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Evolutionary history of East African fresh water gastropods interpreted from the fauna of Lake Tanganyika and Lake Malawi

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with 1 figure and 7 plates in the text

Abstract: The long-lived Lake Tanganyika has a molluscan fauna that differs from other lakes in the area and from short lived lakes in general. Lake Malawi similar in shape, climatic conditions, size, and depth has a different molluscan fauna. The radula and ontogeny of the endemic (thalassoid) gastropods of Lake Tanganyika reveal the presence of at least seven separate groups that probably represent monophyletic lineages derived from at least seven original immigrants to the lake: (1) the Paramelaniinae sensu stricu (with *Paramelania*), (2) the Spekiinae n. subfam. with *Spekia*, *Stormsia*, and *Bridouxia*, (3) the possible *Cleopatra* relation around *Reymondia*, (4) the viviparous Lavigeriinae with the species of *Lavigeria*, (5) the minute sand- and thicket-dwelling Syrnolopsidae with *Syrnolopsis*, *Anceya*, and *Martelia*, (6) the Tanganyiciinae n. subfam. with *Tanganyicia rufofilosa* that has been described as having a brood pouch in the head-foot and would therefore represent a possible member of the Thiaridae, (7) the *Neothauma* group of viviparids. An eighth group has species living also outside of the lake with the basommatophoran *Bulinus* and *Burnupia*. A minute hydrobiid was newly discovered while the mostly monotypic genera *Tiphobia*, *Mysorelloides*, *Limnotrochus* and *Chytra* are thalassoid species, but were not encountered alive and may represent additional groups (probably two). While the radiation of fresh water caenogastropods characteristic of Lake Tanganyika has commonly been assigned to mainly one single family Thiaridae with exception of *Neothauma*, it has become evident that the thalassoid species are not monophyletic, but rather of polyphyletic origin. None of the species appear to be closely related to any of the species of the Thiarinae, even though the representative of this taxon, *Melanoides* is living in the larger tributaries of the lake. *Neothauma* appears to have been more widespread in the past, but with exception of the basommatophorans all others are restricted to actual Lake Tanganyika.

Lake Malawi in contrast, which appears to be of about four million years of age has no unique gastropod fauna that differentiates it from other lakes and even ponds and rivers of the region. The special fauna here has no endemic genera, and even the species here are the same or similar to those of the outside. Basically *Lanistes*, *Melanoides*, *Bellamya* and *Gabbiella* represent caenogastropods of the lake, and all four demonstrate a morphological spectrum which may represent a speciation still close to the founder, but could also represent only intraspecific variability. With exception of *Gabbiella* the founder species of all groups are also living in the lake. Comparison to fossil faunas of about two million years of age indicate that the fauna since then has little changed. A similar picture arises when fossil species found connected to the other lakes of the East-African Rift are compared with those of Lake Tanganyika. The fauna of the Lake Malawi type has been recognized here and their

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deposits ranging back into the Miocene, based on the genera *Pila*, *Lanistes*, *Bellamya*, *Gabbiella*, *Cleopatra* and *Melanoides*. It, thus, becomes evident that most of the gastropods that live in modern Lake Tanganyika have not come from these, but entered the lake during or prior to the Miocene and, thus, at least 5 million years ago when other genera dominated fresh water sources in Africa. A comparison of the described species with those known from Africa and described by Brown (1980, 1994) can be utilized to reconstruct a model of evolution of East African lake gastropods in Tertiary time.

Zusammenfassung: Im alten Tanganyikasee lebt eine Molluskenfauna, die sich von jener anderer See der Region und von dem noch nicht so alten aber klimatisch und der Gestalt nach ähnlichen Malawisee unterscheidet. Unterschiede in der Gestalt der Radula wie dem Ablauf der Ontogenese der sogenannten thalassoiden Schnecken des Tanganyikasees lassen das Vorhandensein von mindestens sieben getrennten Gruppen erkennen, die wahrscheinlich jeweils monophyletische Einheiten darstellen, und von einem ursprünglich in den See von außen gekommenen Einwanderer herzuleiten sind. Die erste Gruppe stellen Paramelaniinae sensu stricu (mit *Paramelania*) dar; die zweite Gruppe sind die Spekiinae n. subfam. mit *Spekia*, *Stormsia*, and *Bridouxia*; in die dritte Gruppe gehören die möglicherweise mit *Cleopatra* verwandten Arten von *Reymondia*; die vierte Gruppe bilden die lebendgebärenden Lavigeriinae mit den Arten von *Lavigeria*; in der fünften Gruppe sind die kleinen, im Sand und in pflanzlichen Dickichten lebenden Syrnolopsidae mit *Syrnolopsis*, *Anceya* und *Martelia* vereinigt; die sechste Gruppe der Tanganyiciinae n. subfam. besteht nur aus der einen Art *Tanganyicia rufofilosa*, die mit einem im Nacken liegenden Brutbeutel versehen sein soll und somit den Thiaridae zugerechnet werden kann; und als siebente Gruppe kann *Neothauma* angesehen werden, die den Viviparidae angehört. In einer achten Gruppe sind solche Arten vereingt, die auch außerhalb des Sees vorkommen, nämlich die Basommatophora *Bulinus* und *Burnupia*. Zudem wurde eine kleine hydrobiide Schnecke neu entdeckt. Über die zumeist nur mit einer Art im See vertretenen thallassoiden Gattungen *Tiphobia*, *Mysorelloides*, *Limnotrochus* und *Chytra* können keine weiteren Auskünfte gegeben werden, da sie nicht lebend angetroffen wurden. Sie mögen zwei weitere unabhängige Gruppen bilden. Im Gegensatz zur häufig vertretenen Annahme, daß die für den Tanganyikasee typischen Caenogastropoda mit der Ausnahme von *Neothauma* einer im See gelegenen Radiation entstammen, die von einem oder wenigen Vertretern der Thiaridae ausgegangen sein soll, wurde ganz deutlich, daß die heutige Fauna polyphyletischen Ursprungs ist. Zudem scheint keine der Arten des Sees sonderlich eng mit einem Vertreter der Thiarinae verwandt zu sein, obwohl ein Vertreter dieses Taxons mit *Melanoides* in den Zuflüssen zum See lebt. Nur *Neothauma* hatte anscheinend in der Vergangenheit einen weit über den See greifende Verbreitung, während mit Ausnahme der Basommatophora alle anderen auf den eigentlichen See beschränkt blieben.

Der Malawisee hat im Gegensatz zum Tanganyikasee eine Geschichte, die nur etwa vier Millionen Jahre zurückgreift. In ihrem Verlauf hat sich eine Schneckenfauna entwickelt, die nicht wesentlich von jener unterschieden ist, die auch in Flüssen und Tümpeln der Region vorkommt. Keine Gattung ist endemisch im See, und auch die meisten Arten der Fauna leben außerhalb des Sees oder haben hier nahe Verwandte. Im wesentlichen stellen *Lanistes*, *Melanoides*, *Bellamya* und *Gabbiella* die Caenogastropoda des Malawisees und weichen in ihrer Gestalt nicht weit vom morphologischen Spektrum ab, welches der Gründerart eigentümlich ist. Alle spiegeln somit noch die innerartliche Vielfalt wider oder kommen ihr doch sehr nahe. Mit Ausnahme von *Gabbiella* lebt auch die Ursprungsart aller anderen Artengruppen noch im See. Der Vergleich mit einer etwa zwei Millionen Jahre alten fossilen Fauna des Sees erweist, daß seither kaum Veränderungen stattfanden. Ein

ganz ähnliches Bild ergibt sich auch, wenn man die bisher bekannten fossilen Arten anderer mit dem ostafrikanischen Grabensystem verbundener Seen vergleicht und mit der Fauna des Tanganyikasees in Relation setzt. Die Schnecken des Malawisees gehören dem gleichen Typus an, wie er seit dem Miocene basierend auf den Gattungen *Pila*, *Lanistes*, *Bellamya*, *Gabbiella*, *Cleopatra* und *Melanoides* für die Region mit Ausnahme des Tanganyikasees kennzeichnend ist. Daraus ergibt sich, daß die meisten der heute im Tanganyikasee lebenden Schnecken schon vor dem Auftreten dieser neueren Fauna im See lebten. Als die seit Miozän die Süßgewässer Afrikas dominierenden Gattungen am See anlangten, war er schon gegen Einwanderung weitgehend abgeschottet. Die endemische Fauna des Tanganyikasees ist somit älter als 5 Millionen Jahre und reflektiert die Zusammensetzung einer vormiozänen Gastropodenfauna Afrikas. Der Vergleich der aus dem Tanganyikasee beschriebenen Arten mit den außerhalb des Sees lebenden Arten Afrikas, wie sie von Brown (1980, 1994) beschrieben wurden, kann genutzt werden, um zu einer modellhaften Rekonstruktion der alttertiären Süßwasserfauna der ostafrikanischen Seen zu gelangen.

Introduction

The East African Rift with Lake Tanganyika, Lake Malawi and also a number of smaller lakes represents an ancient structure that has a geological history ranging back into Mesozoic times. It has been active on and off and, thus, the lakes found in it are of different origin and age. The oldest continuously existent lake is probably Lake Tanganyika, which may have been in existence during most or all Miocene (Rosendahl et al. 1986, Burgess et al. 1988, Tiercelin et al. 1992). It is rather large measuring 650 km in north-south direction and has a width of up to 70 km. The lake surface is about 800 m above sea level, and maximum depth is about 1500 m. Lake Tanganyika is situated in the western branch of the East African Rift System. It has slightly positive water budget and generates a small outflow through the Lukuga River in the southwest. It depends mainly on the Ruzizi River inflow from Lake Kivu in the northern part of the basin. The geological history of Lake Tanganyika ranges back for several million years (Degens et al. 1971). According to Rosendahl et al. (1986) and Burgess et al. (1988) a thickness of more than 4 km sediment have since formed in the lake basin. If the present rates of sedimentation have persisted over the past several million years, the lake should have originated as early as the Oligocene.

Channel and canyon development has occurred in the east-central Lake Tanganyika in about 800 m (Scholz et al. 1990) or 600 m (Burgess et al. 1988) of water. One interpretation is that the Malagarasi River coming from the East downcut hundreds of meters during a Pleistocene lowstand, and the present condition represents a highstand (Scholz et al. 1990). According to Burgess et al. (1988) adjacent to the modern Malagarasi River channels of up to 75 m depth have been incised into the rift sediment. They may have been cut during the last lowstand in the lake level 600 m below present level during late Pleistocene (Hecky & Degens 1973). Another contrasting interpretation is that these channels have been produced subaqueously by turbidity currents down-dip from the delta (Tiercelin et al. 1988). These differences in the interpretation of the lake history is also evident when the extreme drop of lake level 18000 years ago as postulated by GASSE et al. (1989) are contradicted by TIERCELIN et al. (1988) whose results indicate a much smaller drop in water level, if any at all.

Nowadays Ruzizi River entering the lake at its northern end and Lake Tanganyika have similar water chemistry (TIERCELIN et al. 1992). The Ruzizi River came into existence during the late Pleistocene when the Birunga vulcanoes to the north of the lake caused a blocking of the Nile drainage system. Prior to this incident water chemistry of Lake Tanganyika appears to have been different from that of today. Malagarasi River was then a tributary to the Nile. DEGENS et al. (1971) demonstrated that due to this change the main diatom assemblage living in the lake also changed its taxonomic composition. On the Burundi coast near the mouth of the Ruzizi River stromatolitic growth has stopped when water was quite a bit lower than today (CASANOVA & THOUIN 1990). But CASANOVA & HILLAIRE-MARCEL (1992) analysed the stromatolitic crusts and found that sea level several thousand years back was similar to that of today, and fluctuation at top aridity some 2500 years back resulted only in a drop of about 10 m from modern lake level. This is not so much since there is also a constant change in sea level of about 1 to 2 m in connection to the annual change of wet and dry seasons. Stromatolites in thick incrustations on hard substrates are found at depths below about 2 m at the north Tansanian coast. In contrast to conditions further north along the coast of Burundi where these stromatolites are dead (CASANOVA & HILLAIRE-MARCEL 1992), they are quite alive and currently growing in the bay near Kigoma.

Lake Tanganyika is mildly alkaline and non saline with the anomalouse high Mg/Ca ratio largely derived from Lake Kivu (TIERCELIN et al. 1992). The largest river entering the lake is Malagarasi River with less saline water as coming with the Ruzizi River, but higher content in Ca. Deep lake sediments are composed of laminates, organic rich diatomaceous silts and muds (STOFFERS & HECKY 1978). All this indicates that in regard to volume of water, size, and chemistry the lake changed quite a bit during the last few million years, even though exact data on these changes are still not evailable, and COULTER (1994) expressed a contrasting opinion. Lake Tanganyika is permanently stratified and anoxic below water depth of a few hundred meters (HECKY & DEGENS 1973). The shallow water down to about 200 m of depth is oxigenated and bears a rich fauna in which the fishes and the molluscs appear the most conspicuous components (COULTER 1991).

Lake Malawi is smaller than Lake Tanganyika, but still among the world's largest and deepest lakes. It is 580 km long, 30–50 km wide and about 700 m deep (thus, quite a bit shallower than 1500 m deep Lake Tanganyika). Lake Malawi along with the other large lakes of the East African rift system bears resemblance with many ancient rift basins. Mixing of Lake Malawi during the austral winter from May to October is restricted primarily to the upper 250 m. The water column is nearly isothermal, and the lake is anoxic below 250 m (ECCLES 1974). During the windy season the southeast trade winds are channeled by the rift valley, causing wave intensity to be greatest in the northern end of the lake.

The Songwe tuffs are interpreted to reflect the initial rifting at 8–6 Million years (EBINGER et al. 1993). According to BETZLER & RING (1995) there is no evidence for the existence of a lake about four million years ago. Around that time the formation of a major perennial lake began (Bromage et al. 1995) which represents unit 2 of Chiwondo Beds with layers that are rich in gastropods and pelecypods. Here also layers with oncoids and minor stromatolites are present. The hominid remain found in unit 3 of Chiwondo Beds is about 2,4 Million years old, and this whole unit was deposited between 3,7 and 1,5 Million years of age (Schrenk et al. 1993). The molluscan fauna of these deposits was studied by Gorthner (unpubl. manuscript), and it closely resembles that of modern Lake Malawi.

Lake Malawi had low-stand about 20000 years ago (Scholz & Rosendahl 1988). The Lake Malombe periodically fell dry, the last time around 1925 (Dixey 1927). This Lake Malombe is a smaller lake at the southern end of the main Lake Malawi and is connected to it by its southern outflow, the Shire River. This river after passing through Lake Malombe continues into the Sambesi River. According to age determination in shell beds near Mangochi between Lake Malawi and Lake Malombe, Lake Malawi was about 5 m above present level some 6000 years ago when both lakes formed a unit.

Taxonomic part

Here the different groups of gastropods that were found in Lake Tanganyika and Lake Malawi are characterized and placed into relation with what is known from older lakes and lake deposits of the general area of the East African Rift.

Subclass Caenogostropoda Cox, 1959
Superfamily Ampullarioidea Guilding, 1828

Family Ampullariidae Guilding, 1828

The Ampullariidae represent large gastropods of the fresh water which have a ctenidium as well as a lung and can, thus, breathe air and water. Their ontogeny is of the caenogastropod type, but with many special adaptations to yolk feeding. The time when Ampullariidae had marine ancestors with a planktotrophic larval phase may lie way back in history. Since oldest fossil Ampullariidae are known from the Paleocene of Sudan and India, their marine ancestors have lived somewhere in the Mesozoic era or even before that (Bandel 1993). It appears as if they could have evolved and radiated in fresh water of the Gondwanian continent. If they existed on the Indian Plate as well as on the African Plate during the begin of the Tertiary, their common ancestors should have lived in lakes, ponds and streams of the Jurassic Gondwana. In Africa there are about 26 species of the genera *Pila*, *Lanistes*, *Afropomus* Pilsbry and Bequaert, 1927 and *Saulea* Gray, 1867 and 5 species of these live in Asia (Bertold 1991).

feeding habits do not differ between individuals living in the lake from those living in rivers and ponds as was suggested by BERTHOLD (1990). Small differences in the dentition of individual teeth in the radula, a shorter gill in the three lake forms as well the presence of a parasitic copepod in these and its absense outside of the lake was considered of importance by BERTHOLD (1990). It was also suggested lake specimens may not breathe air, which is true, but all of the many individuals collected in depths between 1 and 6 m near Monkey Bay had air bubbles in their mantle cavity. They collect bubbles on their feeding path among oxygen producing algal growths on the lake floor. Due to the decrease in weight of the animal in the water by uplifting of the shell with the bubble of air held in the mantle cavity in individuals of all water depths the animals move rapidly and lightly over the bottom surface (observed down to about 6 m water depth and to 500 m off-shore).

As a result *Lanistes* from Lake Malawi may not represent an independent endemic evolution, but may rather be the expression of what flexibility and adaptational potential lies in the single species *Lanistes ellipticus* which may be the same as *L. ovum*. It has more or less the same shape in rivers and ponds outside of Lake Malawi, but quite a lot of variations when settling the different parts and sediments of the lake.

Family Viviparidae GRAY, 1847

The Viviparidae represent an ancient group of fresh water gastropods that have a large gill which is utilized for gas exchange as well as for collecting food from the water. Females carry developing eggs in the frontal portion of their oviduct. Species are common in Eurasia and Africa and are not found in South America, which may indicate that they have not been living in Mesozoic Gondwana. The Viviparidae are characterized by a rather unique embryonic development (BANDEL 1982, and references therein), which leads to the formation of a rather characteristic shape of protoconch (RIEDEL 1993). Young hatch from the brood pouch with three or more whorls completed. Such protoconchs have been noted on shells in individuals that lived in the pools of the Wealden Facies of the early Cretaceous in central and western Europe (BANDEL 1991), and they had special representatives in the Late Cretaceous of that area (BANDEL & RIEDEL 1994). Most probably the Viviparidae represent an even older family of fresh water gastropods perhaps having their origin in the Paleozoic (BANDEL 1993). The genera *Viviparus* MONTFORT, 1810 and *Bellamya* are rather close to each other in ecology as well as ontogeny, and MANDAHL-BARTH (1972) noted as only distinguishing factor differences observed in the nervous system. Fossil shells can not be differentiated to belong to either genus. *Bellamya* was considered a subgenus of *Viviparus* by THIELE (1929) while WENZ (1938) regarded it to represent an own genus and to belong to an independent subfamily the Bellamyinae. He noted a difference in the ornament of the embryonic shell of *Bellamya* to that of *Viviparus* which has since not been possible to support (BANDEL & RIEDEL 1998). BROWN (1980), for example, figured the early ontogenetic shell of *Bellamya unicolor* which exhibits similar spiral carinae as present in European *Viviparus viviparus* (LINNÉ 1758).

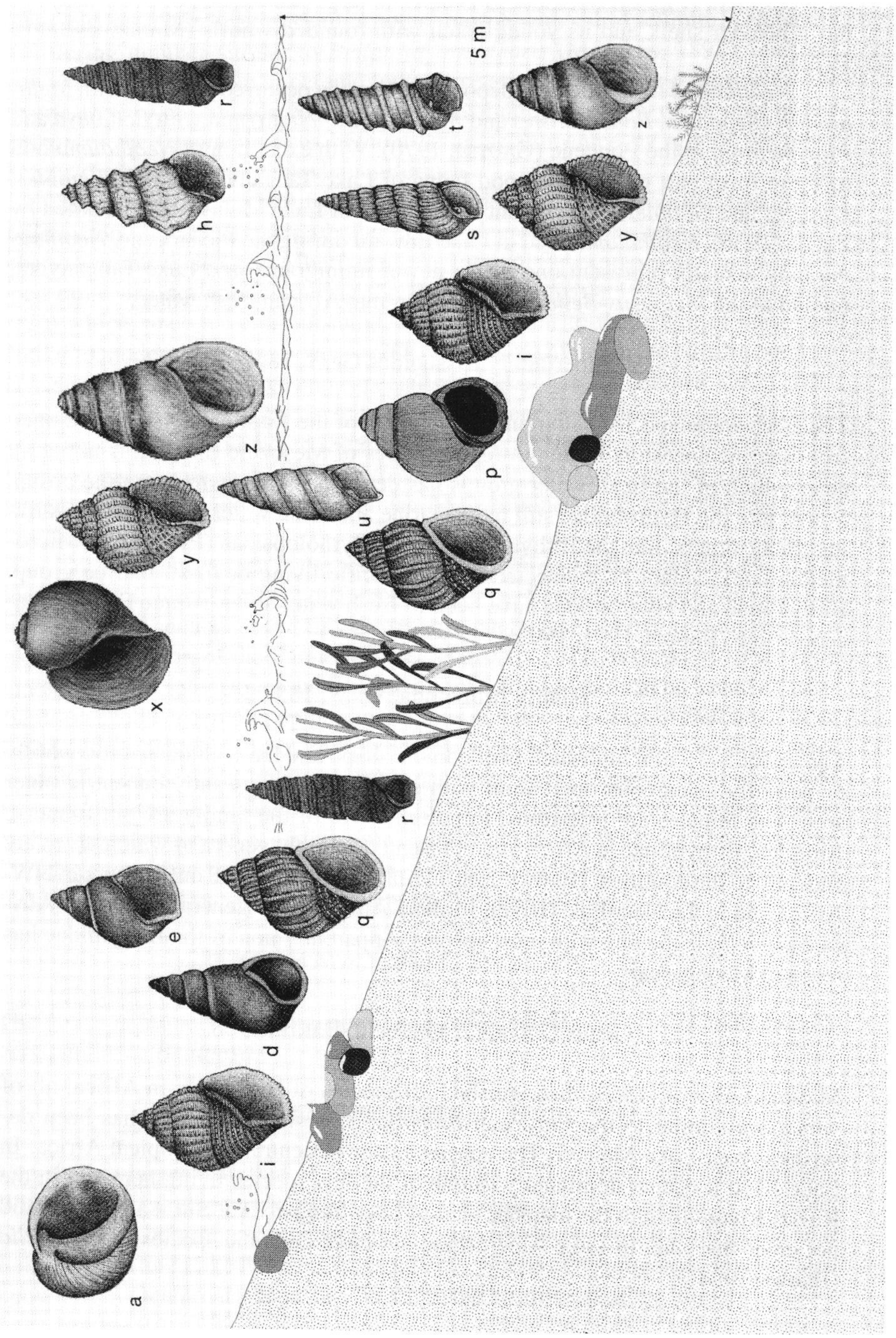
Genus *Bellamya* Jousseaume, 1886

Mandahl-Barth (1972) distinguished four species of *Bellamya* in Lake Malawi by the size of the hatching embryos as well as the size of the adult shell. The largest of these resembles *Neothauma* differing from it by a smaller radula and a thinner shell. Own observations suggest that only one species of *Bellamya* appears to live in several meters of water depth as well as in the marginal pools of the lake. It is also rather common in the Shire River and Lake Malombe. When these filter feeding gastropods grow to full size they begin to increase shell thickness. Such thickened shells have a much higher potential of being preserved on and in the lake sediment than the thin shells of the juveniles. Thick shells, thus, cover scoured lake bottoms while thin and juvenile shells have disappeared due to dissolution. Sandy bottom as well as muddy bottom is settled, and among plant growths individuals of this species are common as well. Fully grown shells usually carry a rounded bodywhorl and bear a narrow open umbilicus. Younger shells commonly show a basal corner and no umbilicus. There is much variation in apical shell angle as well as the presence of spiral ribs, which usually are weakly developed. The most commonly observed morphologic variety near Salima, Cape McLear, and Monkey Bay, and the southern lake end is that with two folds found on the shell flank, one weaker one just below the suture and a stronger one where the flank ends and the base begins. An optimum in shell size and shell thickness was observed in animals living on sandy bottom in two to five meters depth. Smooth and fine shell surfaces are noted on individuals that live in mud and muddy fine sand, while individuals in coarse sand and among plants are more commonly corroded. Corrosion is usually less pronounced than at the shells of accompanying *Lanistes* in the plant substrate, probably due to the more stable position during feeding in *Viviparus*, while *Lanistes* moves about much during its food gathering trips.

Bellamya capillata (Frauenfeld, 1865)

This species with rounded whorls has been called *Viviparus unicolor* Olivier, 1804 by Newton (1910) which actually represents a species from the Nile. It was transferred to the genus *Bellamya* by Gautier (1970). Shells of individuals from Lake Malawi whether fossil or recent can not be distinguished with certainty from the species living in the Nile. Thus, Adam (1959) suggested that *B. unicolor* lives from the delta of the Nile to Lake Malawi, and that it is very similar to late Miocene and Pliocene Viviparidae from Serbia and the Pannonian Lake. *B. capillata* occurs throughout from the oldest bed of Chiwondo some four to three million years ago to the one living in the modern lake. Williamson (1985) suggested that the four recognized endemic species of *Bellamya* living in Lake Victoria all developed from *B. capillata* as well.

Mandahl-Barth (1972) differentiated in Lake Malawi the endemic *Bellamya robertsoni* (Frauenfeld, 1865) and *B. jeffreysii* (Frauenfeld, 1865) from *B. capillata* by having larger and heavier shells and larger shell young hatching. *B. ecclesi* (Crowley and Pain, 1964) is even larger than these and resembles *Neoth-*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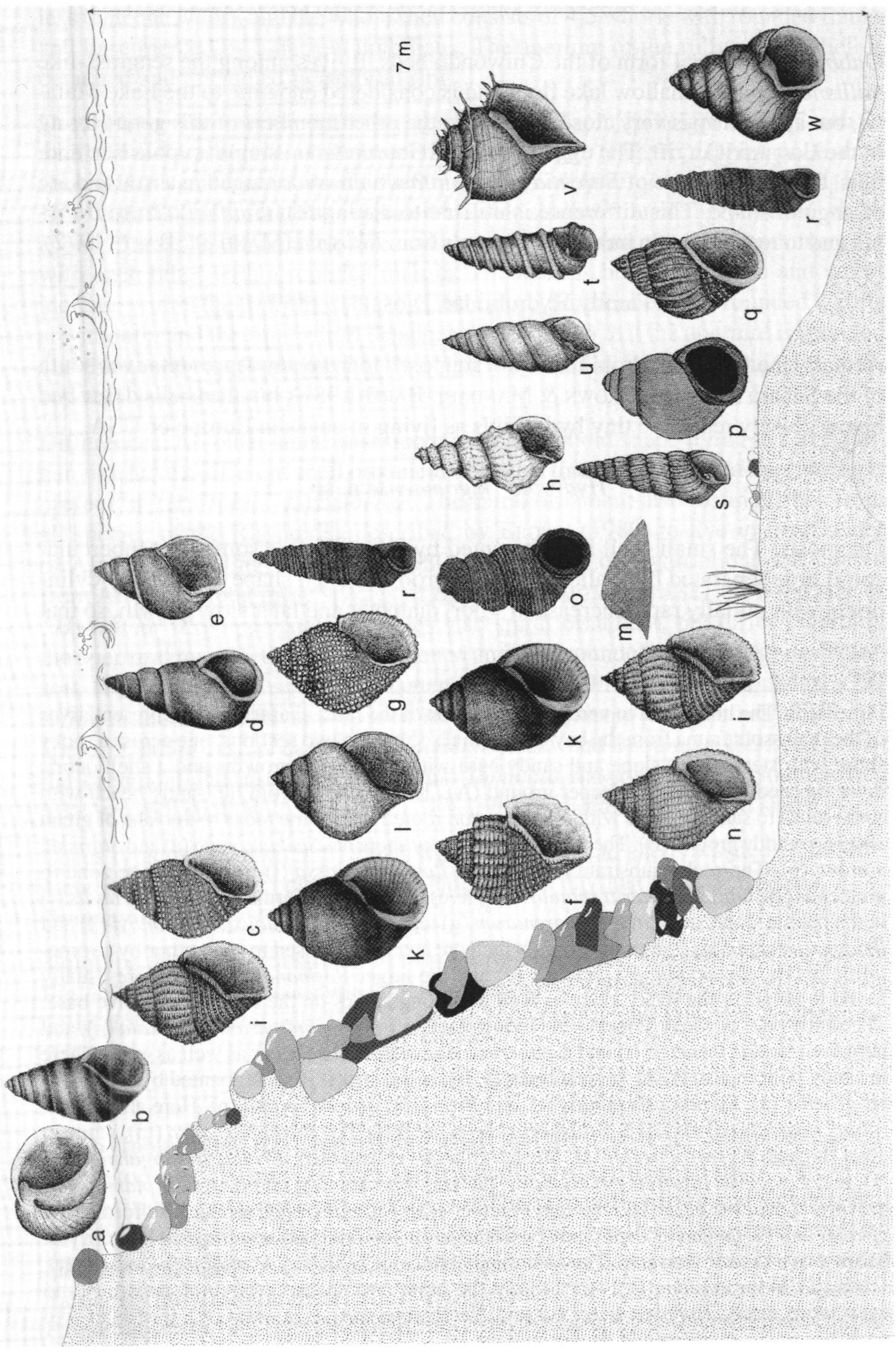
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The Syrnolopsidae are represented with the genera *Syrnolopsis*, *Anceya* and *Martelia*.

Genus *Syrnolopsis* Smith, 1880

The slender shells with up to 9 whorls are up to 9 mm high, but usually smaller around 7 mm in height. Ornament ranges from smooth or spirally ribbed or keeled. The umbilicus is narrow, and the columellar lip has a spiral fold that is more or less well visible in the oval aperture. The operculum is thin and paucispiral. The central tooth of the radula is almost as long as wide. Its frontal cutting edge carries many quite irregular cusps, and its basal platform is of almost semicircular outline. The lateral tooth is of triangular shape with long posterior marginal extension and pointedly serrated upturned cutting edge. The marginal teeth are alike, with long flattened stalk and upturned spoon-like cutting edge with numerous cusps.

Glaubrecht & Bandel (1998) assumed that there is only one variable species, but a reevaluation of several hundreds of individuals from screened sediment revealed three different species or morphs that can best be separated by the initiation of ornament succeeding the embryonic first whorl. Only such individuals that had been living while collected were evaluated. *Syrnolopsis lacustris* has two keels appearing right with first begin of growth lines and with onset of the second whorl, *S. minima* has the appearance of a single median keel in the third whorl while the second whorl bears only growth lines, and *S. gracilis* has no spiral ornament in the early shell portion, while later on a spiral hump, a keel or a smooth whorl side feature the teleoconch. Regarding their occurrence on the soft bottom of the lake there are also differences. Pure sand and silty sand far from rocks or shell coquinas is preferably settled by *S. lacustris* with all its varieties. Where algal thickets are present and near to rocks, boulders, and shell debris *S. minima* becomes more common, and in areas with pebble and shell coquina near to rocky slopes or boulders *S. gracilis* is common together with *S. minima*. Individuals live within and on the first millimeters of sediment, from not far off the beach to greater depth than 10 m (Fig. 1 A, B).

Syrnolopsis lacustris Smith, 1880

The between 5 and 8 mm high and 1.5 to 2 mm wide shell consists of up to 8.5 smooth to spirally ribbed whorls. The only axial element of the ornament are growth lines. Numerous varieties and nearly all intermediate forms from almost smooth to totally spirally ornamented individuals are found, but all of them have two spiral keels or ribs on the second and third apical whorl (Plate 2 E, F). The number of spiral ribs constantly increases with the number of successive whorls, and on spirally ornamented shells there are up to six spiral keels to be found on the last whorl. Very commonly spiral ornament disappears from the fourth or any other further whorl onward. In adult shells there may be a small umbilical slit, or the last part of the whorl detaches from coiling and becomes free. The protoconch is weakly wrinkled or smooth and with one whorl measuring a little less than 0.2 mm across, a pattern of regular growth lines start in the begin and the first spiral keel appears in the middle of the second whorl (Plate 2G) (RIEDEL 1993, GLAUBRECHT & BANDEL 1998).

Differences: The ornamented second whorl distinguishes S. *lacustris* from the two other species, of which *S. minima* usually has a prominent keel on all teleoconch whorls starting within or after the third whorl, and *S. gracilis* is smooth or has a more rounded median ridge in late whorls. *S. lacustris* is slenderer than *S. minima* usually having one more whorl while *S. gracilis* is of similar shape and size.

Syrnolopsis minima BOURGUIGNAT, 1885

The slender shell consists of 7–8.5 whorls and is up to 6 mm long and 2 mm wide (Plate 3A). The keel of the ornament usually begins within the third whorl in median position and migrates into a position just above the suture (Plate 3 B). Commonly there is another, lower keel just below the suture that can more rarely increase in size until both keels are about of equal dimension. This subsutural keel can also be missing, and the main keel remains in median position throughout. In the adult whorl the aperture detaches from the spire and is free exhibiting a polygonal outline. The protoconch is smooth to slightly wrinkled and with one whorl measuring about 0.2 mm across, growth line pattern begins after one whorl without it, and the first spiral keel appears after three rounded whorls are completed (Plate 3B).

Differences: See *Syrnolopsis lacustris. S. lacustris* is very variable in size and ornament, but is usually quite distinct from *S. minima* with its strong spiral keel on each whorl of the teleoconch which appears later in ontogeny, not on the second, but in the end of the third whorl.

Syrnolopsis gracilis PILSBRY and BEQUAERT, 1927

The slender shell consists of 7–8.5 whorls and is between 4 and 6 mm long and up to 2 mm wide. The shell is not ornamented by spiral features and only by fine growth lines, or there may be a rounded or angulated swelling on the median whorl (Plate 2B), or whorls are weakly convex (Plate 2A). In the adult whorl the aperture detaches from the spire and is free exhibiting a rounded to slightly angular outline. The protoconch is delicately wrinkled for more than one whorl. The first whorl measures less than 0.2 mm across and a pattern of regular growth lines appears with 1.3 whorls (Plate 2 C, D). There is no spiral keel.

Difference: *Syrnolopsis gracilis* differs from *S. minima* by not having a sharp keel and never a subsutural spiral rib or keel. The absence of ribs on the early whorls also distinguishes from *S. lacustris*, which may grow to larger size and develop a much more detached aperture on fully grown specimens.

Genus *Anceya* Bourguignat, 1885

The slender shell with 8 to 12 whorls is 4 to 6 mm high, up to 2 mm wide and ornamented by strong axial ribs. A prominent columellar fold features the oval aperture. The edge to the base in fully grown specimens is usually formed by a carination. The operculum is paucispiral with a basal nucleus. The rachidian tooth of the radula has a concave anterior margin, 10 cusps on each side of the median denticle, and a V-shaped basal extension. The lateral tooth has numerous fine and finger-like cusps and a long lateral extension. Marginal teeth are alike and equipped with numerous cusps (Glaubrecht & Bandel 1998). It is not quite clear whether there is only one or more species within this genus. The type is *Anceya giraudi.*

Anceya giraudi Bourguignat, 1885

The turriform shell is ornamented by pronounced axial ribs which decrease in a number on successive whorls and become more widely spaced and more sinuous (Plate 1A). The shell is of light brownish to purplish coloration. The protoconch is almost smooth initially and reveals indistinct fine spiral liration on most of the first whorl that measures about 0.25 mm in width (Plate 1B). Within the first quarter of the second whorl growth lines as well as the first closely spaced transverse ribs (about 40 on the third whorl) appear along with a spiral keel. The axial ribs form a reticulate pattern with initially two spiral keels, the lower of which lies on the angular edge to the base. From the fourth whorl only a single median keel is left, and on the fifth non at all, and the base is rounded. From the sixth whorl onward there are about 12 axial ribs on each whorl. There is a thickened apertural lip on fully grown shells, while the aperture of juveniles is thin.

Plate 1.

A. The turriform shell of *Anceya giraudi* is is ornamented by axial ribs and is 6 mm high.

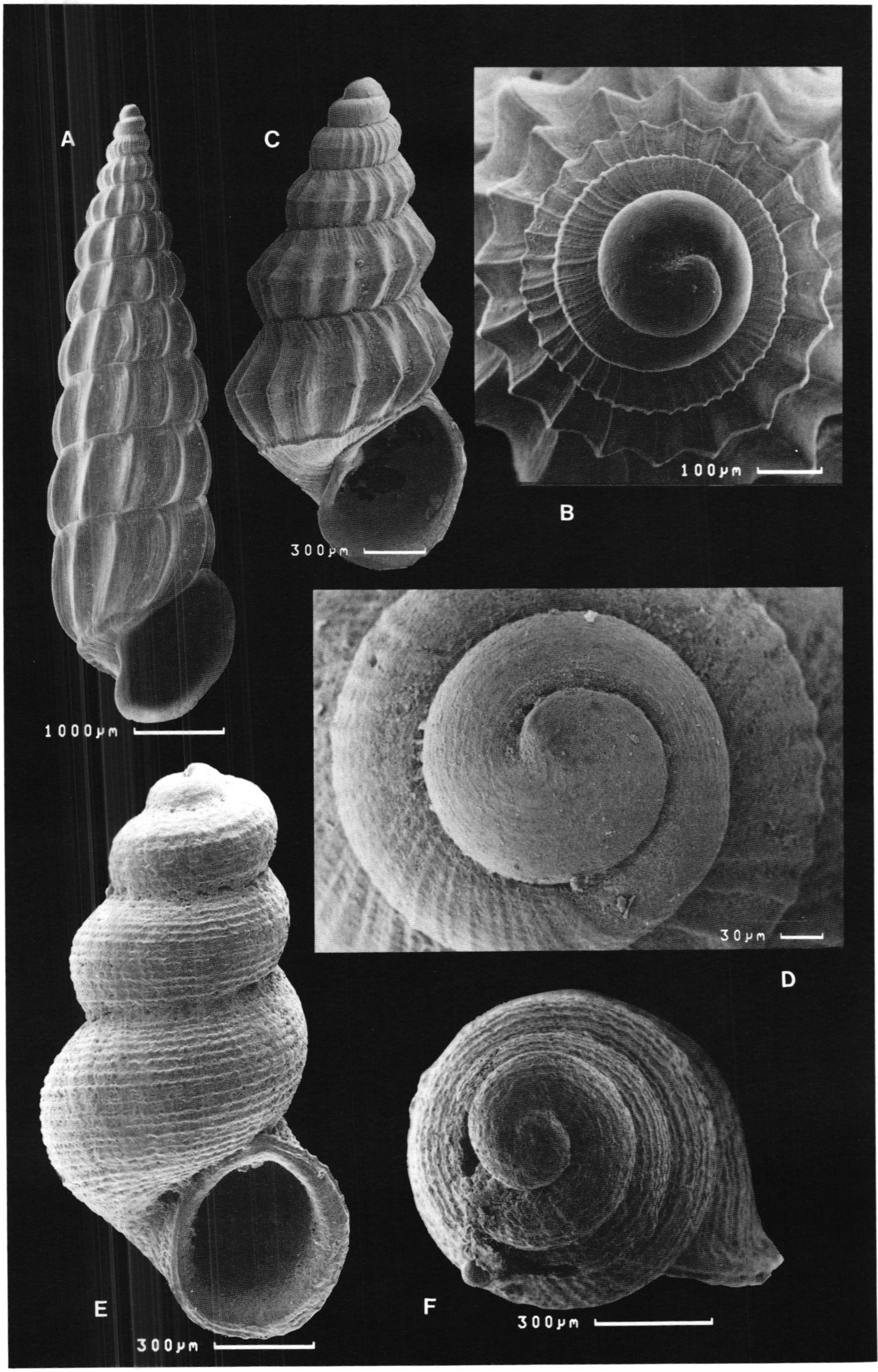
B. The protoconch of *Anceya giraudi* is almost smooth initially and measures about 0.25 mm in width. Within the second whorl growth lines and spaced transverse ribs appear.

C. The shell of *Martelia tanganyicensis* is 4 mm high.

D. The initial part of the protoconch of *Martelia tanganyicensis* is ornamented with spiral ridges and measures 0.2 mm in its first whorl.

E. "*Hydrobia*" *kigomaense* seen in apical view with 1,7 mm high shell from Kigoma. (Holotype)

F. The embryonic shell of "*Hydrobia*" *kigomaense* is smooth and consists of less than one whorl, and the teleoconch is 0,7 mm wide. (Paratype)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Difference and ecology: *Anceya* is of very characteristic shape and can not be mistaken with any other of the thalassoid species. It lives among macrophyllic algae that form thickets between rocks, and in algal thickets that cover rocks from below the zone of wave action to crevices between rocks as well as on gravel and deeper grounds. LELOUP (1953) reported this species to occur widespread to live down to 100 m of depth.

Genus *Martelia* DAUTZENBERG, 1908

The genus is monotypic. The operculum is very thin, translucent and paucispiral with excentrical nucleus near its base.

Martelia tanganyicensis DAUTZENBERG, 1908

The small shell grows up to 4 mm in height and 2 mm in width with about 6.5 strongly ribbed and convex whorls, separated by a depressed suture (Plate 1C). The oval aperture has thickened lips and bears a strong columellar fold. On each of the last three whorls there are about 13 axial ribs with their median portion enlarged to form a carina, and their marginal portions ending before they reach the sutures. The initial part of the protoconch is ornamented with about 14 fine spiral ridges which continue for 1.3 whorls until growth lines appear (Plate 1D). Later numerous axial ribs are added forming a reticulate pattern which is characteristic on the first 2.5 whorls. From here on the axial ribs dominate. The diameter of the first whorl is 0.2 mm (RIEDEL 1993).

Difference and ecology: The juvenile shell portion with its numerous axial ribs resembles that of *Anceya,* but later ornament and shell shape differs in *Martelia tanganyicensis,* so it cannot be misidentified. Living individuals were encountered in about 3 to 5 m depth among macrophyllic algae and among algal thickets that cover rocks and pebbles from below wave base (Fig. 1A, B). Small individuals also occur below stones just below the wave battened zone together with the juveniles of *Spekia* (see below).

Superfamily Cerithioidea FERRUSSAC, 1819

The Cerithioidea of fresh water have developed from marine ancestors, and most probably the different families of fresh water species derived from different taxonomic units of marine species. In the case of the Thiaridae this has been shown (HOUBRICK 1988), and here the marine sister family, the Planaxidae has been recognized (BANDEL & KOWALKE 1997). There are still members of the taxon Thiaridae that have a marine portion of their ontogeny by spending the larval part of their ontogeny in the sea (BANDEL & RIEDEL 1998). A similar case is also noted in the Melanopsidae where one marine species has been noted among several fresh water species from the Late Cretaceous of northern Spain (BANDEL 1993, BANDEL & RIEDEL 1994, KOWALKE & BANDEL 1996). *Zemelanopsis* FINLEY, 1927 from New

Zealand still has planktotrophic marine veliger larvae (Pilkington 1976) while adults prefer fresh water. In the other families of fresh water Cerithioidea the marine sister group is not yet recognized with any certainty, but their derival in the fresh water environment at different times in geological history as been documented (Bandel 1991, 1993). According to Brown (1980) about 25 limnic genera of Cerithioidea may be recognized in Africa, 22 confined to this continent and 16 endemic to Lake Tanganyika.

Family Pleuroceridae Fischer, 1885

The family Pleuroceridae represent fresh water Cerithioidea which have not yet been well differentiated and exclude the Melanopsidae H. and A. Adam's, 1854 and Thiaridae Troschel, 1857.

Subfamily Lavigeriinae Thiele, 1925

Bandel & Glaubrecht (1998) suggested to regard the Lavigeriinae as a monophyletic group that holds the lacustrine genus *Lavigeria* from Lake Tanganyika. Its species are related to the fluviatile *Potadomoides* Leloup, 1953 as suggested by Leloup (1953) and Brown (1980). Both genera exhibit a paucispiral operculum and distinct radula morphology as well as protoconch characters that differentiates *Lavigeria* from all other Tanganyikan gastropods especially the conchologically very similar Paramelaniinae. *Lavigeria* and *Potadomoides* are viviparous uterine brooders (Leloup 1953). Whether *Potadomoides* has evolved from *Lavigeria* stock by leaving Lake Tanganyika or whether the former represents a relict of the ancient river-living group from which *Lavigeria* arose is unknown. The occurrence of species of *Potadomoides* in the lower course of the Melagarasi River and the waters connected to the outflow of Lake Tanganyika (the rivers Luvua and Lualaba) could indicate that it actually evolved from gastropods of Lake Tanganyika. This would be a very interesting problem to solve, since we know of no certain case in which an endemic lake gastropod has given rise to a group living outside of an old lake. The question is still open whether it is possible for such a species to adopt to another type of environment as for example that of a river, as is the case with *Potadomoides*.

Genus *Lavigeria* Bourguignat, 1888

Shells are medium to large, and among the different species reach a size ranging between 8 and to 32 mm height when fully grown. They are solid, ovate or elongated and of conical shape. Regarding the ornament axial elements generally predominating over spiral cords or ridges. These axial ribs are especially pronounced on the apical half of the whorl, while spiral cords predominate basally. The aperture is oval, and the operculum is lamellar, paucispiral to subspiral with excentric nucleus near the base. *Lavigeria* broods embryos until they are miniature adults and hatch crawling. The radula has a characteristic central tooth, and the species of *Lavigeria* show only minute differences in their dentition (BANDEL & GLAUBRECHT 1998).

Six different species were encountered in the bay of Kigoma, each one of them occupying a specific environment. *Lavigeria grandis* exhibit a typical preference for the deeper zone at the rocky slope. It was found only as dead shells among the fused rocks in about 6–7 meters in the rocky slope. To this location they could not have been transported as the washed up shells on the beach with rocky lake bottom below it. *L. nassa* is the most abundant representative found on nearly all hard substrates in the upper littoral zone of Lake Tanganyika. Its juveniles commonly prefer the lower surface of rocks or live in crevices, while fully grown individuals remain on the surface of rocks and boulders among algal covers. They are very common just below wave base to an unknown depth. The operculum is stunted in growth when the individuals of *L. nassa* have reached medium size, and in fully grown individuals it is smaller than half the apertural width. These older individuals also have a wider aperture and cling to the rocks. While the shells of juvenile individuals are rarely covered by algal thickets, those of older individuals usually are totally covered and camouflaged with the surface of the rocks. *L. nassa* changes its strategy from a mobile juvenile hiding from predating fish and crabs in crevices and under rocks to large thick-shelled adults that hold onto the rock so tightly that they cannot easily be picked off either by fish and be crushed by crabs.

Plate 2.

A. *Syrnolopis gracilis* with slender shell that is 5 mm long and has rounded whorls and an aperture that detaches from the spire.

B. *Syrnolopis gracilis* with slender, 6 mm long shell has roundly angulated whorl sides and a basal edge.

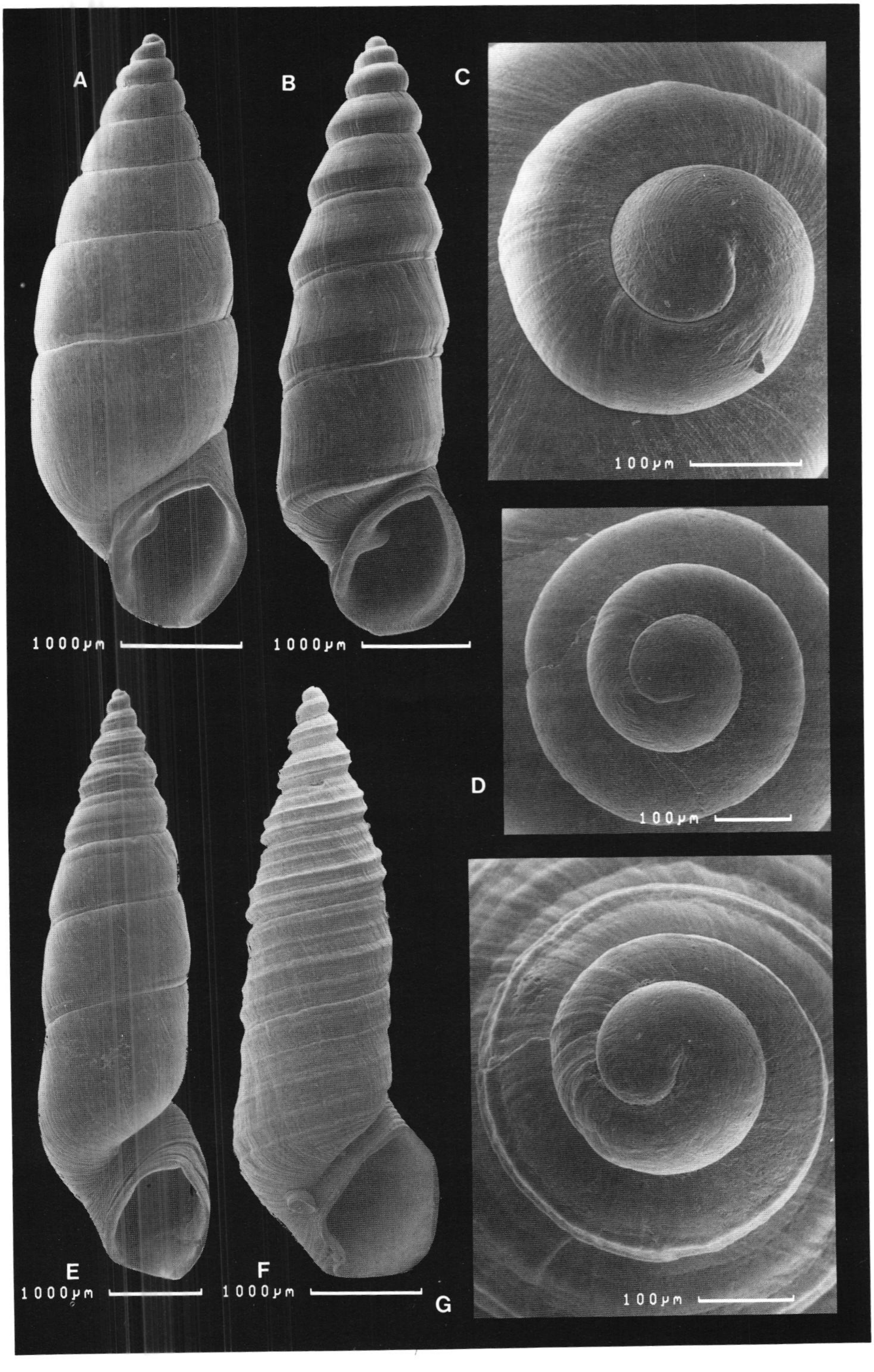
C. The protoconch of *Syrnolopis gracilis* is delicately wrinkled for more than one whorl. The first whorl measures less than 0,2 mm across, and a pattern of regular growth lines appears with 1.3 whorls.

D. The protoconch of *Syrnolopis gracilis* merges with the teleoconch and there is no spiral keel.

E. The shell of *Syrnolopsis lacustris* is 6 mm high, and in this variety it has smooth late whorls and spirally ornamented ones following the protoconch.

F. The shell of *Syrnolopsis lacustris* is 5 mm high, and in this variety has spiral ornament throughout and detached last whorl.

G. The protoconch of *Syrnolopsis lacustris* is weakly wrinkled with one whorl measuring a little less than 0.2 mm across, a pattern of regular growth lines starts in the begin, and the first spiral keel appears in the middle of the second whorl.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While *L. nassa* is found on rocks, *L. livingstoniana* inhabits exclusively sand and soft silty substrate from near-coast to quite some depth. *Lavigeria spinulosa* lives on rocks and boulders within and just below the wave agitated zone with preference for shallower water, while *L. arenarum* lives below about 3 m, also on rocks. *L. arenarum* prefers the underside of stones where rocks are fused by calcareous material that has been deposited by microbial mats forming stromatolitic crusts while *L. spinulosa* also moves on the surface. *Lavigeria littoralis* lives on plants like *Potamogeton* in the shallow water off the sandy beach and also where macrophyllic algae grow on muddy spots between rocks in 3–5 m depth (Fig. 1A, B).

Fossils of *Lavigeria* have been described from Quaternary deposits next to the modern shallow Lake Rukwa by Cox (1939). This lake lies about 150 km to the SW of Lake Tanganyika and is connected to it by a depression containing the Mweru Swamp. This fossil *Lavigeria* called *Edgaria stockleyi* has an illustrated holotype closely resembling shells of modern *L. nassa* (Cox 1939, Pl. 15, fig. 3) while the other specimen attributed to the same species is very close in shape to *Lavigeria livingstoniana* (Cox 1939, Pl. 15, fig. 4). The other two taxa described by Cox (1939) probably represent one and the same species of *Lavigeria* that differs from those living in the lake now by having a basal ridge creating a pseudumbilicus. Such a feature of the shell is not known from the 6 species found to live in Lake Tanganyiaka at present.

Lavigeria nassa (Woodward, 1859)

The shell grows to more than 2 cm in height and a little less than 1,5 cm in width and is of ovate shape with a spire that is shorter than the aperture. Its ornament

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Plate 3.

A. The shell of *Syrnolopsis minima* Bourguignat, 1885 consists of 7–8.5 whorls and is 6 mm long and 2 mm wide.

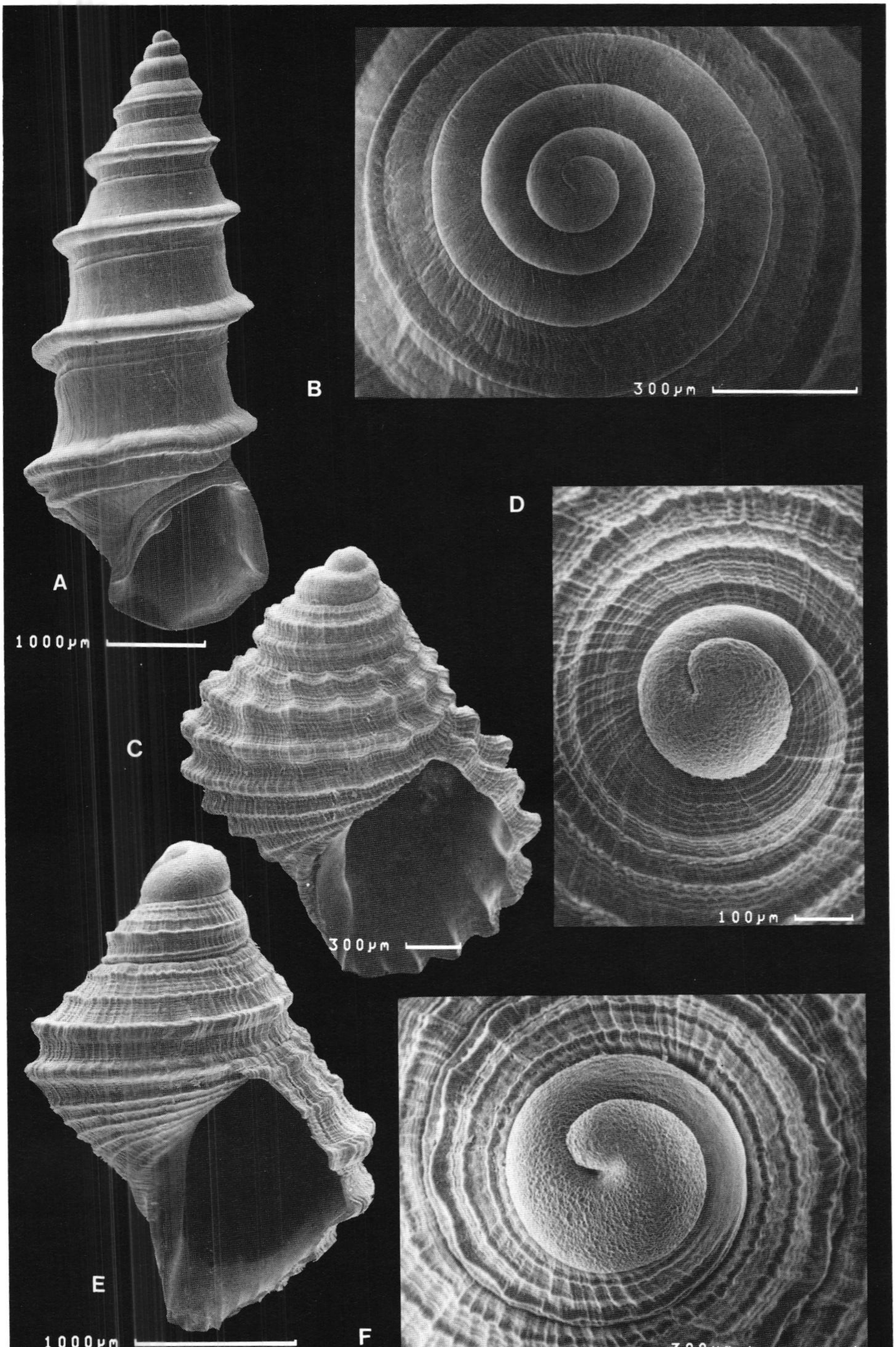
B. The keel of the ornament of *Syrnolopsis minima* usually begins within the third whorl in median position and migrates into a position just above the suture. Apical view.

C. The juvenile shell of *Lavigeria arenarum* is 3 mm high and displays a conical shell shape with rounded base.

D. The protoconch of *Lavigeria arenarum* with about 0.3 mm large first whorl demonstrates the rapid and abrupt initiation of adult-like ornament.

E. The juvenile shell of *Lavigeria nassa* with 3 mm height has an upright initial part that is succeeded by a whorl with growth lines and spiral ribs of which the one on the basal corner is the strongest.

F. The protoconch of *Lavigeria nassa* with about 0,5 mm wide first whorl and ornament of ribs becoming increasingly more pronounced on subsequent whorls.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consists of numerous axial ribs on the upper flank of the whorl and spiral grooves and ridges on the base. The shell is mostly brown, and often shows two dark bands especially well visible on the last whorl. Females may hold up to 25 shelled juveniles which have a shell diameter of about 1.3 mm when they hatch with the first whorl measuring 0.5 mm across (Plate 3 E, F). The ornament of the embryonic shell consists of wrinkles and folds on the first 1.25 whorls and is underlain by coarse crystallites creating a milk-glass impression. The upright initial part is succeeded by more or less regularly spaced growth lines and initiation of spiral ribs of which the one on the basal corner is the strongest. These ribs become increasingly more pronounced on subsequent whorls. With 2.5 whorls up to 8–10 prominent spiral ribs are present forming tubercular expansions when they cross collabral elements, thus, forming a reticulate ornament. Hatching occurs when the third whorl is forming.

Differences: The aperture is slightly sinuated basally, but lacks the denticle-like protrusion as is present in *L. grandis*. The embryonic shell and early juvenile shell differs from that of the other five species of which this shell is known (still unknown form *L. grandis*). *L. nassa* has the largest initial part, and from the third whorl onward a sharp angulation between whorl side and base is formed which is not found in the other species.

Lavigeria grandis (Smith, 1881)

The fully grown shell measures almost 3 cm in height and a little more than 2 cm in width, exhibits a staircase-like spire and whorls with apically protruding axial ribs (Brown 1994, Bandel & Glaubrecht 1998). There are up to six convex whorls, flattened near the suture creating a step-like spire. The prominent sculpture varies from spiral ridges to strongly tuberculate ribs. The lower lip of the aperture is bluntly angular below the twisted columella. A prominent tubercular edge is clearly visible on the columella that creates this angular appearance. This denticle-like protrusion is most prominent at the middle or lower third of the columellar side of the aperture.

Differences: Among these six species of *Lavigeria*, *L. grandis* has the most characteristic shell differing from all other congeneric forms by ornament and large size. The large *L. grandis* differs from the smaller *L. nassa* in that the latter lacks the very prominent tubercular edge on the columella which gives the aperture of *L. grandis* a somewhat angular appearance.

Lavigeria livingstoniana (Giraud, 1885)

The elongated and slender shell measures about 12 mm in height and 7 mm in width and consists of 5 whorls. Ornament consists of about 15 strong and elevated axial ribs on the last whorl which dominate the whorls of the spire. Basally spiral cords appear that are interrupted by the axial elements. In fully grown individuals the operculum is little smaller than the aperture; thus, when withdrawn into the shell it seals the aperture tightly right behind the outer lip, and when the animal is crawling, the operculum is covered by an epipodial sheet. As soon as the crawling juveniles leave the uterine brood pouch of the female with three whorls completed they live in the same environment as the adults. The initial portion of the protoconch is quite smooth, and diameter of the first whorl is about 0.4 mm. Growth lines start at the end of the first whorl, and with 1.3 whorls two broad spiral ribs appear that grade into the five spiral ribs on subsequent whorls. Together with smaller spiral ridges they form a reticulate ornament with the growth lines (Plate 4 E, F).

Differences: *L. livingstoniana* has smaller, slenderer and more elongated shells than the other species of *Lavigeria*. The shells of *L. spinulosa* are more elongated and slender than that of *L. nassa*, but exhibit a shape similar to *L. livingstoniana*. However, the latter have an ornament dominated by strong and widely spaced axial ribs, whereas *L. spinulosa* is characterized by its regular nodulous sculpture. The protoconch of *L. livingstoniana* is quite unique among *Lavigeria* by having a small and low intial portion and axial ribs, and nodes appear on the third whorl and not on the second as in *L. spinulosa*. The rounded shape of the shell of the hatching young distinguishes well from *L. nassa*.

Lavigeria spinulosa (Bourguignat, 1885)

The shell with six whorls is about 13.5 mm high and 8 mm wide. It is black and has a very regular ornament of white-tipped tubercles where spiral ridges are regularly intersected by axial ribs. The aperture is callous and white, contrasting the violet *L. arenarum*. The operculum in fully grown individuals seals the shell quite some way behind the aperture. The embryonic shell is covered by a strong groove and wrinkle pattern to about 1.2 whorls when growth lines start, and three strong spiral ribs initiate with the central one first. The first whorl measures about 0.4 mm across. Spiral ribs become more numerous on subsequent whorls until strong axial ribs cross over, forming a characteristic reticulate ornament that dominates the shell from the end of the second whorl onward. (Plate 4 A, B).

Differences: *L. spinulosa* and *L. arenarum* have darker shells than the other species of *Lavigeria*, and *L. arenarum* is purple inside the aperture, which is not the case in *L. spinulosa* (within dead shells this color difference fades rapidly). The shell of *L. spinulosa* is more elongated and slenderer than that of *L. nassa*, but exhibits a shape similar to *L. livingstoniana*. However, the latter have an ornament dominated by strong and widely spaced axial ribs, whereas *L. spinulosa* is characterized by its regular nodulous sculpture. Regarding protoconch morphology *L. spinulosa* is rather similar to that of *L. littoralis* and differs from that of *L. nassa* with regard to smaller size of the initial whorls and more rounded transition to the base. Regarding *L. arenarum* the first whorl is larger in *L. spinulosa,* and ornamental pattern of the teleoconch begins more rapidly in the former.

Lavigeria arenarum (BOURGUIGNAT, 1885)

The shell grows to 8 mm height and 6 mm width, and therefore appears almost globular with the last of the six whorls quite large. Ornament consists of about 8 prominent spiral ridges, crossed by axial ribs, creating a regularly ornament with white tipped tubercles on a reddish-brown shell. The largely holostome aperture has a violet tinge which is very strong in living animals, but fades in dried shells. The protoconch demonstrates an upright first whorl that is smaller than that of *L. spinulosa*. It is succeeded by an ornament of three prominent spiral keels and numerous minor ones which feature the second whorl measuring only 0.3 mm across before, on the third whorl, axial ribs appear and form nodes where they cross the keels (Plate 3 C, D).

Differences: The shell of *L. arenarum* is much smaller, more globular and, thus, with wider apical angle than e.g. the shell of *L. spinulosa*, to which it resembles in sculpture. However, the unique violet colour of the aperture and especially of the callus distinguishes *L. arenarum* from other species of *Lavigeria*. The protoconch of *L. arenarum* is also quite characteristic and distinguished from that of *L. spinulosa* in having a smaller first whorl and tubercles appearing on the third whorl, while in *L. spinulosa* tubercles form later. *L. nassa* differs with regard to the size of the initial shell part which is larger, and the angulation formed from the third whorl

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Plate 4.

A. The juvenile shell of *Lavigeria spinulosa* is about 2 mm high with the initial portion rounded. It differs from that of *L. nassa* with regard to a more rounded transition to the base.

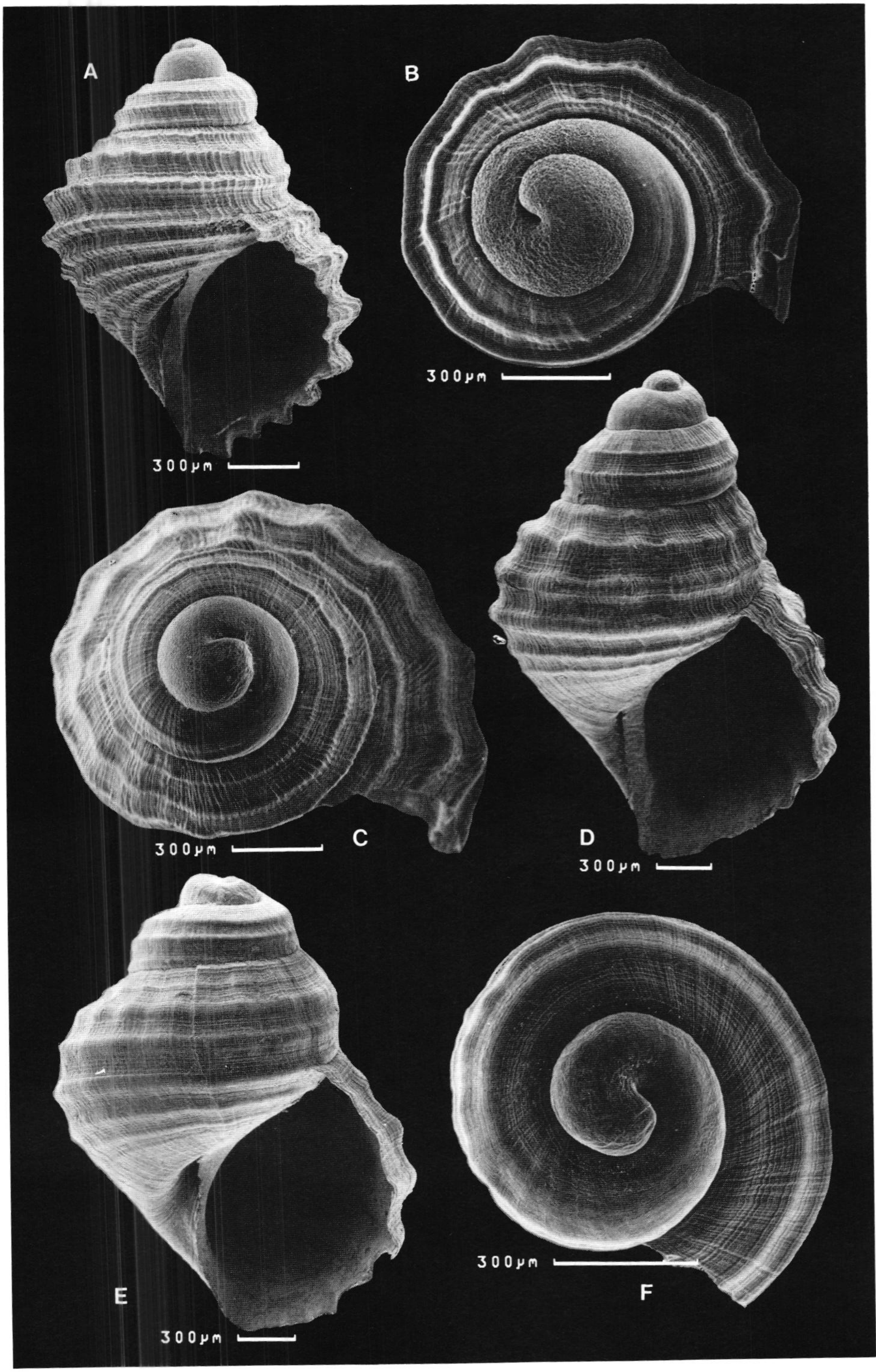
B. The embryonic shell of *Lavigeria spinulosa* is strongly wrinkled to about 1.2 whorls when growth lines start, and three strong spiral ribs initiate with the central one first. The first whorl measures a little less than 0.5 mm in width. The protoconch is similar to that of *L. littoralis*.

C. The juvenile shell of *Lavigeria littoralis* is 1.5 mm wide with 0.4 mm wide first whorl that is strongly wrinkled in the first 1.2 whorls before growth lines start.

D. The juvenile shell of *Lavigeria littoralis* is 3 mm high with four spiral ribs initiating after the smooth initial part and becoming increasingly elevated, with axial ridges crossing, forming a reticulated ornament with elevated tubercles at cross-points. It differs from the early shell of *L. nassa* by having a smaller intitial part and forming no strong angulation on the third whorl.

E. The juvenile shell of *Lavigeria livingstoniana* measures about 3 mm in height and represents a crawling juvenile as it leave the uterine brood pouch of the female. The protoconch has a small and low intial portion, and the rounded shape of the shell of the hatching young distinguishes well from *L. nassa*.

F. The initial portion of the protoconch is of *Lavigeria livingstoniana* has a diameter of the first whorl of about 0.4 mm. Growth lines start at the end of the first whorl, and with 1.3 whorls two broad spiral ribs appear.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onward. *L. livingstoniana* has a more rounded protoconch with low down initial whorl differing from the triangular shape of *L. arenarum.*

Lavigeria littoralis (Bourguignat, 1888)

The up to 13 mm high and a little less than 8 mm wide shell is elongated to ovate with slightly curved sides and depressed sutures. The ornament is regularly nodulous with axial ribs crossed by spiral grooves and spiral ridges predominating on the basis. The aperture has a white callus. The protoconch has a 0.4 mm wide first whorl and is strongly wrinkled in the first 1.2 whorls before growth lines start. Then four spiral ribs initiate which become increasingly elevated, with axial ridges crossing in the third and following whorls, forming a reticulated ornament with elevated tubercles at cross-points (Plate 4C, D).

Differences: *Lavigeria littoralis* reaches only the size of a half grown *L. nassa,* and its shell is significantly thinner and has no thickened apertural lip such as usually found in *L. nassa.* Shells of the latter species are generally broader than those of *L. littoralis*. Also the light-brown color in *L. littoralis* is distinct from the mostly darker *L. nassa.* Regarding the shape of the protoconch *L. littoralis* is well differentiated from *L. nassa* by having a smaller initial part and forming no strong angulation on the third whorl, but it is very close to that of *L. spinulosa* to which, however, is little resemblance when the shell is more grown.

Tiphobiinae n. subfam.

Diagnosis: Tiphobiinae are represented by a large thin shelled monospecific species that broods its young and has an anteriorly elongated aperture. The brooding mode, as well as the rather peculiar shell morphology with apertural spout distinguishes *Tiphobia* rather well from *Paramelania*, and thus, from the only certain save genus of the Paramelaniinae. But little is known of the life, anatomy, and origin of *Tiphobia,* so the subfamiliar status of the genus remains uncertain. *Lavigeria* representing the Lavergeriinae also retains its young in a uterine brood pouch until they hatch but has rather different shell shape and much more solid shell construction. *Lavigeria* has no apertural spout, as is characteristic for *Tiphobia*, but rounded margins of the outer lip. The thick shell and rounded apertural outline is also found in case of *Lavigeria livingstoniana* that lives on and in soft substrate as is the case in *Tiphobia.*

Genus *Tiphobia* Smith, 1880

The genus comprises only one species that is endemic to Lake Tanganyika.

Tiphobia horei Smith, 1880

The shell is large (about 35 X 25 mm) and thin (specimen encountered on the beach in Ujuji), and a half grown specimen was encountered in the sediment screened from near the beach of the bay near Kigoma (Fig. 1A). Only a few kilometres to the south, at the landing place for fishing boats at the beach of Ujiji, shells are common and apparently *Tiphobia* lives here together with *Neothauma* not far from the beach on muddy sand bottom. The spines on the apical corner of the whorl as well as the elongated columellar lip of the aperture are distinctive and distinguish this species from all other thalassoid ones. *Tiphobia* has been reported to be a uterine brooder (see BROWN 1980). The protoconch sculpture of *Tiphobia* was figured by RIEDEL (1993) and reveals the distinct wrinkle pattern indicating a very late calcification of the shell as in *Lavigeria*.

Subfamily Paramelaniinae THIELE, 1925

The subfamily Paramelaniinae as originally suggested by THIELE (1929) in his tribus Paramelanieae includes not only *Paramelania,* but also *Reymondia*, *Spekia*, *Bridauxia*, *Tiphobia* and *Tanganyicia*. The latter five are here placed into different subfamilies, which according to shell shape and radula morphology are not closely related to *Paramelania*. The fossil *Pyrgulifera* may belong to the stem group of the Paramelaniinae, as was suggested by BANDEL & RIEDEL (1994) and BANDEL & GLAUBRECHT (1998). Whether *Myosorelloides*, *Bathanalia*, *Limnotrochus* and *Chytra* belong in close taxonomic relation to *Paramelania* still has to be elucidated.

Genus *Paramelania* E.A.SMITH, 1881

The shell is large, solid, ovate to narrowly conic. Its sculpture is variable with axial ribs and spiral cords. The aperture is ovate, holostome, with strong, white callus and marginal thickening. The operculum is concentric with spiral nucleus. The radula is taenioglossate, small, with central tooth that has a v-shaped basal platform and multiple cusped anterior cutting edge. The lateral tooth has a long outer posterior extension and numerous prominent cusps on its cutting edge that is continuous on the frontal margin of the extension. The inner and outer marginal teeth are quite similar to each other.

In general, the shell of *Paramelania* is very similar to that of *Lavigeria,* but always has a holostome aperture with smooth margin. The concentric operculum, the shape of the radular teeth and also the absence of a brood pouch clearly differentiate *Paramelania* from *Lavigeria*.

Paramelania crassigranulata (SMITH, 1881)

The white to light yellow, about 19 mm high and 12 mm wide shell with 9 whorls has an evenly nodular ornament of axial ribs crossed by about 14 spiral cords on the last whorl. The second and third whorl is ornamented by a reticulate pattern, formed by axial growth lines which are crossed by two spiral ribs. Later the number of spiral ribs increases, and axial ribs predominate. The aperture is ovate, holostome with thickened white margin and columellar callus. The operculum is brown and concentric with spiral nucleus, and the animal can withdraw deeply into the shell before it tightly seals it.

Differences and ecology: *Paramelania damoni* (Smith, 1881) is larger measuring 35 mm in heigth and 21 mm in width, with 10 whorls which are ornamented in a similar way to *P. crassigranulata* (Smith 1881, Cohen 1988, Brown 1994). The ornament is distinguished by a sutural step and a subsutural row of low spines. *P. damoni* is very variable in shape, and its stepped spire resembles to some extent *Lavigeria grandis*, but differs by the character of the aperture. According to Brown (1994) *Paramelania iridescens* (Moore, 1898) has a more slender shell than *P. damoni* and a more uniformly nodular sculpture as in *P. crassigranulata*.

Paramelania crassigranulata was found in the deeper zone at the rocky slope cooccurring with *Lavigeria grandis*. While *L. grandis* was only encountered as dead shells among the fused rocks in about 6–7 meters, *Paramelania* was found alive among the sandy patches within the rocky slope and among *Vallisneria* rooted in the sand down to about 3–8 meters of depth. Here the snails bury in the sand or move among the plants (Fig. 1A).

Genus *Mysorelloides* Leloup, 1953

Mysorelloides multisulcata (Bourguignat, 1888)

The about 10 mm high shell is ovate with conical spire and strong spiral ridges. Only a single fragmentary shell with 5.5 whorls and 5 mm height and 4 mm width was discovered in the shell debris below the rock slope in 3–5 m of depth near Kigoma. The protoconch was illustrated and described by Riedel (1993). On the second whorl two spiral ribs appear inserting in the area with first growth lines that succeed the initial shell whorl. The spiral ribs increase in number and form acute ridges separated from each other by rounded furrows. The base is flattened and pierced by a rounded umbilicus that is surrounded by two minor spiral ribs. The aperture is of circular shape. The operculum is corneous and spiral (Brown 1980). The radula of *Mysorelloides multisulcata* resembles that of *Chytra kirkii, Limnotrochus thomsoni* and both *Bathanalia* species (Leloup 1953) among the thalassoid gastropods. The central tooth accordingly has numerous fine cusps on its cutting edge.

Differences: The conical shell shape with open umbilicus of *Mysorelloides multisulcata* differs from that of all other thallassoid species that were encountered in the bay near Kigoma. It resembles most that of *Bathanalia,* but has no row of spines in its ornament, while the whorls in *Limnotrochus* and *Chytra* are flattened and not of convex shape as in *Mysorelloides.*

Genus *Bathanalia* Moore, 1898

The two species recognized in the genus *Bathanalia* (*B. howesii* Moore, 1898 and *B. straeleni* Leloup, 1953) are 12 or 25 mm high and appear to be restricted to the southern shores of Lake Tanganyika (Brown 1980). They were not encountered in the bay near Kigoma, and differ from *Mysorelloides*, *Chytra* and *Limnotrochus* by having a spinous or tuberculate keel on the middle whorl flank. *Bathanalia* shells resemble those of the latter species by also having a rounded open umbilicus on the flattened base.

Genus *Chytra* MOORE, 1897

The monotypical genus is endemic in Lake Tanganyika.

Chytra kirki (SMITH, 1880)

The 15 mm high shell with conical shape and rounded aperture resembles that of *Myosorelloides* and *Limnotrochus* in ornament, shell thickness and presence of an open umbilicus. *Chytra* differs by having flattened sides, a conical shape with as great width as height. *Chytra kirkii* and *Limnotrochus thomsoni* are reported to be propably oviparous (see BROWN 1980). RIEDEL (1993) illustrated the embryonic whorls for both species and refrained from commenting on their reproductive mode that could not be derived from the evaluation of the protoconch sculpture.

Genus *Limnotrochus* E. SMITH, 1880

The monotypical genus is endemic in Lake Tanganyika.

Limnotrochus thomsoni SMITH, 1880

The 19 mm high and 14 mm wide shell has conical shape like *Chytra* to which it resembles, but differs by being higher than wide. *Limnotrochus*, *Chytra*, *Mysorelloides* and *Bathanalia* are similar to each other in shell shape and may represent a unit of the thalassoid gastropods. With current knowledge of their ontogeny, ecology and anatomy it is not safe to assume to which one of the here distinguished units they may belong. It is also possible that they are related to *Potadoma* SWAINSON, 1840 which lives in forest streams in tropical West Africa and has been living in the Rift area about 3,5 Million years ago (WILLIAMSON 1985) or to *Melanatria* BOWDICH, 1822 that lives in mountain streams in forests of Madagascar.

Spekiinae n. subfam.

Diagnosis: The shell shape is variable, hydrobiform to neritiform, and ornament consists of well visible or microscopic spiral lirae, or the surface is predominantly smooth. The early teleoconch has a spiral rib. The character uniting the members of the genera *Spekia*, *Stormsia* and *Bridouxia* is the shape of the central tooth of the radula which has a characteristic median gap in its cutting edge.

Genus *Spekia* BOURGUIGNAT, 1879

Spekia is characterized by its smooth, grey, banded and depressed, neritiform shell that differs from the species of *Bridouxia* with similar central tooth, but rounded trochiform shell shape. Only *Bridouxia rotundata* is also of depressed shape, but has a conical spire and is much smaller when fully grown. The extremely long and strong radula of *Spekia* has a broad, wing-shaped central tooth lacking the central cusps (GLAUBRECHT & BANDEL 1998) and differs therefore from that of *Paramelania*, *Lavigeria* and *Reymondia*.

Spekia zonata (WOODWARD, 1859)

The grey-green shell of about 14 mm width and height is depressed smooth, dome-shaped with large last whorl. The outer lip of the aperture is oblique, and the basal area is concave. The operculum is concentric with small spiral nucleus of only 2 turns. Young hatch from their gelatinous spawn with a protoconch of the first whorl measuring 0.35 mm in diameter. The surface of its initial portion is almost smooth with only delicate and minute grooves surrounded by faint ridges and weak wrinkles. First growth lines appear within 0.75 whorls (RIEDEL 1993, GLAUBRECHT & BANDEL 1998). Freshly hatched young have an open umbilicus, later it is closed (Plate 5 A, B).

Differences and ecology: *Spekia* is distinguished from all other thalassoid gastropods by its smooth, grey, banded and depressed, neritiform shell. It is found on almost every larger rock in the bay of Kigoma that is washed by the waves on the beach regardless of surrounding substrate being hard or sandy (Fig. 1A, B). Thus, the individuals of this species may cross even far stretches of sandy beaches to reach isolated stones when conditions are calm. Individuals may leave their preferred habitat in the wave zone and move across sand to *Potamogeton* growth rooted at about 2 m of depth. When disturbed *S. zonata* pulls itself to the substrate by its foot and clings to it.

Plate 5.

A. The juvenile shell of *Spekia zonata* measures about 1 mm in width and height.

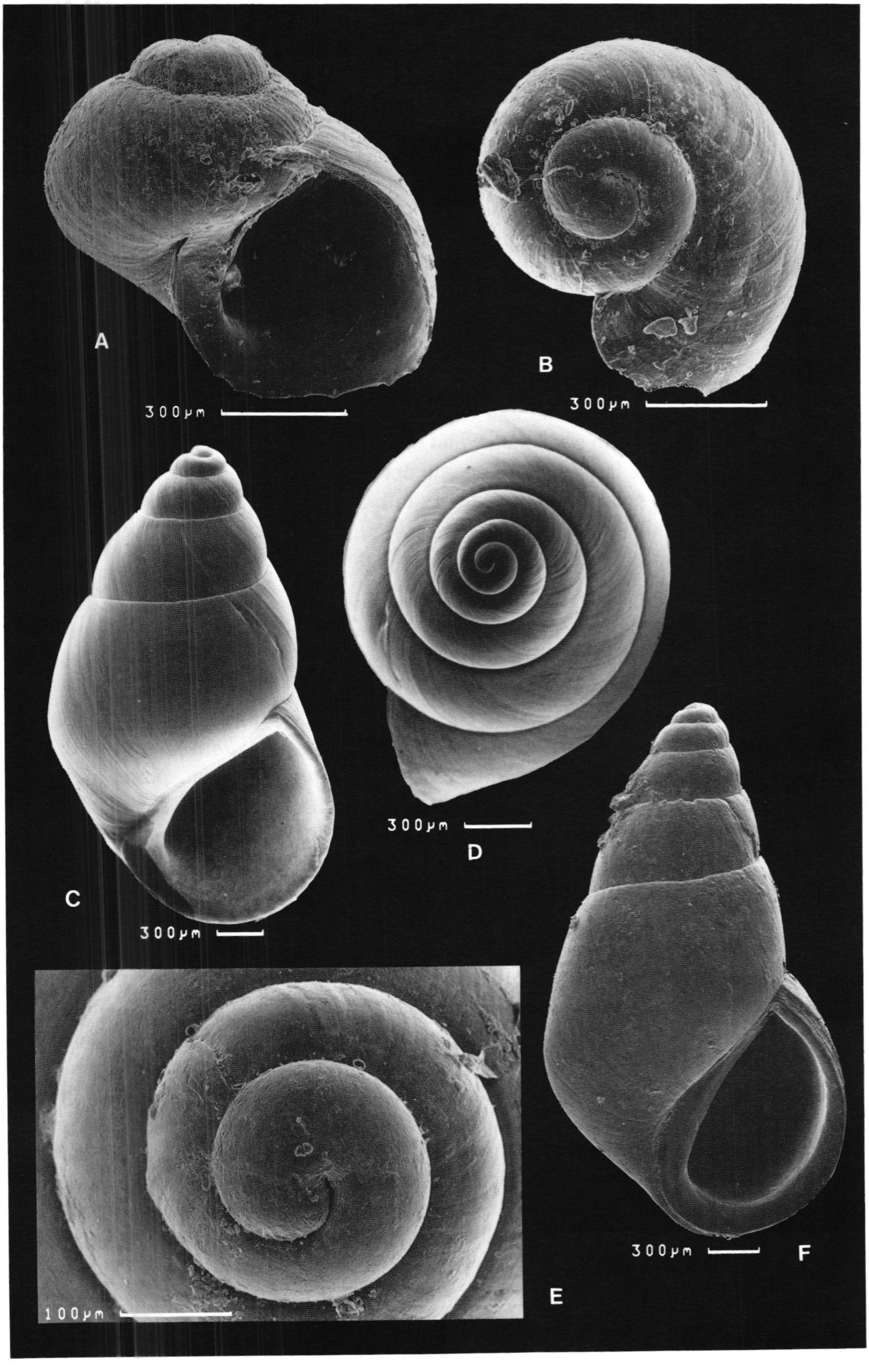
B. Young of *Spekia zonata* hatch with a protoconch of the first whorl measuring 0.35 mm in diameter. The initial portion is almost smooth with only delicate and minute grooves surrounded by faint ridges and weak wrinkles. First growth lines appear within 0.75 whorls.

C. The shell of *Reymondia pyramidalis* with 5 whorls measures little more than 5 mm in height with the aperture rounded and thickened, but less expanded than in *R. horei*.

D. The apical view of *Reymondia pyramidalis* has a smooth embryonic shell grading indistinctly in the smooth teleoconch.

E. The shell of *Stormsia minima* has a smooth initial part. Growth lines begin rather indistinctly after the first whorl and increase in strength with about one and a quarter whorl. The shell is 1,5 mm wide.

F. The shell of *Stormsia minima* is 4 mm high with the aperture provided with an evenly rounded, thickened outer lip.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Genus *Stormsia* Leloup, 1953

Stromsia is a monotypic, very small, but quite conspicuous, rock-dwelling gastropod from the wave zone of Lake Tanganyika. The operculum is concentric with spiral nucleus. *Stormsia* is distinguished from other species of Lake Tanganyika by its small size and from similar *Reymondia* and *Bridouxia* by the regular brown spiral bands of the shell.

Stormsia minima (Smith 1908)

The shell is about 2.5 to 3 mm high and 1.5 mm wide, consists of 5.5 whorls with greyish-white colour and three brown spiral bands. The aperture has an evenly rounded outer lip that is thickened in the adult (Plate 5 F) and thin in not fully grown specimens. The narrow callus of the inner lip covers the columellar slit in the fully grown shell. Individual egg capsules are attached to the lower side of rocks, are cupola-like with oval shape, and 0.8 mm in diameter. They hold three eggs each that measure 0.2 to 0.3 mm in diameter. Young hatch crawling with an about 0.25 mm large shell that has a smooth initial part (Plate 5 E). Growth lines may begin rather indistinctly after the first whorl and increase in strength with about one and a quarter whorl (Riedel 1993, Glaubrecht & Bandel 1998).

Differences and ecology: The tiny *Stormsia minima* lives among the surf beaten rocks in the upper littoral zone usually in large population. *Stormsia* is only found on wave battened rocky shores without sand, while *Spekia* and *L. nassa* also occurs on rocks surrounded by sand. *S. minima* feeds algae on rocks near or even above water level. Only *Spekia zonata* goes further up into the slash zone. Similar shells are present in *Bridouxia tanganyicensis* and *B. grandidieriana,* but both differ from *Stormsia* by being larger, less slender, having no brown spiral bands and an inner lip of the fully grown shell that does not cover an umbilical slit. Also their living environment is a different one (see in the following).

Genus *Bridouxia* Bourguignat, 1885

The shell has conical to almost globose shape with ornament of more or less well developed spiral lirae crossed by collabral ones. The operculum has a concentric outer zone and paucispiral nucleus. In the radula the central tooth lacks a central cusp and has a posteriorly bulging basal platform, the lateral teeth are marginally moderately extended, and the slender marginal teeth resemble each other with paw-like cutting edge. The initial part of the protoconch is weakly ornamented, while after begin of growth lines a spiral rib appears. On the teleoconch the spiral ribs multiply jointly with growth lines forming a more or less pronounced reticulate ornamentation that is well developed in *B. ponsonbyi*, rather delicate in *B. rotundata* and very indistinct in *B. tanganyicensis* and *B. grandidieriana*. With exception of the last species, synonyms have been discussed by Glaubrecht & Bandel (1998).

Ecology: The four species of the genus *Bridouxia* live in different environments which overlap in case of *B. ponsonbyi* and *B. rotundata*. These commonly are found together on the same stone. They live among rocks in about 2 m of depth where cyanobacterial growth forms stromatolithic crusts. While *B. ponsonbyi* appears restricted to stones, *B. rotundata* is also present on gravel and shell debris in greater depth. *B. tanganyisensis* is common among macrophyllic algae that form thickets between rocks at about 4 m of depth and also on the stands of *Potamogeton* in the shallow water off the sandy beach, here together with the common *Lavigeria littoralis* and the more rare *Bulinus truncatus*. *Bridouxia grandidieriana* prefers algal growths that cover shell debris and smaller rocks in water from two meters of depth to unknown depth (Fig. 1 A, B).

Bridouxia ponsonbyi (Smith, 1889)

The shell consists of up to 6.5 whorls, measures about 6 mm in height and 4 mm in width. Ornament consists of about 30 spiral grooves and broad ribs crossed by transverse collabral folds creating a reticulate pattern (Plate 7A). The aperture of the fully grown shell has a rounded and thickened outer lip while the inner lip forms a callus that is broader on its columellar side. In juvenile shells of the lips are thin. The protoconch has a faint groove and ridge ornament until prominent growth lines appear at about 1.25 whorls (Plate 7B). The first whorl measures about 0.25 mm in diameter. With about 1.5 whorls a spiral rib intitiates, succeeded by other ribs and numerous spiral lirae still within the second whorl. Later collabral ribs appear, creating the characteristic reticulate ornament of the teleoconch. The young hatch with one-threequarters to two whorls completed.

Differences: *B. ponsonbyi* has a characteristic reticulate ornament that distinguishes it from all other thalassoid species, and it is the largest of the four species of the genus *Bridauxia*. It has been noted with the same name by Brown (1980) and Brown & Mandahl-Barth (1987).

Bridouxia rotundata (Smith, 1904)

The small depressed shell measures a little more than 3 mm in height and 2.5 mm in width, is reddish-brown, nearly globose and consists of less than 4.5 whorls. Ornament consists of microscopic reticulate sculpture while the shell appears smooth with the naked eye. The aperture of the adult is holostome with thickened outer lip and callous inner lip that forms a columellar plate covering the narrow umbilical slit (Plate 7 C). Not fully grown shells have thin lips. The protoconch is initially wrinkled, and the first whorl measures almost 0.3 mm across. Growth lines are well developed at about 1.5 whorls, and here or a little later a median rib initiates (Plate 7 D). It is succeeded by other numerous and very delicate spiral lirae crossed by faint axial lines. This species has the synonym *Stanleya neritoides* (Smith, 1880).

Difference: While the shells of *Bridouxia ponsonbyi* have strong spiral grooves, *B. rotundata* appears smooth shelled. The shell of *B. rotundata* is depressed while that of the others species of *Bridouxia* are more conical.

Bridouxia tanganyicensis (Smith, 1889)

The up to 4 mm high and 2 mm wide shell is slender and turriform, narrowly conical with 5 whorls and of brown coloration with a subsutural, white, spiral band. In fully grown shells the aperture has a thickened margin and columellar callus. Juveniles have a thin apertural lip and lack callus (Plate 6 C). Ornament consists of faint spiral and axial sculpture not seen with the naked eye. Females produce egg capsules of about 0.3 to 0.5 mm in diameter that hold 3–4 white eggs. These small gelatinous egg masses were commonly attached to the shells of *Lavigeria littoralis*. From it the young hatch crawling with a shell that reveals a faint wrinkled sculpture on its initial part and growth lines right after the first about 0.25 mm wide whorl. Here also a median rib begins that is well developed in the second to fourth whorl and later disappears (Plate 6D).

Differences: *Bridouxia tanganyicensis* resembles *Bridouxia grandidieriana* closely, but differs in shell proportion in being slenderer. Its coloration is darker, and it does not have the columellar slit present in the latter.

Plate 6.

A. The juvenile shell of *Reymondia horei* is a little more than 3 mm high and ornamented by faint growth lines, and faint spiral grooves.

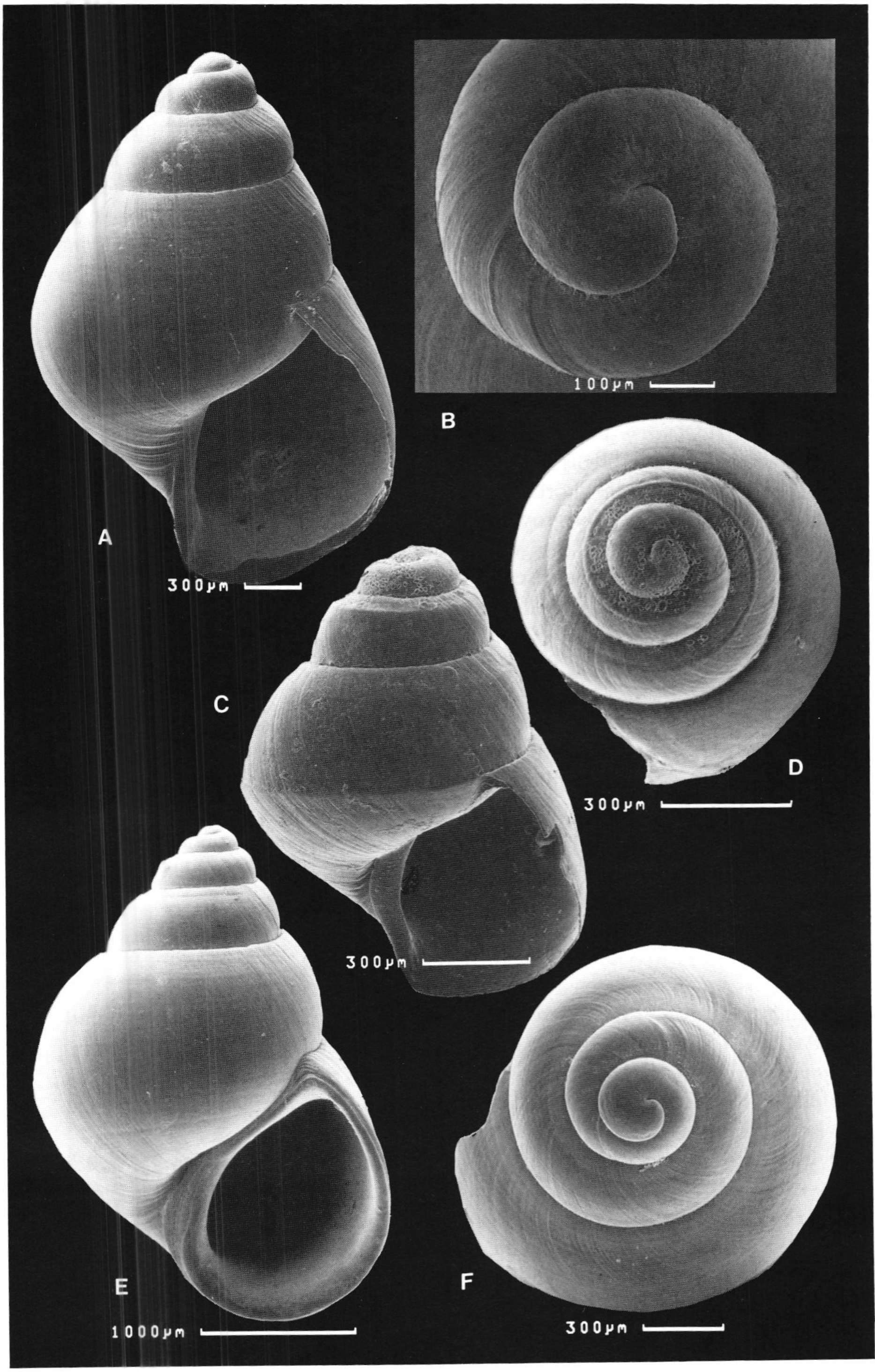
B. The protoconch of *Reymondia horei* has a smooth initial part, measures about 0.3 mm across in the first whorl, and growth lines begin in the second whorl.

C. The juvenile shell of *Bridouxia tanganyicensis* with 1,5 mm height, and the early median rib ending before the fourth whorl.

D. The protoconch of *Bridouxia tanganyicensis* reveals a faint wrinkled sculpture on its initial part and growth lines right after the first about 0.25 mm wide whorl. A median rib begins in the second whorl that later disappears.

E. The up to 4 mm high and 3 mm wide shell of *Bridouxia grandidieriana* has the aperture with thickened margin of the outer lip and is callus-covered at the columellar lip.

F. The protoconch of *Bridouxia grandidieriana* has an initial shell that is slightly wrinkled to the onset of growth lines when a median rib appears that is displaced toward the suture with further growth and disappears on the third whorl. The first whorl measures about 0.3 mm in diameter.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Bridouxia grandidieriana (Bourguignat, 1885)

The up to 4 mm high and 3 mm wide shell consists of five whorls and is commonly quite a bit smaller (2.5 x 2 mm). It is of roundish oval shape with the aperture almost as high as the remainder of the shell (Plate 6E). Coloration is a transparent light brownish grey, and there is a subsutural greyish-white spiral band. In the fully grown shell the aperture has a rounded and thickened margin of the outer lip and is callus-covered at the columellar lip. Some shells have a columellar slit, in others it is covered by the callus of the inner lip. Ornament is restricted to faint spiral lines on juvenile shells and fine growth lines, so that, in fact, the surface appears polished. The initial shell is slightly wrinkled to the onset of growth lines when an indistinct median rib appears that disappears on the third whorl. The first whorl measures about 0.3 mm in diameter, and the spiral rib initiates in the last portion of the second whorl (Plate 6F).

Differences: *Bridouxia grandidieriana* closely resembles *B. tanganyicensis* in size, number of whorls, and shell ornamentation. It differs in having a lighter coloration and more rapid increase in whorl diameter, so that it is relatively broader and has a higher aperture in the fully grown shell. *B. grandidieriana* lives on hard substrate, mostly rocks, while *B. tanganyicensis* lives on vegetation. The spiral rib appears a little later than is the case in *B. tanganyicensis* and ends earlier as well, being well visible only in part of the third whorl of *B. grandidieriana*.

Subfamily Paludominae Stoliczka, 1868

The genus *Cleopatra* which is essentially an African genus may belong to the Paludominae. *Cleopatra* is distributed from lower Egypt to Zululand, westwards to Senegal, southwards to Namibia (Brown 1980). Members of the *Cleopatra* group differ from those of *Lavigeria* regarding the operculum which is concentric with a spiral nucleus, and in not having a uterine brood pouch. Paludominae may be distinguished from the Paramelaniinae by the shape of their radular teeth, but the difference of both taxa is not resolved as yet.

Genus *Cleopatra* Troschel, 1856

According to Brown (1980) there are about 20 species of *Cleopatra* distributed over Africa, of which two species, *C. bulimoides* (Olivier, 1804) and *C. ferruginea* (I. and H.C. Lea, 1850) have extensive ranges. *C. bulimoides* occurs from the delta of the Nile to Lake Albert in Uganda and *C. ferruginea* from the Cape Province to Kenya.

There are two species living in the lakes of the rift. One is *Cleopatra cridlandi* Mandahl-Barth, 1954 living in Lake Victoria, and the other is *Cleopatra mweruensis* Smith, 1893 living in Lake Mweru. The genus had representatives in the Lake Malawi or tributaries which issued into it in the past (Gorthner, unpublished manuscript). It neither occurs in that lake now nor in Lake Tanganyika. According to Brown &

MANDAHL-BARTH (1987) *Cleopatra* is known from the Malagarasi delta with individuals that probably belong to *C. ferruginea.* There are also several species of *Cleopatra* in Madagaskar which indicates the antiquity of the presence of the genus in Africa. *Cleopatra* in ancient Lake Turkana was involved in a speciation event at a late Miocene level that produced quite extraordinarily shaped species (WILLIAMSON 1985, Plate 5E) which did not live on after the event ended.

Reymondiinae n. subfam.

Diagnosis: The shell is of slender conical shape and almost smooth. The central tooth in the radula differs strongly from that found in other thalassoid taxa like the Spekiinae, Lavigeriinae and Paramelaniinae. It is broad and quadrangular with large median cusp and few cusps on the cutting edge. Lateral teeth have short posterior lateral extensions and bear a spatulate main cusp on their upturned cutting edge. Marginal teeth are slender and differ from each other with regard to the dentition of their apices. The subfamily is based on the two endemic species of *Reymondia* extant in Lake Tanganyika.

Genus *Reymondia* BOURGUIGNAT, 1885

Description: The shell is small to medium-sized (5–15 mm high), of slender conical shape. Whorls are smooth, weakly convex, and the aperture is thickened in fully grown individuals. The operculum is concentric with paucispiral nucleus. There is no spiral rib present on the juvenile shell.

In respect of radula morphology, protoconch sculpture and protoconch size *Reymondia horei* and *R. pyramidales* are very similar to each other. However, the adult shell of *R. pyramidalis* is always smaller (about half size) than that of *R. horei*, and it has one whorl less (5.5 and not 6.5). That they differ in reality and *R. pyramidalis* is not simply a juvenile of *R. horei* is documented by the presence of a thickened and slightly widened apertural lip of fully grown specimens. This species pair is rather unusual in occupying the same living space. *R. horei* and *R. pyramidalis* are present throughout a zone of about 1 m below surface down to around 5 m in the rocky slope area. Their greatest abundance lies in shallow water of the pebble beach with or without sand. When wave action is minimal, individuals of *R. horei* – as well as *R. pyramidalis* – may move across the upper exposed surface of rocks and also crawl over sand to distant hard substrates or *Potamogeton* growths.

Reymondia horei (SMITH, 1880)

The conical shell with 6.5 whorls measures about 13 mm in height and 6 mm in width. The weakly curved smooth whorls are reddish-brown with one white subsutural band. Ornament consists of faint growth lines, and faint spiral grooves usually present on juveniles (Plate 6A) and commonly eroded on adults. The operculum can be withdrawn deeply into the shell, sealing it far behind the aperture.

Nearly spherical egg capsules of about 0.5 in diameter are attached to rock surface, and from them young hatch crawling. The protoconch has a smooth initial part, measures about 0.3 mm across in the first whorl, and growth lines begin in the second whorl (Plate 6B). Very delicate spiral lines appear on later whorls, but create only indistinct reticulate pattern with the growth lines. The protoconch merges indistinctly into the teleoconch.

Difference: The shells of the two species of *Reymondia* are rather similar to those of other genera, especially *Bridouxia*, but the protoconch is not succeeded by juvenile whorls that carry a spiral rib, as is characteristic to the four species of *Bridouxia* described here. The similarity of shell shapes, as well as the difference in radula morphology that exists between the species of *Bridouxia* and *Reymondia* had also been noted by Brown & Mandahl-Barth (1987).

Reymondia pyramidalis Bourguignat, 1888

The shell habitus is like that of *R. horei,* but fully grown individuals are only up to 6 mm high and 4.5 mm wide and consist of 5.5 whorls. The aperture is also well rounded and thickened (Plate 5C), but appears slightly less expanded and less thickened than in *R. horei*. The protoconch measures only about 0.2 mm in the first whorl, and growth lines become distinct well within the second whorl. Transition in the teleoconch is very indistinct (Plate 5D).

Plate 7.

A. The juvenile shell of *Bridouxia ponsonbyi* with about 2,5 mm height shows the ornament of spiral grooves and broad ribs crossed by transverse collabral folds creating a reticulate pattern.

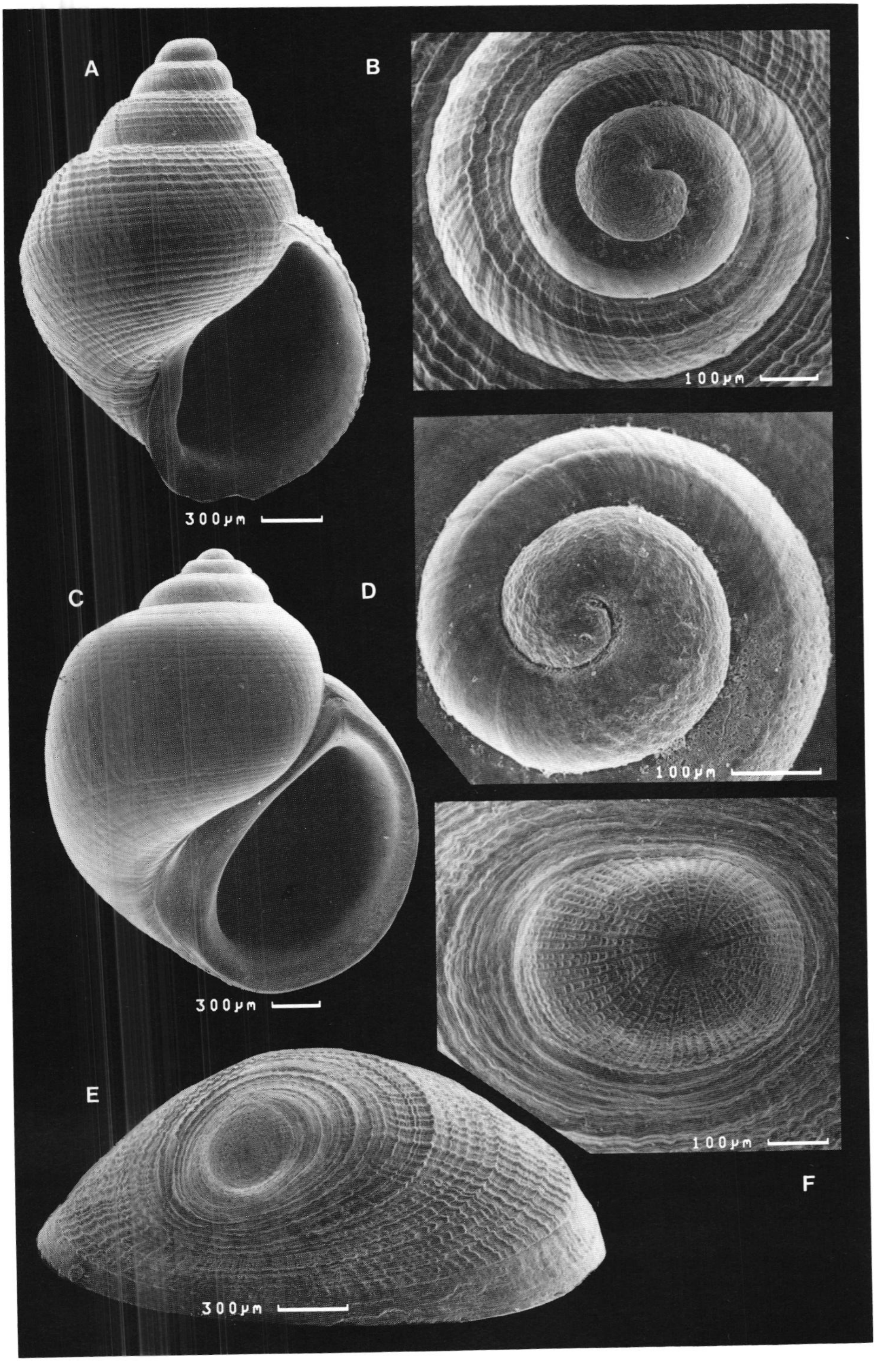
B. The protoconch of *Bridouxia ponsonbyi* has a faint groove and ridge ornament until prominent growth lines appear at about 1.25 whorls. The first whorl measures about 0.25 mm in diameter. With 1.5 whorls a spiral rib intitiates, succeeded by other ribs and numerous spiral lirae still and later collabral ribs.

C. The fully grown shell of *Bridouxia rotundata* measures a little more than 3 mm in height and 2.5 mm in width.

D. The protoconch of *Bridouxia rotundata* is initially wrinkled, and the first whorl measures almost 0.3 mm across. Growth lines are well developed at about 1.5 whorls, and a median rib initiates.

E. Apical view of *Burnupia caffra* with the limpet shell measuring about 2.5 mm in diameter. The apex is inclined to the right and forms a hump on the cap-like shell.

F. The embryonic shell cap of *Burnupia caffra* is ornamented by radial ribs and concentric growth lines forming a fairly regular reticulation with each other. It measures 0.5 mm in maximum diameter and is well differentiated from the teleoconch.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Difference and ecology: The shell of *Reymondia pyramidalis* is shorter by one whorl than that of *R. horei*. *Bridouxia ponsonbyi* can be separated from the similar sized *Reymondia pyramidalis* by its reticulate ornament. The radula of *Bridouxia* is quite different from that of *Reymondia*, which possesses a stout median denticle in its quadrangular central tooth while *Bridouxia* lacks a median cusp and has a more wing-shaped central tooth. *Reymondia* has a smooth embryonic shell while that of *Bridouxia* reveals at least one conspicuous spiral keel as ornament.

Family Thiaridae Troschel, 1857

According to Morrison (1954) the Thiaridae comprise only species in which males are rare, and the females have a brood pouch separate from the uterus. Here the genus *Melanoides* has a cosmopolitan species *M. tuberculata* which is present in most of Africa (Brown 1980). The majority of the remaining about 30 congeneric species are restricted to Lake Malawi and the Congo Basin. Bandel & Kowalke (1997) demonstrated that a potential ancestor to *Melanoides* lived in Europe during the Eocene with the genus *Melanotarebia* Bandel and Kowalke, 1997. Apparently the Thiarinae later on concentrated in SE Asia where there are still many species living. They reflect the transition from marine environment to fresh water (Bandel et al. 1997). Houbrick (1987, 1992) recognized similarities between marine brood pouch bearing Planaxidae on one side and the Thiaridae with similar brood pouch on the other hand.

Subfamily Thiarinae Troschel, 1857

The subfamily is based on the genus *Thiara* Röding, 1798 that has great similarity with *Melanoides* (Thiele 1928, Wenz 1938).

Genus *Melanoides* Olivier, 1804

Observations in Lake Malawi during 1995 indicated that juvenile individuals of *Melanoides* are common in many regions of the lake. These are usually quite brittle and demonstrate that they will to a large extent be totally disintegrated before they can be preserved in the sediment. Living juveniles can be discovered here and there and are commonly found in great numbers in coastal pools that form rapidly during lake level changes throughout the year. Large individuals with fully grown and thick-walled shell were found to occur on sandy and muddy surfaces and among plant growth between protecting boulders within the lake.

Remarks: Williamson (1981, 1985) described fossil *Melanoides* from Lake Turkana in northwestern Kenia. Here he noted a number of species which in their variability have gone even further than those found in Lake Malawi today. Some of these varieties of *Melanoides* from Lake Turkana are quite unusual, among these a small sized variety that resembles Syrnolopsinae of Lake Tanganyika. These morphs or species are found in layers intercalated with such that have more "usual" shells of *Melanoides* like those of *M. tuberculata.* WILLIAMSON suggested that *Melanoides* had migrated to Africa right at that time in the Late Miocene and formed new species during two speciation events in Lake Turkana, which did not survive after the end of these periods. *Melanoides tuberculata* is also found in Madagascar. But like its relatives on the Pacific Islands it may have reached Madagascar with drinking water or on plants carried by humans. According to TCHERNOV (1975) *Melanoides tuberculata* reached the region of Lake Galilee in fresh water during the Late Miocene, and in its present distribution in the Mediterranean region it traces the border of the Miocene lands as present during the Messinian phase.

Melanoides tuberculata (MÜLLER, 1774)

M. tuberculata appeared in the basal sediments of the Chiwondo beds of Lake Malawi, at about the same time it appeared in the Turkana fauna (WILLIAMSON 1981, 1985) during the Late Miocene. MANDAHL-BARTH (1972) distinguished 9 species living in Lake Malawi mainly based on differences in width and denticulation of the central tooth of the radula. While SMITH (1877) had recognized 7 species based on shell differences, and BOURGUIGNAT (1889) distinguished even 29 species, the most common of which is *M. tuberculata.* CROWLEY & PAIN (1964) suggested that only 6 species with different shell shapes are living in the lake, all others represent variations of these.

Melanoides admirabilis SMITH, 1880 may perhaps represent one of the many morphs of *M. tuberculata* and lives in the large tributaries of Lake Tanganyika (BROWN, 1990), but it does not enter the actual lake. BROWN & MANDAHL-BARTH (1987) expressed their surprise about *Melanoides* not having entered actual Lake Tanganyika, while it is usually found in great abundance in fine sediments of other lakes of the East African Rift. Two fossil species called *Platymelania bifidicincta* (COX, 1926) and *P. brevissima* (COX, 1926) had originally been described by ADAM (1959) and again reported from the Pleistocene of the Lake Edward-Lake Albert Rift (GAUTIER 1970). They resemble very short representatives of the *Melanoides* varieties that live nowadays in Lake Malawi. Similarily as is the case in *Bellamya* in *Melanoides* the different shapes may reflect the flexibility within the species rather than speciation events, but what exactly creates the periodical morphological bursts is not at all known and needs to be studied in detail.

Tanganyiciinae n. subfam.

Diagnosis: The shell is ovate, conical with last whorl deviating, and young are brooded in a pouch that has its opening on the side of the head. The taxon is based on the genus *Tanganyicia* from Lake Tanganyika.

Difference: In contrast to the Thiarinae with slender turriform shell documented to have not changed much since Eocene, the shell of the Tanganyiciinae is shorter, ovate, conical in shape. The later have similarities with Thiaridae of the South American *Hemisinus* (SWAINSON, 1840) group (WENZ 1938).

Genus *Tanganyicia* Crosse, 1881

The genus is monotypic. According to Morrison (1954) *Tanganyicia* is the only representative of the Thiaridae in Lake Tanganyika while the other Cerithioidea of the lake belong to different families of which he considered two further ones. Regarding shell shape *Tanganyicia* is quite different from the other thalassoid gastropods. Brooding of young occurs also in *Lavigeria*, but here the brood pouch lies in the lower part of the oviduct and not in the head/neck as in *Tanganyicia*.

Tanganyicia rufofilosa (Smith, 1880)

The ovate shell is between 10 and about 16 mm high and 10 to 12 mm wide with a short conical spire and the last whorl detaching from the spire so that the aperture is of oval shape with continuous thickened rim. There is a shallow spout-like groove on the anterior and posterior apertural end. The initial whorl is well rounded, and growth lines appear with more than 1.5 whorls. The protoconch sculpture of *Tanganyicia* figured by Riedel (1993) reveals the distinct wrinkle pattern indicating a very late calcification of the shell as resembles that found among Thiarinae, but also in the Lavigeriinae. The first four whorls are well rounded and produce a naticoid shell with round and open umbilicus. In the fifth whorl the inner lip begins to cover the umbilicus resembling then what is known as *Stanleya neritoides* (Smith, 1880) (Wenz 1938, Fig. 2047), and at its end the whorl detaches to the fully grown stage. Now the shell is higher than wide and becomes much thickened. Ornament consists of dark spiral lines on a smooth whorl surface with fine growth lines that become more irregular in the latest detached shell portion. The open umbilicus is surrounded by an angulation.

Differences and ecology: In Kigoma only dead individuals were encountered on the beach and in the shell debris washed from sand below a rocky slope in 3–5 m depth. According to Moore (1898) there is a brood pouch below the right tentacle. Brown (1980) described its living place as among rocks in the littoral zone.

Subclass Heterostropha Fischer, 1885
Order Basommatophora Keferstein, 1864

Of the fresh water gastropods of the Basommatophora representatives of the families Lymnaeidae, Ancylidae, and Planorbidae occur in the waters of the East African Rift.

Family Lymnaeidae Rafinesque, 1815

According to Mandahl-Barth (1987) the pools and swamps near Lake Tanganyika and Lake Malawi hold *Lymnaea (Radix) natalensis* Krauss, 1848 that is widely distributed between Egypt and South Africa (Brown 1980). It does not enter Lake Tanganyika and was also not noted in Lake Malawi, even though it is rather common in marginal swamps and ponds next to these lakes.

Family Planorbidae RAFINESQUE, 1815

Only one member of the genus *Bulinus* enters Lake Tanganyika, and there are also few species or one variable one in Lake Malawi. In pools and swamps next to Lake Tanganyika BROWN and MANDAHL-BARTH noted *Bulinus scalaris* (DUNKER, 1845), *Biomphalaria sudanica* (MARTENS, 1870), *Biomphalaria pfeifferi* (KRAUSS, 1848), *Afrogyrus corteus* (BLAINVILLE, 1826), *Ceratophyllus natalensis* (KRAUSS, 1848), and *Segmentorbis angustus* (JECKELI, 1874).

Genus *Bulinus* MÜLLER, 1781

The outer shell shape resembles that of the Physidae in being sinistrally coiled. There are about 30 species in Africa (BROWN 1980). The basis of classification is the revision of MANDAHL-BARTH (1957, 1958).

Bulinus succinoides (SMITH, 1877)

In Lake Malawi *Bulinus* was encountered only in shore-ponds that formed behind the beach ridges washed up by the waves of the lake. Here they may be very common and found on plants as well as moving on the muddy thin layer that covers the sand in these warm and fertile shallow ponds. When the ponds are flooded again and become integrated in the lake, *Bulinus* dies and its thin shells are usually rapidly destroyed in the surf and by dissolution. According to BROWN (1980) there are several endemic species belonging to the *Bulinus tropicus* complex as well as to the more thick-walled and globose *Bulinus nyassanus* (SMITH, 1877) with almost flat apical area which was seen commonly in shallow Lake Malombe connected to lake Malawi by the Shire river, but not found alive in actual Lake Malawi, where it supposedly lives in shallow water. This species or species group from Lake Malawi exhibits individuals with rather thick shell.

Species *Bulinus truncatus* (AUDOUIN, 1827)

This species is found in Africa from the Nile Delta to Lake Tanganyika and also occurs in southern Europe and the Middle East. The radula was described by BURCH & JEONG (1984). According to BROWN (1980) the species lives in a variety of water bodies, including seasonal pools, irrigation systems, lakes, south to the Lake Malawi area.

In Lake Tanganyika *B. truncatus* lives in the growths of *Potamogeton* plants jointly with *Lavigeria littoralis* and *Bridouxia tanganyicensis* (Fig. 1B). As was checked by BROWN (pers. com.) this little gastropod is definitely the same as present in many places outside of Lake Tanganyika in Africa.

Family Ancylidae

These basommatophoran gastropods are limpet shaped. The protoconch is also limpet shaped and rather large. In difference to the Ancylidae the protoconch of *Acroloxus* Beck, 1837 (Acroloxidae) is not indented, which may distinguish the shells of Ancylidae and Acroloxidae (Riedel 1993).

Genus *Burnupia* Walker, 1912

Burnupia lives in central and southern Africa, and may be considered to represent subgenus of *Ancylastrum* Bourguignat, 1853. It is characterized by radiate rows of punctae in its ornament. The apex of *Burnupia* is always situated right from the length axis (Brown, 1980). The protoconch and teleoconch in shape and ornament of *Burnupia caffra* from Lake Tanganyika is very similar to that of the Cretaceous *Ancylina cretacea* (Tausch, 1886) from Santonian deposits in Hungary (Bandel & Riedel 1994, Pl. 16, figs. 1–4).

Burnupia caffra (Krauss, 1848)

The little limpet measures about 2.5 mm in maximum and 2 mm in minimum width with almost regularly oval aperture. The prominent apex is far inclined to the right and forms a hump on the evenly cap-like shell (Plate 7E). Juveniles are thin, and the shell later becomes quite solid and well calcified. The embryonic cap is ornamented by radial ribs and concentric growth lines forming a fairly regular reticulation with each other. It is of somewhat variable shape in different individuals usually of oval outline with up to 0.5 mm in maximum diameter. From an initial circular shell cap which sometimes forms a depression radial rows of pits are arranged right to the onset of the teleoconch (Plate 7F). On the teleoconch the radial ribs are very numerous, but collabral growth increments in more or less regular pattern are more dominant. *Burnupia* in the bay near Kigoma lives in shallow water from about 2 m downwards (Fig. 1A). The species was obtained alive from a depth of 70 to 100 m in Lake Tanganyika by Leloup (1953). Brown & Mandahl-Barth (1987) assumed that *Burnupia caffra* living in Lake Victoria is conspecific.

Difference and ecology: In the shallow, 3–5 m deep water at the sandy beach right in front of the Inns of Africa at Kigoma the basommatophorans *Bulinus truncatus* and *Burnupia caffra* were found. While *Bulinus* was found alive, *Burnupia* has been encountered from screened sand both near the rocky slope and more sandy areas (25 specimens). Fresh shells are common next to sea-grass-like *Vallisneria* rosettes, and the little limpet may therefore have lived attached to the blade-like leaves of these browsing growth from their surface. The species occurs from South Africa to Ethiopia (Brown 1980).

Remarks: The similar small limpet-like basommatophoran *Ferrissia* Walker, 1903 has been found to live in the Malagarasi delta next to Lake Tanganyika by Leloup

(1953). It should differ from *Burnupia caffra* by the ornament of the protoconch since *Ferrissia* does not show radial rows of pits (Brown 1980).

The environmental setting of the gastropods of Lake Tanganyika

Lake Tanganyika forms a deep trough. Accordingly, this rift lake has steep rocky shores, interspersed by shallow sandy beaches and swampy river estuaries. This frequent alternation of sandy and rocky stretches of coastline in Lake Tanganyika as a whole was found near Kigoma en miniature. Kigoma is situated in a relatively shallow bay which, however, opens further east to an extremely steep slope where one of the deepest sub-basins of Lake Tanganyika is found that has a depth of about 1310 m. In the bay just to the south of Kigoma Bandel & Glaubrecht (1998) and Glaubrecht & Bandel (1998) described most of the gastropods that were encountered alive. A rocky slope is developed on the northern bay side that drops to great depth and also forms a rocky slope with rocks and pebbles fused to each other by calcarous crusts of living cyanobacterial stromatolites. Next to the rocky shore sandy or pebble strewn beach is succeeded by rocky bottom with sand between rocks and by larger stretches of sand until deeper down, beginning in 3–6 m depth, larger areas of rocky bottom are exposed. Between them sandy and silty bottom is often covered by dense thickets of macrophyllic algae while on more shallow sandy bottoms smaller and larger *Potamogeton* growths are rooted in the sand with their up to 3 m long stalks erect and with their tops reaching lake surface. Further to the south the bottom of the bay is formed by soft sandy and silty sediment and here settled by bioturbating endobenthic organisms. This small bay apparently represents a characteristic environment in which most of the gastropods of Lake Tanganyika occur alive with exception of those that prefer muddy ground near streams that enter the lake as is the case near Ujiji just to the south of Kigoma.

Woodward (1859) was the first to receive shells collected by Speke on the shores of Lake Tanganyika, and he expressed amazement in describing such remarkable fresh water molluscs. Boss (1978) suggested that a snail from the coast near Bujumbura would have to cover a distance like from London to Vienna in order to reach the southern coast of the lake. But this is apparently not an argument for speciation since most species appear to be the same at both ends of the lake and in areas in-between as well. Leloup (1953) suggested that the radiation of the melaniid gastropods of the Tanganyika has taken millions of years. This is certainly true.

Brown (1980) suggested that there are more than the 20 thalassoid species placed in 16 genera living in Lake Tanganyika as had been suggested by Leloup (1953). According to Brown there are more than 25 of such species, and Brown & Mandahl-Barth (1987) noted 60 species that live close to or in the lake of which 36 are endemic. Own observations indicated that in the bay of Kigoma there are at least 19 genera of which only the two basommatophoran genera with the species *Bulinus truncatus* and *Burnupia caffra* also live outside of the lake. Of the 27 species encountered in the bay of Kigoma six were only found as dead shells, all others were encountered in their characteristic living environment with several to many individuals. In the lake there are at least four more endemic species of the genera *Paramelania, Bathanalia, Limnotrochus* and *Chytra.*

The bay of Kigoma provided the following species:
Anceya giraudi
Bridouxia grandidieriana
Bridouxia ponsonbyi
Bridouxia rotundata
Bridouxia tanganyicensis
Bulinus truncatus
Burnupia caffra
"Hydrobia" kigomae
Lavigeria arenarum
Lavigeria grandis
Lavigeria littoralis
Lavigeria livingstoniana
Lavigeria nassa
Lavigeria spinulosa
Martelia tanganyicensis
Mysorelloides multisulcata
Neothauma tanganyicensis
Paramelania crassigranulata
Reymondia horei
Reymondia pyramidalis
Spekia zonata
Stormsia minima
Syrnolopsis gracilis
Syrnolopsis lacustris
Syrnolopsis minuta
Tanganyicia rufofilosa
Tiphobia horei

Definitely also present as endemic genera in the lake are:
Bathanalia
Chytra
Limnotrochus

Brown (1980) expressed the opinion that the thalassoid gastropods of Lake Tanganyika have descended from a number of ancestral species which lived in central Africa before the formation of the lake and which belonged to the same stock as the modern Thiaridae. Amongst the living thiarids the genus *Potadomoides* was considered by Leloup (1953) and Brown (1980) to have the strongest claim, they be considered in relation to this ancestry. This genus now is found only in the Malagarasi delta of Lake Tanganyika and in the rivers of eastern Congo. Based on the new data from the bay next to Kigoma it was noted that *Potado-*

moides may well be a relative to *Lavigeria* of the endemic genera of the lake, but it is difficult to state a relation to the other genera because of differences in breeding and radula morphology. *Potadomoides* as well as *Lavigeria* cannot be regarded as closely related to thiarids represented by the genus *Thiara* as found at the Indian Ocean coast of Africa or to *Melanoides* as found all over Africa in streams and ponds, but not the Lake Tanganyika. Thiaridae sensu strictu, as suggested by Morrison (1958) and confirmed by Houbrick (1987, 1988, 1990, 1992), have a characteristic brood pouch that lies behind the head in the head-foot. The only species among the thalassoid gastropods that may perhaps be related to the Thiarinae is *Tanganyicia*, but here the shell shape indicates some distance, so it may better be placed in a subfamily by its own, the Tanganyiciinae with probable relation to the Thiaridae.

Model of the settlement of Lake Tanganyika

It can be concluded that the thalassoid gastropods of Lake Tanganyika represent a unique assemblage of several, at least seven independent ancient lineages of African fresh water gastropods. The first of these, the Paramelaniinae with *Paramelania* can in the future possibly be connected to the ancient group around *Pyrgulifera* that has been recognized in the Cretaceous of Europe and North America (Tausch 1885, Bandel & Riedel 1994). Its last representatives in Europe, that we know of, lived in the Eocene of Hungary (Kecskémeti-Körmendy 1972, Oppenheim 1892). Ancient migration paths of fresh water gastropods existed in the area of the East African Rift from the Late Cretaceous onwards (Wycisk et al. 1990). Whether the genera *Mysorelloides*, *Limnotrochus* and *Chytra* can be related to the Paramelaniinae, as is suggested by the morphology of the cutting edge of their central tooth of the radula remains to be evaluated. The conical shell with simple aperture and open umbilicus of the representatives of these genera indicates that they form a group by themselves. There exists a certain similarity to the Cretaceous genus *Szaboella* Bandel and Riedel, 1994. A third group are the Spekiinae with *Spekia*, *Stormsia*, and *Bridouxia*. They are interconnected by the shape of their radula with characteristic central tooth. Also the shape and ornament of the early ontogenetic shell unites them, with one whorl representing the primary embryonic shell and the presence of a single spiral rib with begin of growth lines, which may or may not give rise to the adult ornament. Otherwise shell shape in this group varies from slender conical to low neritiform.

The fourth group is formed by the two species of *Reymondia*. The Reymondiinae could possibly be related to the common African *Cleopatra*, that has settled on this continent so early, that its representatives have been established in mountain streams of Madagascar as well as differentiated the genus *Pseudocleopatra* Thiele, 1928 in West Africa (Brown 1980). The fifth group is formed by the ovoviviparous Lavigeriinae with the species of *Lavigeria* which all are still close to each other in shape and anatomy. They are related to *Potadomoides* that lives in rivers connected to Lake Tanganyika. Apparently *Tiphobia* has a similar development of young in a uterine brood pouch, but otherwise it is not close in shape and mode of life to Lavigeriinae and represents an additional, the sixth group of thalassoid gastropods (?Tiphobiinae). *Tanganyicia* has been described as having a brood pouch in the head-foot and would therefore represent a possible member of the Thiaridae, but its shell shape differs strongly from other known members of this family, especially those that migrated in Late Miocene time to Africa coming from Asia, so that it forms its own subfamily Tanganyiciinae. Similarities may be noted with some members of the *Hemisinus* SWAINSON, 1840 relation living in northern South America and Central America and the Antilles or with *Sulcospira* TROSCHEL, 1857 from Indonesia.

The minute sand- and thicket-dwelling Syrnolopsidae with *Syrnolopsis*, *Anceya*, and *Martelia* have enough characters in common, especially their small turriform shell shape and the characteristic columellar swelling that they form the eighth group. Syrnolopsidae probably are no members of the Cerithioidea since *Syrnolopsis* was found to be hermaphroditic (pers. communication Tanya Sitnikova). These data support classifications as presented by THIELE (1929) and WENZ (1938). According to these Syrnolopsidae are closer to the Pyrgulidae and, thus, probably represent members of the Rissoidea. The *Neothauma* group of viviparids is an own ninth group that appears to be closely related to the common *Bellamya.* And only the tenth and eleventh group with representatives of the basommatophoran *Bulinus* and *Burnupia* have species living in the lake that also live outside of it in streams and ponds of tropical and southern Africa. *Burnupia* is very close to the Cretaceous *Ancylina* BANDEL and RIEDEL, 1994 that lived in fresh water swamps of islands in the Tethys Ocean, which were also the home of *Pyrgulifera* and *Szaboella* resembling *Paramelania* and *Limnotrochus* respectively. The minute hydrobiid, that was newly discovered to be present in the lake may represent a member of cave dwelling species, and it cannot yet be evaluated whether it actually lives in the lake or is washed in from subterranean source. Also its place in the system of the rissoaform gastropods still remains to be evaluated when more of its anatomy becomes known.

While this radiation of fresh water caenogastropods characteristic of Lake Tanganyika has commonly been assigned to mainly one single family Thiaridae with exception of *Neothauma*, it has become evident that the thalassoid species are not monophyletic, but rather of polyphyletic origin. None of the species appear to be closely related to any of the species of the Thiarinae even though the representative of this taxon, *Melanoides* is living in the larger tributaries of the lake and has done so for about the last three million years. *Neothauma* appears to have been more widespread in the past, but with exception of the basommatophorans, all others are restricted to actual Lake Tanganyika. A systematic assignment of these thalassoid groups to the known fresh water families outside of Lake Tanganyika indicate that regarding the Cerithioidea among them their placement within the different branches of the superfamily is still problematic and needs further studies. The Lake Tanganyika gastropod radiation of one single family Thiaridae, as was assumed by several authors, thus, has never happened. This is in accordance with paleontological data which indicate that several independent groups of

Cerithioidea have entered the fresh water environment coming from the sea during Jurassic and Cretaceous time (BANDEL 1991, 1992, BANDEL & RIEDEL 1994). Accordingly the remarkable conchological as well as anatomical variety of the thalassoid gastropods is probably due to a polyphyletic origin of its members. Thus, neither the enormous morphological spectrum nor the ecological adaptations can be viewed any longer as the result of an exclusively intralacustrine speciation and adaptive radiation within Lake Tanganyika.

There is a clear separation of such species living in lake proper from those species only found in associated water bodies around the lake. BROWN (1994) suggested that there is a fundamental difference in ecological adaptation between the snails living in the main lake and those of the peripheral marshes and tributaries. It is a still unresolved phenomenon that those taxa most widespread in Africa in general did usually not enter Lake Tanganyika. Accordingly, species of *Cleopatra* and *Melanoides*, as well as *Potadomoides* are not living in the lake. Among the other fresh-water gastropods only *Bulinus truncatus* and *Burnupia caffra* of the Basommatophora entered the lake, and they are the only species that do not live exclusively in Lake Tanganyika, but also outside of it. Species of *Lanistes*, *Pila*, *Bellamya*, *Gabbiella*, and *Melanoides* for example remained confined to ponds rivers and lakes outside of Lake Tanganyika, some actually in contact with the lake.

Model of the settlement of Lake Malawi

In 1994 we found only four species and their varieties in Lake Malawi, one with the polymorphic *Lanistes*, a second with polymorphic *Melanoides tuberculata*, and a third with moderately polymorphic *Viviparus (Bellamya),* and a fourth with *Gabbiella*. The coastal ponds usually in addition also contain *Bulinus*. GORTHNER (unpublished manuscript) stated that the present Lake Malawi holds 9 gastropod species.

According to the revision of MANDAHL-BARTH (1972) cited by BROWN (1980) there are 27 species of gastropods living in the lake belonging to 9 genera. BROWN (1980) presented a list containing *Bellamya capillata* and 3 endemic species of this genus, *Lanistes ovum* and *L. ellipticus,* and three endemic species of *Lanistes*, the endemic *Gabbiella stanleyi*, *Melanoides tuberculata* and 8 endemic species of *Melanoides*. Of the about 40 species of *Melanoides* that had been suggested to live endemic in Lake Malawi by BOURGUIGNAT (1889), MANDAHL-BARTH (1972) accepted only 9 species, but it may well be that all these are only variations of the single species *M. tuberculata*. BROWN (1980) further noted *Lymnaea natalensis*, *Biomphalaria pfeifferi*, *Ceratophallus natalensis*, *Gyraulus costulatus*, *Segmentorbis angustus*, *Bulinus globosus* and three further endemic species of *Bulinus* to live in the lake. The basommatophorans are almost all found also in ponds nearby, with exception of two endemic species of *Bulinus*. As BROWN (1980) stated, unlike Lake Tanganyika, Lake Malawi has no endemic genera of gastropods. Only three species apparently live exclusively in deeper water, these being *Lanistes nasutus*, *Gabbiella* sp., and *Bulinus ecclesi*. The sea grass-like *Vallisneria* plants host *Lanistes ovum*, *Melanoides tuberculata*, *Gabbiella stanleyi* and *Bullinus nyassanus* (=*succinoides*).

It may well be that the case of the most common widespread and visible gastropod in Lake Malawi represented by *Lanistes*, as discussed above, can serve as example for the speciation of the other "endemic" species. As in the case presented by BERTHOLD (1990, 1991) there may not be four species as suggested by this author, but perhaps only two species, one of them endemic to the lake, if at all. Regarding *Melanoides* with its many so called endemic species, it very much appears to be the case of one, very variable species *M. tuberculata*, even though it is quite unknown, why there are so many very different looking morphs to be found on the beachdrift of parts of the lake.

The gastropods found in Lake Malawi are those or are closely related to those that are characteristic for Africa since the Miocene. Perhaps a new immigration wave of the Viviparidae with V*iviparus* may have changed into *Bellamya*, and the Bithyniidae of Eurasia sent their representatives that changed into *Gabbiella* and relation on their way south. *Melanoides* arrived coming from Asia, and *Cleopatra* as well as *Lanistes* and *Pila* had developed from African or at least Gondwanian source. The history and evolution of *Bellamya* as distinct genus from *Viviparus* still needs to be elucidated, since *Bellamya* has been present in Asiatic lakes for a long time. The paleobiogeographic history of the basommatophorans is still so little known that it cannot be interpreted at present. There is very much convergence found within the lymnaeid, flatly coiled planorbid, sinistral bulinid and limpet-like ancylid shapes of these fresh water gastropods that has similar shapes at least since Late Cretaceous times (BANDEL & RIEDEL 1994), that this group of gastropods may be very difficult to utilize in the future as well.

Conclusions

The gastropods of Lake Tanganyika represent the living members of ancient groups of fresh water gastropods that have been living in Africa prior to a new wave of immigrants which came during or before Miocene time. This later immigration has totally changed the composition of the African fresh water community from the Nile to South Africa, from the coast of the Indian Ocean to the coast of the Southern Atlantic. The only exception is North Africa outside of the Nile valley which has Mediterranean character (BROWN 1980) and is, thus, Eurasian in its faunal composition. Regarding Lake Tanganyika the only exception to this picture is presented by both members of the Basommatophora found in Lake Tanganyika, which are not endemic. Whether they are new components to the lake or whether they have simply not changed in the course of time, cannot be stated. Both strategies appear possible when other lakes with endemic speciation are consulted. For example the fossil Steinheim Lake in Germany had a conspicuous evolution of planorbid species, while *Lymnaea* and *Pseudamnicola* did not change at all (see NÜTZEL & BANDEL 1993, FINGER 1998).

Madagascar was isolated from Africa at least since Paleogene time, and this can also be seen reflected in its gastropod fauna. While *Melanoides*, *Pila* and *Lanistes* living in the cultured lowlands could well have reached Madagascar with human settlement, and species here and on the mainland are very similar or the same, *Melanatria* Bowdich, 1822, *Potadoma* Swainson 1840, and *Cleopatra* live in streams of the primary forest and probably represent modern species evolved from members of the early African fauna. They strongly differ from species present on the African continent. From this it may be assumed, that ancestral species of *Melanatria*, *Potadoma* and *Cleopatra* could also have been related to some of the groups now found in Lake Tanganyika.

A migration path could well have opened with the Nile, when it became connected to the portion of it that had contact to the East African Rift. *Bellamya* and *Gabbiella* reached South Africa, but never made it across to Madagascar. *Melanoides* also arrived late in Africa, perhaps also using the Nile after having reached the Near East. Williamson (1985) noted that in the late Miocene to Plio-Pleistocene fresh water mollusc fauna from the Turkana Basin, in two restricted horizons, underwent a wholesale phenotypic reorganization. This change affected *Bellamya*, *Pila*, *Cleopatra* and *Melanoides*. Especially *Melanoides* and *Cleopatra* changed very much and within these levels. The original species, from which all these changes started disappeared and returned again after the endemic fauna became extinct. These original species were close to modern *Bellamya unicolor, Pila ovata*, *Cleopatra bulimoides*, and *Melanopsis tuberculata*. The disappearance of the originator species seems to be an important factor that indicates the point of development in which a real change had occurred. Such a situation is found in Lake Tanganyika, where all of the endemic groups exist without the species from which they could have originated. Williamson's example as well as the case of the Steinheim lake indicate, that the evolution of new species does not have to take a long time, as assumed by Hubendick (1952), but has since developed in Lake Tanganyika to such a degree that the different lineages have reached the rank of subfamilies as was also suggested by Hubendick. The situation in Lake Malawi differs. Here the originator to species or morphs within a genus is still living in or near the lake. These are still largely the same that have been living in the fossil Lake Turkana, fossil and modern Lakes Albert and Edward, and modern Lake Victoria, and they belong to the genera *Bellamya*, *Pila*, *Lanistes*, *Gabbiella*, *Melanoides*, *Cleopatra*, *Bulinus*, and *Burnupia*/*Ferrissia*. The number of potential founder species to an endemic speciation is, thus, about the same as was reconstructed for ancient Lake Tanganyika. But Lake Tanganyika has, a long time ago, closed access to the actual lake to many species. How this is done remains mysterious, but it is the case. A similar feature is also noted in Lake Baical among modern lakes (Röpstorf, pers. com.), and it was documented for Lake Steinheim that existed during Miocene times in Germany (Nützel & Bandel 1993, Finger 1998).

Thus, Lake Tanganyika has preserved an ancient fresh water gastropod fauna that originated from species which no longer live in more short lived environments in the East African region. This lake had already closed itself to new settlement when a faunal turnover occurred during Miocene time. Only very few species could pentrate through this mysterious barrier, perhaps *Neothauma* being an early exception and the basommatophorans later ones. The gastropod fauna has changed in the lake and developed new species, and most of them have remained within the lake and have not affected the changes going on around them. One exception may be *Potadomoides* that could have migrated from the lake into the neighboring rivers and developed from the *Lavigeria* stem group. In reconstructing the fresh water fauna that has lived before the Miocene in Africa, the living fauna of Lake Tanganyika can be of great help once Paleogene fossils are known.

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