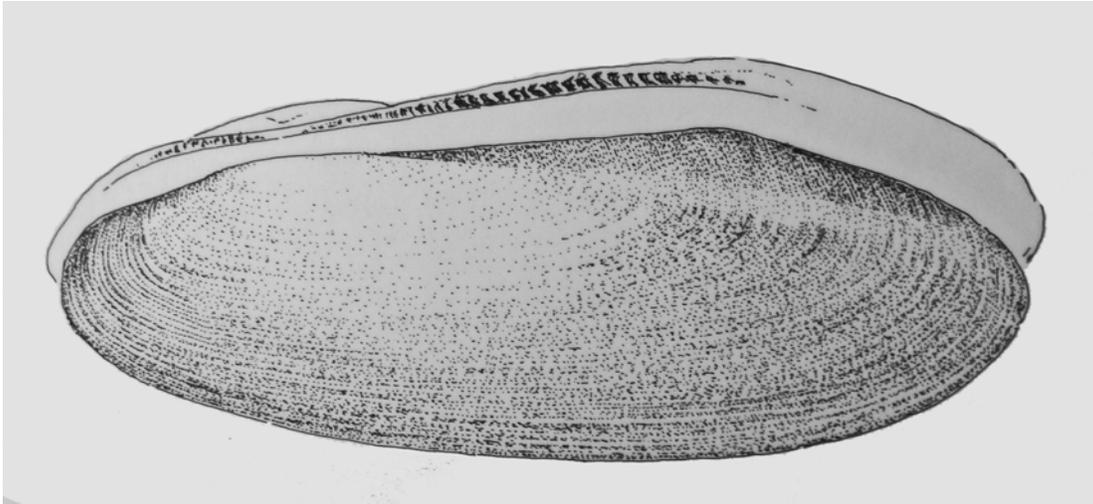


Figure 32. *Iridina williamsoni* sp. nov. Holotype (L = 108 mm).

Distribution. Upper Semliki - Ishango area (L. Edward, Congo); Sinda-Mohari area (Semliki Plain, Congo); Nyamavi area (L. Albert, Uganda)

Description. Medium sized, strongly elongated, rectangular iridiniid. The height about 1/5 of the length. Beak wide and low. Anterior end small, narrow and evenly rounded. Posterior end stretched out into a rounded point along the shell's horizontal axis, constituting about 1/5 to 1/6 of the total length. Dorsal and ventral margin subparallel. The posterior margin is straight with a faint angle descending into the posterior end. Ventral margin weakly curved, nearly straight in the median part. Surface is glossy, smooth except for slight concentric growth wrinkles. Hinge plate relatively thin, weakly pleiodontiform with irregular and small teeth usually restricted to the posterior side.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|-----------------------------|
| Holotype | 108 | 22.0 | 20 | Adam, 1957, Pl.VIII, Fig. 4 |

Type. Specimen figured by Adam (1957, Pl. VIII, Fig. 4).

Type locality. 'Senga, in front of the Kasaka river, 1.0 to 3.6 m above the river' in Lepersonne, 1970, p. 186, Upper Semliki area, L. Edward, Congo (J. de Heinzelin *collevis*, de Heinzelin Mission, 1950-51).

Stratigraphy and age. Lusso Fm (Lusso III), Sinda Fm Member C, Nyamavi Fm., Member VII. Late Pliocene (Molluscan Association G5a-b and GX').

Remarks. In the late Pliocene deposits a strongly elongated iridiniid appears in the deposits of Palaeolake Kaiso and Palaeolake Lusso, usually represented by poorly preserved fragments that were mistaken as *Iridina adami* by Gautier (1970a). Williamson correctly remarked that it was a different species. It lacks the typical elongated anterior tube of *Iridina adami* and although strongly elongated posteriorly it can be markedly higher than the latter species. Adam (1959) identified the fossil material as *Mutela cf. rostrata* (Rang, 1835) which it indeed resembles in its general form (Bajoje, 1992). But the fossil specimens here named *Iridina williamsoni* grow to a much larger size (up to a length

of 160 mm), lack the typical rostrum and have a considerably broader hinge with weak and irregular teeth. Since most of these specimens have a pleiodontiform hinge, admittedly poorly developed, the species is ranged under *Iridina*. *Iridina williamsoni* was not a lacustrine endemic but one of the many new faunal elements that entered the Albertine Basin at the end of the Pliocene.

Species *Iridina lepersonnei* Adam, 1959

Synonymy

Pliodon sp. nov. (Cox, 1926, p. 69, Pl. IX, fig. 5 a-b).

Pleiodon sp. (Connolly, 1928, p. 206).

Pliodon sp. (Fuchs, 1934, p. 147).

Pliodon sp. (Cahen, 1954, p. 342).

Iridina (Pliodon) sp. (Adam, 1957, 137).

Iridina lepersonnei (partim) (Adam, 1959, 63-66, Pl. IX, figs. 3-5).

Mutela cf *rostrata* (partim) (Adam, 1959, p.60, Pl.VIII, fig. 5).

Aspatharia sp. (partim) (Adam, 1959, 60-62, Pl. VIII, fig. 3).

Iridina (Pliodon) ovata (Gautier, 1965 (*non* Swainson), 140 – 143, Pl. VI, figs. 1-2, fig. 4).

Pleiodon ovatus (Gautier, 1970a, 123-128, Pl. V, figs 8 – 13; Pl. VI, figs. 1, 2, 4).

Pleiodon ovatus (Williamson, 1990, p. 136).

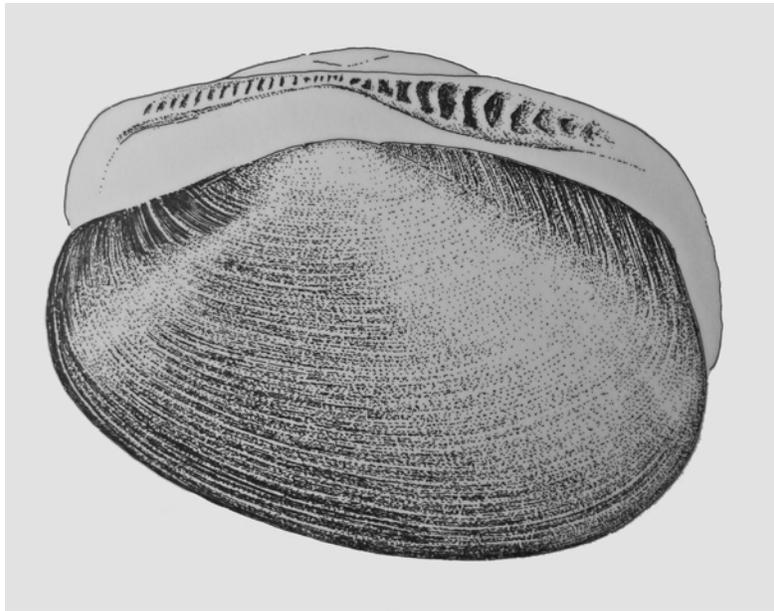


Figure 33. *Iridina lepersonnei* Adam, 1959 (L = 78 mm) from Gautier's Site 8, Sinda Mohari.

Material. BMNH: L. 40267: 1 internal mold (coll. Cox, 1926). **UM:** NY 46'90 (NY 32): 6 specimens; NY 310'90 (NY 40): 1 specimen; NY 70'92: 2 specimens; NY 91'92: 2 specimens; NY 83'92: 1 specimen; NK 1177'89 (NK 4): 3 specimens; NK 556'89 (NK 123): 5 specimens; NK 868'89 (NK 19): 4 specimens; NK 849'89 (NK 47): 1 specimen; NK 854'89 (NK 74): 1 specimen; NK 679'89 (NK 76): 1 specimen; NK 861'89 (NK 20): 1 specimen; NK 451'89 (NK106): 1 specimen; NK 900'89 (NK 28): 1 specimen; NK 347'89 (NK 21): 1 specimen; NK 91'89 (NK 78): 2 specimens; NK 434'89 (NK 26): 1 specimen; NK 634'88 (NK 106): 1 specimen; NK 687'88 (NK 110): 1 specimen; NK 371'88 (NK 38): 1 specimen; NK 677'88 (NK

108): 1 specimen; NK 1456'89 (NK 38): 1 specimen; NK 2238'89 (NK 120): 1 specimen; NK 1532 (NK 13): 2 specimens; NK 1208'89 (NK 4): 2 specimens; NK 1181'89 (NK 31): 1 specimen; NK 1382'89 (NK 52): 1 specimen; NK 1651'89 (NK 38): 1 specimen; NK 273'89 (NK 115): 2 specimens; NK 159'89 (NK 90): 1 specimen; NK 717'89 (NK 115): 1 specimen; NK 649'89 (NK 39): 1 specimen; NK 637'89 (NK 62): 1 specimen; NK 638'89 (NK 62): 1 specimen; NK 305'89 (NK 119): 2 specimens; NK 305'89 (NK 119): 1 specimen; NK 289'89 (NK 120): 1 specimen; NK 889'89 (NK 9): 8 specimens, ?1 specimen; NK 465'89 (NK 106): 1 specimen; NK 254'88 (NK 14): 1 specimen; NK 273'89; NK91'89: 1 specimen; HO 25'89 (HO 8): 3 specimens; HO 25'89 (HO 8): 1 specimen; KS 39'89 (KS A?): 4 specimens; KS 63'89 (KS A): ?1 specimen; KS 12'90 (KS B): 1 specimen; KS 49'90 (KS B): 1 specimen; KY 30'90 (KY 1): 1 specimen; KY 17'90 (KY 1): 1 specimen; KN 200'88: 1 specimen; KN 162'88: 1 specimen. **MCA:** RG 16.694 (? Kaiso, Site D band W): 1 doubtful specimen; RG 16.695 (? Kaiso, Site E): 1 doubtful fragment; RG 169.691 (? Kaiso, Site F): 1 doubtful specimen; RG 16.693 (? Kaiso, Site between E and F): 2 small shells and a doubtful fragment; RG 16.692 (Kaiso, Site 1): 4 specimens and a doubtful internal mold; RG 16.696 (Kaiso, Site 3): 1 juvenile, one fragment and one doubtful internal mold; RG 16.584 & RG 16.690 (Kaiso, Site 1): 1 specimen, one fragment and an internal mold; RG 16.780 (Wasa-Kisegi, N. Nyaburogo I Site 1): 3 fragment; RG 16.778, RG 16.580 (Wasa-Kisegi, N. Nyaburogo I Site 2): 6 fragmentary specimens; RG 16.782 & RG 16.579 (Wasa-Kisegi, N. Nyaburogo I, Site 3): 8 fragmentary specimens and fragments; RG 16.776 (Wasa-Kisegi, ?N. Nyaburogo I/II Site 1): 1 poorly preserved specimen; RG 16.777 (Wasa-Kisegi, ? downstream N. Nyaburogo I Site 1): 1 fragment; RG 16.781, RG 16.582 (Wasa-Kisegi, Kisegi Fault Site 2): 16 fragmented specimens; RG 16.646, RG 16.581 (Kazinga Site A 3): 12 poorly preserved specimens; RG 16.577 (? Kazinga Site D): 1 poorly preserved specimen; Sinda Mohari, Site 8: 9 specimens; Sinda Mohari, Site 40 I: 3 fragments; Sinda Mohari, Site 40 I: 9 specimens (coll. Gautier, 1965); MC867: Uganda: L. Albert, "Cliff south of River Howa" (Exp. Wayland, identification by Connolly, 1928): one internal mold; MC 2402, 05, 09 & 10, Lep. 464: Nyamavi N° 68, Nyamavi camp: several bivalve specimens, internal molds and fragments; MC 2430, Lep. 466, Nyamavi N° 466, north of Nyamavi camp: 3 bivalve specimens; MC 2551, Lep. 500: Mohari-Sinda N° 102, right bank of the Mohari, upper limonite layer: dubious specimen; MC 2591, Lep. 521: Mohari-Sinda N° 129, right bank of the Gety: one specimen; MC 2592, Lep. 522: Mohari-Sinda N° 129, right bank of the Gety: a few specimens; MC 2600 Mohari-Sinda, N° 134, northern side of the Sinda; MC 2608, Lep. 525: Mohari-Sinda N° 134, northern side of the Sinda: a few specimens; MC 2619, Lep. 527: Mohari-Sinda N° 139, between Munene I et II: several doubtful specimens; MC 2635: Mohari-Sinda, cliffs north of the Sinda (Lep 531B); MC 2657, Lep. 531c: Mohari-Sinda N° 145-156, cliffs north of the Sinda: some doubtful fragments; MC 2684, Lep. 551: MC 2664, Lep. 553: Mohari-Sinda N° 171, between Sinda and Ndira: a few specimens; MC 2695b, Lep. 553B: Mohari-Sinda N° 171, between Sinda et Ndira: an internal mold; MC 2642, Lep. 555: Mohari-Sinda N° 186, between Sinda and Ndira (ravine of N° 171): some doubtful specimens; MC 2479, Coll. Delpierre: Mohari-Sinda, left bank of the Gety river (= Lep. 117): a doubtful specimen; MC 2495, coll. Delpierre; locality unknown: 2 specimens; RG 16.694 (?Kaiso, Site D band W): 1 doubtful specimen; RG 16.695 (? Kaiso, Site E): 1 doubtful fragment; RG 169.691 (? Kaiso, Site F): 1 doubtful specimen. **LPG:** P4705, Mahiga Ravine East, 949 m (G3c): 1 specimen; P4714, Nyakasia Ravine, western slope, 960 m (G3): internal mold.

Distribution. Upper Semliki - Ishango area (L. Edward, Congo); Kazinga - Bushabwanyama area (L. Edward, Uganda); Wasa-Kisegi area (Toro Region, Uganda); Sinda-Mohari area (Semliki Plain, Congo); Irimba-Maginda area (Semliki Plain, Congo); Nkondo area (L. Albert,

Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda); Kaiso Village-Hohwa area (Lake Albert, Uganda); Nyamavi area (Lake Albert, Congo).

Description. ‘Shell equivalve, somewhat flattened, inequilateral, the length of the posterior part about twice the size of that of the anterior part. Beaks only weakly protruding. Dorsal margin almost straight, somewhat convex, rising gradually posteriorly until about the last third of the shell’s length, then descending towards the posterior end that is situated about half of the total height of the shell. Basal margin regularly convex. Anterior part somewhat truncated, posterior end rather acuminate. Hinge with an interrupted series of rather heavy teeth, markedly developed in the posterior part’ (translated from Adam, 1959).

To this we add that the teeth are smaller and not so incised anteriorly, that the posterior teeth are few in number (8-9) but very large and that the shell is globose, thick and heavy.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------------------|--------|--------|----------|-----------------------------------|
| Holotype | 68 | 37.5 | + 23 | MC 2409 Adam, 1959 Pl. IX, Fig. 5 |
| Lectotype | 74 | 39 | 25.5 | MC 2321 |
| Sinda Mohari, S. 8 | 78 | 49 | 34 | Gautier, 1965, Pl. VI, Fig. 2 |
| Sinda Mohari, S. 8 | 90 | 55 | 35 | Gautier, 1965, p. 141 |
| Sinda Mohari S. 40 I | 58 | 39 | 23 | Gautier, 1965, Pl. VI, Fig. 1 |

Type locality. Site L 464 of Lepersonne (1970), Nyamavi N° 68, Nyamavi Camp, Lake Albert, Congo (J. de Heinzelin *collevis*, Mission J. de Heinzelin, 1950-52).

Stratigraphy and age. Oluka Fm, Nkondo Fm, Warwire Fm, Nyaburogo Fm, Kaiso Village Fm, Kyeoro Fm, Nyakabingo Fm, Lusso Fm (LI & LII), Nyamavi Beds III to VII and the Sinda Beds. Late Miocene to terminal Pliocene. Molluscan Association G3 to G5a and GX’. Recently it was collected at Koku (West Nile, Uganda) in the most northern part of the Albertine basin (see appendix 2).

Remarks. In our opinion, the generic position of this species- either *Iridina* or *Pleiodon*- is not fully solved. Gautier (1965) synonymized *Iridina lepersonnei* with extant *Pleiodon ovatus* (Swainson, 1823), a living fossil found in a few rivers in West Africa (Sierra Leone, Senegambia), but the two species show barely any similarities. *Iridina lepersonnei* is distinctly wedge shaped and relatively short instead of ovate-elongate, it has a shell thickness about 3 times that of *Pleiodon ovatus*, a much broader and more curved hinge plate and larger and fewer teeth posteriorly and less regular anterior teeth. *Iridina lepersonnei* is considered here to be a lacustrine endemic form which may have evolved from the fluvio-lacustrine *Iridina subelongata* soon after Palaeolake Obweruka was formed. The thick shell and extremely broad hinge plate constituted an excellent protection against external dangers and the species is the most abundant naiad in the Albertine deposits. Against this in-lake evolution hypothesis stands the fact that it is the only large bivalve that survived both the NK-27 Extinction Event and the Ruwenzori-Rising Extinction Event (only in Palaeolake Kaiso). Which may suggest that populations of this species also lived outside the lake, as *Pseudobovaria mwayana* did, and repeatedly recolonised the lacustrine environment.

Williamson (1990) also recorded *Iridina lepersonnei* (as *Pleiodon ovatus*) from deposits of the Middle Lusso Formation (LII), namely from sites Senga 1, Kanyavughorwe 6, Tshibiridi 6, and Kishishio 2 of Verniers & de Heinzelin (1990).

Species *Iridina wasai* nov.

Diagnosis. See description.

Synonymy

Iridina cf *exotica* (Adam, 1957, p. 136, Pl. VII, fig 10).

? *Mutela* sp. (partim) (Adam, 1957, pp. 133-134, Pl. VIII, fig. 4).

? *Mutela* cf *rostrata* (partim) (Adam, 1959, pp. 60-61).

Pleiodon (*Cameronia*) *spekii* (Gautier, 1970a, pp. 130-134, Pl. VI fig. 3a-b, 5-8).

Pleiodon sp. (Gautier, 1970a, p134).

Pleiodon spekii (Musisi, 1991, p. 205)

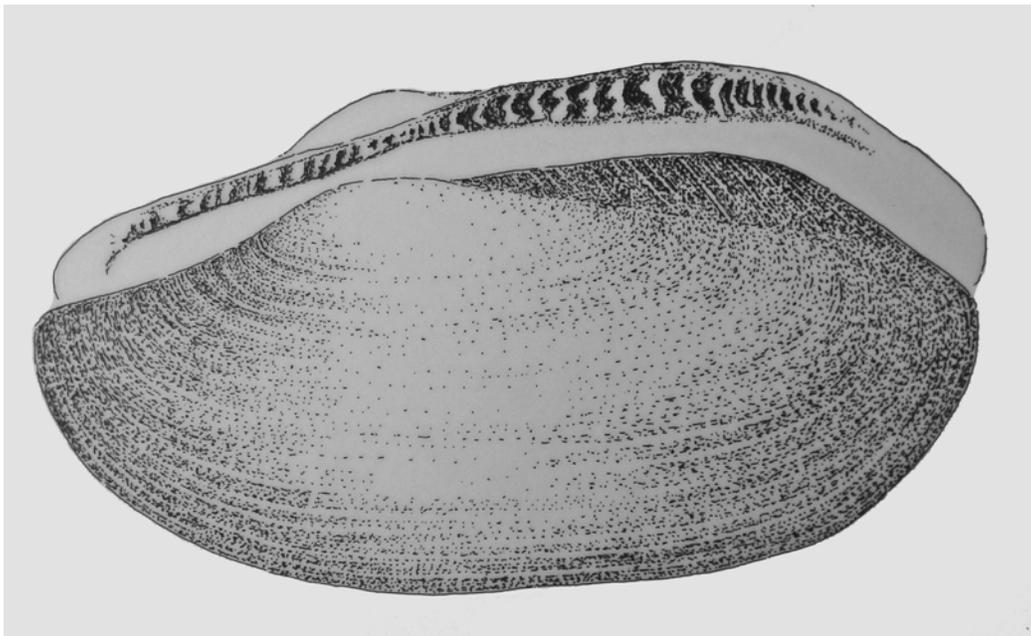


Figure 34. *Iridina wasai* sp. nov. (L = ca 93 mm) Holotype.

Material. **BMNH:** L.40266: 1 internal mold (Kaiso). **UM:** NY 236'90 (NY 22): 1 specimen; NY 289'90 (NY 55): 1 specimen; NY 70'92 (NY83): 1 specimen, NY 68'92 (NY83): 6 specimens; NY 70'92 (NY83): 2 specimens; NY 40'92 (NY67): 6 specimens; NY 110'92 (NY83): 1 specimen; NY 53'92 (NY82): 3 specimens; NY 70'92 (NY83): 4 specimens; NY 77'92 (NY67): 2 specimens; NK 556'89 (NK 123): 1 specimen; KI 95'92 (KI15): 1 specimen; KI 57'92 (KI11): 1 specimen; KI 31'92 (KI12): 3 specimens. **MCA:** RG 16.790 (Wasa-Kisegi, N. Nyaburogo I Site 1): 35 fragmentary specimens and fragments; RG 16.791, RG 16.586 (Wasa-Kisegi, N. Nyaburogo I/S. Nyaburogo II, Site 1): many complete specimens and fragments; RG 16.794 (Wasa-Kisegi, N. Nyaburogo I/S. Nyaburogo II Site 2): 19 fragmentary specimens and fragments; RG 16.793, RG 16.588 (Wasa-Kisegi, N. Nyaburogo I/II Site 2): 12 fragments; RG

16.792, RG 16.585, RG 16.587 (Wasa-Kisegi, N. Nyaburogo II Site 1): 75 fragmentary specimens and fragments; RG 16.797 (Wasa-Kisegi Fault Site 1): 1 specimen and one fragment; RG 16.798, RG 16.583 (Wasa-Kisegi, Kisegi Fault Site 2): 15 fragments and specimens; RG 16.796 (Wasa-Kisegi, ? N. Nyaburogo I/Kisegi R. Site 2): 2 fragments; RG 16.795 (Wasa-Kisegi, ? N. Nyaburogo I/Kisegi R. Site 3): 1 fragment; RG 16649: Kazinga Site Z; RG 16650: Kazinga Site A2. **LPG:** P 347: *ca* 30 large specimens collected by J. Musisi in 1989 in the Kazinga area at the type locality of the Kamahe Formation, i.e. in a gully along the northern bank of the Kamahe River, *ca* 600 m upstream from its confluence with the Ntabagwe River (Kisegi District, Uganda); P 2103: 4 specimens from Wasa-Kisegi, N. Nyaburogo, Nyaburogo II, Site I of Gautier (1970a).

Distribution. Kazinga - Bushabwanyama area (L. Edward, Uganda); Kisegi area (Toro region, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda)

Description. Medium sized, equivalve, strongly inequilateral shell; height about 1/2 of the length, diameter about 1/3 of the height. Beak relatively sharp and slightly projecting above the dorsal ridge, situated at about 1/3 of the total length. Dorsal posterior margin slightly raised. Posterior end obliquely truncate, produced into a point at about half the height, where the posterior ridge reaches the posterior margin, the margin straight to slightly concave in the upper part and convex and regularly curved below the point. Ventral margin nearly straight in the middle and sharply upward curving anteriorly, forming a sharp angle with the concave anterior dorsal margin. Ornamentation plicatulate, consisting of irregular growth lines only. Hinge plate slightly curved with large well-developed teeth in the posterior part and irregular weakly developed teeth anteriorly.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------|--------------|--------------|--------------|--------------|
| Holotype | <i>ca</i> 93 | <i>ca</i> 45 | <i>ca</i> 25 | RG 16585 |
| Paratype A | <i>ca</i> 79 | <i>ca</i> 39 | <i>ca</i> 29 | RG 16585 |
| Paratype B | <i>ca</i> 80 | <i>ca</i> 42 | - | RG 16587 |

Type. RG 16585 (Pl. VI, fig 5 of Gautier 1970a).

Type locality. North Nyaburogo II Site 1 of Gautier (1970a), Wasa-Kisegi area (Uganda) (collected by members of the Baker Centenary Expedition, 1963).

Stratigraphy and age. Upper Oluka Fm, Lower Nyaburogo Fm, Kazinga Fm, Kamahe Fm. Late Miocene – Early Pliocene, Molluscan Association G3b-c.

Etymology. Named after the nearby Wasa River (Toro, Uganda).

Remarks. Gautier (1970a) identified the fossils as *Pleiodon (Cameronia) spekii*, occurring today in Lake Tanganyika. They differ however from this Tanganyikan species by their smaller size (*Iridina spekii* attains a length of more than 160 mm), much thinner shells (about 0.5 times the thickness of *Iridina spekii*), the median position of the posterior point which is lower in *Iridina spekii*, the considerably narrower beaks, the straight or concave instead of incurved ventral

margin and the larger anterior part.

The occurrence of *Iridina wasai* appears to have been restricted to the time period encompassing the early stage of Palaeolake Obweruka, i.e. prior to the NK-27 Extinction Event. *Iridina wasai* was not a lacustrine endemic but occurred not only in shallow oxygen-rich littoral stretches of the lake but also in estuaries and other aquatic fringe habitats. For although it is relatively common in the Wasa-Kisegi area, all the fossils are poorly preserved (mainly as internal molds) in ferruginous silts or silty sands, indicative of diagenesis in shallow oxygenated sediments. The presence at the northeastern margin of Palaeolake Obweruka around 4 Ma of many fluvio-lacustrine shells may be indicative of a large drowned estuary in that region during the early Pliocene.

Species *Iridina atrox* nov.

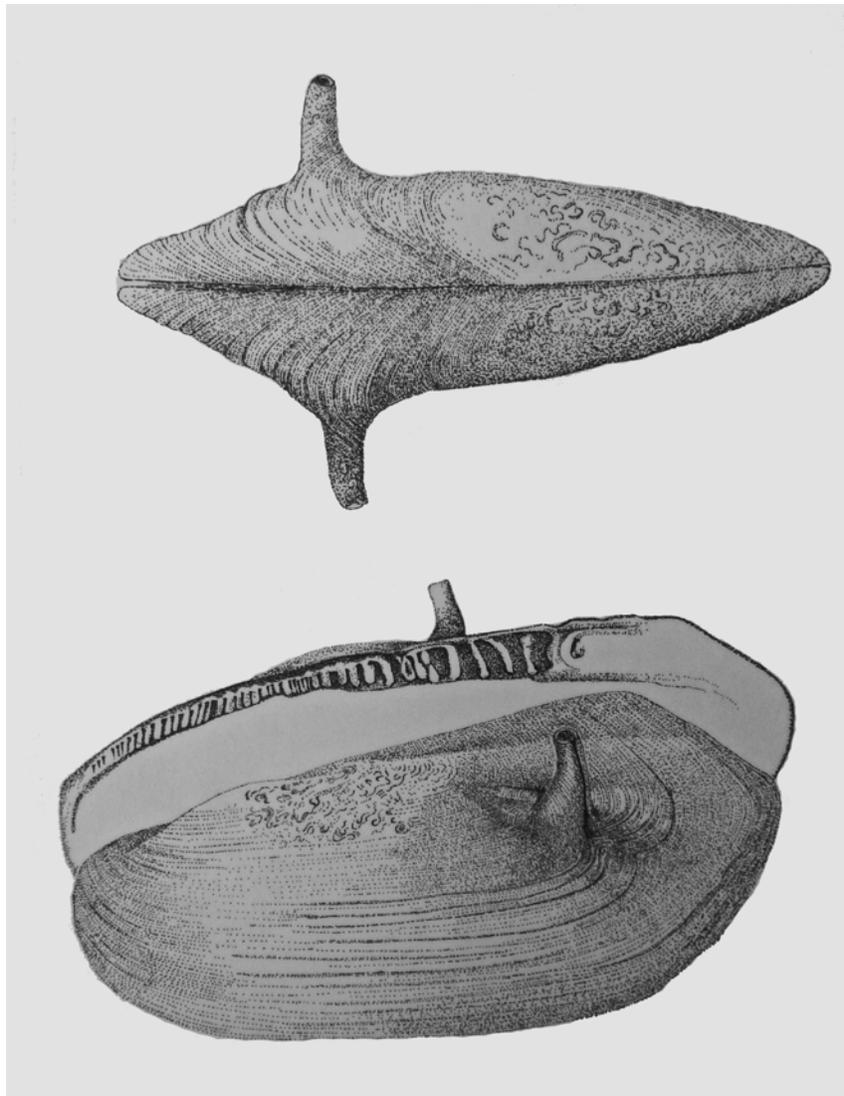


Figure 35. *Iridina atrox* sp. nov. Holotype (L = 50.2 mm) with reconstructed spines based on specimen RG 16575.

Diagnosis. See description.

Synonymy

Pleiodon ovatus (partim) (Gautier, 1970a, p. 125, Pl. V, Figs. 8a-b).

Material. **UM:** KN 3'88 (KN 1): 1 fragmentary specimen and a valve; NK 398'89 (NK 103): 1 specimen (type). **MCA:** RG 16.575: Kazinga, Site C, fragment with posterior spine.

Distribution. Kazinga - Bushabwanyama area (L. Edward, Uganda); Nkondo area (L. Albert, Uganda).

Description. Relatively small equivalve and strongly inequilateral shell. Height about half the length, diameter without the spines about 2/3 of the height. Beak narrow and protruding slightly above the dorsal margin, positioned far forward, the anterior end being contained about 4.5 times in the total length. Dorsal posterior margin straight and slightly raised. The posterior margin is produced and bluntly pointed at the middle of the shell. A faint posterior ridge runs from the beak to the upper part of the posterior end. Ventral margin straight, subparallel with the dorsal one. Anterior end regularly curved. Ornamentation consisting of a ridge that starts about halfway along the upper part of the posterior side, becoming broader and higher while descending towards the posterior point and detaching itself from the shell as a curved hollow tubercle, open at the ventral side. The part of the shell beyond it is indented. Growth lines regular interrupted by growth wrinkles. Hinge relatively broad posteriorly with irregular but well-developed teeth. Hinge plate below the beak and in the anterior part rather narrow with faint teeth.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|--------------|
| Holotype | 50.2 | 24.0 | 18.1 | NK 398'98 |

Type locality. Site NK 103 of Pickford *et al.*, (1993), Nkondo area, L. Albert, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition, 1988-1993).

Stratigraphy and age. Kazinga Fm, Nkondo Fm (Late Miocene – Early Pliocene, Molluscan Association G3b-c).

Etymology. *atrox* (Latin) meaning cruel.

Remarks. The type specimen is small, perhaps not fully grown. The fragmentary larger shells from Kazinga (from site KN of Pickford *et al.*, 1993 and Site C of Gautier, 1970a) indicate that *Iridina atrox* reached a length of *ca* 75 to 80 mm, which is still small for an iridinid. This species, considered by us to be an endemic of Palaeolake Obweruka, was confined to the same period as *Iridina wasai*, from which it evolved. The only functional explanation we can propose for the curved tubular extensions on both sides of the animal is that they acted as a defence against predators. In a live position these spines must have been hidden just below the surface and hence their utility for better anchorage would have been minimal. Freshwater clams with such type of spines are extremely rare. *Iridina atrox* is the only known representative among the Iridinidae.

Iridina atrox may have been more common as the limited material listed here suggests since many internal molds of *Iridina* could not be identified to the species level. For example Gautier (1970a) lists from Kazinga Site C four specimens of his '*Pleiodon ovatus*', namely the fragment of *Iridina atrox* with the well-developed spine (RG 16.575) and 'three very doubtful and poorly preserved specimens (RG 16647)', which indeed may well be internal molds of *Iridina atrox*.

Species *Iridina palaeospekii* nov.

Diagnosis. See description.

Holotype. UM: NK 1176'89 (NK 4): 1 specimen.

Distribution. Nkondo area (L. Albert, Uganda).

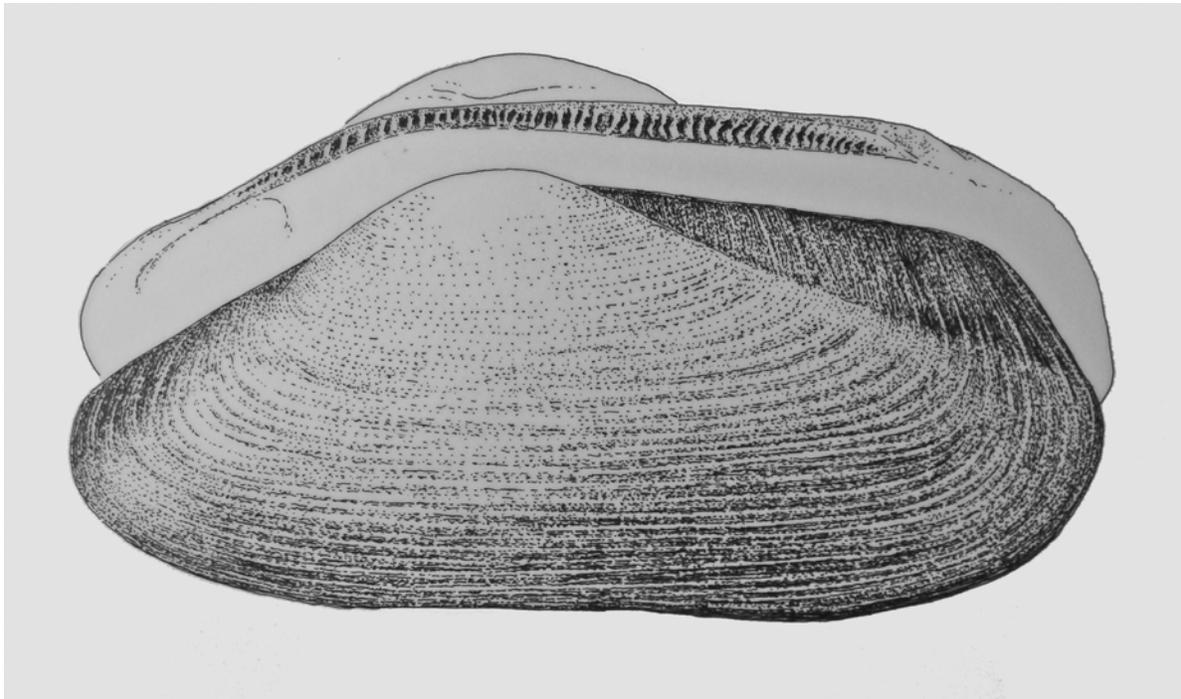


Figure 36. *Iridina palaeospekii* sp. nov. Holotype (L = ca 147 mm).

Description. Very large, markedly inequilateral shell. Length ca 2.5 times the height, height ca 1.4 times the diameter. Beak situated in the anterior 1/3 of the total length, broad and distinctly protruding above the dorsal margin. A broad and rounded ridge runs from the beak to the basal posterior point, the part of the shell above it is somewhat sunken. Dorsal and ventral margins subparallel, dorsal posterior margin straight, ventral margin incurved. Posterior end only slightly produced with a rounded point at the base, the part above the point weakly concave. Anterior end with a broadly rounded point, dorsal anterior margin straight and downward sloping. No visible ornamentation as the shell is partly dissolved. Hinge very similar to extant *Iridina spekii*, posterior part straight with ca 20 well-developed teeth, anterior part curved with only a few well-developed teeth near the beak.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|--------------|
| Holotype | ca 147 | 60 | 44 | NK 1176'89 |

Type locality. Site NK 4 of Pickford *et al.*, (1993), Nkondo area, L. Albert, Uganda (M. Pickford *collevis*, Uganda Palaeontology Expedition 1989-1993).

Stratigraphy and age. Nkondo Formation, Nkondo Member (Late Miocene – Early Pliocene, Molluscan Association G3a).

Etymology. Name refers to the close morphological affiliation with Modern *Iridina spekii* from L. Tanganyika.

Remarks. Only one specimen of this large *Iridina* species was recovered. *Iridina palaeospekii* clearly stands very close to the extant *Iridina spekii*, endemic to L. Tanganyika, and as concerns its dimensions and general shape, resembles closely the outline drawn in Leloup (1950, Fig. 48j) of a specimen of *Iridina spekii* collected at Station 167 (locality: Vua, L. Tanganyika). Although we are not able to exclude that it is conspecific with *Iridina spekii*, we prefer to describe *Iridina palaeospekii* as a distinct species. It differs from the extant *Iridina spekii* by its much longer posterior dorsal margin (about 1.5 times the length of that of *Iridina spekii*), the more basally situated posterior point and the strongly sloping straight anterior dorsal margin, which is curved in *Iridina spekii*. These relatively minor morphological differences may be due to the fact that *Iridina palaeospekii* lived in a fluvial habitat while *Iridina spekii* inhabits a lacustrine environment and must be considered as a relict that is likely derived from a fluvial *Iridina palaeospekii* ancestor with a wide range in the Pliocene.

Genus *Mutela* Scopoli, 1777

Type species. *Mytilus dubius* Gmelin, 1791: 3363 based on the original non-Linnean description of 'le Mutel' by Adanson, 1757: 234, pl. 17, fig. 4. Type locality: Senegal.

Diagnosis. Shell without a wing, with small and smooth areola (Haas, 1969a). See also dichotomous key.

Occurrence. Recently widespread in tropical and subtropical Africa. As fossil known in African deposits since the early Tertiary.

Remarks. Edentate iridinids that are identical in form with Modern *Mutela* are extremely rare in the fossil record. The only confirmed occurrences are from the Upper Cretaceous-Lower Tertiary Nubian Sandstones in Egypt (Newton, 1909), from the Eocene Continental Terminal series in Niger (unpublished material), from the Early Pliocene Ebole Member in the Manonga Basin (Tanzania) (Van Damme & Gautier, 1997) and from Terminal Pliocene to Lower Pleistocene deposits in the Albertine Basin (Uganda) (present paper). It should be stressed that in collections of Albertine bivalve material a substantial percentage of the fossils consists of fragments with the hinge hidden or eroded and that hence *Mutela* may have been overlooked.

As already stated, part of the Modern *Mutela* species with irregular small tuberculi on the hinge plate that are ranged under *Mutela* may actually represent *Iridina* with a strongly reduced pseudotaxodont hinge. Molecular research is necessary to elucidate the relationships between some extant *Mutela* species (e.g. *Mutela bourguignati* and *Mutela alluaudi*), with tuberculi (= reduced teeth?) on the hinge and *Iridina* (see also Van Bocxlaer & Van Damme (2009).

Species *Mutela cf alluaudi* Germain, 1909

Type. *Mutela alluaudi* Germain 1909: 544, pl. 8, fig. 45. Type locality: Lake Albert.

Synonymy

Mutela cf alluaudi (Gautier, 1970a, pp. 119 –120, Pl. IV, fig. 15; Pl. V fig. 1-6).

Material. MCA: RG 16.572 (Wasa-Kisegi, S. Rwebishengo Site 1): 14 specimens, 16 fragments; RG 16.764, RG 16.570 (Wasa-Kisegi, S. Rwebishengo Site 2A): 2 calcareous specimens, 5 limonitised specimens, 28 fragments; RG 16.569 (Wasa-Kisegi, S. Rwebishengo Site W.B.): 3 fragments and 2 specimens; RG 16.769, RG 16.568 (Wasa-Kisegi, N. Behanga II Site 1): 7 specimens and 15 fragments; RG 16.774 (Wasa-Kisegi, N. Behanga II site 2A): 3 specimens; RG 16.772 (Wasa-Kisegi, Behanga II Site 1): 2 specimens; RG 16.770 (Wasa-Kisegi, Behanga II Site 2): 4 specimens and 21 fragments; RG 16.767, RG 16.573 (Wasa-Kisegi, Behanga II Site 3): 1 specimen and 6 fragments; RG 16.768, RG 16.571 (Wasa-Kisegi, Behanga II Site 4): 6 specimens and 18 fragments; RG 16.771 (Wasa-Kisegi, Behanga II Site 5): 1 fragment; RG 16.773 (Wasa-Kisegi, N. Behanga I Site 2): 1 fragment. **LPG:** P 2103, Wasa Kisegi, Site 2A, S. Rwebishengo: 5 specimens.

Distribution. Wasa–Kisegi area (Toro region, Uganda).

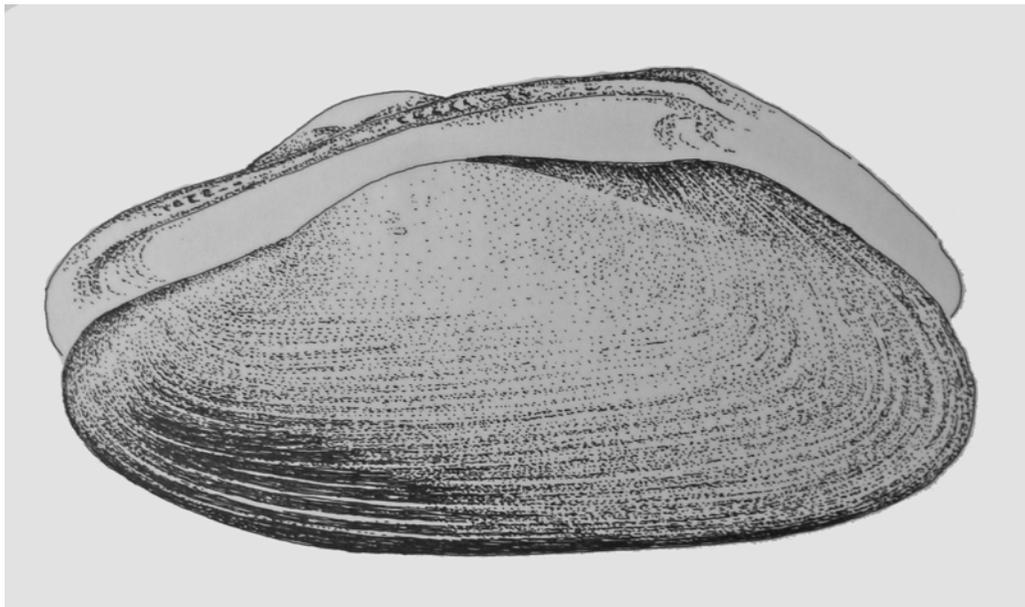


Figure 37. *Mutela cf alluaudi* Germain, 1909 (L = ca 56 mm) from the site ‘S. Rwebishengo 1’.

Description of the fossil material (specimen RG 16775). 'Relatively small inequilateral equivalve shell; probably rather delicate; dorsal margin straight; prosogyre and faintly prominent umbones situated between two thirds and half of the length from the anterior end; anterior end broadly rounded; dorsal and ventral margin slightly to strongly divergent (rostrate) towards the posterior end; oblique posterior end meets ventral margin in a rounded angle; hinge without teeth although probably some faint tuberculi may be present (cf *S. Rwebishengo* Site 1); length about twice the height, height about 1.5 times the diameter' (Gautier, 1970a).

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------------------------|--------|--------|----------|--------------|
| S. Rwebishengo 1 Holotype | + 56 | + 30 | + 17 | RG 16775 |
| S. Rwebishengo 2A | + 81 | + 40 | - | RG 16764 |
| S. Rwebishengo WB | + 61 | + 28 | + 19 | RG 11765 |
| Behanga II 3 | + 59 | + 28 | + 18 | RG 11767 |
| Behanga II 4 | + 70 | + 37 | +23 | RG 11571 |

Stratigraphy and age. Nyabusosi Formation, Lower Pleistocene, Molluscan Association G6.

Remarks. This species is placed by us in the genus *Mutela* instead of *Iridina* even though it possess some tuberculi on the hinge. This is because it is nearly identical to Modern *Mutela alluaudi* Germain, 1909, from Lake Albert and to *Mutela bourguignati* Bourguignat, 1885, from Lake Victoria. These Modern species are considered to belong to *Mutela*, although as Graf & Cummings (2007b) state: 'both share conspicuous pseudotaxodont hinge dentition'. We therefore maintain the present generic status for this fossil species that morphologically stands closest to *Mutela alluaudi* but may represent the ancestral lineage of both *Mutela alluaudi* and *Mutela bourguignati* (hence the cf).

In the Albertine deposits this species is confined to the Wasa Kizegi region, either in monotypic associations or with *Etheria elliptica*. The material described by Gautier (1970a) from Makoga (Wasa Kisege) has been omitted because it cannot be identified. There are no indications of a lacustrine environment during the time of deposition and it is likely that these shells lived in a fluvio-paludal or unstable lake environment that succeeded Palaeolake Kaiso.

Species *Mutela dubia* (Gmelin, 1791)

Type. *Mytilus dubius* Gmelin, 1791. Type locality: fresh water lakes from the interior of Senegal.

Synonymy

Mutela sp. (partim) (Adam, 1955, pp. 37, 46, 89, 90, 94).

Mutela sp. (partim) (Adam, 1957, p. 133-134).

Mutela nilotica? (Gautier, 1970a, p. 122, Pl. IV, fig. 14).

Mutela nilotica (?partim) (Williamson, 1990, p. 128).

Material. **BNS:** part of the material from the site ‘Senga, in front of the Kasaka, 1.0 to 3.6 m from the river’. **MCA:** RG 16566: Wasa-Kisegi, Behanga II, Site 5, one fragmentary elongated valve. **LPG:** P4702, ridge at Katanda, downstream: fragments and 2 molds in block of ferruginous sandstone.

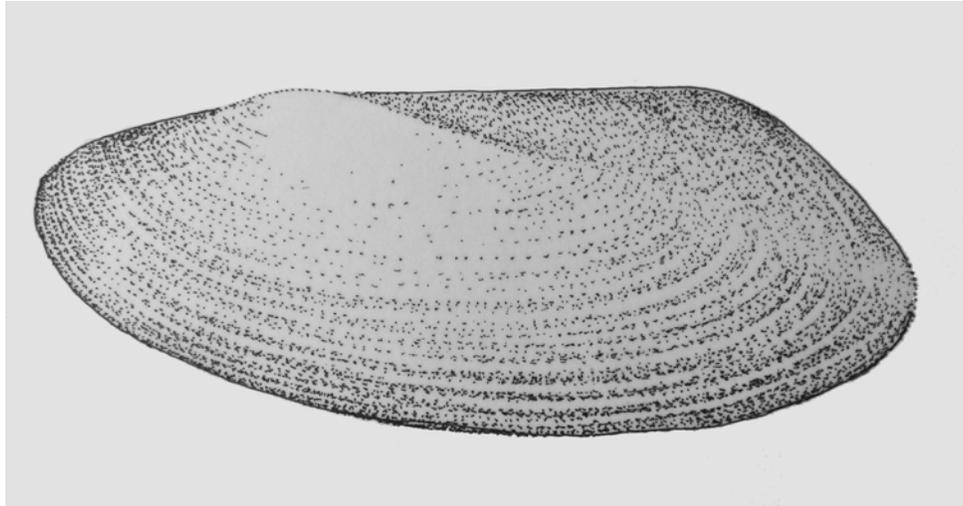


Figure 38. *Mutela dubia* (Gmelin, 1791) (L = ca 102 mm). Specimen P 4702 from the site ‘Ridge at Katanda’.

Distribution. Upper Semliki - Ishango area, (L. Edward, Congo); Kisegi area (Toro region, Uganda)

Description of fossil material (*specimen P 4702*). Medium sized, rather thin, equivalve and strongly inequilateral iridiniid. Length about 2.4 times the height, height about 1.8 times the diameter. Beak situated near the anterior one fourth of the length, low, not or hardly protruding above the dorsal margin. Dorsal posterior margin straight and slightly raised, posterior end with a blunt angulation at the base, a broad rounded ridge running from the beak to this posterior angle. Ventral margin regularly and weakly curved. Anterior end rounded. Anterior dorsal margin straight and level with the dorsal posterior margin. Ornamentation consisting of irregular growth lines. Hinge edentate.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------------|--------|--------|----------|--------------|
| Ridge at Katanda | ca 102 | 43 | 24 | P 4702 |
| Behanga II 5 | ca 105 | 47 | - | RG 16566 |

Stratigraphy and age. Lusso Formation (L II & L III), Nyabusosi Formation. Terminal Pliocene-Early Pleistocene, Molluscan Association GX’ and G6.

Remarks. The material at our disposition is limited and fragmentary. According to the currently used taxonomy it should be attributed to *Mutela dubia*, into which it is here placed with some reservations considering the present taxonomic chaos that the *Mutela dubia* ‘clade’ is in.

Mandahl-Barth (1988) and Daget (1998) considered *Mutela dubia* to be a species with a wide distribution that can be subdivided into three or four geographical races, namely *Mutela dubia dubia* (Gmelin, 1791) (western Congo Basin, Chad Basin, West Africa), *Mutela dubia nilotica* (Cailliaud, 1823) (Nile Basin), *Mutela emini* Martens, 1897 (L. Albert) and possibly *Mutela garambae* Pilsbry & Bequaert, 1927 (eastern Congo Basin, Lualaba). This lumping is in our opinion incorrect and future molecular and morphological research may show that *emini* (to which the fossil material compares best) and *garambae* are distinct from *dubia* and *nilotica* (see also comments by Graf & Cummings, 2007c). Williamson (1990) recorded *Mutela nilotica* from deposits ranging through the Middle and Upper Lusso Formation and the Lower Semliki Formation (Sites Katanda 3, 12, 13, Senga 1, 5, 6, Senga 13, Senga 15, Senga 16, Kanyavughorwe 6, Tshibiridi 7, Kishishio 2, Mupanda 1B/3 and Mupanda 4 of Verniers & de Heinzelin, 1990), and considered the Albertine irididids, respectively described by former authors as *Mutela nilotica* (= *Mutela dubia*, *ibi*), *Mutela alluaudi* (= *Mutela cf alluaudi*, *ibi*) and *Mutela alata* (= *Pteromutela cummingsi*, *ibi*), all to belong to the same species. This view has not been shared in this study. It is here concluded that most of Williamson's material pertains to the same species, which is here provisionally identified as *Mutela dubia*. These differences in taxonomic interpretation are of no importance to the biozonation and evolutionary history presented here, since there is general agreement that anodont naiads of the genus *Mutela* only appear in the Albertine Basin in Late Pliocene-Early Pleistocene times, after Palaeolake Obweruka had split up into Palaeolakes Kaiso and Lusso and a process of intrabasinal evolution was replaced by one of pulses of extra-basinal invasions.

Species ?*Mutela nyamaviensis* nov.

Diagnosis. See description.

Holotype. MC 2433 Nyamavi N° 466 (Lep. 466) N. of Nyamavi Camp, see figure of ? *Mutela alata* in Adam (1959, Pl. X, Fig. 4).

Synonymy

Mutela sp. (partim) (Adam, 1955, pp. 37, 46, 89, 90, 94).

?*Mutela alata* (partim) (Adam, 1959, pp. 61-62, Pl.X, figs 4-6).

Mutela nilotica (partim) (Williamson, 1990, p. 128).

Material. MCA: Holotype and MC 2411: Nyamavi Camp (Lep 464/III) Nyamavi N° 68: 1 incomplete specimen; MC 2686: Mohari Sinda N° 555 (L 186), between Sinda and Ndira: 2 incomplete specimens.

Distribution. Nyamavi area (L. Albert, Congo); Sinda-Mohari area (Lower Semliki, Congo).



Figure 39. ?*Mutela nyamaviensis* sp. nov. Holotype with reconstructed anterior part (L = + 62 mm).

Description. Relatively small, thin shelled inequilateral iridimid. Length about 1.5 times the height, height about 2 times the diameter. Beak sharp, small and not extending above the dorsal margin. Dorsal posterior margin slightly raised. Posterior end strongly produced, with a blunt point near the base. The posterior side is divided by a broad and raised fold running from the beak to the posterior point, the part of the posterior side above the fold is slightly convex. Ventral margin regularly and weakly curved. Anterior end unknown. Ornamentation consisting of regular plicae and a heavy, oblique posterior fold. Hinge probably anodont but additional material is needed for a definite opinion.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|---------|----------|--------------|
| Holotype | + 62 | ca 42.5 | ca 21 | MC 2433 |

Type locality. Site Lep. 466, Nyamavi N° 466, north of Nyamavi Camp (L. Albert, Congo) (J. Lepersonne *collevis*, Lepersonne Mission, 1939-1940).

Stratigraphy and age. Upper Nyamavi Beds, Member VI; Sinda Beds, Member C. Terminal Pliocene, Molluscan Association G5a.

Remarks. The fossil material consists of one almost complete shell and the posterior part of 3 specimens. They appear to belong to a small iridimid (estimated maximal length ca 70-80 mm) that resembles somewhat the recent *Mutela carrei* (Putzeys, 1898), presently ranged under *Mutela legumen* (Rochebrune, 1886) (see Graf & Cummings, 2007b). *Mutela carrei* and ?*Mutela nyamaviensis* both bear a posterior ridge. But the ridge is a mere sharp fold in *Mutela carrei* (= *legumen*) while in the fossils it is developed into a broad welt. Adam (1959) placed these small specimens, without any trace of a dorsal wing, together with the large winged iridimids collected at the same sites under ?*Mutela alata* (= *Pteromutela cummingsi*, *ibi*). The fossils belong however to a distinct species that most likely lived in a river adjacent to Palaeolake Kaiso. More material is necessary to establish with certainty that it belongs to the genus *Mutela*. The holotype is not available for the scientific community as it was loaned to Dr. Williamson and after his

death it appears to have been lost.

Genus *Pteromutela* Starobogatov, 1970

Type species. *Mutela hargerii* Smith, 1908: 13, fig. 4. Type locality: Lake Moero.

Diagnosis. Posterior dorsal margin with a wing. See also dichotomous key.

Occurrence. Recently confined to tropical southern Africa, i.e. in the northeastern part of the Zambezi drainage, the Luapula drainage and the Cuanza River (Graf & Cummings, 2007c). As fossil known only from Late Pliocene deposits of the Albertine Basin .

Remarks. We are aware that the presence or absence of a wing in an unionoid may be an ecophenotypic variation, e.g. in function of stream velocity as in the well documented case of the hyriid *Alathyria jacksoni* (Balla & Walker, 1991). However, the ecophenotypic lacustrine morphs of the Modern alate *Mutela* species, *M. alata* and *M. hargerii* do have a relative higher wing than the fluvial morph, but the wing is decidedly present in both phenotypes and is hence a genetically fixed trait. Of the third winged species, *M. wistarmorrisi*, only the fluvial morph is known (Graf & Cummings, 2007b). An additional important argument to consider *Pteromutela* distinctive is the restricted yet well-delineated geographic range Winged, thin-shelled mutelids with an edentulous, blade-like hinge, only occur in the region which is presently or was in the past connected to the Zambezi drainage. The appearance of *Pteromutela* in the Albertine Basin would in that context either be indicative for an invasive pulse from the south/southwest during the Late Pliocene or for a wider range of the genus.

Species *Pteromutela cummingsi* nov.

Diagnosis. See description.

Synonymy

? *Mutela alata* (partim) (Adam, 1959, pp. 61-62, Pl. X, figs 1-6).

Material. MCA: MC 2683, Lep. 550: Mohari-Sinda N° 165, on the plains margin west of the Sinda: fragment of a very large specimen, MC 2686, Lep. 553: Mohari-Sinda N° 171, between Sinda and Ndira: some large specimens; MC 2701, Lep. 554: Mohari-Sinda N° 185, between Sinda and Ndira (ravine of hill N° 171): several fragments and one specimen; MC 2710, Lep. 555: Mohari-Sinda N° 186, between Sinda and Ndira (ravine of hill N° 171): several fragments; ?MC 2496, Coll. Delpierre: Nzebi at the base of the Bogoro escarpment, immediately north of the Kisega (or Kasego), halfway between the Karugamania and the Nyamavi regions: two fragments (no stratigraphical context and dubious identification since the specimens have been lost).

Distribution. Sinda-Mohari area (Semliki Plain, Congo); Nyamavi area (L. Albert, Congo), ?Karugamania area (L. Albert, Congo).

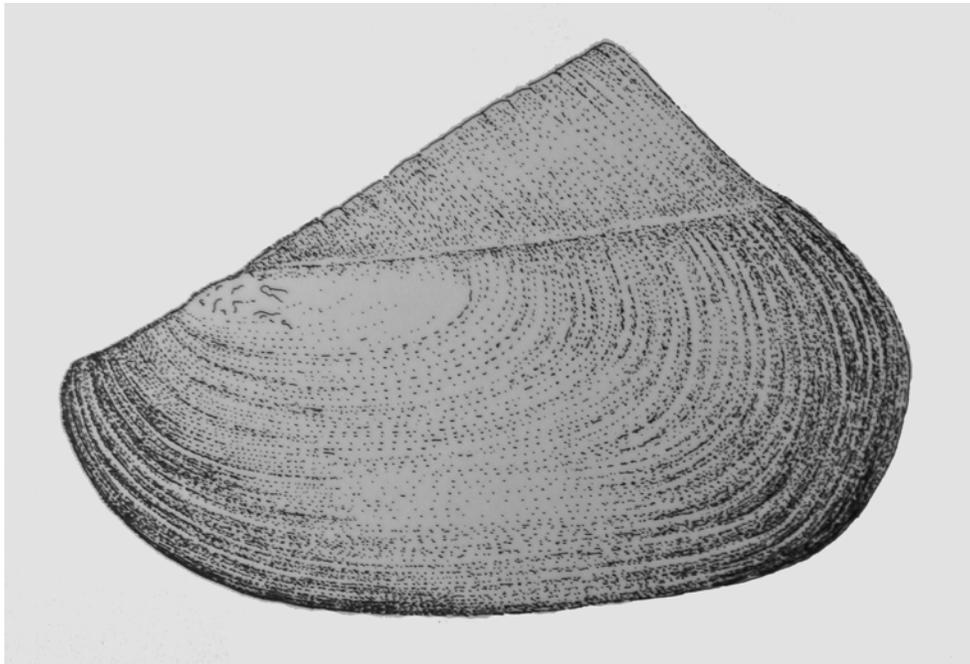


Figure 40. *Pteromutela cummingsi* sp. nov. Holotype, reconstructed (L = ca 135 mm).

Description. Large but very thin, flattened, inequilateral and trapezoidal iridiniid. Length about 1.6 times the height, maximal height about 6 times the diameter. Height of shell at the beak ca 49 mm, greatest length of the shell positioned about 1/3 of the height below the beak. Beak small and low, not projecting above the dorsal margin. Posterior dorsal margin straight and steeply raised, upper posterior part forming a large, flat wing, weakly concave posteriorly and strongly flattened. The fold at the base of the wing runs subparallel to the ventral margin. The posterior end below the wing is produced and broadly and evenly rounded. Ventral margin almost straight. Anterior end short, regularly curving into the ventral margin and straight to weakly concave and downward sloping dorsally. Ornamentation consisting of fine growth lines and irregular plicae, the surface of the shell being glossy. Hinge very narrow and weak, anodont.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|----------|--------|--------|----------|--------------|
| Holotype | ca 135 | + 84 | ca 16 | MC 2686 |

Type. Specimen MC 2686, see ?*Mutela alata* in Adam, (1959, Pl.X, fig. 3).

Type locality. Site L 171 of Lepersonne (1959), Sinda Mohari, between Sinda and Ndira (L. Albert, Congo) (J. Lepersonne *collevis*, Lepersonne Mission, 1939–40).

Stratigraphy and age. Sinda Beds, Member C; Upper Nyamavi Beds, Member VI. Late Pliocene (Molluscan Association G5b).

Etymology. Named in honor of Dr. Kevin Cummings, Illinois Natural History Survey, for his contributions to bivalve phylogeny and taxonomy.

Remarks. This large naiad is only known from a few specimens from the Mohari-Nyamavi region (SW of L. Albert) and no specimen with a complete anterior side has been preserved. Adam (1959) erroneously identified the fossils as ?*Mutela alata* (Lea, 1864). This endemic of Lake Malawi – Lake Malombe is characterized by a relatively thick and heavy shell and the winged lacustrine form reaches a maximal length and height of 94 x 54 mm (Mandahl-Barth, 1988). The Albertine specimens differ from *Mutela alata* by their much larger size, smaller diameter and very thin shell. The only other known iridiniid with a marked wing is *Mutela hargerii* (Smith, 1908) from the Lake Mweru-Bangweulu Basin (Congo). Its dimensions given by Pilsbry & Bequaert (1927) are 91 x 55 x 13 mm with a height at the beaks of 26 mm. *Pteromutela cummingsi* resembles *Pteromutela hargerii* by the thin shell and small diameter but it is about a third larger and the height of the shell below the wing is considerably greater. The occurrence of a winged iridiniid in the northeastern part of the Congo drainage system indicates that winged *Mutela* species, presently confined to the latitude of the Zambesi region, extended during the Late Pliocene throughout the Congo system. Since *Pteromutela cummingsi* is a fluvial species, as are *Pteromutela hargerii* and *Pteromutela wistarmorrisi* (Graf & Cummings, 2007b), the posterior wing cannot be considered to be an ecophenotypic adaptation to environmental conditions. The suggestion of Graf & Cummings (2006b) that within the present genus *Mutela* some species groups may merit generic distinction, e.g. *Pteromutela* Starobogatov, 1970, for the group of winged *Mutela* species, has here been further elaborated.

Finally it should be pointed out that the stratigraphic position of *Pteromutela cummingsi* is somewhat uncertain. It is confined to the Sinda-Mohari/Nyamavi region, i.e. to the northern sub-basin, where it is found in sites co-occurring with *Neothauma adami* and *Neothauma edwardianum* according to Lepersonne (1970), implying an age of 3.5 to 3.0 Ma (Van Damme & Pickford, 1999). During his mission in 1939-1940, Lepersonne and his team only made surface collections over quite extensive areas (Gautier, pers. comm., 2010). In view of the differences in the type of fossilisation of the material from these sites (from limonite in oolitic matrix to calcium carbonate in ochre coloured ferruginous silt), these fossils may be from different strata and *Pteromutela cummingsi* may be somewhat younger (ca 2.5 Ma) than the viviparids mentioned above.

Genus *Aspatharia* Bourguignat, 1885

Type species. *Anodonta rugifera* Dunker, 1858: 225. Type locality: Como River, Gabon.

Diagnosis. See dichotomous key.

Occurrence. At present the representatives of this genus are mainly confined to West Africa and the Congo Basin with the highest diversity in West Africa. This distribution also seems to have been the case in the past, since *Aspatharia* is very rare in East and Central African fossil deposits.

Remarks. The oldest but unconfirmed record of this genus or an ancestral taxon may be *Unio crossthaitei* Newton, 1909, described from the Early Cretaceous Nubian Sandstone Series in Aswan (Egypt) (Newton, 1909) and from the Lower Cretaceous Continental Intercalaire Series at Fort Flatters (Algeria) as '*Unio crossthaitei*' (genus indet.) by Mongin (1963). The latter author states that, although the hinge is not visible, '*it appears to show the presence of an extensive ligamentary surface and a long, sharp posterior hinge plate*'. The general shape, size,

the thick shell and the presence of vertical striae also point to *Aspatharia* according to Mongin. Modell (*in litt.* in Mongin, 1963) ranges this species together with the specimens from the Continental Intercalaire Series in Niger, described as *Unio planus* Roemer, 1836, by Mongin (1963), in the subfamily Aspathariinae Modell, 1942.

The oldest certain record of the genus is from Lower Pliocene deposits of the Mursi and Kanapoi Formations (*ca* 4.1 Ma) in the Lake Turkana Basin (Van Damme, 1976, Van Bocxlaer & Van Damme, 2009).

Species *Aspatharia pfeifferiana* (Bernardi, 1860)

Type. *Margaritana pfeifferiana* Bernardi, 1860. *Terra typica*: Gabon.

Synonymy

Aspatharia ?sinuata (Adam, 1959, pp. 58, Pl.VII, fig. 5).

Material. MCA: MC 2471 (Lep. 484): Nyamavi N° 75, Nyagomba river, 1 bivalve specimen.

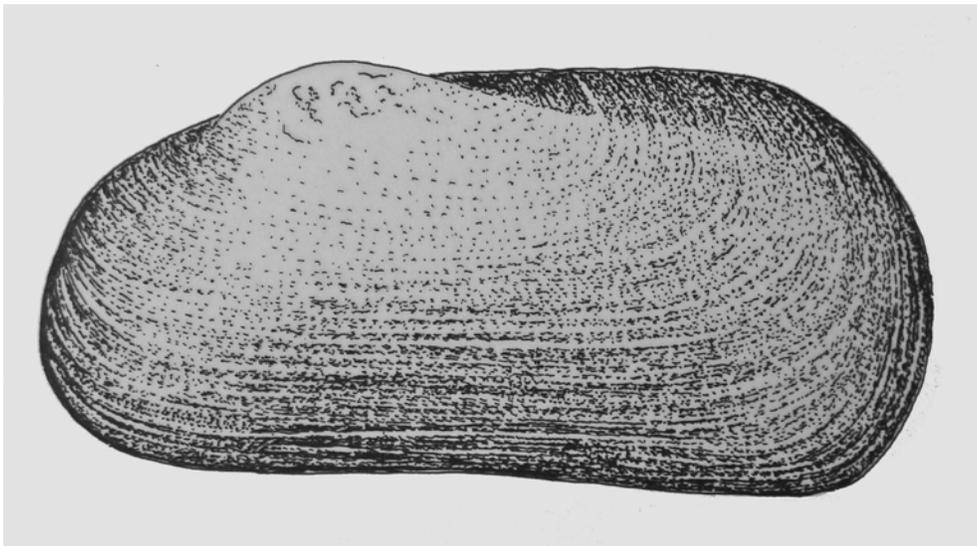


Figure 41. *Aspatharia pfeifferiana* (Bernardi, 1860). Specimen MC 2471 from Nyamavi N° 75 (L = *ca* 72 mm).

Distribution. Nyamavi area (L. Albert, Congo).

Description of the fossil material (*specimen MC 2471*) Shell trapezoidal and inequilateral, relatively thin and small for an *Aspatharia*. Length about 2 times the height, height about 1.5 times the diameter. The anteriorly situated beaks are broad and low, scarcely projecting above the hinge line. Posterior margin slightly elevated above the beak and almost straight. Posterior end produced into a rounded point in the basal part. Ventral margin clearly incurved. Dorsal end short and rounded with the anterior dorsal margin strongly downward sloping. The surface of the shell is covered with fine regular growth lines and is concentrically plicatulate.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|---------------|--------|--------|----------|--------------|
| Nyamavi N° 75 | ca 72 | 35 | 22 | MC 2741 |

Stratigraphy and age. Upper Nyamavi Beds, Member V or VI, Late Pliocene, Molluscan Association G5a.

Remarks. Adam (1959) identified this specimen with hesitation as the extant *Aspatharia sinuata* (Martens, 1883) from which it indeed cannot be distinguished morphologically. But *Aspatharia sinuata* was considered by Mandahl-Barth (1988) to be probably synonymous with *Aspatharia pfeifferiana*. Typical *sinuata* shells are only found in southern (Shaba Province) and eastern Congo (L. Albert region and the Albert Nile), while the range of *Aspatharia pfeifferiana* (*sensu* Mandahl-Barth, 1988) covers the entire Chad-Chari and Congo Basin, the Okavango and South Zimbabwe. Modern *Aspatharia sinuata* mainly differs from *Aspatharia pfeifferiana* by the stronger ventral incurvation and the lower beak. These characteristics are clearly present in the fossil specimen, and their persistence through time constitutes an argument for the distinctiveness of *Aspatharia sinuata*. For a definite opinion more fossil material is needed. Some authors consider *Aspatharia pfeifferiana* to be conspecific with *Aspatharia dahomeyensis* (Lea, 1859), a widespread West African species (see Daget, 1998 for discussion). On the basis of extant material at our disposal it seems to us however that *Aspatharia pfeifferiana* and *Aspatharia dahomeyensis* are two quite distinct species. We agree with Graf & Cummings (2006b, 2007c) that Modern *Aspatharia pfeifferiana* is best regarded as a ‘species complex’.

The single Albertine fossil comes from the northern basin and co-occurs with *Neothauma adami*, which in this basin is a marker for Molluscan Association G5a, i.e. Late Palaeolake Obweruka times. It is safe to assume that *Aspatharia pfeifferiana* was an inhabitant of surrounding swamps or tributaries of Palaeolake Obweruka but did not live in the lake proper.

Genus *Chambardia* Servain, 1890

Type species. *Chambardia letourneuxi* Servain, 1890: 307; pl. 7; fig. 1-2. Type locality: Old Nile bed near Ramses. Lower Egypt.

Diagnosis. See dichotomous key.

Occurrence. At present the representatives of this genus are spread throughout subtropical Africa, with the centre of diversification in Eastern Africa. Possibly present in the Cretaceous - Lower Tertiary deposits of Egypt and Niger (see under *Aspatharia*). The earliest confirmed occurrence is in the Middle Miocene Mohari Formation (Albertine Basin, Congo).

Remarks. The genus *Aspatharia* was formerly subdivided on the basis of anatomical and conchological characteristics into two subgenera, namely *Aspatharia* Bourguignat, 1885, and *Spathopsis* Simpson, 1900 (see Pilsbry & Bequaert, 1927), which were subsequently elevated to generic rank (Daget, 1961). The name *Chambardia* (*ex* Bourguignat) Servain, 1890, however has precedence over *Spathopsis* (see Daget, 1998).

Species *Chambardia triangulata* (Gautier, 1965)

Synonymy

Caelatura sp. (Verdcourt, 1963, p.30, fig. 62).

Aspatharia ? *wissmanni* (partim) (Adam, 1959, pp. 7, 8, 130, 151).

Aspatharia triangulata (Gautier, 1965, pp. 136-138, Pl. III, figs 8a-b, 9; Pl.IV, figs. 1-3).

Aspatharia ? *wissmanni* (Gautier, 1965, pp. 135-136, Pl. III, fig. 7).

Aspatharia ? *triangulata* (Gautier & Van Damme, 1973, pp. 48-49, Pl. I, fig. 11; Pl. II, figs. 3-7).

Material. UM: NK 2238'89 (NK 120): 1 specimen (?), KI 24'92 (KI 9): 5 specimens some flattened; KI 46'92 (KI 5): 1 mold; **MCA:** RG 11783-85 (Sinda-Mohari, Site 13): about 80 valves and 200 fragments; RG 11782: 2 doublets and fragments of large shells (Coll. Lepersonne); MC 2299, Lep. 446/I: Karugamania N° 48, outcrop on the base of the escarpment of Bogoro, Lower Miocene of the Karugamania: fragment.

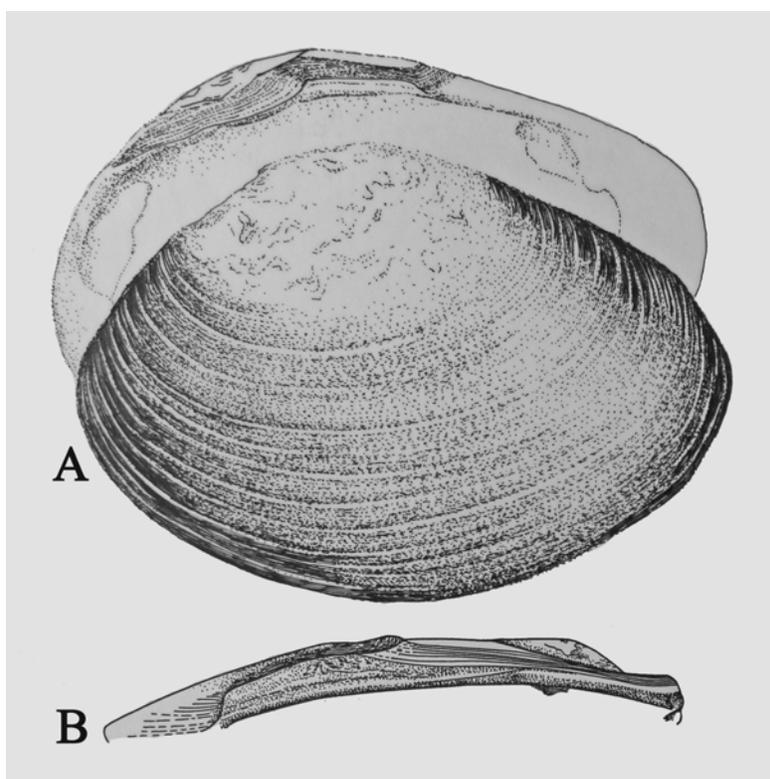


Figure 42. *Chambardia triangulata* (Gautier, 1965). A) Holotype (L = 32.1 mm). B) Details of the hinge (from Gautier & Van Damme, 1973).

Distribution. Kisegi area (Toro region, Uganda); Sinda-Mohari area (Semliki Plain, Congo) (A. Gautier *collevis*, Ganda-Congo Expedition, 1960).

Description. 'Equivalve shell with height about two thirds of the length, thickness about two thirds of the height. The general shape is trigonal with a subelliptical anterior end, ventral margin slightly curved. The prosogyre umbones are heavy and situated at about one third from the anterior end. The posterior end is more pointed. The slightly curved hinge plate is normally

rather broad with an anterior sinus and bears a lamellate, elongate thickening on the left valve. This thickening fits in under the less developed right valve's hinge plate. A marked ligamental groove (fossette) exists behind the umbones. The beaks show a V-shaped corrugation (cf Pilsbry & Bequaert, 1927, p. 412, subgenus *Aspatharia*). (Gautier, 1965, p. 137).

To this must be added that the H/L and D/H ratios given pertain to the dwarfed Mohari form, in which the length is about 1.5 times the height and the height about 1.6 times the diameter. In the large Kisegi form the length is 1.3 times the height and the height 1.8 times the diameter.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|-------------|--------|--------|----------|--------------|
| Holotype | 32.1 | 22.0 | 13.6 | RG 11783 |
| Paratype A | 28.6 | 18.2 | 11.6 | RG 11784 |
| Paratype B | 24.4 | 17.4 | 11.6 | RG 11785 |
| Kisegi KI 9 | ca 71 | ca 55 | + 31 | KI 24'92 |
| Kisegi KI 9 | 55.5 | 44.5 | 26.2 | KI 24'92 |
| Kisegi KI 5 | 41.2 | 36.0 | 22.3 | KI 46'92 |

Type locality. Mohari, Site 13 of Gautier (1965), Semliki Plain, Congo (A. Gautier *colleivit*, Ganda-Congo Mission, 1960).

Stratigraphy and age. Mohari Fm & Kisegi Fm, Middle Miocene, Molluscan Association G1.

Remarks. Like many iridinids this species seems to be highly variable in size. The type and paratypes of *Chambardia triangulata* from the Mohari Formation must be considered as adult but dwarfed shells. Larger specimens (arranged by Gautier, 1965 under *Aspatharia ?wissmanni*) occur in the Mohari Fm but only as fragments. In the Kisegi Formation *Chambardia triangulata* grows larger and becomes less triangular and more ovate. The Early Miocene material from Winam (*ex* Kavirondo, Rusinga Island, Kenya) described by Verdcourt (1963, fig. 61) as *Caelatura* sp., also belongs to *Chambardia triangulata*. This species was not a lacustrine form but was apparently widespread in fluvio-paludal biotopes of the Palaeo-Congo drainage during Early and Middle Miocene times. The fragmentary specimen MC 2299 (Lep. 446/I) identified by Adam (1957) as *A. ?wissmanni* is also a *Chambardia triangulata*. Material probably belonging to this species has been collected in the West Nile sector of the Albertine Graben near the Sudan border (see appendix 2).

Species *Chambardia wissmanni* (Martens, 1883)

Type. *Spatha wissmanni* Martens, 1883. *Terra typica*: Lubilash River, Congo.

Synonymy

?Aspatharia rubens wissmanni (Adam, 1955, p. 39).

Aspatharia ? wissmanni (partim) (Adam, 1957, pp. 7, 8, 130, 151, Pl. VI, fig. 9).

Aspatharia ? wissmanni (partim) (Adam, 1959, Pl.VII, fig. 6 & 7).

?Iridina lepersonnei (partim) (Adam, 1959, p. 63, Pl.IX, fig. 3 & 4).

Aspatharia wissmanni (Williamson, 1990, p. 38).

Material. UM: NY 546'87 (NY 14): 1 specimen; NY 108'87 (NY 18): 1 specimen; NY 889'89

(NY 19): 1 specimen; KY 18'90 (KY 1): 1 specimen. **MCA**: MC 2413, Lep. 464/II: Nyamavi N° 68, Nyamavi camp: one right valve; MC 2710, Lep. 555: Mohari-Sinda N° 186, between Sinda and Ndira (ravine of N° 171): 1 large specimen and an internal mold; MC 2299: Karugamania N° 75, Nyangomba River; MC 2664: Mohari-Sinda N° 171, between Sinda and Ndira; MC 2321: Nyamavi N° 467, hill north of Nyamavi Camp. **BNH**: Senga, in front of the Kasaka, 1 m to 3,60 m from the river: numerous specimens; 1000 m downstream of Senga, right bank (L. 317): 3 valves and some fragments.

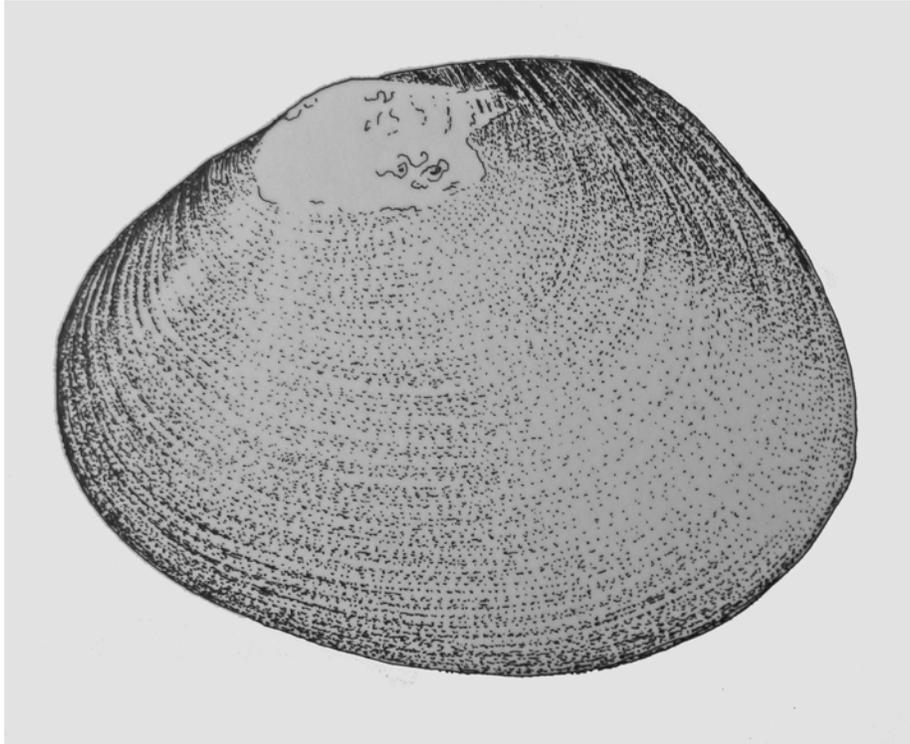


Figure 43. *Chambardia wissmanni* (Martens, 1883). Specimen MC 2710 from Sinda-Mohari between Sinda and Ndira (L = 102 mm).

Distribution. Upper Semliki-Ishango area (L. Edward, Congo); Sinda-Mohari area (Semliki Plain, Congo); Nyaburogo-Nyabusosi area (L. Albert, Uganda); Kyeoro area (Lake Albert, Uganda).

Description of fossil specimen (MC 2710). Shell ovate, equivalve, slightly inequilateral, with the beak situated almost centrally, the posterior part only slightly longer than the anterior part. Beak wide and low, often corroded, only slightly extending above the dorsal margin. Posterior dorsal margin short and almost straight, posterior end obliquely truncate, produced and rounded below. The basal margin is convex with the greatest curvature in the middle, and anteriorly curving upward towards the anterior blunt end. Anterior dorsal margin straight with sharply downward sloping end. The hinge plate is broad but very short, covered with cuticular laminae with the posterior end of the hinge plate abruptly truncated by the deep triangular sinulus, anteriorly identical to that of extant *Chambardia wissmanni*.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|---------------------------------------|--------|--------|----------|--------------|
| Sinda-Mohari, between Sinda and Ndira | 102 | 79 | - | MC 2170 |

Stratigraphy and age. Kyeoro Fm; Nyamavi Beds, Member VI; Sinda Beds, Member B; Upper Nyaburogo Fm; Lusso Fm (LII and LIII). Upper Pliocene–Early Pleistocene, Molluscan Association G5a-c and GX-X’

Remarks. Modern *Chambardia wissmanni* (Martens, 1883) is often considered to be conspecific with *Chambardia rubens* (Lamarck, 1819), but according to Mandahl-Barth (1989) it differs from the latter by the shorter and stronger hinge plate and more ponderous and more regularly oval shell.

The diagnostic characters separating the Modern forms appear to be consistent. But this is not so evident in the fossil material. In the Plio-Pleistocene deposits of the Turkana Basin *Chambardia* populations occur that show characters of both *Chambardia rubens arcuata* and *Chambardia wissmanni* (Van Bocxlaer & Van Damme, 2009). The Albertine fossils closely resemble extant *Chambardia wissmanni*, in particular *Chambardia wissmanni bangalorum* Pilsbry & Bequaert, 1927 (pp. 424-425, text fig. 93), the only difference being that the fossils are usually somewhat smaller, in particular those from the older deposits. Williamson (1990) recorded *Aspatharia wissmanni* from different sites in the Middle and Upper Lusso Formation, which are characterized by the dominance of ‘Nilotic’ elements (*Melanoides tuberculata*, *Corbicula fluminalis*, etc.), namely at sites Katanda 3, Katanda 12, Katanda 13, Senga 1, Kanyavughorwe 6, Tshibiridi 6 and Kishishio 2 of Verniers & de Heinzelin (1990).

Species *Chambardia trapezia* (Martens, 1897)

Type. *Spatha trapezia* Martens, 1897. *Terra typica*: Lake Victoria.

Synonymy

Aspatharia cailliaudi (Gautier, 1970a, pp. 117-119, Pl. IV, figs 9, 10, 12 & 13).
Aspatharia cailliaudi (Williamson, 1990, p. 83).

Material. MCA: MC 2471, Nyamavi N° 75, Nyangomba River (Lep. 484): 1 specimen.

Distribution. Nyamavi area (Lake Albert, Congo).



Figure 44. *Chambardia trapezia* (Martens, 1897). Specimen MC 2471 from Nyamavi (L = ca 72 mm).

Description of fossil specimen (MC 2471). Medium sized, trapezoidal iridiniid. Length about twice the height, height about 1.6 times the diameter. Beaks wide, gibbose, slightly projected and situated anteriorly in the first 1/3 of the shell. Posterior dorsal margin straight and slightly turned upward. Posterior end truncated, the exterior margin convex. Ventral margin markedly incurved in the middle of the length axis. Anterior end regularly but strongly curved and convex, merging dorsally into the short antero-dorsal margin, sloping downwards from the umbo. Ornamentation absent except for irregular growth wrinkles.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|---------------|--------|--------|----------|--------------|
| Nyamavi N° 75 | ca 72 | 35 | 22 | MC 2471 |

Stratigraphy and age. Upper Nyamavi Beds, Member VI or VII; Late Pliocene or Early Pleistocene, Molluscan Association GX or GX’.

Remarks. Gautier (1970a) used the monograph of Mandahl-Barth (1954) on the freshwater molluscs of Uganda as a prime reference for the identification of his fossil naiads. He, and subsequently Williamson (1990), ranged the ellipsoid *Chambardia* fossils under *Aspatharia cailliaudi*, because of the strong morphological similarity with a Modern specimen from Lake Albert, identified as *Aspatharia cailliaudi* by Mandahl-Barth (1954, fig. 79). In his later study on African bivalves, Mandahl-Barth (1988) stated that this identification was erroneous and that the Modern Lake Albert material should be considered as a new subspecies of *S. trapezia*, namely *Spathopsis trapezia ovoidea* Mandahl-Barth, 1988. The Albertine fossil specimen closely resembles the extant nominate subspecies of *Chambardia trapezia*, including the dimensions. This nominate form occurs in Lake Victoria, the Victoria Nile and Lake Kyoga. *Chambardia trapezia* has also been found in the Lower Pliocene Mabaget Fm (Tugen Hills, Kenya) (De Groeve, 2005).

The type of preservation of the Albertine fossil (original shell partly dissolved) and matrix (ferruginous sandy silts) indicates that the species lived mainly in shallow marginal waters such as pools, swamps and small lakes bordering the large palaeolakes. The stratigraphic position of the single fossil is uncertain. Lepersonne (1970) placed it in the Nyamavi Beds VII with a query. It was collected in area Lep. 484 where *Neothauma adami* was also recovered (Lepersonne, 1970), which is a guide fossil in the Lake Albert sub-basin for deposits of Upper Pliocene age, it may hence be from Nyamavi Member VI.

Family Etheriidae Deshayes, 1830

Presently three or four monotypic genera of these sessile irregularly shaped bivalves are recognized within this family, all occurring on fragments of Gondwana (Graf & Cummings, 2006b).

Genus *Etheria* Lamarck, 1807

Type species. *Etheria elliptica* Lamarck, 1807: 401, pl. 29 & 31. Type locality: Indian Ocean.

Diagnosis. Usually shaped like an oyster, surface smooth or with tube-like extensions.

Occurrence. Recently widespread over tropical and subtropical Africa and also on Madagascar. Conspicuously absent from the African fossil record till the end of the Early Miocene (18 Ma) (Van Damme, 1984).

Remarks. The absence in strata predating 18 million years maybe incidental. Since *Etheria elliptica* also occurs on Madagascar (Graf & Cummings, 2009a) it could be postulated that the species invaded Africa from that location, which, in our opinion, is highly unlikely.

Species *Etheria elliptica* Lamarck, 1807

Type: *Etheria elliptica* Lamarck, 1807. *Terra typica*: Indian Ocean (erroneous locality).

Synonymy (pre-Middle Pleistocene material from the Albertine Rift only)

Aetheria elliptica (Cox, 1926, p. 67).

Etheria elliptica (Connolly, 1928, p. 206).

Aetheria elliptica (Fuchs, 1934, pp. 108, 148).

Aetheria sp. (Cahen, 1954, p. 342).

Aetheria elliptica (Adam, 1955, pp. 35, 39, 40, 42, 49, 53, 56, 62, 66, 83-86, 89-90, 94-95, 98, 100, 120).

Etheria elliptica (Adam, 1957, pp. 137-140, Pl. VI, fig. 8).

Etheria elliptica (Adam, 1959, pp. 67-69).

Etheria elliptica (Gautier, 1965, pp. 148-149, Pl. VI, fig. 8, Pl. VIII, fig. 5).

Etheria elliptica (Gautier, 1970a, pp. 134-136, Pl. VIII, figs 5-7).

Etheria elliptica (Gautier & Van Damme, 1973, pp. 134-136, Pl. VIII, figs 5-7).

Etheria elliptica (Williamson, 1990, p. 38).

Material. BMNH: L. 40259-62 (Kaiso), 4 specimens. **BNH** L. 327, Kambukakabale: a few specimens and fragments, Mupanda, L. 328): several fragments; 1000 m east of the river mouth, Lusso: fragments; 1500 m east of the river mouth: fragments; Kanyatsi, lake beach, washed gravel: several rolled fragments, Kanyatsi, inland near the trenches (probably L. 274, L. 274-275, L. 280 and L. 281): several rather large specimens up to 140 mm, some with spines and two fragments (L. 274-275); beach at Nyakasia ravine, about 40 m from the lake (L. 283-285): fragments; Ravine K.9 (L. 292): fragments; Senga, in front of the Kasaka, 1.0 m to 3.6 m from the river: many specimens some 150 mm long, of about the same length and width, some well preserved specimens wearing spines; Ravine east of Kanyatsi (L. 279): one fragment; upstream from Senga, right bank (L. 315): some specimens, one bearing spines; 1000 m east of Ishango, 30 to 40 m from the lake (L. 273 and L. 302): one fragment; Lake beach near Nyakasia ravine, 65 to 80 m from the lake (L. 283): some fragments; (?) Ravine K., 80 to 100 m from the lake (L. 288): several fragments (L.); Head of the Kiavimara Ravine: one fragment; Track from the barge of Kiavinionge, about 24 m from the river (L. 277): some fragments; large cliffs of Kihandaghati, *Etheria* level: several bleached specimens. **UM:** NY 44°90 (NY 68): 3 specimens; NY 225°90 (NY 30): 1 specimen; NK 2514°89 (NK 60): 1 specimen; NK 2620°89 (NK 28): 1 specimen; NK 577°89 (NK 122): 1 specimen; NK 2466°89 (NK 23): 1 specimen; NK 322°89 (NK 13): 1 specimen; NK 858°89 (NK 74): 1 specimen; NK 1653°89 (NK 38): 1 specimen; NK 563°88 (NK 96): 2 specimens; NK 557°88 (NK 94): fragment; NK 564°88 (NK 97): 10 fragments; NK 848°88 (NK15): 5 rolled specimens; KN 10°88 (KN 2): 22 specimens; KN 90°88 (KN 6): 1 specimen; KN 88°88 (KN 6): 1 specimen; KN 201°88 (KN 8): 1 specimen; KN 2°88 (KN 1): 1 specimen; KN 166°88 (KN 7): 1 specimen. **MCA:** MC 2400, Lep. 464/I: Nyamavi N° 68, camp Nyamavi: well preserved specimen. MC 2404, Lep. 464/II: Nyamavi N° 68, Nyamavi camp: fragments and a good specimen.; RG 11809, Sinda Mohari: a fragmentary specimen; MC 2364, Lep. 464/III: Nyamavi Camp N° 68,: fragments; MC 2413, Lep. 464/III: Nyamavi Camp N° 68: fragments; MC 2357, Lep. 464: Nyamavi Camp N° 68: fragment; MC 2431, Lep. 466 north of Nyamavi Camp: fragments; MC 2432, Lep. 467, north of Nyamavi Camp: 2 large almost circular valves; MC 2433, Lep. 467: north of Nyamavi camp: a few fragments, MC 2435, Lep. 469: Nyamavi N° 58, east flank of the Kaheri: 2 fragments; MC 2453, Lep. 476: Nyamavi N° 63, hill west of the Kaheri: fragments; MC 2312, Lep. 483: Nyamavi N° 75, Nyangomba river: doubtful fragments; MC 2320, Lep. 484: Nyamavi N° 75, Nyangomba River: fragments, one with spines; MC 2469, Lep. 484: Nyamavi N° 75, Nyangomba River: several fragments; MC 2473, Lep. 485: Nyamavi, N° 76, hill west of the Kaheri: 2 fragments one with spines; MC 2474, Lep. 486: Nyamavi N° 76, hills west of the Kaheri: two specimens with spines; MC 2489, Lep. 490: Nyamavi N° 81, at the base of the escarpment: one specimen; MC 2562, Lep. 509: Mohari-Sinda, N° 109, Kalindu: fragments; MC 2569, Lep. 510: Mohari-Sinda N° 107, east flank of the Kalundu: fragments; MC 2677, Lep. 544: Mohari-Sinda N° 162, right bank of the Sinda (downstream): doubtful fragments; MC 2684, Lep. 551: Mohari-Sinda N° 166, on the margin of the plain west from the Sinda: one fragment; MC 2687, Lep. 553: Mohari-Sinda N° 171, between Sinda and Ndira: a few fragments; MC 2694, Lep. 553B: Mohari-Sinda N° 171, between Sinda and Ndira: two specimens with spines and some fragments; MC 2625, Lep. 555: Mohari-Sinda N° 186, between Sinda and Ndira (ravine of N° 171): 2 specimens; MC 2639, Lep. 555: Mohari-Sinda N° 186, between Sinda and Ndira (ravine of N° 171): fragments; MC 2589, Lep. 557: Mohari-Sinda N° 187, south of the Sinda, on the plains margin: fragment; MC 2504, Coll. Delpierre: Mohari-Sinda, Hill 739, left bank of the Sinda (downstream): a block with fragments; RG 16596: Kaiso, Site D: large fragment with obsolete spines; Kaiso, Site 1: 1 complete specimen and 4 fragments; RG 16701: Kaiso, Site 2: 1 specimen; RG 16702: Kaiso Site 3: 1 small fragment; Kaiso, Site I: 2

fragmentary small specimens; RG 16811: Makoga Site G.C.: 5 fragments; RG 16754: Makoga Site A.G.: 1 specimen in ironstone; RG 16799, S. Rwebishengo Site 1: 7 non-limonitized fragments and specimens and 14 limonitized specimens; RG 16800, S. Rwebishengo Site 2A: 10 non-limonitized specimens, RG 16801 S. Rwebishengo, Site WB: 15 limonitized specimens; RG 16810: N. Behanga II, Site 1: 3 fragmentary specimens; RG 16807: N. Behanga II, Site 2A: 3 fragments; RG 16805: N. Behanga II, Site 1: 54 non limonitized fragmentary specimens and 23 limonitized fragments; RG 16803: N. Behanga II, Site 2: 18 calcareous fragments and 48 limonitized fragmentary specimens; RG 16802: N. Behanga II, Site 3: 22 fragmentary specimens; RG 16804 N. Behanga II, Site 4: 3 fragmentary specimens; RG 16808: N. Behanga II, Site 5: 5 fragmentary specimens; RG 16812: N. Nyakabingo I Site 1: one fragmentary specimen; Kazinga Site 3: one small fragment; RG 16651 Kazinga Sites A & C: 1 fragment. **LPG:** P 4695, 250 m N. of Kanyatsi excavation trench (G5b): rolled fragment; P 4696, 55 m N. of Kanyatsi excavation trench (G5b): fragment; P 4703, eastern edge of Mahiga Ravine West (G3): 1 specimen and a fragment, 1000 m; P 4704, eastern edge of Mahiga Ravine West, 10-23 m lower (G3): fragments; P 4727, Nyakasia-Kakungu, 937 m (G3): fragment; P 745c, Mupanda, 1 m above the Semliki (MP_B) G5a: a few rolled valves; P 745d, 30-60 m South of Mupanda Gully, 13 m above the Semliki (MP_C) G5a: fragments.

Distribution. Upper Semliki-Ishango area (L. Edward, Congo); Kazinga-Bushabwanyama area (L. Edward, Uganda); Sinda-Mohari area (Semliki Plain, Congo); Wasa-Kisegi area (Toro, Uganda); Nkondo area (L. Albert, Uganda); Nyaburogo-Nyabusosi area (L. Albert, Uganda); Kaiso Village-Hohwa area (Lake Albert, Uganda); Nyamavi area (Lake Albert, Congo).

Stratigraphy and age. Mohari Fm, Nyakabingo Fm, Kagusa Beds, Nkondo Fm, Warwire Fm, Lusso Fm (LI-LIII) (see also Williamson, 1990), Semliki Fm, Nyamavi Beds, Senga Beds. Middle Miocene to Upper Pleistocene, Molluscan Associations G1 to G7.

Remarks. Williamson (1990) recorded *Etheria elliptica* through the entire range of the Lusso Formation. The *Etheria* material found in the Albertine Basin is highly variable as is typical for this species but all specimens recovered are relatively small (100-150 mm) and rounded to ovate. They have either a flattened side indicating that they adhered to stones, other *Etheria* shells or tree roots (similar to extant specimens from Lake Victoria) or both sides are convex with spines. This non-adnate form, originally described as *Etheria elliptica* forma *tubifera* Sowerby, 1825, is relatively common and must have lived in the Albertine palaeolakes. Most *Etheria* shells of the adnate form show wear from being rolled during transport and were probably carried into the lakes by flowing water. The very large elongated specimens, reaching 250 mm or more, such as found in fluvio-lacustrine deposits of the Turkana Basin (Van Damme, 1976) and indicative of the presence of *Etheria* reefs are absent in the Western Rift deposits. Although *Etheria* is found throughout the known fossil record of the Albertine Basin, its frequency rate differs strongly in time. While being virtually absent from the Middle to Late Miocene deposits (one single rolled fragment in the Mohari Fm), it becomes gradually more abundant from the Early Pliocene onward and is most abundant in the Late Pliocene-Early Pleistocene deposits. The geographic distribution of this species in the basin is also irregular. It is most frequent in the Nyamavi-Sinda-Mohari region on the Congo side of the Albertine Basin, which is indicative of the presence of a large estuary or estuaries in that region. It is absent from the Kyeoro area.

Subclass Heterodonta Neumayr, 1884
Order Veneroida H. Adams & A. Adams, 1856
Superfamily Corbiculacea Gray, 1847
Family Corbiculidae Gray, 1847
Genus *Corbicula* Megerle von Mühlfeld, 1811

Type species. Megerle von Mühlfeld; 1811: 56 with *Corbicula fluminalis* (Müller, 1774) as type by monotypy and original designation. Type locality: Euphrates.

Diagnosis. Triangular shells with concentric growth rings and hinge teeth below the umbo.

Occurrence. At present distributed all over Africa, most of Eurasia and N. America (often transported by Man). Appears in the African fossil record at about 2.6 Ma.

Remarks. The taxonomic status of the African *Corbicula* species has been called an extraordinary tangle by Connolly (1939). A recent anatomical and molecular study (Korniushin, 2004) on Asian and African representatives of the genus has shown that the *Corbicula* populations occurring in the Nile Basin, western Africa and part of the Congo Basin, are genetically not distinct from the Asiatic *Corbicula fluminalis*. Korniushin therefore rejected *Corbicula consobrina* (Cailliaud, 1827) and *Corbicula fluminalis consobrina*, the names commonly used for *Corbicula* populations north of the equator (Daget, 1998) as invalid. The author did recognize *Corbicula fluminalis africana* (Krauss, 1848) as genetically distinct but geographically confined to southeastern Africa. The fossil Albertine material should thus be identified as *Corbicula fluminalis* and not as *Corbicula consobrina*.

Species *Corbicula fluminalis* (Müller, 1774)

Type. *Tellina fluminalis* Müller, 1774. *Terra typica*: Euphrates River.



Figure 45. *Corbicula fluminalis* (Müller, 1774). Specimen RG 16600 from Kaiso (L = 11 mm).

Synonymy (Pre-Holocene material from the Albertine Basin only).
Corbicula consobrina (Adam, 1955, pp. 36, 39, 65, 66, 84, 96, 100, 118).

Corbicula consobrina (Adam, 1957, pp. 140-145, Pl. VI, fig. 10; Pl. VII figs 7-9).

Corbicula consobrina (partim) (Adam, 1959, pp. 69-70).

Corbicula consobrina (Gautier, 1965, pp. 137-138, Pl. VII, figs. 9-12).

Corbicula consobrina (Williamson, 1990, p. 38).

Material. **MCA:** RG 16.680 (Kaiso, Site F): several molds on gravelly ironstone blocks; RG 16.600 (=RG 16.703) (Kaiso surface between E and F): 1 specimen; RG 16.814, RG 16.599, RG 16.599 bis (Wasa-Kisegi, Makoga Site A.G.): 7 molds on pisolithic ironstone; RG 16.816 (Wasa-Kisegi, N. Behanga II Site 2B): 1 specimen and 1 doubtful specimen; RG 16.704 (Wasa-Kisegi, N. Behanga I Site 1A): 1 damaged specimen in slag-like ironstone; RG 16.816 (Wasa-Kisegi, N. Behanga I Site 1B): 1 poorly preserved specimen. **UM:** KS 36'86 (Kaiso A): 1 specimen. **BNH:** Senga, in front of the Kasaka, 1.0 to 3.6 m from the river: 1 valve; L 279, Ravine east of Kanyatsi (L. 279): a small valve; upstream of the ford at Katanda, right bank: a few internal molds; (?) downstream of Katanda, right bank (L 312): a ferruginous block with several internal molds and imprints. **LPG:** P 4692, Kanyatsi Ravine, western slope, 940 m (G5b): 1 specimen; P 4693; Kanyatsi Ravine, western slope, 937 m (G5b): 1 specimen; P 4701, Crest at Katanda, downstream (G5b): several specimens in block of ferruginous sandstone; P 4702, Crest at Katanda, downstream (G5b): idem.

Distribution. Upper Semliki-Ishango area (L. Edward, Congo); Kaiso Village-Hohwa area (Lake Albert, Uganda); Wasa-Kisegi area (L. Albert, Uganda).

Description. The fossil specimens are small, almost equilateral and triangular to rounded triangular with close-set fine concentric ribs.

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------------|--------|--------|----------|--------------|
| Makoga A.G. | 14 | 15.4 | - | RG 16599 |
| Makoga A.G. | ca 20 | ca 19 | - | RG 16599 |
| Kaiso E to F | 11 | 12.5 | - | RG 16600 |
| N. Behanga II/2B | 19.5 | + 20 | ca 18 | RG 16704 |

Stratigraphy and age. Lusso Formation (LII & LIII), Semliki Formation, Kaiso Village Formation, Nyabusosi Formation, Rwebishengo Formation. Late Pliocene to Middle Pleistocene, Molluscan Association G5b, G5c, GX', G6 and G7.

Remarks. The Albertine fossil material is here identified as *Corbicula fluminalis*, following Korniusshin (2004). According to Williamson (1985) the genus first appears in Africa around 3.2 Ma in the Turkana Basin, from which time on it is very common in that basin. However, a revision of the stratigraphy of East Turkana (Brown & Feibel, 1986) and an ongoing PhD study on the Turkana molluscs (see Van Bocxlaer *et al.*, 2008) indicates that the oldest occurrence of *Corbicula* is in deposits of the Lower Burgi Fm about 2.6 - 2.5 Ma. The date of the first invasion of the Albertine Basin by this Asiatic clam is equally situated around 2.5 Ma (Pickford *et al.*, 1993). *Corbicula* is thus a reliable geochronological guide fossil for Late Cenozoic African deposits, its presence indicating that their age is less than 2.6 Ma. At present, *Corbicula* occurs all over Africa with the exception of the West African rivers in the Gulf of Guinea and Lake Tanganyika, the two areas in Africa with ancient Miocene relict faunas. According to Leloup

(1950), *Corbicula* is restricted in the Lake Tanganyika area to the thalwegs of the estuaries and the surrounding waters but is absent in the true lacustrine habitats.

Williamson (1990) recorded *Corbicula* from the Lower Semliki sites Katanda 3, 12, 13, Senga 1, Kanyavughorwe 6, Tshibiridi 7 and Kishishio 2 of Verniers & de Heinzelin (1990). All the 'subfossil' and 'Gamblian' *Corbicula* material mentioned from the Albertine Basin as *Corbicula radiata* by von Martens (1897), Germain (1912, 1916), Pilsbry & Bequaert (1927), Schouteden (1933), Darteville & Schwetz (1947) and Darteville (1948) comes from the Holocene terraces around Lake Edward and is not discussed here. The identifications of *Corbicula consobrina* by Adam (1959; Pl. VIII, fig. 6) from the Lower Semliki deposits pertain to small *Coelatura* shells.

Family Pisidiidae Gray, 1857 (= Sphaeriidae, auctores)
Genus *Eupera* Bourguignat, 1854

Type species. *Pisidium moquinianum* Bourguignat, 1854: 663.

Diagnosis. Small ovate shells with relatively small protruding umbo.

Occurrence. Tropical and subtropical Africa. The oldest fossil known from Africa is from the Late Miocene of the Albertine Basin (present study).

Remarks. Due to its minute size rarely collected.

Species *Eupera* sp. indet.

Material. UM: NK 2236'89 (NK 120): 1 fragmentary specimen.

Distribution. Nkondo area (L. Albert, Uganda).

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|-------------------|--------|--------|----------|--------------|
| Referred specimen | + 4.8 | 3.0 | 2.8 | NK 2236'89 |

Stratigraphy and age. Nyaweiga Member of the Nkondo Formation (Late Miocene-Lower Pliocene, Molluscan Association G3b); Lusso Formation (LIII) and Semliki Formation (*vide* Williamson, 1990), Late Pliocene-Early Pleistocene, Molluscan Association G5c-G6.

Remarks. The single specimen at our disposal lacks part of the posterior side and its hinge is not visible. Identification to the species level is therefore impossible. In size and general appearance it is similar to extant *Eupera ferruginea* (Krauss, 1848), a species found all over Africa. Williamson (1990) recorded *Eupera* sp. from deposits at the top of the Lusso Formation (LIII) and the Lower Semliki Formation, at the sites Katanda 3, 12, 13, Senga 16 and Kanyavughorwe 6.

Genus *Pisidium* Pfeiffer, 1821

Type species. *Tellina amnica* Müller, 1774.

Diagnosis. Small ovate shells with broad umbo

Occurrence. All over Africa and on all other continents. Oldest African fossil known is from the Middle Miocene of the Albertine Basin (present study).

Remarks. Due to its minute size often overlooked. The genus *Pisidium* is under-represented in the Albertine lacustrine deposits due to the fact that most molluscs are preserved in oolitic ironstone, the diameter of the granules being not much smaller than *Pisidium* species. They were thus only fossilized exceptionally, for example in the rare assemblages in which shells have not been decalcified (Mohari Formation and some sites belonging to the Lusso Formation). A second reason for their scarcity in collections is that suitable deposits were not sieved for small shells.

Species *Pisidium (Afropisidium) lepersonnei* Gautier & Van Damme, 1973

Synonymy

Pisidium (Afropisidium) lepersonnei (Gautier & Van Damme, 1973, pp. 51-52, Pl. II, figs. 8-9).

Material. MCA: RG 11805, Sinda Mohari (Lep. 145): one left valve; RG 11806 Sinda Mohari (Lep. 145): one right valve, RG 11807: Sinda Mohari (Lep. 145): two juvenile valves.

Distribution. Sinda-Mohari area (Semliki Plain, Congo).

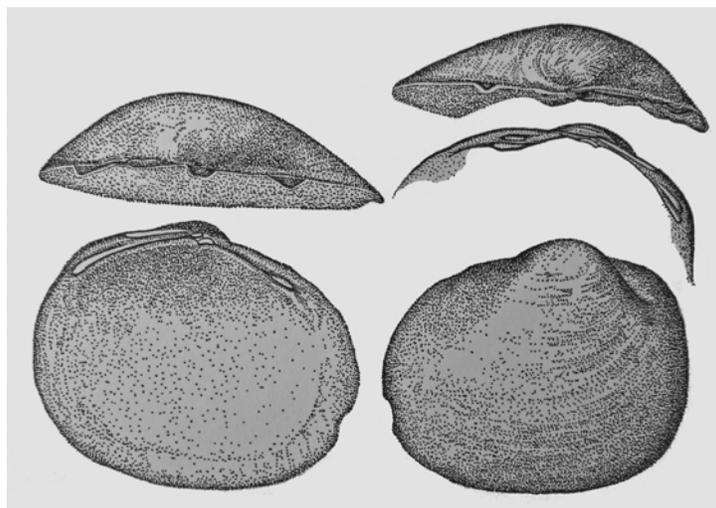


Figure 46. *Pisidium (Afropisidium) lepersonnei* Gautier & Van Damme, 1973. Holotype (L = 2.3 mm) (from Gautier & Van Damme, 1973).

Description. ‘Right valve: shell thin, moderately convex (convexity index: $100 \times D/H = 36$). Dorsal margin rather long (1.5 mm), weakly curved, forming a rounded angle with the anterior and posterior margin, posterior dorsal margin truncate, anterior margin slightly pointed. Greatest length slightly below the middle of the height of the shell. Umbo small, low (only protruding 0.1 mm above the dorsal margin), weakly prosogyre. Sculpture: weak concentric striation.

*Dentition: Right valve: hinge plate long (A1-P1= 1.5 mm), about 3/5 of total length, three times broader at the lateral teeth than in the middle. C3 relatively long (0.2 mm), weakly curved, somewhat thickened posteriorly. Posterior laterals straight, small, parallel, P3 near P1. Anterior laterals weakly curved; A1 long, small, with proximal end curved inward; A3 short but well-developed. Ligament pit large (0.5 mm; $\pm 1/5$ of the shell length) narrow and extrovert on both ends (ligament probably visible in live animal, cf *Pisidium pirothi*) ventrally lined with ligament fold.*

Left valve: Apices of A2 and P2 markedly distally placed (A2-P2 = 1.4 mm); P2 long and straight proximally (towards C3); A2 proximally curved inward. Cardinals C2 and C4 short, both ± 0.1 mm, C4 straight, C2 somewhat angularly curved'. (Kuiper in Gautier & Van Damme, 1973).

Dimensions (in mm)

| | Length | Height | Diameter | Reference N° |
|------------------------|--------|--------|----------|--------------|
| Holotype (left valve) | 2.3 | 1.9 | 0.6 | RG 11805 |
| Paratype (right valve) | 2.3 | ca 1.9 | 0.6 | RG 11806 |

Type locality. Site L. 145 of Lepersonne, Sinda- Mohari (Semliki Plain, Congo) (A. Gautier *collevis*, Ganda-Congo Expedition, 1960).

Stratigraphy and age. Mohari Formation, Middle Miocene, Molluscan Association G1.

Remarks. *Pisidium lepersonnei* lived in the swamps and temporary lakes of Middle Miocene age. The position of the ligament pit is indicative of the subgenus *Afropisidium*, which contrary to the name, has a circum-tropical distribution. *Pisidium lepersonnei* resembles the extant African species *Pisidium pirothi* Jickeli, 1881, but the latter possesses a nepionic shell without concentric striation.

Species *Pisidium* spp. indet

Material. UM: NK 329'89 (NK): 3 specimens of two different species. LPG: P4768: 2 fragmentary valves of two different species.

Stratigraphy and age. Nkondo Formation (Lower Pliocene, Molluscan Association G3a), Lusso Formation (L II) (Terminal Pliocene, Molluscan Association G5b).

Remarks. The shells from the lower Pliocene deposits were found in a block of fine ferruginous bituminous sediment also containing many *Gabiella* specimens and plant remains. This deposit was formed in shallow calm water with a mainly organic bottom. Such deposits probably originated from standing waters bordering Palaeolake Obweruka and not from the palaeolake itself. The terminal Pliocene specimens were found inside the non-decalcified shells of *Neothauma edwardianum* (Adam, 1957). The presence of *Pisidium* in these typically lacustrine shells clearly shows that the genus was present in Palaeolake Lusso. One of the species seems to be closely related to, or identical to, *Pisidium lepersonnei*, being of the same size and possessing the typical prominent external ligament and the excentrically placed beak. The other species is smaller, more ovate and with a more centrally placed beak. In general shape it is reminiscent of

specimens of the *Pisidium viridarium* Kuiper, 1956, - *Pisidium kenianum* Preston, 1911, group. Since the hinge is not visible or is partially destroyed in the fossil specimens, identification is impossible.

DISCUSSION

Historical Reconstruction of the Afrotropical Bivalve Fauna during Late Cenozoic Times

The composition of the dominant unionoid families that lived on the Afro-Indian continent during the Cretaceous, namely Unionidae, Etheriidae, Hyriidae or Iridinidae, still remains in doubt. However, it is certain that the period that the continent was making contact with Laurasia, the bivalve palaeoheterodont fauna was highly diverse, considerably more than at any point during the early and middle Tertiary.

In sharp contrast, the earliest known Tertiary assemblages (Palaeocene to Eocene) are very poor, consisting of Iridinidae only, in which *Pleiodon* was dominant. The fossil evidence shows that the fauna was homogenous over vast distances, occurring from east to west in the region of the Tropic of Capricorn.

Tens of millions of years later, the Early to Middle Miocene assemblages in equatorial Africa (Kenya), still show the same poverty, with *Pleiodon*, *Iridina* (dominant), *Chambardia*, *Aspatharia* (presence uncertain) (Iridinidae) and *Etheria* (Etheriidae) (rare).

Fossils with unionid morphology or dentition remain conspicuously absent. The explanation that the absence of the Unionidae, i.e. an entire family, is due to preservational bias or particular palaeolimnological conditions, has become difficult to maintain in light of the considerable quantity of fossil bearing sites, usually yielding well preserved fossils, including such minute shells as *Pisidium*.

From equatorial Africa, the following geological units (arranged by localities) with fossil bivalves of Early to Miocene age are known: Kulu Fm, Hiwegi Fm, Wayondo Fm (richest association) and Kiahera Fm (Early Miocene, Rusinga Island, L. Victoria, Kenya) (Verdcourt, 1963; Gautier, 1965; Kat, 1987; Van Couvering & Van Couvering, 1976; Van Damme, 1976; Pickford, 1986), Chianda Beds on the Uyoma Peninsula (Early Miocene, L. Victoria, Kenya) (Pickford, 1986), from the Karungu Fm (Early Miocene, Karungu, Kenya) (Pickford, 1986), from the Nyakach Fm (Middle Miocene, Nyakach, Kenya) (Pickford, 1986), from Napak II, VI & VIII (Early Miocene, Napak, Uganda) (Bishop & Whyte, 1962; Pickford, 1986), from the Ngorora Fm (Middle Miocene, Tugen Hills, Kenya) (De Groeve, 2005), the Lower Turkana Basalt (Middle Miocene, Loperot, L. Turkana, Kenya) (Van Damme, 1976, 1984), the Mohari Fm (Middle Miocene, Mohari-Sinda, Congo) (Gautier, 1965, Gautier & Van Damme, 1973, Pickford *et al.*, 1993; this paper) and the Kisege Fm (Middle Miocene, Toro, Uganda) (Pickford *et al.*, 1993; this paper).

Dramatic changes in the molluscan fossil record, in particular the bivalve fauna, started in Africa in the Late Miocene and continued throughout the Pliocene. Although these events are also recorded in other regions such as the Turkana Basin and the Tugen Hills, the main information is stored in the Albertine fossil record. This record's uniqueness resides in the fact that it is so

complete and so long, covering the period from the Late Middle Miocene till the Early Pleistocene (i.e. from about 12 to 1.8 million years, or perhaps as old as 15-18 Ma see Fig. 2). But of equal importance for our understanding of continent-wide events is the fact that the Albertine record contains abundant evidence about the composition and changes in the bivalve community that occurred in the Palaeo-Congo basin *sensu lato*. Since this hydrographic system extended from the region of Tugen Hills - Mount Elgon in the east to the Atlantic Ocean in the west, the Albertine record is representative for most of equatorial Africa.

The faunal changes here described are corroborated by evidence from fossiliferous Terminal Miocene and Pliocene deposits in other parts of Africa, each of which however covers only a fraction of the period preserved in the Albertine record. Of these more fragmentary records, the one of the Turkana Basin is by far the most complete and the best studied (Van Damme, 1976, Williamson, 1979, 1981; Van Bocxlaer *et al.*, 2008; Van Bocxlaer & Van Damme, 2009). However, it should be pointed out that only during relatively brief lacustrine phases in this basin, i.e. less than 10% of the accumulated length of *ca* 2.5 Ma, preservational conditions were favourable for molluscs (Van Bocxlaer *et al.*, 2008). Bivalve associations from stratigraphic series covering a shorter time span are known from the Malawi Basin (Chiwondo Fm, maximal time span from *ca* 3.5 to 2.5 Ma) (Gautier, 1970b; Gorthner, 1994; Schrenk *et al.*, 1995), from the Afar Depression (*ca*. 2.5 Ma, Van Damme, 1984), unnamed deposits with an age of *ca* 5 Ma from the Awash Basin, Ethiopia (unpublished material at the Research Unit Paleontology, Ghent, collected by Dr. T. White), the Baringo Basin (Chemeron Beds, *ca* 3.5 Ma) (Van Damme, 1984), the Manonga-Wembere Depression, Tanzania (Ibole Member, Wembere Fm, originally considered to be *ca*. 5.5 to 5.0 Ma (Van Damme & Gautier, 1997) (Fig. 47) but probably considerably younger (Verniers, pers. comm., 2010), the Tugen Hills, Kenya (Lukeino and Mabaget Fms, respectively 6.0 to 5.7 Ma and *ca* 4.7 Ma) (De Groeve, 2005) and possibly from scattered outcrops in the Chad Basin with highly dubious ages (which are probably Middle or Late Pleistocene) (Van Damme, 1984).

The first significant change that occurred in the bivalve community around 8 to 5 million years is the appearance of unionid taxa; not a single genus, but several of them. Two of these, namely *Coelatura* and *Nitia*, have persisted till the present, *Coelatura* today being the most speciose African genus (*ca* 26 species). But during the Late Miocene – Early Pliocene period not only did these genera appear but equally so did other genera such as *Pseudobovaria*, *Gautieraia*, *Nkondonaia* and *Obwerukunio*.

During the Late Pliocene, around 2.5 Ma, another unionid genus *Pseudodiplodon* appears in the Albertine basin as well as the schizodont genus *Corbicula*.

Synchronous occurrences from other regions have been recorded respectively for *Coelatura* (Mabaget Fm, Tugen Hills, De Groeve, 2005), *Pseudobovaria* (unnamed deposits in Ethiopia, T. White *collevis* and in deposits at the base of the stratigraphic column in the Turkana Basin, Van Damme, 1976), *Pseudodiplodon* and *Corbicula* (Turkana Basin, Van Damme, 1976; Van Bocxlaer *et al.*, 2008). The genus *Nitia* is also found in the Early Pliocene deposits at the base of the stratigraphic column in the Turkana Basin (Van Damme, 1984).

The time of appearance in the Albertine Basin of these bivalves thus appears to reflect continent wide faunal changes. These coincide with major wet phases. The Zeit Wet Phase was a long-

lasting period of increased precipitation (between 7.5 and 4.5 million years) during which freshwater groups, such as fish, dispersed over Eurasia and Africa (Böhme, 2004; Stewart, 2009; Van Damme & Van Bocxlaer, 2009). As Böhme (2004) wrote, this migration (of snakehead fish : Channidae) could have been related to the intensification of the Asian monsoon that brought summer precipitation to the migratory pathways of these fishes in East Africa–Arabia and East Asia.

During the next wet peak in eastern Africa, namely around the beginning of the Pleistocene (ca 2.7 to 2.5 Ma) (Trauth *et al.*, 2005, 2007, 2009), the intensity of transcontinental and intercontinental movements again greatly increased with west African faunal elements extending deeply into east Africa (e.g. the rainforest tree *Antrocaryon* and the river forest freshwater snail *Potadoma*) and the Asian element *Corbicula* making its appearance (Williamson, 1985; Van Bocxlaer *et al.*, 2008; Van Damme & Van Bocxlaer, 2009). This is also the period that the enigmatic unionid genus *Pseudodiplodon* appears in both the Albertine and Turkana Basins.

A third relatively minor faunal mobilisation occurred during the next wet phase around 1.8 Ma (Trauth *et al.*, 2005, 2007, 2009). This is the period that the unionid genus *Grafunio* appears in the Albertine Basin together with a *Melanoides* species (*M. rwebishengoensis*, Van Damme & Pickford, 2003), formerly only known from the Turkana Basin (*M. howelli*, nomen nudum in Van Damme, 1976), and with *Iridina williamsoni*, a species that probably gave rise to *I. omoensis*, Van Bocxlaer & Van Damme, 2009 during the same period in the Turkana Basin (Van Bocxlaer & Van Damme, 2009).

There thus exists clear evidence that during these major wet phases intercontinental as well as transcontinental dispersals were activated. Based on marked similarities with Asian tropical faunal elements, the most plausible scenario for the appearance of genera such as *Coelatura*, *Nitia* and *Pseudobovaria*, appears to be that they invaded Africa from Eurasia. But for Late Miocene unionid genera such as the sulcate and tubercular *Gautieraia*, *Nkondonaia* and the flattened *Obwerukunio* as well as the Early Pleistocene *Grafunio* no putative related taxa are known from Eurasia. As to the Late Pliocene/Early Pleistocene *Pseudodiplodon*, its possible affinity to the tropical Asian *Chamberlainia* is indeed just a suggestion.

If some of the unionid genera that appeared in Equatorial Africa at the end of the Miocene are not of Asian origin, then where did they come from? The answer to this question is that they may have persisted or evolved in other parts of Africa since the Late Cretaceous, but were only able to spread during Late Miocene times with improving interbasinal connections. An argument to support this hypothesis is the recent occurrence in Africa of other problematic unionids which may have been around for a long time. This may be the case of the two anodontine unionoids, namely *Brazzaea* Bourguignat, 1885 (for which the monotypic subfamily Brazzaeinae Leloup, 1950 was established) and *Pseudospatha* Simpson, 1900 (monotypic subfamily Pseudospathinae Leloup, 1950), that are living fossils in Lake Tanganyika. Possibly due to their extremely thin shell they have not been preserved in the fossil record. Another candidate may be the genus *Germainaia* Graf & Cummings, 2009a, endemic to Madagascar. Graf & Cummings (2009a) stated that the family position of this genus was uncertain (Unionidae or Hyriidae) since it does not resemble any other recent African genus. However, considering the former unionid diversity observed in the Albertine record, this argument loses much of its strength.

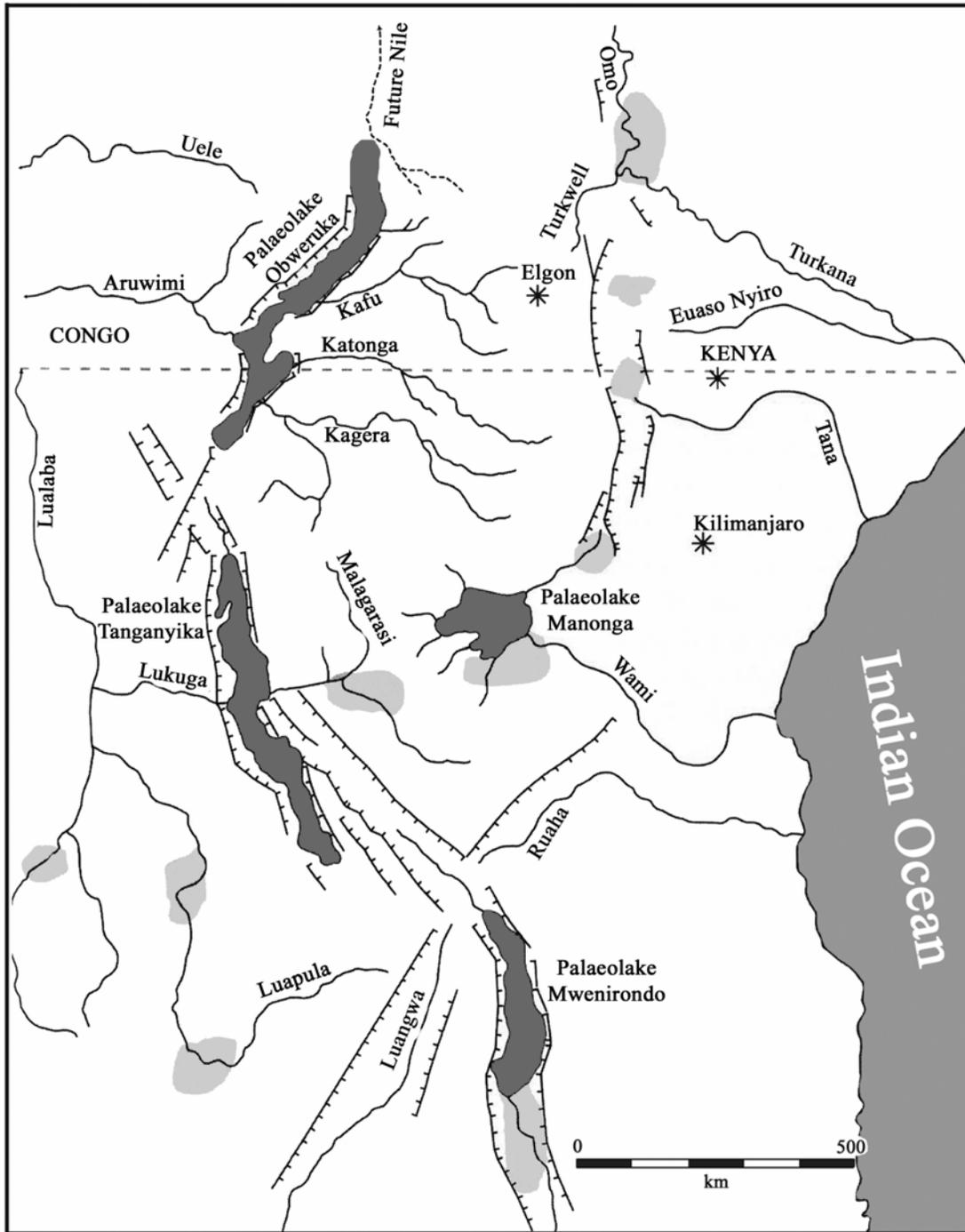


Figure 47. Reconstruction of the Late Miocene hydrographic network of East-Central Africa showing the occurrence of long-lived palaeolakes (dark grey) and ephemeral lakes and swamps (light grey). Palaeolake Obweruka drained westwards into the Congo drainage, and extended from the Sudan border in the north, to the Rwanda border in the south. This hydrographic network largely determined the biogeographic affinities of the molluscan faunas of Palaeolake Obweruka (after Van Damme & Pickford, 2003).

The hypothesis that some of the unionid genera that appear from Late Miocene times onward in the tropical African fossil record may have come from other parts of Africa instead of Asia suggests that the Early Tertiary African fauna may not have been strongly impoverished but instead may have been strongly partitioned until the Neogene.

Most of the unionid genera that make their appearance in Late Miocene to Early Pleistocene times have become extinct. The unionid genus that was the most successful during Pliocene times was undoubtedly *Pseudobovaria*, which lasted from *ca.* 5 to 1.5 - 1.4 Ma. Since the Middle Pleistocene *Coelatura* is the only widespread, diversified and dominant unionid genus, *Nitia* being restricted to the Nile basin and its former connections (e.g. the Chad Basin) and others such as *Grandidieria* or *Prisodontopsis* being highly confined.

In contrast to the Unionidae, the Iridinidae do not show any shifts at the genus level, only in intergeneric dominance. In Late Miocene – Early Pliocene times the frequency rate had already shifted between *Pleiodon* and *Iridina* from a ratio of *ca.* 1 to 10 to exclusively *Iridina* in the Albertine Basin (this paper) and an overwhelming dominance of the same in the Turkana Basin (Van Bocxlaer & Van Damme, 2009). Aspathariinae are represented mainly by representatives of the genus *Chambardia* while *Aspatharia* is extremely rare, not only in the Albertine but also in the Turkana Basin. This may have an ecological explanation, the latter genus being predominantly fluvial.

Representatives of the genus *Mutela*, as this taxon is defined here, remain absent till the Early Pleistocene to replace *Iridina* over most of its eastern African range during the Pleistocene. Considering the number of Modern *Mutela* with a blade-like hinge and *Pteromutela* species in the region of the Lower Congo and the Zambesi and other southern rivers, we suggest that the centre of evolution of thin hinged iridinids may be southwestern tropical Africa.

Winged iridinids with a relict hinge occur for the first time in the fossil record during Late Pliocene times but may be much older considering the extreme fragility of the shells. Their present geographic clustering and the fact that their fossil record appears to extend over more than 2.5 million years prompts us to use Starobogotov's (1970) taxonomic arrangement.

Why *Mutela* replaced *Iridina* in eastern Africa is a question that for the moment must remain unanswered. The shift in dominance from pseudotaxodont iridinids to edentulous ones could be hypothesized as being an ecophenotypic reaction to environmental changes. This would imply that the hinge types, which indeed seem to intergrade, are not related to important genetic differences. But there are different alternative explanations, a tempting one being the change in the fish fauna during the Pleistocene, the hitherto extremely frequent genus *Sindacharax* (Characidae) becoming extinct and hence the possible unavailability of a previous major host for *Iridina*.

According to the present distribution of the family Etheriidae (S. America, India, Madagascar and Africa) the monotypic genus *Etheria*, endemic to Africa and Madagascar, should represent an ancient faunal element that evolved on the African continent after the continent had broken away from the other parts of Gondwana. However, it is only from Early Pliocene times that the species appears to become hugely successful.

Finally, since the Late Pliocene the invasive heterodont *Corbicula* filled a niche that was apparently unoccupied because it seems not to have caused any upset in the rest of the bivalve fauna; it was thus not a harmful exotic. However, after the disappearance of *Pseudobovaria*, *Corbicula* rather than *Coelatura* seems to have filled its niche.

Evolution of the Bivalve Fauna in the Palaeolakes of the Albertine Rift

It is a general observation that the evolutionary history of the unionoids, in contrast to that of many freshwater gastropods or of, for example, secondarily freshwater representatives of some veneroid families (Cardiidae, Dreissenidae), does not display examples of brief but intensive radiations but as a rule is restricted to anagenetic processes.

Anagenetic evolution appears also to have occurred in Palaeolake Obweruka, but when it did take place it was rapid (geologically speaking) and unique.

Once it formed during Late Miocene times, Palaeolake Obweruka rapidly reached its enormous size and an impressive depth (a thickness of 6 km of sediment is inferred from seismic surveys). As in Lake Tanganyika, the part of the lake bottom surface that was available to benthic organisms must have been a small fraction of the total surface, situated below the oxygen rich parts. The number of unionoid taxa that succeeded in invading Palaeolake Obweruka at the onset was very limited, namely one unionid, *Pseudobovaria mwayana*, and two iridiniids, *Iridina moharensis* and *Iridina subelongata*. While *Pseudobovaria* remained unaltered (possibly not venturing into the lake proper), the evolutionary transformation of the iridiniids was spectacular: *Iridina moharensis* became more elongated and thin shelled with its anterior side stretched out into a tubular and hollow rostrum, the result being *Iridina adami*. The other iridiniid, *Iridina subelongata* evolved towards the other extreme, namely to a relatively short, wedge-like and extremely thick shelled form, *Iridina lepersonnei*.

Both were highly successful, being the most common bivalve fossils in the basin. While the lacustrine adaptations in *Iridina lepersonnei* are of a common well known type, i.e. as a function of improved hold in the sediment plus augmented protection against predators, this is not the case for *Iridina adami*. Gautier (1965, 1970a) and Pickford *et al.*, (1993) state that this species was the only mollusc they found in the blue-gray clays of the stratigraphic sequence in the Albertine basin. These clays are considered to have accumulated in reduced, hypoxic to anaerobic conditions (de Heinzelin & Verniers, 1996), hence at a depth below or around the mixolimnion.

These observations of *in situ* animals lend support to the hypothesis, first formulated by Seilacher (1990), that *Iridina adami* may potentially be one of the few freshwater chemosymbionts that ever existed (see under *Iridina adami* in the taxonomic part).

The third iridiniid species that succeeded in invading Palaeolake Obweruka during the earliest phase (Nkondo Member of the Nkondo Fm) is *Iridina wasai*. This relatively small iridiniid evolved into *Iridina atrox*, unique amongst the etherioids because of the presence of a single curved hollow tubercle on the posterior part of each shell. The most logical explanation for this ornamentation seems to be one of defense against molluscivorous predators, which in Palaeolake Obweruka were abundant and diversified (Van Neer, 1994; Van Damme & Pickford, 2004).

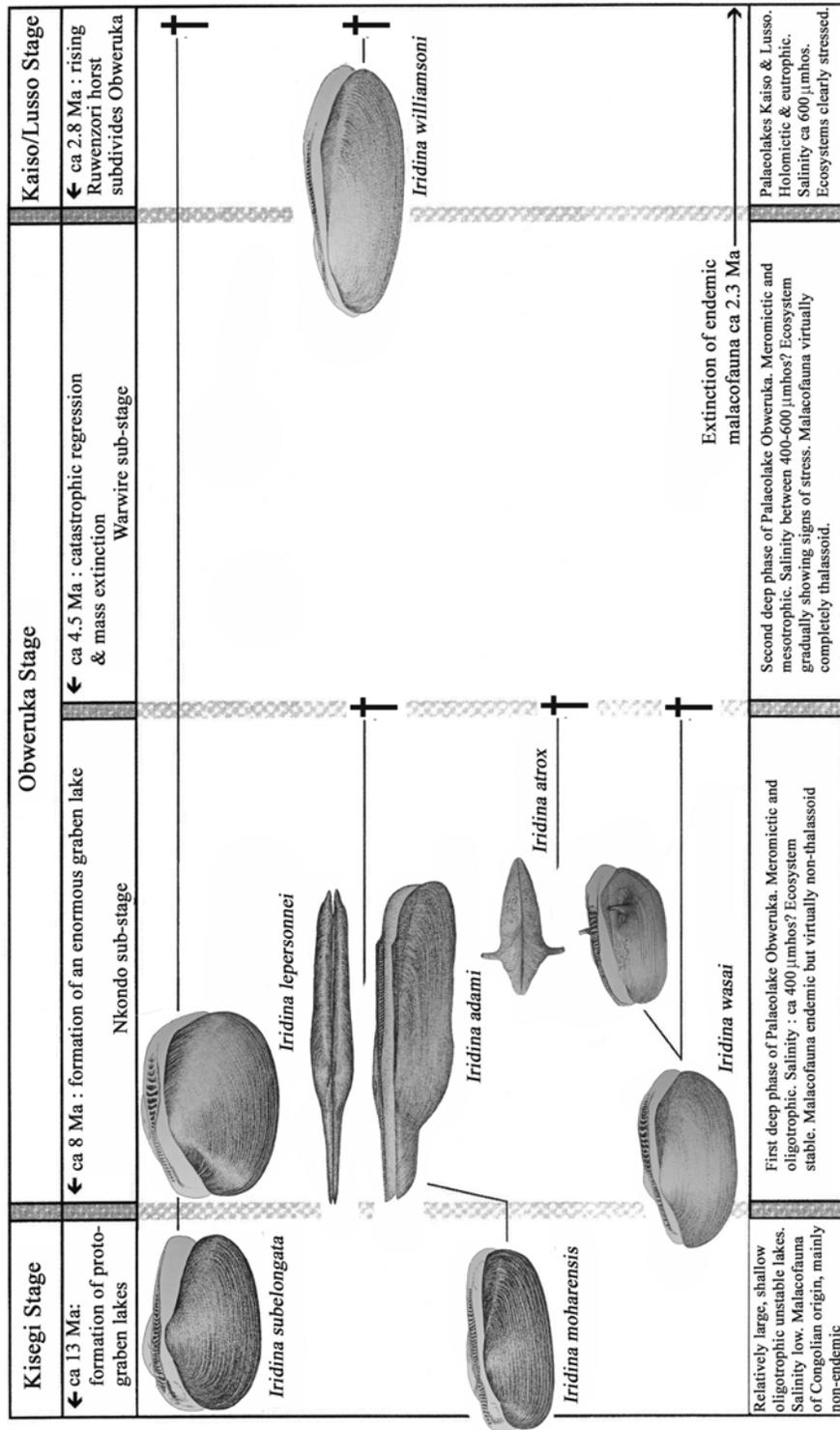


Figure 48. Summary of evolutionary changes in the Iridinidae (*Iridina*) that took place within the Albertine palaeolakes, giving rise to uniquely ornate species (*Iridina atrox*), heavily shelled species (*Iridina lepersonnei*) and to thin shelled (putative) chemosymbiotic species (*Iridina adami*).

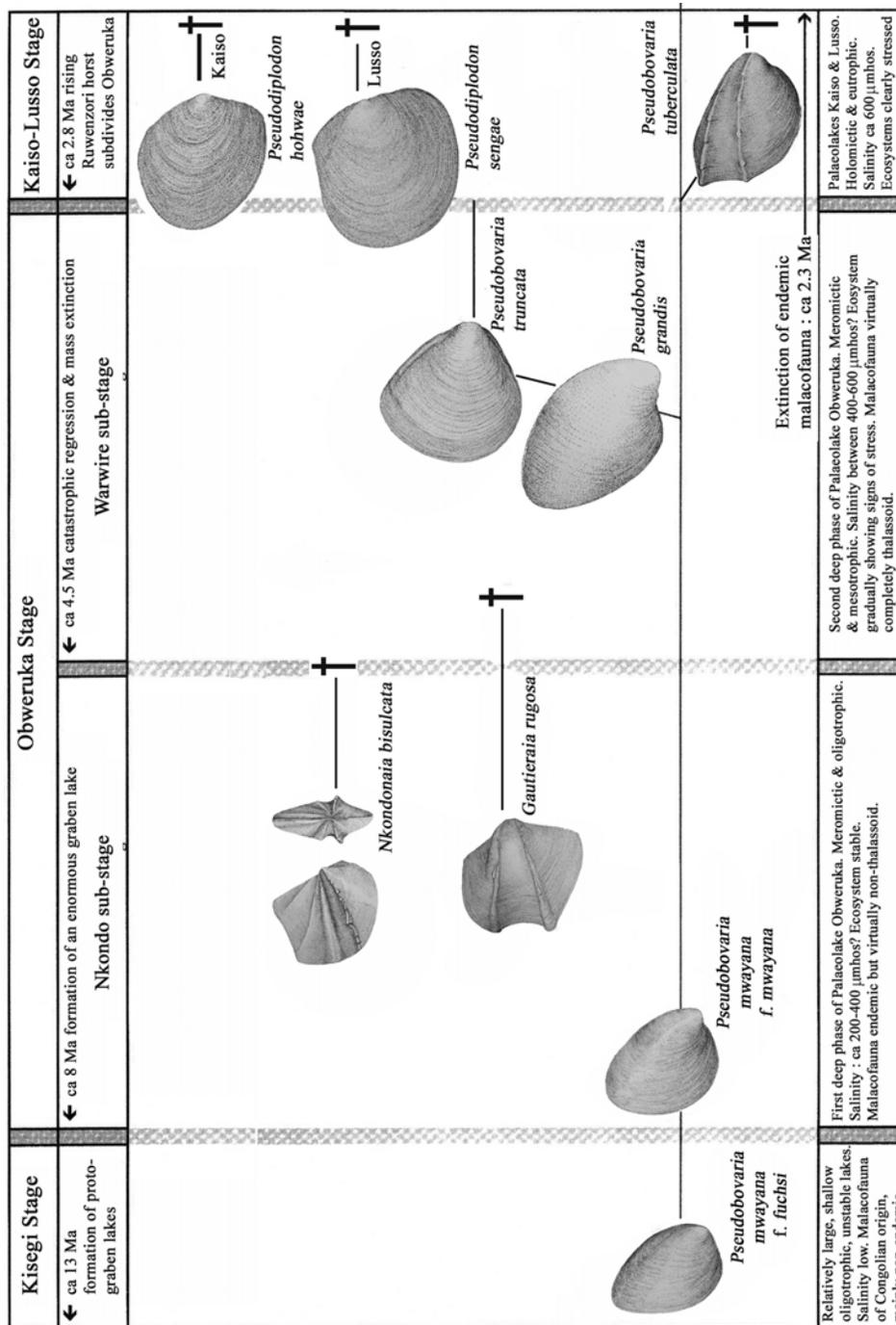


Figure 49. Summary of evolutionary changes in the Unionidae (*Pseudobovaria*) that took place within the Albertine palaeolakes during the earliest stages giving rise to non-ornate thick shelled species (*Pseudobovaria grandis*) and thin shelled, flattened (putative) chemosymbiotic species (*Pseudobovaria truncata*). Also shown are the other ornamented naiads *Nkondonaia* and *Gautieria* and the flat-shelled *Pseudodiplodon sengae* and *Pseudodiplodon hohwae* during the later stages. The latter three genera are considered to have invaded the basin, possibly from the Far East, as there appears to be no suitable African lineages to which they can be linked.

Elsewhere, tubular extensions are only known among the etherioids in *Etheria elliptica* forma *tubifera*, in which the purpose of such ornamentation is unknown.

Two unionid genera also colonised Palaeolake Obweruka during the subsequent Nyaweiga Member of the Nkondo Fm around the beginning of the Pliocene. These are *Gautieraia* and *Nkondonaia*, two unionids with a median sulcus and two ridges with knobs or spines. Possibly *Gautieraia* may have invaded from Asia and possibly *Nkondonaia* may have evolved from *Gautieraia*, but the fossil record is too sparse to provide an answer one way or the other.

During the NK-27 extinction event, when due to an unknown but catastrophic event around 4.5 Ma most of Obweruka's malacofauna died out, all the above mentioned ornate species as well as *Iridina adami* became extinct, only the estuarine/lacustrine *Pseudobovaria mwayana* and *Iridina lepersonnei* survived.

After the lacustrine ecosystem was restored, during the ensuing two million years, the bivalve fauna remained markedly impoverished compared to the pre-extinction phase. Only a single iridiniid, *Iridina lepersonnei*, and a single unionid genus, *Pseudobovaria* occurred. During the final stage of Palaeolake Obweruka, a limited evolutionary event did occur in this genus, first with the appearance of *Pseudobovaria grandis*, differing from the ancestral *Pseudobovaria mwayana* by its larger form and the lamellate pseudocardinals. Such adaptations are common in unionids inhabiting large lakes. The form that evolved from *Pseudobovaria grandis*, namely *Pseudobovaria truncata*, had a particular habitus with a central umbo and an eccentric sulcus. Such a shell morphology is strikingly convergent with that of the marine chemosymbiotic *Thyasira flexuosa* (Montagu) as figured in Kauffman (1969). But these convergences constitute insufficient evidence to infer such an adaptation in *Pseudobovaria truncata*.

A second cataclysm affected the malacofauna around 2.8 Ma as a result of the rise of the Ruwenzori Horst and accompanying tectonic activity. Palaeolake Obweruka was subdivided into southern and northern sub-basins, occupied by two smaller lakes, Palaeolake Lusso in the south and Palaeolake Kaiso in the north. It is in these two smaller basins that after a long period of infilling, renewed tectonic activity finally formed the present Lakes Edward and Albert. In Palaeolakes Lusso and Kaiso, *Iridina lepersonnei* persisted and at the end of the existence of the palaeolakes, new widespread iridiniids, namely *Iridina williamsoni* and *Mutela dubia* appear. Evolutionary changes did not occur in the unionid fauna, the taxa (*Pseudodiplodon*, *Coelatura*, *Corbicula*) or forms (*Pseudobovaria mwayana* f. *tuberculata* or a convergent morph) also having been recorded from the Turkana Basin (Van Damme, 1976, Van Bocxlaer *et al.*, 2008).

Evolutionary events in the Albertine Basin, except for some minor adjustments, thus ended during the second stage of Palaeolake Obweruka.

A Note on the Origin and Intra-basinal Evolution of the Bivalve Fauna of Lake Tanganyika

There exists a general consensus that Lake Tanganyika is a long-lived lake that is extremely old, with age estimates ranging from 12 to 6 Ma (see discussion in Van Damme & Pickford, 2003). These authors pointed out that in the gastropods, in contrast to Palaeolake Obweruka or for that matter other palaeolakes such as Palaeolake Pannon (Austria-Hungary), intensive evolutionary change (resulting in thalassoid morphs) remained strictly confined to a single family, the

Paludomidae (formerly ranged in the Thiaridae). In the case of the bivalves, the same observation can be made: no intensive radiation took place in Lake Tanganyika and all its bivalve taxa should be considered as relicts of a former widespread fauna. Nishida (1991) came to similar conclusions for the cichlid fishes and Wilson *et al.*, (2004) also refuted the notion that the present endemic paludomid taxa originated within the lake from a single ancestor. The fossil evidence suggests that the bivalve fauna of L. Tanganyika consists of relict fluvial species that have remained in virtually complete stasis. For none of the monotypical genera shows any particular thalassoid adaptations, neither to predation nor to life in hypoxic conditions. The only exception appears to be the genus *Grandidieria* that probably branched into a number of morphotypes within the lake, possibly forming a species clade, adapted to different sediment types ranging from soft muds to coarse sublittoral sands in turbulent zones. The fact that *Grandidieria* produces no larvae but juvenile shells that settle immediately (Kondo, 1990) does indeed greatly favour isolation and genetic drift. A molecular investigation should elucidate this matter.

CONCLUSIONS

The Albertine fossil bivalve record is unique and essential for our understanding of what changes took place in the freshwater bivalve fauna of the African continent over the last 15 million years.

It is safe to state that prior to the Late Miocene, the African malacofauna – certainly in eastern Africa but quite likely also in the rest of the continent - was in stasis, homogenous over vast distances and showing little diversity. The only naiads known from that early period are Iridinidae and Etheriidae. This ended in the period under consideration with the appearance of a considerable amount of previously absent genera - all Unionidae - and *Corbicula fluminalis*. Marked morphological similarities with Asian unionids, in particular between the African *Coelatura* (Coelaturinae) and the Asian *Parreysia* (Parreysiinae), combined with the appearance of certifiable Asian taxa such as *Corbicula*, constitute solid arguments for an Asian origin of part of these newcomers in the African fossil record. However, it cannot be excluded that some of these unionid taxa are ancient African elements that were confined to other parts of the continent, until the Late Miocene-Pliocene. From that period onward, due to a combination of wet phases and the intermittent creation of hydrographic links caused by increased tectonic activities, dispersal capacities increased enormously. Surprisingly, the number of taxa that did spread over most of east and central Africa remained relatively restricted. This is the conclusion that can be drawn from comparing the Albertine fossil record with those from the Turkana Basin, the Malawi Basin and the Ethiopian Rift. For instance, though the quantities of fossil bivalves in the Pliocene Turkana Basin are considerably higher than in the Albertine Basin, the number of genera in this basin and in the other African fossil sites is significantly lower than in the Albertine Basin. The genera which successfully extended over most of Africa are *Coelatura*, *Nitia*, *Pseudobovaria*, *Pseudodiplodon*, *Mutela*, *Pleiodon*, *Iridina*, *Chambardia*, *Aspatharia*, *Etheria* and *Corbicula* (Pisidiidae excluded). The question hence remains why extinct unionid genera such as *Grafunio*, *Nkondonaia*, *Gautieraia*, *Obwerukunio* from the Albertine Basin as well as Modern genera such as *Brazzaea* and *Pseudospatha* from Lake Tanganyika and *Prisodontopsis* from Lake Mweru-Lower Luapula have only been found in the Congo Basin. Are they the result of a rather spectacular unionid evolution within this ancient basin or should it be assumed that all these taxa cited above are descendants from Asian invasives that appeared during the Late Cenozoic but were accidentally only preserved in the Congo Basin? The latter seems unlikely, particularly because of the absence of related Asian forms. An invasion from Indotropical Asia during the

Late Cenozoic thus seems to us to be the best explanation for the appearance of a number of unionid genera, but not for all of them.

After a peak during Pliocene times, bivalve diversity plunged on a continental scale with the disappearance of most of the Pliocene unionid taxa and a relictualisation of the iridiniid genera *Pleiodon* and *Iridina*.

Bivalve diversity also increased markedly in Africa during Late Miocene to Terminal Pliocene times, due not only to the apparently increased dispersion of taxa, but also to evolutionary processes in particular in the eco-insular lake ecosystems that were formed in the rift. In relatively short-lived palaeolakes such as the ones that occurred in the Turkana Basin (the most long-lived lake in that basin had a maximal duration of *ca.* 200,000 years) endemic unionid species did evolve in both the Iridiniidae and the Unionidae, but morphological changes between ancestral/daughter lineages were modest and quite predictable, falling within the ordinary lacustrine adaptational patterns that are repeated in time and space (Van Damme, 1976, Van Bocxlaer & Van Damme, 2009). If anything, the observation that freshwater bivalve evolution worldwide is characterized by rampant convergence, is fully confirmed by the African fossil records except for that of the Albertine Basin.

In Palaeolake Obweruka, in contrast, the intensity of change – although rapid in geological terms - is unequalled. A morphology such as the tubular projections on *Iridina atrox* is unique and so is the extremely lengthened hollow rostrum of *Iridina adami*, possibly indicative of a chemosymbiotic lifestyle. The intriguing aspect is that in Palaeolake Obweruka spectacular morphs evolved not only in all gastropod families (Ampullariidae, Viviparidae, Paludomidae, Pachychilidae) but also – and as rapidly - in Unionidae and Iridiniidae, two families that are morphologically conservative with a high degree of convergence.

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REFERENCES

- Adam, W., 1955 - In : de Heinzelin, J., (Ed.) Le fossé tectonique sous le parallèle d'Ishango. *Exploration du Parc National Albert, Mission J. de Heinzelin de Braucourt (1950)*, **1**: 36-94.
- Adam, W., 1957 - Mollusques quaternaires de la région du Lac Edouard. *Exploration du Parc National Albert, Mission J. de Heinzelin de Braucourt (1950)*, **3**: 1-171.
- Adam, W., 1959 - Mollusques pléistocènes de la région du Lac Albert et de la Semliki. *Annales du Musée Royal du Congo Belge (Tervuren, Belgique)*, **25**: 1-148.
- Adams, H., 1866 - List of the shells collected by Samuel White Baker, Esq., during his recent exploration in Central Africa. *Proceedings of the Zoological Society of London*, **1866**: 375-376.
- Adams, H., & Adams, A., 1958 - Freshwater Musells. In: *The Genera of Recent Mollusca; Arranged According to their Organization*. John van Voorst, Paternoster Row, London, vol. **2**: 489-511.
- Bajope, B., 1992 - Mollusques fossiles de la région de Sinda à l'Est du Zaïre. *African Study Monographs, Supplement*, **17**: 19-25.
- Balla, S. & Walker, K. 1991 - Shape variation in the Australian freshwater mussel *Alathyria jacksoni* Iredale (Bivalvia, Hyriidae). *Hydrobiologia*, **220 (2)**: 89-98.
- Berggren, W., Kent, D., Swisher, C., & Aubry, M.-P., 1995 - A revised Cenozoic geochronology and chronostratigraphy In: Berggren, W., Kent, D., Aubry, M.-P., & Hardenbol, J., (Eds) *Geochronology, Time Scales and Global Stratigraphic Correlation, SEPM Special Publication*, **54**: 1-212.
- Bernardi A.C., 1860 - Descriptions d'espèces nouvelles. *Journal de Conchyliologie*, **4**: 331-332.
- Bieler, R., Carter, J.G., & Coan, R.V., 2010 - Classification of bivalve families. In: Bouchet, P., Rocroi, J., Bieler, R., Carter, J.G. & Coan, R.V., (Eds) *Nomenclator of bivalve families with a classification of bivalve families, Part 2. Malacologia*, **52(2)**: 1-184.
- Bishop, W.W., & Whyte, F., 1962 - Tertiary mammalian faunas and sediments in Karamoja and Kavirondo, East Africa. *Nature*, **196**: 1283-1287.
- Bogan, A.E., & Hoeh, W.R., 2000 - On becoming cemented: evolutionary relationships among the genera in the freshwater bivalve family Etheriidae (Bivalvia: Unionoida). In : Harper, E.M., Taylor, J.D., & Crame J.A., (Eds) *The Evolutionary Biology of the Bivalvia. Geological Society of London Special Publication*, **177**: 159-168. Geological Society, London.
- Bogan, A.E., & Roe, K.J., 2008 - Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future directions. *Journal of the North American Benthological Society*, **27**: 349-369.
- Bogan, A.E., 2008 - Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Global diversity of freshwater animals. Hydrobiologia*, **595**: 139-147.
- Böhme, M., 2004 - Migration history of air-breathing fishes reveals Neogene atmospheric circulation patterns. *Geological Society of America*, **32(5)**: 393-396.
- Bourguignat, J.R., 1854 - Aménités malacologiques 14-20. *Revue Magasin de Zoologie* **6 (2)**: 658-676. Published separately, with a different pagination, as a part of "Aménités malacologiques 1".
- Bourguignat, J.R., 1883 - Histoire malacologique de l'Abyssinie. *Annales des Sciences Naturelles, Zoologie et Paléontologie*, **15 (2)**: 1-154, pl. 7-11.
- Bourguignat, J.R., 1885 - *Espèces nouvelles et genres nouveaux découverts par les Rév. Pères*

- missionnaires dans les grands lacs africains Oukéréwé et Tanganyika*. Tremblay, Paris, 39 pp.
- Brown, F.H., & Feibel, C.S., 1986 - Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *Journal of the Geological Society of London*, **143**: 297-310.
- Brusatte, S. L., & Sereno, P. C., 2006 - Basal abelisaurid and carcharodontosaurid theropods from the Elrhaz Formation (Aptian-Albian) of Niger. *Journal of Vertebrate Paleontology, Supplement* **26**: 46A.
- Burke, K., & Gunnell, Y., 2008 - The African Erosion Surface : a continental scale synthesis of geomorphology, tectonics, and environmental change over the past 180 million years. *Geological Society of America, Memoir*, **201** : 1-66.
- Cahen, L., 1954 - *Géologie du Congo Belge*. Liège. Annual Meeting October 27-30, 2002, Colorado Convention.
- Caillaud, F., 1823-1827 - *Voyage à Méroé et au Fleuve Blanc au-delà de Fâzoql dans le midi du royaume de Sennâr, à Syouah et dans cinq autres oasis*. Imprimerie Royal, Paris.
- Canudo J., Barco, J-L, Pereda-Suberbiola, Ruiz-Omeñaca, J., Salgado, L., Fernández-Baldor, F., & Miguel Gasulla, J., 2009 - What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. *Bulletin de la Société Géologique de France*, **180 (1)**: 5-11.
- Connolly, M., 1928 - The Mollusca of Lake Albert Nyanza. Fossil species. *Journal of Conchology, London*, **18**: 171-208.
- Connolly, M., 1939 - A monographic Survey of South African non-marine Mollusca. *Annals of the South African Museum*, **33**: 1-660.
- Conrad, T. A., 1834 - Description of a new genus of freshwater shells. *Journal of the Academy of Natural Sciences of Philadelphia*, Ser. 1, **7**: 178-180.
- Conrad, T.A., 1853 - A synopsis of the family of Naiades of North America with notes and a table of some of the genera and subgenera of the family according to their geographical distribution and description of genera and subgenera. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **6**: 243-269.
- Cox, L.R., 1926 - Fossil Mollusca. In: Wayland, E.J. (Ed.) *The Geology and Palaeontology of the Kairo Bone-Beds. Geological Survey of Uganda Department, Occasional Paper*, **2**: 53-71.
- Cox, L.R., 1955 - Lamellibranchia from the Nubian Sandstone Series of Egypt. In: Attia, M. (Ed.) *Topography, Geology and Iron-ore deposits of the District East of Aswan*. Report on the Egyptian Mineral Resources, Department of Geological Survey. Appendix: 237-239.
- Cox, L.R., 1969 - ?Family Desertellidae, Superfamily Unionacea Fleming, 1828. In: Cox *et al.*, (Eds) *Treatise of Invertebrate Paleontology Part N Mollusca 6: Bivalvia. Geological Society America*, N467.
- Crosse, H., 1881 - Faune malacologique du Lac Tanganyika. *Journal de Conchyliologie*, **29**; 105-139, Supplement, 277-306.
- Cummings, K.S., & Bogan, A.E., 2006 - Unionoida: Freshwater Mussels. In : Sturm, C.F., Pearce, T.A., & Valdés, A., (Eds) *The Mollusks: A Guide to Their Study, Collection, and Preservation*, Chapter **25**: 313-325. American Malacological Society, Universal Publishers.
- Daget, J., 1961 - Note sur les *Spathopsis* (Mutelidae) de l'Ouest Africain. *Journal de Conchyliologie*, **191**: 63-77.
- Daget, J., 1998 - *Catalogue raisonné des Mollusques bivalves d'eau douce africains*. Backhuys Publishers/Orstom: Leiden/Paris, 329 pp.
- Dartevelle, E., 1948 - Contribution à la faune malacologique des terrasses de la région des lacs Edouard et Kivu. *Bulletin du Service Géologique de Congo Belge et Ruanda-Burundi*, **3**:

- Dartevelle, E., & Schwetz, J., 1947 - Contribution à l'étude de la faune malacologique des grands lacs Africains. Première étude. Les Lacs Albert, Edouard et Kivu. *Mémoires de l'Institut royal colonial belge, Nature et Sciences Série 8°*, **14(4)**: 1-48.
- De Groeve, E., 2005 - *De laat-Cenozoïsche zoetwatermollusken van de Tugen Hills (Kenia): taxonomie, paleoecologie en paleozoögeografie*. Unpublished MA Dissertation, Ghent University, Belgium, 121 pp.
- de Heinzelin, J., & Verniers, J., 1996 - Realm of the upper Semliki (Eastern Zaire). An essay on historical geology. *Annales du Muséum Royal de l'Afrique Central, Sciences Géologiques*, **102**: 1-87.
- de Heinzelin, J., 1955 - Le fossé tectonique sous le parallèle d'Ishango. *Exploration du Parc National Albert, Mission J. de Heinzelin de Braucourt (1950)*, **1**: 1-130.
- Deshayes, P.G., 1830 - Mollusques. Mollusca. *Encyclopédie Méthodique, Histoire Naturelle des Vers*, vol. 2: 471-550. Paris.
- d'Orbigny, A., 1835 - Synopsis terrestrium et fluviatilium molluscorum, in suo per Americam meridionalem itinere, ab. d'Orbigny, collectorum. *Magazine de Zoologie, Classe 5*, (61-62) 1-44.
- Dufour, S.G., & Felbeck, H., 2003 - Sulphide mining by the superextensile foot of symbiotic thyasirid bivalves. *Nature*, **426**: 65-67.
- Dunker, W., 1858 - Einige neue species der Naiaden. *Malakozoologische Blätter*, **5**: 225-229.
- Feibel, C.S. 1997 - A terrestrial auxiliary stratotype point and section for the Plio-Pleistocene boundary in the Turkana Basin, East Africa. *Quaternary International*, **40**: 73-79.
- Fleming, J., 1828 - *History of British Animals*. Edinburgh, 565 pp.
- Frierson, L.S., 1913 - Two new species of *Parreysia* from Kamerun, Africa. *Nautilus*, **27**: 85-86.
- Fuchs, V.E., 1934 - The geological work of the Cambridge Expedition to the East African lakes, 1930-1931. *Geological Magazine*, **72**: 97-122, 145-166.
- Fuchs, V.E., 1936 - Extinct Pleistocene Mollusca from Lake Edward, Uganda, and their bearing on the Tanganyika problem. *Journal of the Linnean Society, London*, **40**: 93-106.
- Gautier, A., 1965 - Geological investigation in the Sinda-Mohari (Ituri, N.E. Congo), a monograph on the geological history of a region in the Lake Albert Rift. *Ganda-Congo Publications, Ghent, State University, Belgium*, pp. 1-161.
- Gautier, A., 1966 - Geschiedenis en evolutie van de zoetwatermolluskenfauna in de Albert- en Edwardmeren-slenk. *Natuurwetenschappelijk Tijdschrift* **48**: 3-24.
- Gautier, A., 1970a - Fossil freshwater Mollusca of the Lake Albert - Lake Edward Rift. *Annales du Muséum Royal de l'Afrique Central, Tervuren, Sciences Géologiques*, **67**: 1-169.
- Gautier, A., 1970b - The freshwater molluscs from the Chiwondo Beds (Malawi). A preliminary report. *Quaternaria*, **13 (3)**: 325 - 330.
- Gautier, A. & Van Damme, D., 1973 - A revision of the Miocene freshwater molluscs of the Mohari Formation (Sinda-Mohari, N. E. Zaire). *Annales du Muséum Royal de l'Afrique Central, Tervuren, Séries 8°*, *Sciences Géologiques*, **75**: 43-62.
- Germain, L., 1909 - Descriptions de mollusques nouveaux de l'Afrique équatoriale. *Bulletin du Muséum Natioanl d'Histoire Naturelle de Paris*, **15 (8)**: 539-544.
- Germain, L., 1911 - Les Unionidae de Madagascar. *Bulletin du Muséum Natioanl d'Histoire Naturelle de Paris*, **17**: 136-140.
- Germain, L., 1912 - Sur quelques mollusques recueillis par M. le Dr Gromier dans le lac Albert-Edouard et ses environs. *Bulletin du Muséum d'Histoire Naturelle, Paris*, **18**: 77.
- Germain, L., 1916 - Faunule malacologique du Lac Albert-Edouard. *Bulletin du Muséum*

- d'Histoire Naturelle, Paris*, **22**: 193.
- Ghilardi R.P., & Simões, M.G., 2002 - Foram os Bivalves do Grupo Passa Dois (Exclusive Formação Rio do Rasto), Neopermiano, Invertebrados Tipicamente Dulcícolas? *Pesquisas em Geociências*, **29(1)**: 1-16.
- Giribet, G., & Wheeler, W., 2002 - On bivalve phylogeny: a high level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebrate Biology*, **126 (4)**: 271-324.
- Gmelin, J.F., 1791 - *Caroli a Linné, Systema naturae per regna tria naturae*. Editio decima tertia. Leipzig, Germany: **1(6)** class 6, Vermes: 3021-3910.
- Gorthner, A., 1994 - Grenzen paläontologischer Systematik und Stratigraphie in lakustrischen Biotopen am Beispiel rezenter und fossiler Mollusken des Malawisees. *Neues Jahrbuch der Geologie und Paläontologie, Monatshefte*, **8**: 487-500.
- Goumar, J., 1956 - Nouvelle espèce d'*Unio* plissé du Crétacé supérieur du Soudan français. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **28(2)**: 248-254.
- Graf, D.L., 2000 - The Etherioidea revisited: a phylogenetic analysis of hyriid relationships (Mollusca: Bivalvia: Palaeoheterodonta: Unionoidea). *Occasional Papers of the University of Michigan Museum of Zoology*, **729**: 1-21.
- Graf, D.L., & Cummings, K., 2006a - Palaeoheterodont diversity (Mollusca: Trigonioidea + Unionoidea): what we know and what we wish we knew about freshwater mussel evolution. *Zoological Journal of the Linnean Society*, **148**: 343-394.
- Graf, D.L., & Cummings, K., 2006b - Freshwater mussels (Mollusca: Bivalvia: Unionoidea) of Angola, with description of a new species, *Mutela wistarmorrisi*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **155**: 163-194.
- Graf, D.L., & Cummings, K., 2007a - Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoidea). *Journal of Molluscan Studies*, **73**: 291-314.
- Graf, D.L., & Cummings, K., 2007b - Preliminary review of the freshwater mussels (Mollusca: Bivalvia: Unionoidea) of northern Africa with an emphasis on the Nile. *Journal of the Egyptian German Society for Zoology*, **53D**: 89-118.
- Graf, D.L., & Cummings, K., 2007c - *Zambongo! Freshwater mussels of the Congo and Zambezi Rivers of Africa*. Philadelphia, PA, The MUSSEL project, 104 pp.
- Graf, D.L., & Cummings, K., 2009a - Actual and alleged freshwater mussels (Mollusca: Bivalvia: Unionoidea) from Madagascar and the Mascarenes, with description of a new genus, *Germainaia*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **158**: 221-238.
- Graf, D.L., & Cummings, K., 2009b - Unionoidea *cum grano salis*. Available at: <<http://bama.ua.edu/~musselp/>>.
- Graf, D.L., & Cummings, K., 2010a - The MUSSEL Project Database. Available at: <<http://bama.ua.edu/~musselp/>>.
- Graf, D.L., & Cummings, K., 2010b - Comments on the value of COI for family-level freshwater mussel systematics: a reply to Hoeh, Bogan, Heard & Chapman. *Malacologia*, **52**: 191-197.
- Graf, D.L., & Ó Foighil, D., 2000 - The evolution of brooding characters among the freshwater pearly mussels (Mollusca: Bivalvia: Unionoidea) of North America. *Journal of Molluscan Studies*, **66**: 157-170.
- Haas, F., 1936 - Binnen-Mollusken aus inner-Afrika, hauptsächlich gesammelt von Dr. F. Haas während der Schomburg-Expedition in den Jahren 1931-1932. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **431**: 1-156.

- Haas, F., 1962 - Zur Unionidenfauna Afrikas. *Archiv für Molluskenkunde*, **91** (4/6): 215-216
- Haas, F., 1969a - Superfamily Unionacea. In : Hennig, W., (Ed.) *Das Tierreich, eine Zusammenstellung und Kennzeichnung der rezenten Tierformen*. **88**: 1-663, Walter de Gruyter & Co., Berlin.
- Haas, F., 1969b - Superfamily Unionacea Fleming, 1828 – In: Cox *et al.*, (Eds) Treatise of Invertebrate Paleontology, Part N, Mollusca 6. Bivalvia. *Geological Society America*: N411-N466.
- Hartman, J., 2001 - An unusual freshwater bivalve from the uppermost Cretaceous of Montana: a previously unexplored ecological niche in the Hell Creek Formation. *GSA Annual Meeting*, November 5-8, 2001, Abstract 82-0. <http://gsa.confex.com/gsa/2001AM/finalprogram/abstract_23134.htm>.
- Henderson, J., 1935 – Fossil non-marine Mollusca of North America. *Geological Society of America Special Paper*, **3**: 1-313.
- Hoeh, W.R., Bogan, A.E., & Heard, W.H., 2001 - A phylogenetic perspective on the evolution of morphological and reproductive characteristics in the Unionoida. pp. 257-280. In : Bauer, G, Wächtler, K, (Eds) Ecology and Evolution of the Freshwater Mussels Unionoida. *Ecological Studies*, **145**. Springer-Verlag, Berlin.
- Hoeh, W.R., Bogan, A.E., Heard, W.H. & Chapman, E.G. 2009 - Palaeoheterodont phylogeny, character evolution, diversity and phylogenetic classification: a reflection on methods of analysis. *Malacologia*, **51**: 307-317.
- Iredale, T., 1934 - The freshwater mussels of Australia. *Australian Zoologist*, **8**: 57-78.
- Kat, P., 1987 - Biogeography and evolution of African freshwater molluscs: implications of a Miocene assemblage from Rusinga Island, Kenya. *Palaeontology*, **30**: 733-742.
- Kauffman, E.G., 1969 - Form, Function and Evolution. In: Cox *et al.*, (Eds) Treatise of Invertebrate Paleontology, Part N, Mollusca, 6: Bivalvia: *Geological Society America*: 129-205.
- Kondo, T., 1990 - Reproductive biology of a small bivalve *Grandidieria burtoni* in Lake Tanganyika. *Venus*, **49**: 120-125.
- Korniushin, A., 2004 - A revision of some Asian and African freshwater clams assigned to *Corbicula fluminalis* (Müller, 1774) (Mollusca: Bivalvia: Corbiculidae), with a review of anatomical characters and reproductive features based on museum collections. *Hydrobiologia*, **529**: 251-270.
- Krauss, F., 1848 - *Die Südafrikanischen Mollusken*. Ebner & Seubert. Stuttgart, 140 pp.
- Kuiper, J.G.S., 1956 - *Pisidium viridarium*, eine neue Art aus Ost-Afrika. *Archiv für Molluskenkunde*, **85** : 61-63.
- Küster, H.C., 1862 - Die Gattung *Limnaeus* etc. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*, 2nd Edit. 1(17).
- Lamarck, J.B., 1799 - Prodrome d'une nouvelle classification des coquillages. *Mémoires de la Société d'histoire naturelle de Paris*, **1**: 63-91.
- Lamarck, J.B., 1807 – Sur l'Aethérie, nouveau genre de coquille bivalve de la famille des Cemacés. *Annales du Muséum d'Histoire Naturelle, Paris*, **10** : 398-408.
- Lamarck, J.B., 1819 - *Histoire naturelle des animaux sans vertèbres*. Histoire Naturelle des Animaux sans Vertèbres **6(1)**: vi + 343 pp. Author: Paris.
- Lapparent, A.F., & Mongin, D., 1959 - Sur de nouveaux Mollusques d'eau douce découverts dans le 'Continental intercalaire' du Sahara central. *Comptes Rendus de l'Académie des Sciences de Paris*, **249**: 832-834.
- Lea, I., 1856 - Description of a twenty-five new species of exotic Uniones. *Proceedings of the*

- Academy of Natural Sciences of Philadelphia*, **8** : 92-95.
- Lea, I., 1859 - Description of a twenty-one new species of exotic Unionidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **11** : 151-154.
- Lea, I., 1864 - Descriptions of six new species of Unionidae from Lake Nyassa, Central Africa, &c. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **16** : 108-109.
- Leloup, E. 1950 - Exploration hydrobiologique du lac Tanganika (1946-47). Lamellibranches. Résultats Scientifiques de l'Exploration Hydrobiologique du Lac Tanganika (1946-1947). *Institut Royal des Sciences Naturelles de Belgique*, **3**: 1-153.
- Lepersonne, J., 1959 - Données géologiques et stratigraphiques et comparaison entre le Lac Albert et le Lac Edouard. In : Adam, W., (Ed.) Mollusques pléistocènes de la région du Lac Albert et de la Semliki. *Annales du Muséum Royal, Congo Belge*, **25**: 78-119.
- Lepersonne, J., 1970 - Revision of the fauna and the stratigraphy of the fossiliferous localities of the Lake Albert - Lake Edward Rift (Congo) *Annales du Muséum Royal de l'Afrique Centrale, Tervuren, Sciences Géologiques*, **67**: 170-207.
- Lydeard, C., Mulvey, M., & Davis, G., 1996 - Molecular systematics and evolution of reproductive traits of North American freshwater Unionacean mussels (Mollusca: Bivalvia) as inferred from 16S rRNA gene sequences. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences*, **351**: 1593-1603.
- Mandahl-Barth, G., 1954 - The freshwater mollusks of Uganda and adjacent territories. *Annales du Musée Royal du Congo Belge, Sciences Zoologiques*, **32**: 1-206.
- Mandahl-Barth, G., 1988 - *Studies on African Freshwater Bivalves*. Danish Bilharziasis Laboratory, Charlottenlund, 161 pp.
- Martens, E. von, 1883 - Vorlegung einiger centralafrikanischer, von Dr. Böhm und Lieutenant Wissmann gesammelten Conchylien. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, Mai: 71-74.
- Martens, E. von, 1897 - Beschalte Weichthiere Deutsch Ost-Afrikas. In: Möbius, K., (Ed.) *Deutsch Ost-Afrika*. **4** (1): 1-270. Berlin, Dietrich Reimer (Ernst Vohsen).
- McMichael, D.F., & Hiscock, I.D., 1958 - A monograph of the freshwater mussels (Mollusca: Pelecypoda) of the Australian region. *Australian Journal of Marine and Freshwater Research*. **9**: 372-508.
- Megerle von Mühlfeld, J.K., 1811 – Entwurf eines neuen System's der Schalthiergehäuse. Erste Antheilung. Die Muscheln. *Der Gesellschaft Naturforschender Freunde zu Bzrlin Magazin für die neuesten Entdeckungen in der gesammten Naturkunde*, **5** (1) : 38-72.
- Miko, I., 1999 - *Dynamique sédimentaire des formations détritiques et ligniteuses du Continental Terminal dans le Bassin des Iullemmeden (Niger)*. Unpublished PhD dissertation, Geological Department, Abdou Moumouni University, Niamey, 320 pp.
- Modell, H., 1942 - Das natürliche System der Naiaden. *Archiv für Molluskenkunde*, **74**: 161-191.
- Mongin, D., 1954 - Sur diverses lamellibranches d'eau douce récoltés dans le 'Continental intercalaire' du Sahara. *Comptes Rendus de l'Académie des Sciences de Paris*, **239**: 771-773.
- Mongin, D., 1963 - Les mollusques du 'Continental Intercalaire' (Mésozoïque) du Sahara Central, Lamellibranches. *Mémoires de la Société Géologique de France*, **96**: 1-40.
- Mongin, D., 1977 - Quelques précisions taxonomiques sur les Unionacea du Crétacé inférieur du Sahara (Afrique). *Archives des Mollusques*, **108**: 63-66.
- Mongin, D., & Lapparent, A.F., 1968 - Etude paléontologique des Lamellibranches limniques récoltés dans le Crétacé inférieur du Niger. *Bulletin de la Société géologique de France*, **10**: 148-155.
- Morris, P.J., 1996 - Testing patterns and causes of faunal stability in the fossil record, with an

- example from the Pliocene Lusso Beds of Zaire. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **127**: 313-337.
- Morris, P.J., & Williamson, P.G., 1988 - *Pleiodon* (Conrad) (Bivalvia: Mutelidae: Pleiodoninae) from the late Cretaceous of Montana: a first North American record for the Mutelidae. *Journal of Paleontology*, **62** (5): 758-765.
- Müller O. F., 1774 - *Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaceorum, non marinorum, succincta historia*. Volumen alterum. pp. I-XXVI [= 1-36], 1-214, [1-10]. Havniae & Lipsiae. (Heineck & Faber).
- Musisi, J., 1991 - *The Neogene and Quaternary Geology of the Lake George - Edward Basin, Uganda*. Unpubl. PhD Dissertation. Faculty of Sciences, VUB-Brussels University, 299 pp.
- Nagel, K-O., 1991 - On some freshwater molluscs (Gastropoda and Bivalvia) from Sierra-Leone. *Journal of Conchology*, **34**: 31-36.
- Neuville, H., & Anthony, R., 1906 - Contribution à l'étude de la faune malacologique des lacs Rodolphe, Stéphanie et Marguerite. *Bulletin de la Société Philomatique de Paris*, **9**(8): 1-26.
- Newton, R.B., 1909 - Fossils from the Nubian Sandstone of Egypt. *Geological Magazine*, **6**: 353-397.
- Nishida, M., 1991 - Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes. Inference from allozyme data. *Experientia*, **47**: 974-979 -
- Obaje, N.G., 2009 - Geology and Mineral Resources of Nigeria. *Lecture Notes in Earth Sciences*, **120** : 221 pp. Springer Verlag, Berlin.
- Pain, T., & Woodward, F., 1964 - A monograph of the African bivalves of the genus *Pleiodon* Conrad (= *Iridina* authors), Mollusca-Mutelidae. *Annales du Muséum Royal de l'Afrique Central*, **8**: 1-33.
- Pallary, P., 1924 - Supplément à la faune malacologique terrestre et fluviatile de l'Egypte. *Memoir de l'Institut de l'Egypte*. **7**: 1-61.
- Parodiz, J.J. & Bonetto, A.A., - 1963 - Taxonomy and zoogeographic relationships of South American naiades (Pelecypoda: Unionacea and Mutelacea). *Malacologia* **1** (2): 179-213.
- Pfeiffer, C., 1821 - *Naturgeschichte deutscher Land- und Süßwasser-Mollusken Erste Abtheilung*, **1-10**, 1-134, (1-2) Weimar (Landes-Industrie-Comptoir).
- Philippi, R. A., 1845-1847 - *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien*. Vol. 2. Theodor Fischer: Kassel, Germany.
- Philipsson, L.M., 1788 - *Dissertatio historico-naturalis: Nova testaceorum genera, ad publicum examen defert Laurentius Münster Philipsson scanus*. Lundae. 23 pp.
- Pickford, M., 1986 - Cainozoic Palaeontological Sites of Western Kenya. *Münchner Geowissenschaftliche Abhandlungen (A) Geologie und Paläontologie*, **8**: 1-151.
- Pickford, M., Senut, B., & Hadoto, D., 1993 - Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 1, Geology. Orléans, *CIFEG Occasional Publication*, **24**: 1-190.
- Pilsbry, H., & Bequaert, J., 1927 - The Aquatic Molluscs of the Belgian Congo. *Bulletin of the American Museum of Natural History*, **53**: 69-602.
- Preston, H., 1911 - Description of thirty-six new species of land and freshwater shells from British East Africa, chiefly from Mount Kenya and the neighbouring district. *Annals and Magazine of Natural History*, (8) **7**: 463-476.
- Putzeys, S., 1898 - Diagnoses de coquilles nouvelles provenant de l'Etat indépendant du Congo. *P.-V. Société de Malacologie Belgique*, **27**: 25-28.
- Rafinesque, C.S., 1820 - Monographie des coquilles bivalves fluviatiles de la Rivière Ohio

- contenant douze genres et soixante-huit espèces. *Annales Générales des Sciences Physiques, Bruxelles*, **5(13)**: 287-322.
- Rang, M. 1835. Mémoire sur quelques acéphales d'eau douce du Sénégal, pour servir à la malacologie de l'Afrique occidentale. *Nouvelles Annales du Muséum d'Histoire Naturelle, ou Recueil de Mémoires...* etc. **4**: 297–320.
- Rochebrune, A.T., 1886 - Sur quelques lamellibranches nouveaux provenant du Congo et de ses tributaires. *Bulletins de la Société Malacologique de France*, **3**: 1-14.
- Roe, K.J., & Hoeh, W.R., 2003 - Systematics of freshwater mussels (Bivalvia: Unionoida). In: Lydeard, C., & Lindberg, D.R., (Eds) *Molecular Systematics and Phylogeography of Mollusks*. Smithsonian Series in Comparative Evolutionary Biology. Smithsonian Books, Washington: 91-122.
- Rosenberg, G., Bogan, A.E., & Spamer, E.E., 1990 - *Coelatura* Conrad 1893, *Caelatura* Conrad 1865 and *Coelatura* Pfeiffer 1877 (Mollusca). A tale of two diphthongs. *Nautilus*, **104**: 29-32.
- Savazzi, E., & Peiyi, Y., 1992 - Some morphological adaptations in freshwater bivalves. *Lethaia*, **25**: 195-209.
- Scholz, H., & Glaubrecht, M., 2004 - Evaluating limnic diversity: toward a revision of the unionid bivalve *Coelatura* Conrad, 1853 in the Great Lakes of East African and adjacent drainage systems (Mollusca, Bivalvia, Unionidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, **80**: 89-121.
- Schouteden, H., 1933 - Les mollusques aquatiques vivants et subfossiles de la région du lac Kivu. *Bulletin de l'Institut royal colonial belge*, **4**: 519.
- Schrenck, F., Bromage, T., Gorthner, A., & Sandrock, O., 1995 - Palaeoecology of the Malawi Rift: vertebrate and invertebrate faunal contents of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution*, **28** (1): 59-70.
- Scopoli, J.A., 1777 - *Introductio ad Historiam naturalem sistens genera Lapidum, Plantarum et Animalium*. Prague, 506 pp.
- Seilacher, A., 1990 - Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology*, **3**: 289-311.
- Sereno, P., Larsson, H., Sidor, C., & Gado, B., 2001 - The Giant Crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, **294** (5546): 1516-1519.
- Sereno, P., Wilson, J., & Conrad, J., 2004 - New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society of London B*. 03PB1064.1-6, published online.
- Servain, G., 1890 - Des Acéphales lamellibranches fluviatiles du système Européen. *Bulletin de la Société Malacologique de France*, **7**: 281-323.
- Simpson, C.T., 1900 - Synopsis of the Naiades or pearly freshwater mussels. *Proceedings of the United States National Museum*, **22**: 501-1044.
- Simpson, C.T. 1914 - *A Descriptive Catalogue of the Naiades or Pearly Freshwater Mussels*. Parts I-III. Bryant Walker, Detroit Michigan, 1540 pp.
- Smith, E.A., 1908 - Descriptions of new species of freshwater shells from Central Africa. *Journal of Molluscan Studies*, **8**: 12-15.
- Sowerby, G.B., 1825 – Some account of a fourth species of *Aetheria*. *Zoological Journal of London*, **1**: 522-523.
- Starobogatov, Y., 1970 - Mollusca (Bivalvia). Mollusc fauna and zoogeographical partitioning of continental water reservoirs of the world. *Instituta Zoologi, Akademiya Nauk SSSR*, Nauka, Leningrad, 284 pp.

- Stefanescu, S., 1896 - Terrains tertiaires de Roumanie. Contribution à l'étude des faunes sarmatique, pontique et levantine. *Mémoires de la Société géologique de France, Paléontologie*, **15**: 1-147.
- Stewart, K.M., 2009 - Fossil fish from the Nile and its Southern Basins. In : Dumont, H.J., (Ed.) *The Nile: Origin, Environments, Limnology and Human Use*. Series: Monographiae Biologicae, **89** : 677-704, Springer, Netherlands.
- Suárez, J. M., 1999 - O sítio fóssilífero de Pirapozinho, São Paulo. In: Schobbenhaus, C., Campos, D.A., Queiroz, R.T., Winge, M., & Berbert-Born, M., (Eds) *Sítios Geológicos e Paleontológicos do Brasil*. <<http://www.unb.br/ig/sigep/sitio071/sitio071.pdf>>.
- Swainson, W.A., 1823 – Remarks on *Iridina*. *Philosophical Magazine*, **61**: 112-113.
- Swainson, W.A., 1840 - *A Treatise on Malacology: or the Natural Classification of Shells and Shell-fish*. Longman, Orme, Brown, Green & Longman, Paternoster Row, London, 419 pp.
- Tantawy, A., Keller, G., Adate, T., Stinnesbeck, W., Kassab, A., & Schulte, P., 2001 - Maastrichtian to Paleocene depositional environment of the Dakhla Formation, Western Desert, Egypt: sedimentology, mineralogy, and integrated micro- and macrofossil biostratigraphies. *Cretaceous Research*, **22** (6): 795-827.
- Tomlin, J.R. le B., 1928 - *Pseudavicula* Simpson preoccupied. *Nautilus*, **42**: 66.
- Trauth, M.H., Larrasoana, J.C., & Mudelsee, M., 2009 - Trends, rhythms and events in Plio-Pleistocene African climate. *Quaternary Science Reviews*, **28**: 399-411.
- Trauth, M.H., Maslin, M.A., Deino, A. & Strecker, M.R., 2005 - Late Cenozoic moisture history of East Africa. *Science*, **309**: 2051-2053.
- Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., Bergner, A.G.N., & Dühnforth, M., 2007 - High- and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. *Journal of Human Evolution*, **53**: 475-486.
- Van Bocxlaer, B. & Van Damme, D., 2009 - Palaeobiology and evolution of the Late Cenozoic molluscs of the Turkana Basin: Iridinidae Swainson, 1840 and Etheriidae Deshayes, 1830 (Bivalvia: Etherioidea). *Journal of Systematic Palaeontology*, **7**: 129-161.
- Van Bocxlaer, B., Van Damme, D., & Feibel, C.S., 2008 - Gradual versus punctuated equilibrium evolution in the Omo-Turkana Basin molluscs: evolutionary events or biological invasions? *Evolution*, **62** (3): 511–520.
- Van Couvering, J.A., & Van Couvering, J.A.H., 1976 - Early Miocene mammal fossils from East Africa: Aspects of geology, faunistics and palaeoecology. In: Isaac, G., & McCown, E., (Eds) *Louis Leakey and the East African Evidence*, Berkeley, University of California Press, pp. 155-207.
- Van Damme, D., 1976 - *Taxonomie, Ecologie en Evolutie van de Fossiele Zoetwatermollusken van het Rudolfmeerbekken (Ethiopië, Kenia)*. Unpublished PhD Dissertation, Ghent University, Belgium, 310 pp.
- Van Damme, D., 1984 - The Freshwater Mollusca of Northern Africa: Distribution, Biogeography and Palaeoecology. *Developments in Hydrobiology*, **25**: 1-164. The Hague, Junk.
- Van Damme, D., & Gautier, A., 1972 - Molluscan Assemblages from the Late Cenozoic of the Lower Omo Basin, Ethiopia. *Quaternary Research*, **2**: 25-37.
- Van Damme, D., & Gautier, A., 1997 - Late Cenozoic Freshwater Mollusks of the Wembere-Manonga Formation, Manonga Valley, Tanzania. In : Harrison, T., (Ed.) *The Neogene Paleontology of the Manonga Valley. A Window into the Evolutionary History of East Africa*. Topics in Geobiology, **14**: 351-360.
- Van Damme, D., & Pickford, M., 1994 - The Late Cenozoic Freshwater Molluscs of the

- Albertine Rift, Uganda-Zaire: Evolutionary and Palaeoecological Implications. In: Senut, B., & Pickford, M., (Eds) *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. II: Palaeobiology*. Orléans, CIFEG, Occasional Publication, **29**: 71-87.
- Van Damme, D., & Pickford, M., 1995 - The Late Cenozoic Ampullariidae (Mollusca, Gastropoda) of the Albertine Rift Valley (Uganda-Zaire). *Hydrobiologia*, **316**: 1-32.
- Van Damme, D., & Pickford, M., 1999 - The late Cenozoic Viviparidae (Mollusca, Gastropoda) of the Albertine Rift Valley (Uganda-Congo). *Hydrobiologia*, **390**: 171-217.
- Van Damme, D., & Pickford, M., 2003 - The late Cenozoic Thiaridae (Mollusca, Gastropoda, Cerithioidea) of the Albertine Rift Valley (Uganda-Congo) and their bearing on the origin and evolution of the Tanganyikan thalassoid malacofauna. *Hydrobiologia*, **498**: 1-83.
- Van Damme, D., & Van Bocxlaer, B., 2009 - Freshwater molluscs of the Nile Basin, past and present. In : Dumont, H.J., (Ed.) *The Nile: Origin, Environment, Limnology and Human Use*. Monographiae Biologicae, **89**: 585-630. Springer Verlag, Dordrecht.
- Van Neer, W., 1994 - Cenozoic fish fossils from the Albertine Rift Valley in Uganda. In: Senut, B., & Pickford, M., (Eds) *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. II: Palaeobiology*. Orléans, CIFEG, Occasional Publication, **29**: 89-124.
- Verdcourt, B., 1963 - The Miocene non-marine Mollusca of Rusinga Island, Lake Victoria, and other localities in Kenya. *Palaeontographica*, (A) **121**: 1-37.
- Vermeij, G.J., 1993 - *A Natural History of Shells*. Princeton, N.J. Princeton University Press.
- Verniers, J., & de Heinzelin, J., 1990 - Stratigraphy and geological history of the upper Semliki: a preliminary report. *Virginia Museum of Natural History, Memoir*, **1**: 17-39.
- von Ihering, H., 1912 - Analyse der Süd-Amerikanischen Heliceen. *Journal of Natural Sciences, Philadelphia*, **15**: 473-500.
- Watters, G., 2001b - The Evolution of the Unionacea in North America, and its Implications for the Worldwide Fauna. In : Bauer, G., & Wächtler, K., (Eds) *Ecology and Evolution of Freshwater Mussels, Unionoidea*. Ecological Studies, Berlin: Springer Verlag, **145**: 281-307.
- Williamson, P.G., 1979 - *Evolutionary Implications of Late Cenozoic Mollusc Assemblages from the Omo-Turkana Basin, North Kenya*. Unpublished PhD Dissertation, University of Bristol, UK, 376 pp.
- Williamson, P.G., 1981 - Palaeontological documentation of speciation in Cenozoic Mollusks from Omo-Turkana Basin. *Nature*, **293**: 437-443.
- Williamson, P.G., 1985 - Evidence for an early Plio-Pleistocene rainforest expansion in East Africa. *Nature*, **315**: 487-489.
- Williamson, P.G., 1990 - Late Cenozoic mollusc faunas from the north western African Rift (Uganda-Zaire). *Virginia Museum of Natural History, Memoir*, **1**: 125-139.
- Wilson, A.B., Glaubrecht, M., & Meyer, A., 2004 - Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society London, Biological Sciences*, **271**: 529-536.
- Zieritz, A., in prep. - *Variability and function of unionoidean shell shape and sculpture*. PhD dissertation Aquatic Ecology Group, Department of Zoology, Cambridge.
- Zieritz, A. & Aldridge, D., 2009 - Identification of ecophenotypic trends within three European freshwater mussel species (Bivalvia: Unionoidea) using traditional and modern morphometric techniques. *Biological Journal of the Linnean Society*, **98** (4): 814-825.

Appendix I. List of fossil bivalves from the Albertine Rift, Uganda-Congo.

- Bivalvia Linné, 1758 (Buonanni, 1681)
Heteroconchia Hertwig, 1885
Palaeoheterodonta Newell, 1965
Unionoida Stoliczka, 1871
Unionoidea Fleming, 1828
Unionidae Fleming, 1828
 Pseudobovaria Adam, 1957
 Pseudobovaria mwayana f. *typica* Fuchs, 1936
 Pseudobovaria mwayana f. *fuchsi* Adam, 1957
 Pseudobovaria mwayana f. *tuberculata* (Adam, 1957)
 Pseudobovaria grandis nov.
 Pseudobovaria truncata nov.
 Pseudodiplodon Adam, 1957
 Pseudodiplodon sengae Adam, 1957
 Pseudodiplodon hohwae nov.
 Coelatura Conrad, 1853
 Coelatura cf. *stanleyvillensis* (Pilsbry & Bequaert, 1927)
 Coelatura cf. *hauttecoeuri* (Bourguignat, 1883)
 Coelatura scholzi nov.
 Grafunio nov.
 Grafunio dageti nov.
 Gautieraia nov.
 Gautieraia rugosa nov.
 Nkondonaia nov.
 Nkondonaia bisulcata nov.
 Nitia Pallary, 1924
 Nitia cf. *monceti* (Bourguignat, 1883)
 Obwerukunio nov.
 Obwerukunio pliocenica nov.
Etherioidea Deshayes, 1830
Iridinidae Swainson, 1840
 Pleiodon Conrad, 1834
 Pleiodon tavernieri (Gautier, 1965)
 Iridina Lamarck, 1819
 Iridina moharensis Gautier, 1965
 Iridina subelongata Gautier, 1965
 Iridina adami Gautier, 1965
 Iridina williamsoni nov.
 Iridina lepersonnei Adam, 1959
 Iridina wasai nov.
 Iridina atrox nov.
 Iridina palaeospekii nov.
 Mutela Scopoli, 1777
 Mutela cf. *alluaudi* Germain, 1909
 Mutela dubia (Gmelin, 1791)
 ? *Mutela nyamaviensis* nov.
 Pteromutela Starobogatov, 1970
 Pteromutela cummingsi nov.
 Aspatharia Bourguignat, 1885
 Aspatharia pfeifferiana (Bernardi, 1860)
 Chambardia Servain, 1890
 Chambardia triangulata (Gautier, 1965)
 Chambardia wissmanni (Martens, 1883)
 Chambardia trapezia (Martens, 1887)

Etheriidae Swainson, 1840

Etheria Lamarck, 1807

Etheria elliptica Lamarck, 1807

Heterodonta Neumayr, 1884

Veneroidea H. Adams & A. Adams, 1856

Cobiculacea Gray, 1847

Corbiculidae Gray, 1847

Corbicula Megerle von Mühlfeld, 1811

Corbicula fluminalis (Müller, 1774)

Pisidiidae Gray, 1857

Eupera Bourguignat, 1854

Eupera sp. indet.

Psidium Pfeiffer, 1821

Psidium (*Afropsidium*) *lepersonnei* Gautier & Van Damme, 1973

Psidium spp. indet.

Appendix 2.

Brief Report on Late Miocene Molluscs from West Nile, Uganda

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ABSTRACT

In 2008, a brief survey of sediments in West Nile District, Uganda, led to the discovery of several fossiliferous outcrops. Molluscs from these deposits comprise lineages that are characteristic of the Nkondo Formation further south. This discovery indicates that Palaeolake Obweruka extended as far north as the Sudan border, and that, faunally speaking, the West Nile sector of the Albertine Graben was in close hydrographic connection with the main part of the Albertine Rift further south.

INTRODUCTION

Fossil molluscs were collected from several outcrops in the West Nile District, Uganda (Fig. 1). The main sites are at Koku, Dellu, and “Line 4” (a seismic line) (Fig. 2).

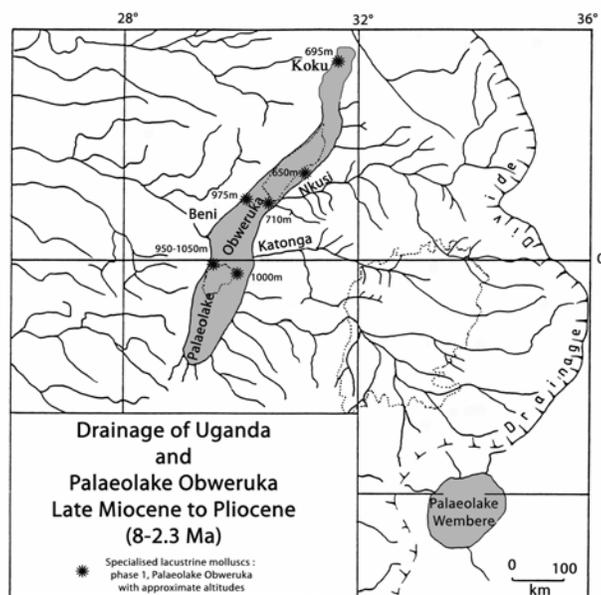


Figure 1. Late Miocene to Pliocene drainage network of Central Africa, showing the location of fossiliferous deposits in West Nile District, Uganda.

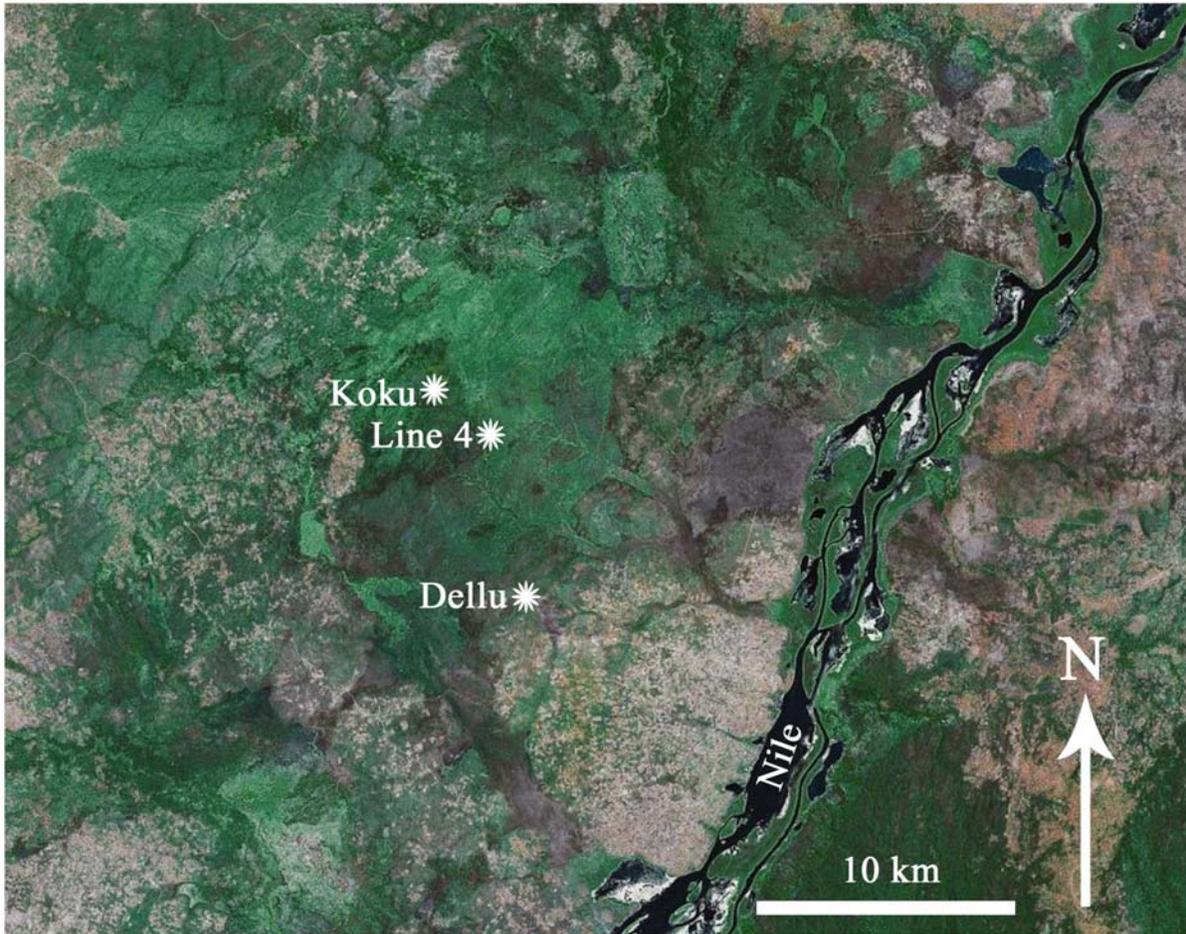


Figure 2. West Nile area, Uganda, with location of Late Miocene and Pliocene molluscs (modified from Google Earth).

THE BIVALVES

Family Unionidae

***Nkondonaia bisulcata* Van Damme & Pickford, 2010**

Material: Deltu: 3 inner molds of adult doublets (20 x 11 mm)

Identification: although the material consists of internal molds only, the small size of the shells with a posterior wing and imprints of the two sulci clearly identify them as *Nkondonaia bisulcata* (Fig. 4B).

Remarks: *Nkondonaia bisulcata* is a small unionid that is known only from Albertine deposits ranging in age from 7.5 to 5.5 Ma.

Family Iridinidae
***Iridina lepersonnei* Adam, 1959**

Material. Koku: 2 fragmentary doublets of adult shells (+ 80 x 40 mm), 1 juvenile shell?; Dellu: 5 fragmentary internal molds of adult doublets (estimated max. length: 90 mm) and 4 smaller doublets of possible young specimens (doubtful identification).

Identification: the large doublets show the typical wedge shape of *Iridina lepersonnei* as well as the huge pseudotaxodont hinge.

Remarks: *Iridina lepersonnei* occurs in the Albertine sequence from the earliest deposits of Palaeolake Obweruka (7.5 Ma) to those of Palaeolakes Lusso and Kaiso (2.5 Ma).

***Iridina adami* Gautier, 1965**

Material. Koku: 4 fragmentary doublets and 1 internal mold with pseudotaxodont hinge

Identification: the fragmentary doublets are characterised by the low height, the parallel dorsal and ventral margins, a rostrum at the posterior end and fine but distinct, regular teeth on the pseudotaxodont hinge (Fig. 3A-D). The identification as *Iridina adami* is certain.

Remarks: *Iridina adami* is a fossil species endemic to Palaeolake Obweruka, with a time range from 7.5 to 4.5 Ma. The species became extinct during the NK-27 Extinction Event. It appears to have been confined to deep parts of the lake.

***Chambardia triangulata* (Gautier, 1965)**

Material. Koku: 1 mold of a doublet (3.8 x 2.5 mm). Line 4 – West Nile: 2 internal molds (doubtful identification).

Identification: the triangular relatively flat shells with a blunt umbo appear to belong to *Chambardia triangulata*. The identification remains somewhat doubtful because the hinge is not visible (Fig. 3E).

Remarks: *Chambardia triangulata* was until now only known from Early and Middle Miocene deposits.

Family Etheriidae
***Etheria elliptica* Lamarck 1807**

Material: Dellu: small fragment of inner side with typical blister structure.

Identification: the blister structure is unmistakably that of *Etheria elliptica* (Fig. 4A).

Remarks: *Etheria elliptica* ranges in age from Early Miocene to Modern times.

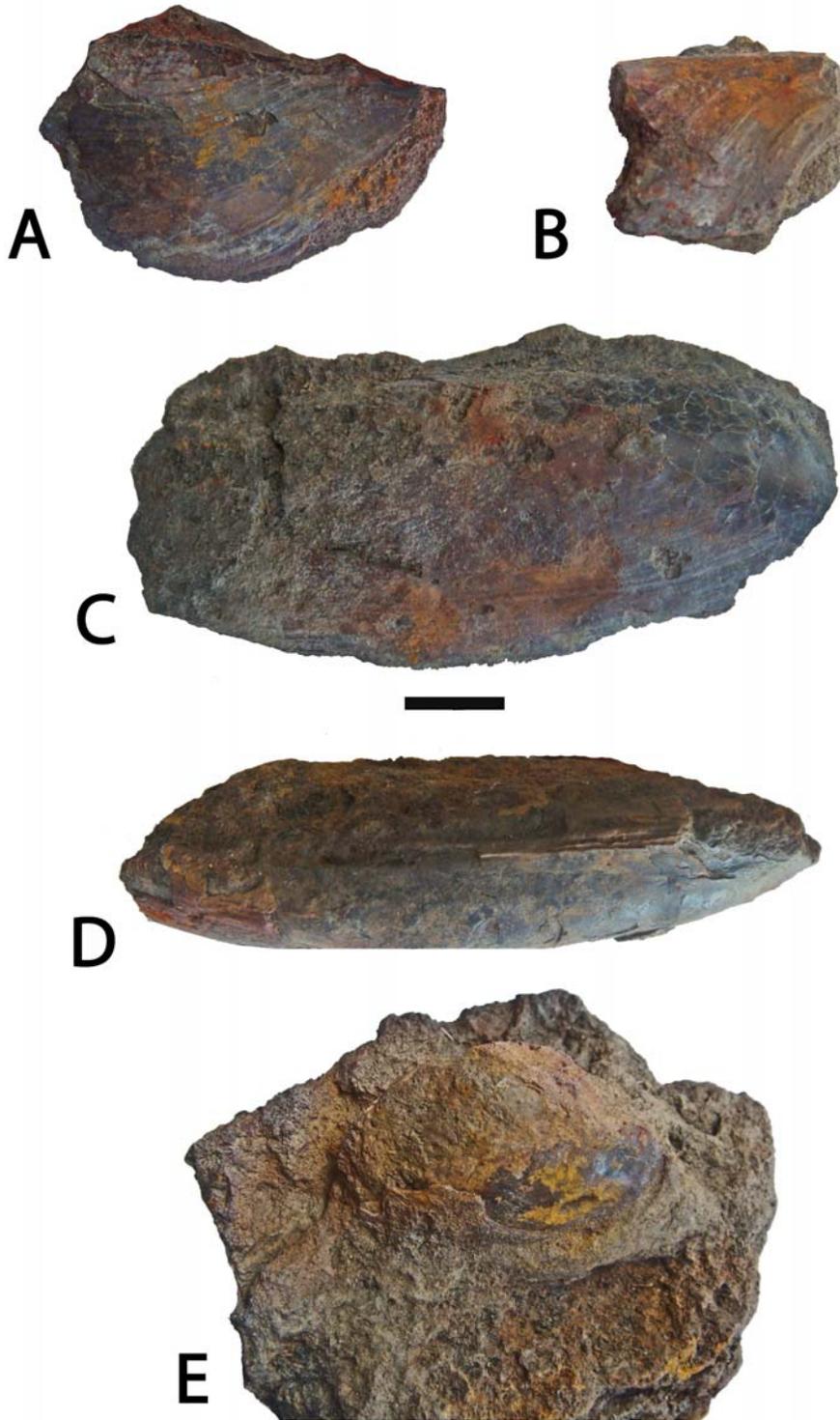
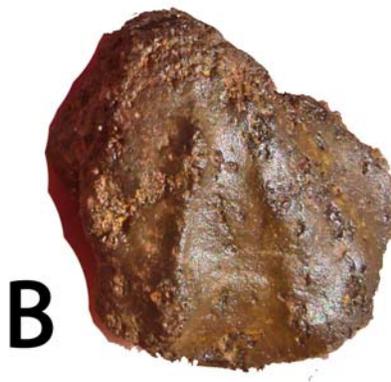


Figure 3. Bivalves from Koku, West Nile District, Uganda. A-B) *Iridina adami*, anterior part showing the tubular rostrum, C) *Iridina adami* shells lacking the rostrum, lateral and dorsal views, E) *Chambardia triangulata*.



A



B

Figure 4. Bivalves from Dellsu, West Nile, Uganda. A) *Etheria elliptica*, B) *Nkondonaia bisulcata*.

THE GASTROPODS

Family Viviparidae

Neothauma dubium (Cox, 1926)

Material: Dellsu: ca. 30 internal molds and several external impressions of shells. Length of largest specimen: 30 mm. Line 4 – West Nile: 20 flattened internal molds and several specimens

in a block of ironstone.

Identification: some imprints of undistorted shells clearly belong to the freshwater snail *Neothauma dubium* (Fig. 5). It is assumed that all other specimens also belong to this species. It cannot be excluded that some of the smaller shells belong to the viviparid *Kaya nodulosus* (Fuchs, 1936).

Remarks: *Neothauma dubium* lived in Palaeolake Obweruka from 7.5 to 4.5 Ma and is not found in deposits postdating the NK-27 Extinction Event. *Kaya nodulosus* has the same time range.

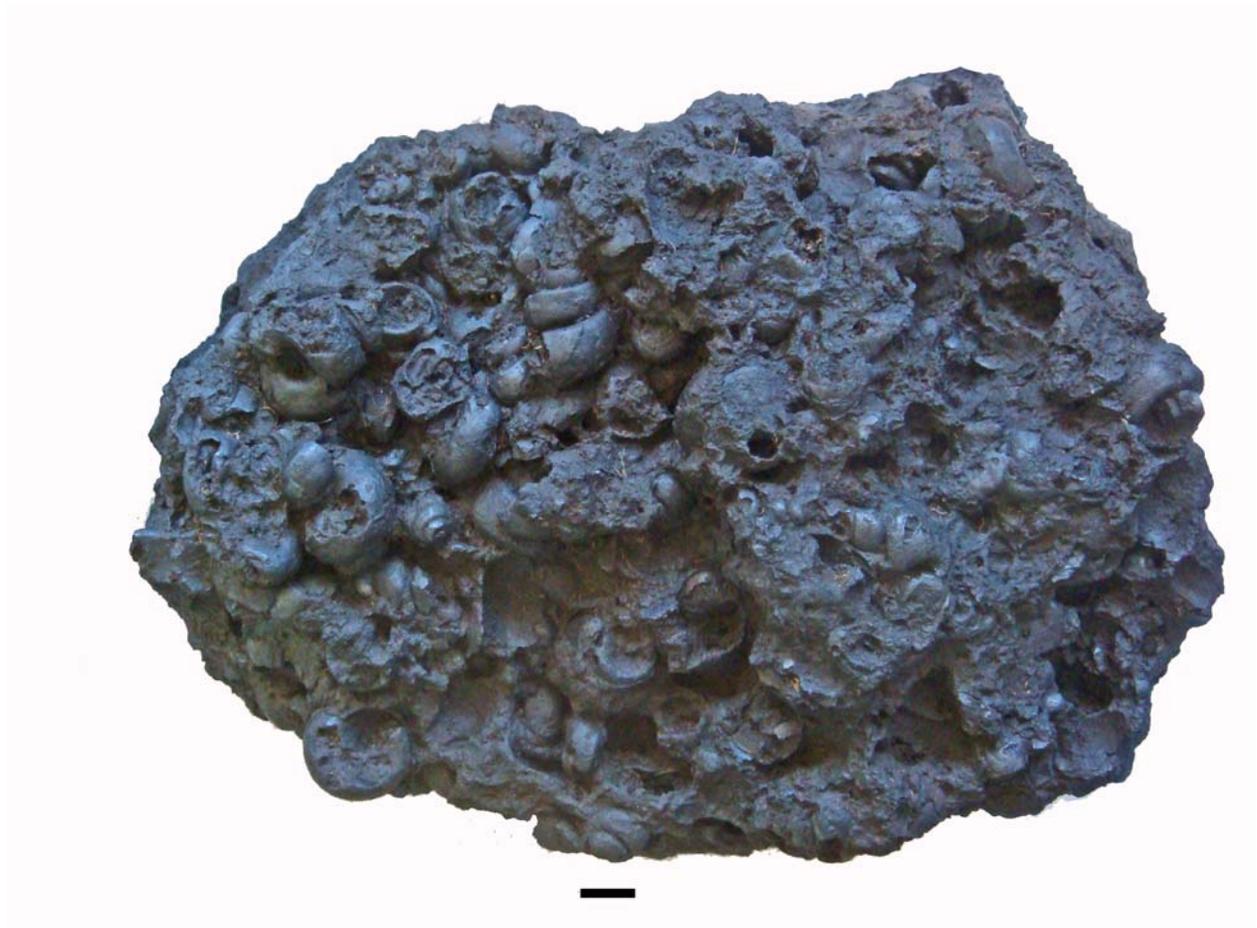


Figure 5. *Neothauma dubium* shells in a block of magnetitic ironstone from “Line 4”, West Nile, Uganda.

BIOCHRONOLOGY

Iridina adami from Koku indicates a Late Miocene age for the deposits. This species is typical of molluscan assemblages G3a – G3c (7.5-4.5 Ma). The presence of *Nkondonaia bisulcata* at Deltu is important because, further south, this species is confined in its temporal distribution to the Nkondo Formation, ca 7.5-5.5 Ma. The specimen of *Chambardia triangulata* could indicate the presence of earlier deposits at Koku, because, further south this species is confined to mollusc association G1 (Mohari, Kisegi, ca 12-10 Ma). Alternatively, the Koku specimen could belong to

a different taxon - its hinge is not clearly visible.

PALAEOENVIRONMENT

Iridina adami is a thin-shelled lineage that is usually found in clay deposits. It likely lived in soft sediment in the anoxic depths of the palaeolake. *Nkondonaia bisulcata* is also a thin shelled form, but at Dellu it occurs in sandy ironstone deposits, along with an abundance of *Etheria elliptica* and gastropods indicative of near shoreline depositional environments.

SUMMARY AND CONCLUSIONS

Molluscs from West Nile District, Uganda, are of interest from several points of view. They indicate that during the Late Miocene period, the West Nile sector of the Western Rift was in intimate hydrographic connection with the main Albertine Graben further south – it was part of Palaeolake Obweruka, as already hypothesised by Pickford *et al.*, 1993 (Pickford & Senut, 1994; Van Damme & Pickford, 1994). Secondly, they provide useful information concerning the age of the deposits that infill the rift in its northern parts, where the sediments are only about 1 km thick, compared to thicknesses of up to 6 km further south in the Albertine Graben. Thirdly, they reveal that the West Nile sector contained deep anoxic conditions as well as shallow, well oxygenated shoreline fringes.

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REFERENCES

- Pickford, M., Senut, B., & Hadoto, D., 1993 - Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 1, Geology. Orléans, *CIFEG Occasional Publication*, **24**: 1-190.
- Pickford, M., & Senut, B., 1994 - Palaeobiology of the Albertine Rift Valley : General conclusions and synthesis. *In* : Senut, B., & Pickford, M., (Eds) Geology and palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 2 : Palaeobiology. Orléans, *CIFEG Occasional Publication*, **29**: 409-423.
- Van Damme, D., & Pickford, M., 1994 - The Late Cenozoic freshwater molluscs of the Albertine Rift, Uganda-Zaire: Evolutionary and palaeoecological implications. *In*: Senut, B., & Pickford, M., (Eds) Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 2. Palaeobiology. Orléans, *CIFEG Occasional Publication*, **29**: 71-87.

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