



SHELL AND OPERCULUM TAPHONOMY OF THE BITHYNIID GASTROPOD *GABBIELLA* IN THE PLEISTOCENE TURKANA BASIN, NORTH KENYA

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ABSTRACT—Shells and opercula of bithyniid gastropods assigned to *Gabbiella* are found in high abundance in the Pleistocene upper Burgi and KBS Members of the Koobi Fora Formation, Turkana Basin, northern Kenya. The systematic paleontology of the Turkana Basin *Gabbiella* is revised herein based on morphological comparison with the opercula of other Recent African bithyniids. The fossils from the upper Burgi and KBS Members are here assigned to *Gabbiella rosea* Mandahl-Barth, 1968, a species not known from the Turkana fossil record before, but extant in this lake today. A sampling and taphonomic bias is identified which influences the relative abundance of *Gabbiella* shells and opercula, as a mesh size of 0.63 mm or less is necessary to capture all opercula preserved in the sediments. Accordingly, opercula were found to be significantly more abundant than shells, indicating a different preservation potential of shells and opercula, as the calcitic operculum is more robust than the aragonitic shell. In contrast to previous arguments that most shellbeds in the Turkana Basin sequence represent undisturbed life assemblages, a taphonomic bias is clearly evident reducing the fidelity of the Turkana Basin mollusk assemblages.

INTRODUCTION

THE FOSSIL mollusk record of the Turkana Basin in the Plio–Pleistocene is known to be one of the best for freshwater mollusks in the world. In Turkana shellbeds are extremely abundant and very rich both in mollusk species and well-preserved specimens. The first extensive documentation and interpretation of this mollusk fauna was presented by Williamson (1979, 1981). In his papers he also described the high abundance of *Gabbiella* shells in the Koobi Fora Formation, assigning all congeneric shells from the upper Burgi and KBS Members to *G. senaariensis* (Küster, 1852).

Although not being mentioned by Williamson (1979), small and calcareous gastropod opercula, isolated from shells, are also very abundant in the upper Burgi and KBS Member deposits of the Koobi Fora Formation in Areas 100 and 102 (see Fig. 1). A direct affiliation of the opercula with any of the Turkana Basin gastropod species is not possible; however, among the extant gastropods of the Turkana Basin only bithyniid gastropods are known to have a small calcareous operculum. Therefore, it is most reasonable to assume that all opercula belong to the only *Gabbiella* species identified before. The first aim of this study is to test this hypothesis by comparing the morphology of the fossil *Gabbiella* shells and opercula from upper Burgi and KBS Members with modern bithyniid shells and opercula from East Africa based on the revision by Mandahl-Barth (1968). The second aim of this study is to estimate the taphonomic bias and fidelity of the mollusk assemblages based on quantitative analyses of the relative abundance of *Gabbiella* shells and opercula. Our results bear relevance as understanding taphonomic processes is paramount for the still controversial paleobiological analysis of the Turkana Basin mollusk assemblages.

Williamson (1981) interpreted the mollusk fauna to be of high importance for evolutionary studies. He distinguished three periods with morphological “excursions” of several to many mollusk taxa, i.e., contemporaneous changes of shell morphology in different lineages of mollusks. Two of these excursions are associated with the Suregei Isolate (SI; i.e., the lower Burgi Member of the Koobi Fora Formation according to modern terminology) and the Guomde Isolate (GI; i.e., the Chari Member of the Koobi Fora Formation according to modern

terminology), respectively. Williamson (1979, 1981) interpreted these excursions as speciation events following the punctuated equilibrium model (see discussions in Fryer et al., 1983; Eldredge and Gould, 1972; Gould, 2002; Van Bocxlaer et al., 2008). This model claims that evolutionary change, rather than being slow and gradual, takes place in bursts after long periods of stasis during which little change occurs (see Eldredge and Gould, 1972; Gould, 2002). The third morphological excursion was interpreted by Williamson (1979, 1982) as a so called “minor adaptive radiation” of several mollusk lineages in the lower Member of the Koobi Fora Formation (i.e., the upper Burgi Member in modern stratigraphic terminology), suggesting in this case speciation in peripheral isolates.

An essential prerequisite for being able to draw and evaluate those conclusions is the taphonomic nature of the shellbeds. Williamson differentiated three facies types for the mollusk beds: 1) life assemblages with no evidence of reworking, i.e., an autochthonous thanatocoenoses; 2) mass flows in prodeltaic settings; and 3) death assemblages with transported and abraded material (Williamson, 1982, 1983). As facies three is mainly restricted to the KBS Member of the Koobi Fora Formation, it has little or no impact on the evolutionary scenarios, according to Williamson (1982, 1983). Although the importance of taphonomic processes for paleobiological analysis was pointed out by Cohen and Schwartz (1983), a detailed analysis of the taphonomic bias of the aquatic fauna of the Turkana Basin was never provided to validate the importance of taphonomic processes for paleobiological analysis. It is not only transport or reworking influencing the fidelity of fossil assemblages. Other taphonomic factors must be analyzed, as well as the potential for and implications of sampling bias. The present study aims to evaluate the importance of taphonomic processes for the formation of the Turkana Basin shellbeds in the Pleistocene.

GEOLOGY AND PALEOHYDROLOGY OF TURKANA BASIN

The history of the Turkana Basin dates back to the early Pliocene when it existed primarily as a fluvially-dominated rift basin. During relatively short time intervals, rift lakes formed in the basin, including the most recent, modern Lake Turkana, which is fed primarily by the Omo River draining from the

Ethiopian Highlands to the south. The Omo River is hypothesized as the major source of freshwater for the last ~ 4.2 million years (Joordens et al., 2011), draining the Turkana Basin from north to south. Altogether five lake phases are identified prior to the emergence of modern Lake Turkana: 1) the first major lake was Lake Lonyumun at about 4.1 Mya that existed for about 100,000 year; 2) Lake Lokochot was the second lake filled within 60,000 years at about 3.4 Mya; 3) the Lake Lokeridede (also known as Lake Kokiselei) between 2.43 and 2.32 Mya has the first important mollusk record; mollusks from that lake are known representing the fauna from the so called Suregei Isolate (SI; Williamson, 1980, see also Van Bocxlaer et al., 2008), a term no longer used in modern stratigraphic terminology; 4) between about 2.0 and 1.5 Mya the Turkana Basin held Lake Lorenyang, which is the focus of the present study; and 5) Lake Silbo is the fifth lake around 0.7 Mya and it contains the so called Guomde Isolate (GI) mollusk fauna (Williamson, 1980, see also Van Bocxlaer et al., 2008).

The sediments of the paleolakes in the Turkana Basin contain most of the mollusk-bearing strata (Feibel, 1999). The entire sedimentary record of these paleolakes comprises the Koobi Fora Formation. The chronostratigraphic framework of the Koobi Fora Formation is based on more than 130 tuffs that are isochronous markers and in some cases suitable for isotopic dating. The formation is subdivided into eight members with major tuff layers acting as separating geologic units. The Burgi Member of the Koobi Fora Formation is subdivided into lower and upper parts separated by a major unconformity. The deposits of the lower and upper Burgi Members have accumulated in two distinct lake phases separated by fluvial sedimentary rocks in the Turkana Basin (Feibel, 1999). The sediments of the lower Burgi Member are deposited in Lake Lokeridede, whereas the sediments of the upper Burgi Member are deposited in Lake Lorenyang.

The Plio–Pleistocene sediments of the Koobi Fora Formation are exposed in several regions around Lake Turkana. For this study the mollusk fossils of the upper Burgi and KBS Members (i.e., deposits of Lake Lorenyang) along the Koobi Fora Ridge were analyzed (Figs. 1, 2). A series of laterally extensive and continuous marker beds facilitates the correlation of sedimentary sequences (Feibel et al., 2009). These marker beds are mollusk or stromatolite beds indicating shallow lake water conditions with low clastic input in nearshore or back-beach settings (Lepre et al., 2007). In the marker beds a gradual increase in algae abundance is evident with the increase of stromatolites. This increase is also indicated by the change in the notation of the marker beds from C-beds (i.e., mollusk-dominated beds) to A-beds (i.e., stromatolite beds).

MATERIAL AND METHODS

The mollusks for this study were collected 2006 and 2010 in Areas 100, 102, and 103 near Koobi Fora (Fig. 1). A complete list of samples is provided in Table 1 indicating the stratigraphic level and geographic position of the material. Bulk samples were taken if possible and dry-sieved in the field and/or laboratory. In the field one mesh screen with about 1.5 mm mesh size was used, for sieving in the laboratory a mesh screen with 0.63 mm mesh size was used. The residues in the sieve were quantitatively sorted under a microscope in the lab.

A Chi-square test was performed on the specimen counts (total abundances per sample) using PAST version 2.13 (Hammer et al., 2001) to determine if shell and operculum abundance differ significantly between samples (see Nehm and Hickman, 2008). Samples sieved with 0.63 mm and 1.5 mm were tested separately. Relative abundance of shells and

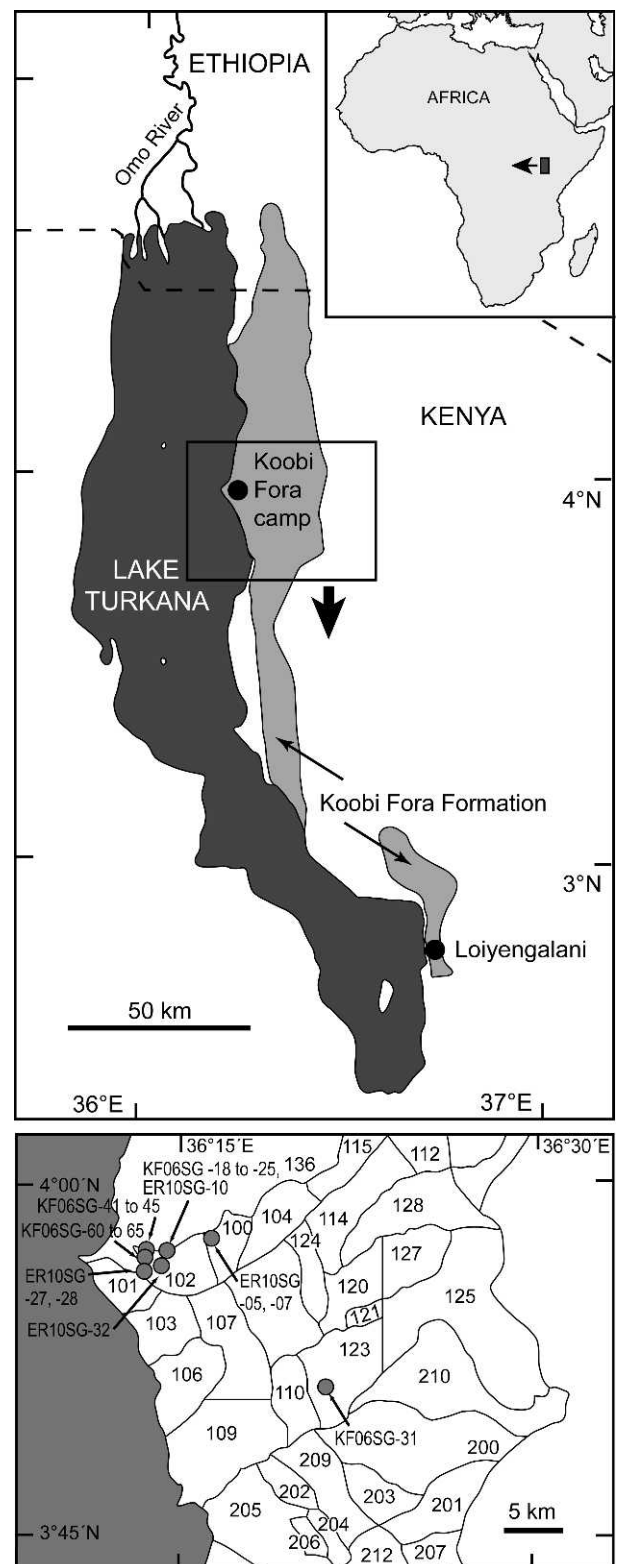


FIGURE 1—Location maps showing Lake Turkana in East Africa, the exposures of the Koobi Fora Formation along the eastern shore of Lake Turkana, the collection areas near Koobi Fora camp, and the collection localities of the *Gabbiella* shells and opercula studied herein (maps compiled after Brown and Feibel, 1991). See Table 1 for the exact geographic position of the localities.

opercula was calculated as their percentage of the sum of shells and opercula from one sample (Table 1).

All shells will be eventually housed in the National Museums of Kenya in Nairobi (NMK). As official NMK accession numbers were unavailable for the study, the figured specimens have RGM numbers referring to the National Museum of Natural History Naturalis in Leiden. Most of the modern species studied herein are from the Mandahl-Barth collection at the former Danish Bilharziasis Laboratory (DBL), now DBL-Centre for Health Research and Development in Copenhagen, Denmark. Additional material was included from the Royal Museum of Central Africa (Musée Royal de l'Afrique Centrale, MRAC) in Tervuren, Belgium, and the Charpentier collection at the Musée de Zoologie in Lausanne, Switzerland. All *Gabbiella* shells and opercula were studied using SEM techniques. Only type material from DBL, MRAC and Lausanne was studied under low vacuum to keep the shell surface unaltered.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1798

Family BITHYNIDAE Gray, 1857

Genus GABBIELLA Mandahl-Barth, 1968

Type species.—*Bithynia stanleyi* variety *humerosa* Martens, 1879.

GABBIELLA ROSEA Mandahl-Barth, 1968

Figure 3.1–3.9, 3.16–3.20

Description.—The fossil *Gabbiella* shells (Fig. 3.1–3.5) from upper Burgi and KBS Members of the Koobi Fora Formation are small. The width ranges from 2.1 to 2.6 mm, the height ranges from 2.7 to 3.2 mm. The shells are globose with sometimes slightly trapezoidal spire flanks. The spire is usually higher than the aperture.

The calcareous opercula of the fossil *Gabbiella* shells (Fig. 3.6–3.9) vary between 0.8 and 1.9 mm in width and between 1.0 and 2.2 mm in height. The spiral nucleus is shifted anteriorly towards the inner lip of the shell. It is very large and occupies almost the entire operculum.

Types.—DBL, catalogue number 53-1445; from Lake Rudolph (Turkana), western shore; leg., Champion.

Occurrence.—Shells and opercula of *Gabbiella rosea* are preserved continuously in all major shellbeds of the upper Burgi Member sampled in Area 100 and 102 (see Table 1 for more details). They occur in the KBS Member also but abundance in the major shellbeds is lower (see below).

Remarks.—Based on the descriptions provided above, the only modern *Gabbiella* species that has shells and opercula identical in shape and size to the fossil specimens is *Gabbiella rosea* (Fig. 3.16–3.20), which is still living in Lake Turkana today (Cohen, 1986). A very distinctive feature is the white or pink shell color from where the species derived its name. Mandahl-Barth (1968) named this species as being new without having an operculum available for description. He described it from the western shore of Lake Turkana, which is confirmed by Lange (2004). After the publication of Mandahl-Barth (1968), more material of *G. rosea* was collected for the DBL including material from Loyangalani, at the southeastern shore of Lake Turkana. A number of opercula are present in this material, both loose and attached to the shells (dry soft tissue still present). They have not been figured nor described in detail before, but are depicted here (Fig. 3.19, 3.20). The spiral nucleus of *G. rosea* is very large and occupies almost the entire operculum. It is situated not in the middle of the operculum but closer to the inner lip of the shell, similar to the fossil specimens from the Turkana Basin.

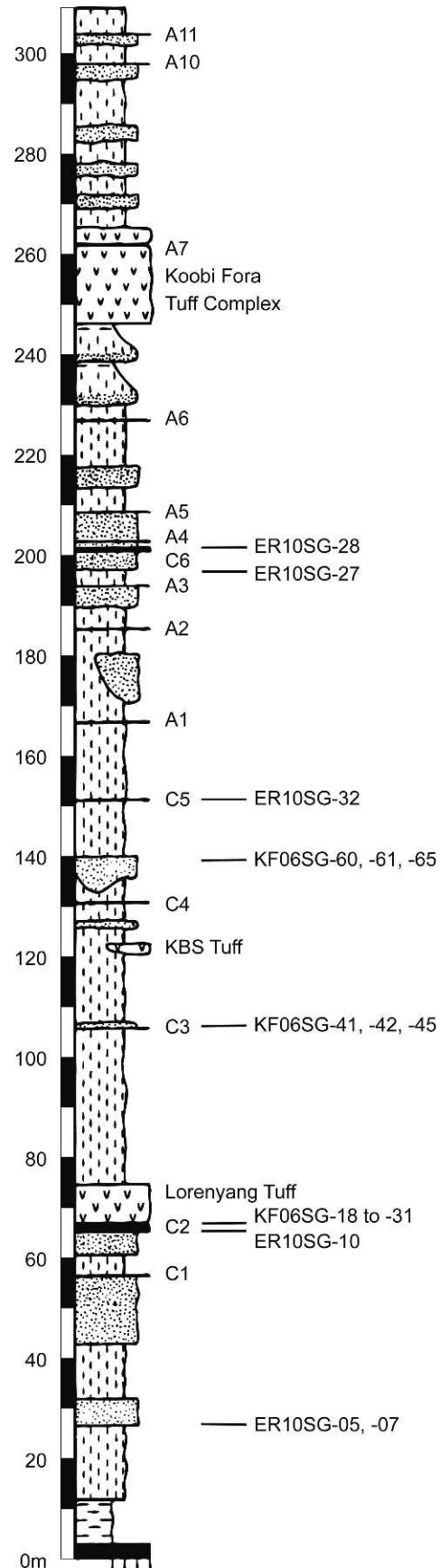


FIGURE 2—Composite stratigraphic column for the Koobi Fora Ridge with some key tuff layers, the mollusk (C) and stromatolite (A) marker beds and the samples of the *Gabbiella* shells and opercula studied herein (column from Feibel, 1999).

TABLE 1—Shell and opercula numbers and relative abundance per sample in stratigraphic order (see Fig. 2 for the stratigraphic position of the samples). The sampling mode is also given. All samples are bulk samples that were either sieved in the field and/or in the lab (minimum mesh size given as well).

Sample	Lat. / Long.	Total abundance		Total	Relative abundance		Sampling mode
		Shells	Opercula		Shell	Opercula	
ER10SG-28	N3°56.393', E36°13.484'	191	3030	3221	0.06	0.94	lab sieved, 0.63 mm
ER10SG-27	N3°56.374', E36°13.507'	0	835	835	0.00	1.00	lab sieved, 0.63 mm
ER10SG-32	N3°56.554', E36°14.005'	15	67	82	0.18	0.82	lab sieved, 0.63 mm
KF06SG-65	N3°56.624', E36°13.638'	38	0	38	1.00	0.00	not sieved
KF06SG-61	N3°56.605', E36°13.674'	755	1347	2102	0.36	0.64	lab sieved, 0.63 mm
KF06SG-60	N3°56.605', E36°13.674'	500	36	536	0.93	0.07	field sieved, 1.5 mm
KF06SG-45	N3°56.838', E36°13.742'	11	623	634	0.02	0.98	lab sieved, 0.63 mm
KF06SG-42	N3°56.838', E36°13.742'	29	2078	2107	0.01	0.99	lab sieved, 0.63 mm
KF06SG-41	N3°56.838', E36°13.742'	6	310	316	0.02	0.98	lab sieved, 0.63 mm
KF06SG-31	N3°51.248', E36°21.198'	25	20	45	0.56	0.44	field sieved, 1.5 mm
KF06SG-25	N3°57.16', E36°14.324'	10	11	21	0.48	0.52	field sieved, 1.5 mm
KF06SG-21	N3°57.16', E36°14.324'	54	1	54	0.98	0.02	field sieved, 1.5 mm
KF06SG-20	N3°57.16', E36°14.324'	396	2	396	0.99	0.01	field sieved, 1.5 mm
KF06SG-19	N3°57.16', E36°14.324'	232	2	232	0.99	0.01	field sieved, 1.5 mm
KF06SG-18	N3°57.16', E36°14.324'	760	4	760	0.99	0.01	field sieved, 1.5 mm
ER10SG-10	N3°57.181', E36°14.347'	88	2615	2703	0.03	0.97	lab sieved, 0.63 mm
ER10SG-07	N3°57.264', E36°16.037'	8	69	77	0.10	0.90	lab sieved, 0.63 mm
ER10SG-05	N3°57.264', E36°16.037'	12	1004	1016	0.01	0.99	lab sieved, 0.63 mm

Gabbiella rosea occurs today in the modern Lake Turkana with other mollusk species that are known from the fossil record as well (Cohen, 1986). Therefore, it is reasonable to assume an earlier invasion into the Turkana Basin. As the Omo River is feeding the Turkana Basin since about 4.2 Mya (Joordens et al., 2011), the same invasion routes for mollusks are open since this time to establish a lacustrine fauna with the establishment of lakes in the Turkana Basin.

Williamson (1979) assigned the upper Burgi Member bithyniids to *Gabbiella senaariensis* (Küster, 1852) (Fig. 3.10–3.12). Therefore, the modern representatives of the species are chosen for comparison and their opercula are studied in order to confirm or reject Williamson's hypothesis on the species' affiliation.

Difficulties exist to identify the type material of *G. senaariensis*, not only because a taxonomic revision of these bithyniids is unavailable to date. As Küster (1852) is referring to the Charpentier collection for his study, the specimens from the Charpentier collection in Lausanne are good candidates for the material available to Küster for his original description of the species. The size of the shells from this collection is relatively small. The specimen on Figure 3.10 is only about 4.5 mm high. However, shells of *G. senaariensis* can grow up to 8.5 mm in height (Mandahl-Barth, 1968) though no fossil bithyniid in the sampled shell beds were found to reach this size.

Williamson (1979, p. 236) reported on "no biometric evidence for regarding it as a distinct form". The shells are slender, with a spire that is higher than the aperture. Thus, shape of modern *G. senaariensis* and the fossil *Gabbiella* shells is very similar, but the difference in size is striking.

The shape of the operculum of *G. senaariensis* is different from the fossil operculum. The spiral nucleus only occupies half of the diameter of the operculum and is more or less centrally placed. As the operculum is a taxonomically important feature in bithyniids, it is evident that the described difference is also important in identifying the fossil bithyniids from the Turkana Basin.

For comparison other modern bithyniids were studied for which either shell and operculum morphology or biogeographic distribution pattern suggests relationships with the Turkana Basin *Gabbiella*. For a complete overview and description of African bithyniid gastropods see Mandahl-Barth (1968) and Brown (1994).

Gabbiella humerosa (Martens, 1879) (Fig. 3.13) is a very common species from the large lakes of the western branch of the East African Rift System (i.e., Tanganyika, Kivu, Albert, Edward,

Victoria) and in the connecting rivers (Brown, 1994). The various subspecies (according to Mandahl-Barth, 1968) and morphs of *Gabbiella humerosa* are variable in shell morphology and considerably smaller than *G. senaariensis*. A further difference is the lower height of the spire compared to the aperture. As a distinctive feature, the operculum has a larger spiral nucleus compared to *G. senaariensis* but a smaller nucleus compared to the fossil operculum.

Jubaia excentrica Mandahl-Barth, 1968 (Fig. 3.14, 3.15) is very similar in shell morphology to *Gabbiella senaariensis* and the operculum is described having an excentrically placed nucleus (Mandahl-Barth, 1968). Today, *J. excentrica* is known only from SW Somalia (e.g., Juba River; see Van Damme, 2008). However, it is reported from Pleistocene deposits of the Lower Omo Basin (Van Damme and Gautier, 1972). Therefore, it is plausible that the species invaded the Turkana Basin even before that time. The *Jubaia* operculum is very different from the operculum of most of the *Gabbiella* species, justifying the erection of the new genus *Jubaia* in which the nucleus is excentrically placed to the right of the middle (Mandahl-Barth, 1968). This gives the opercula a rounded triangular outline shape. This is also the most noticeable difference between the fossil opercula and *J. excentrica*. The spiral nucleus of the fossil specimens is excentric as well, but shifted anteriorly towards the inner lip of the shell.

Like the shells of other *Gabbiella* species, the shape of *Jubaia excentrica* is very similar to the fossil shells. The spire is higher than the aperture, the whorls are convex but slightly shouldered and the umbilicus is almost closed. The shell size of *J. excentrica*, however, is much larger (height of the type specimen about 6 mm).

It is not possible to clearly distinguish the operculum of *Gabbiella parvipila* (Verdcourt, 1958) (Fig. 3.21–3.23) from that of *G. rosea*. Both are characterized by a very large nucleus covering the largest part of the diameter. The drawing of Verdcourt (1958) is incorrect in placing the nucleus towards the outer lip of the shell. Instead, the nucleus is situated very central. Although the operculum of *G. rosea* and *G. parvipila* is more or less identical, the shell morphology of both species is clearly different. The shells of *G. parvipila* are more globose and have a shorter spire compared to *G. rosea*.

ABUNDANCE PATTERN RESULTS AND DISCUSSION

Shells and opercula of *Gabbiella rosea* are preserved continuously in all major shellbeds sampled in Area 100 and

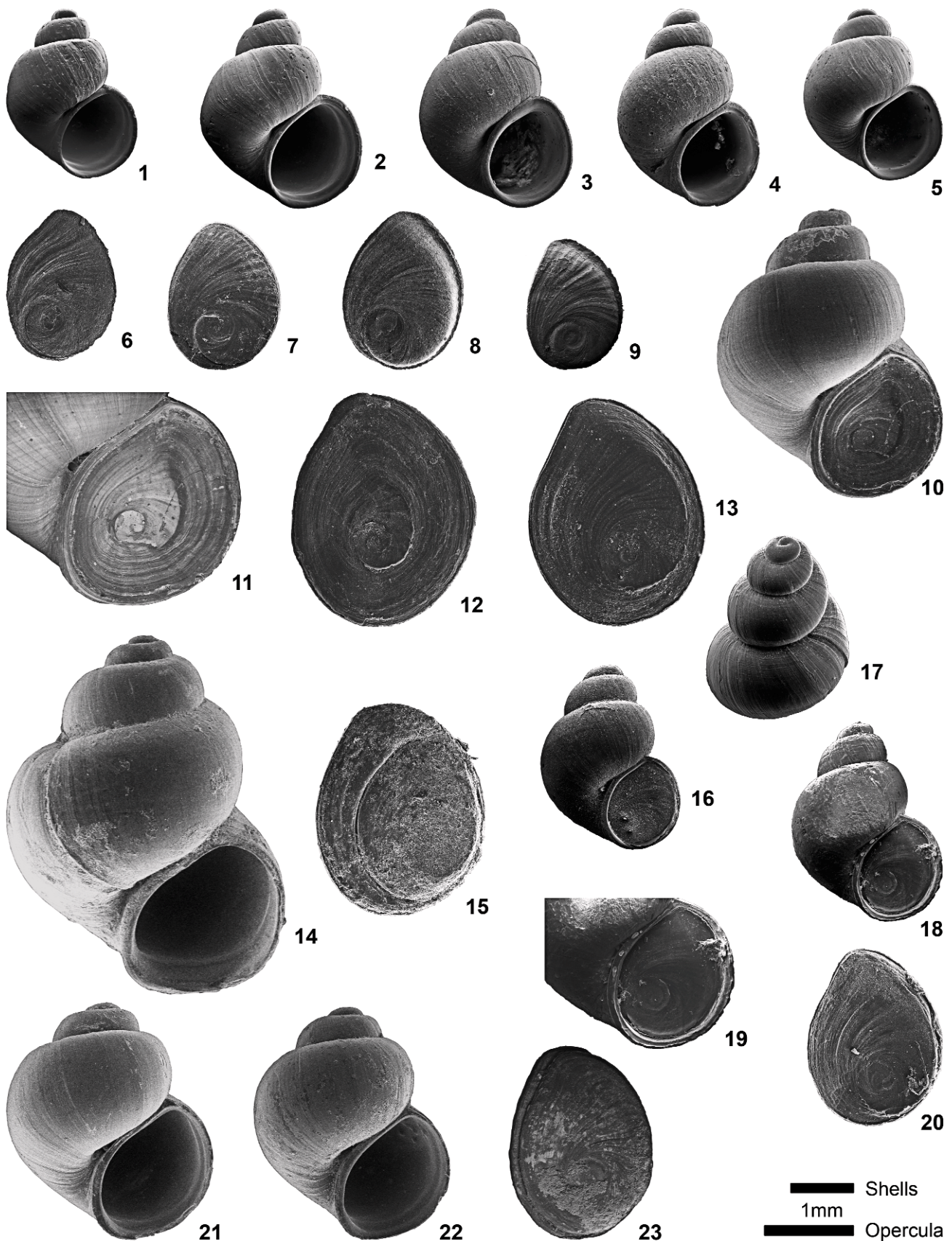


FIGURE 3—Fossil and modern bithyniid shells and opercula from North and East Africa. 1–9, fossil *Gabbiella rosea* Mandahl-Barth, 1968 shells and opercula from the upper Burgi and KBS Members of the Koobi Fora Formation, RGM 609.101 to RGM 609.109: 1, 2, KF06SG-18 to –21; 3–5, 7, KF06SG-61; 6, ER10SG-05; 8, KF06SG-42; 9, ER10SG-10; 10–12, *Gabbiella senaariensis* (Küster, 1852): 10, 11, Lausanne, Collection Charpentier, no 42; 12, DBL 53-1565; 13, *Gabbiella humerosa* (Martens, 1879), DBL 53-1423; 14, 15, *Jubaia excentrica* Mandahl-Barth: 14, type, DBL 53-1517; 15, DBL 53-1519; 16–20, *Gabbiella rosea* Mandahl-Barth, 1968: 16, 17, DBL 53-1447; 18, 19, DBL 53-1446; 20, DBL 53-1483; 21–23, *Gabbiella parvipila* (Verdcourt, 1958), type, MRAC 340.085.

102. However, the abundance pattern of shells and opercula in the various shellbeds of the Koobi Fora Formation is puzzling (Table 1). In all cases where a bulk sample was sieved through the 0.63 mm sieve, shells are significantly less abundant than opercula (Chi-square test, $p \sim 0$). Overall, about 9 percent of all specimens are shells (1,115 shells versus 11,951 opercula). In all cases where a bulk sample was sieved in the field through the about 1.5 mm sieve or not sieved at all, shells are significantly more abundant than opercula (Chi-square test, $p < 0.001$). In these samples, 97 percent of all specimens are shells (2,015 shells versus 76 opercula).

The shells and opercula only rarely occur in the same relative abundance in the section sampled quantitatively. In particular when the abundance of either shells or opercula is very high, the abundance of the counterpart is very low. We identified three possible factors to explain this pattern: 1) separation of shells and opercula due to different transport behavior in currents and waves; 2) different preservation potential of shells and opercula; 3) sampling bias due to the selection of different mesh size for sample processing.

Postmortem transport may explain the different abundance of shells and opercula in fossil assemblages. When the gastropod soft parts decay before the burial of the shell, opercula can easily be separated from the shell. Wave action may then be responsible for a spatial separation and sorting of shells and opercula. The difference in size and shape of both components certainly influences their transport behavior. Opercula are light and flat and are likely transported by very low water currents, and also likely stay longer in the water column as compared to the shells. The waves at the beach of Lake Lorenyang would be ideal to separate shells and opercula over time. The velocity of the water current produced by waves is higher in a shoreward direction than in seaward direction (see May, 1973). Shells and opercula may be transported by the high velocity shoreward current together, but only opercula may be transported by the low velocity seaward current. The shells would then be deposited at the shore while the opercula would be deposited somewhere else.

The postmortem transport model, however, is not well suited to explain the abundance pattern of shells and opercula in the Koobi Fora Formation for several reasons. First, shells and opercula are found together in many shellbeds, which is not expected under a effective transport mechanism to separate them. Second, even if opercula are very abundant and *Gabbiella* shells are almost absent, numerous large shells of other mollusk taxa are present in the same sample. Larger bivalve shells (*Coelatura*, *Pseudobovaria*, sometimes even *Iridina*) and larger gastropods (e.g., *Bellamyia*, *Cleopatra*, *Melanoides*) are at least present if not very abundant in the same samples with high opercula abundance. If postmortem transport is responsible for the different abundance pattern, offshore shell beds with large shells must be present where isolated opercula accumulate. However, most shellbeds of the Koobi Fora Formations are interpreted as nearshore or beach sediments (see Lepre et al., 2007), where winnowing would remove the opercula, if the processes described above are applicable.

The only study we are aware of analyzing abundance pattern of gastropod shells and opercula was published by Nehm and Hickman (2008). They explain the difference in abundance of shells and opercula with a different preservation potential of both components. This is also interpreted to be the main reason for the higher abundance of *Gabbiella* opercula in many shellbeds. The shells of bithyniid gastropods are aragonitic whereas the opercula are calcitic (Anadón, 2006; Penkman et al., 2010, 2011). As calcite is more stable compared to

aragonite, the preservation potential of calcitic objects is higher compared to aragonitic objects. This is obvious in a number of samples where *Gabbiella* shells and opercula occur together. If the degree of shell disintegration is high and the degree of shell integrity is low, opercula are still well-preserved and robust (e.g., ER10SG-07, -27 and -28, personal observation). Thus, the variability in shell condition in different shellbeds is high as opposed to the consistent preservation of opercula in the samples. This argues for a different preservation potential as the main reason for the higher abundance of opercula in many shellbeds.

It is obvious that the mode of collecting and processing samples has a significant influence on the abundance pattern. Given the size range of the opercula (0.8–1.9 mm wide, 1.0–2.2 mm high), a mesh size of about 1.5 mm is not sufficient to capture all opercula in the sample. This is confirmed by the results of J. Joordens (personal commun., 2012) who sieved the sediments of the stratigraphic interval where we took the samples KF06SG-18 to -25 with a 0.63 mm mesh size to extract specimens for geochemical analyses and found a very high abundance of *Gabbiella* opercula. It is also obvious that the arenaceous bioclastic carbonates (e.g., KF06SG-65) are not suitable to identify opercula. Large shells but not very small components like opercula can be identified easily at the surface of the rocks. Therefore, a quantitative paleobiologic and taphonomic analysis of the Koobi Fora Formation mollusk fauna requires the collection of loose bulk samples and the evaluation of the 0.63 mm size fraction.

PALEOECOLOGY AND FIDELITY OF THE TURKANA BASIN MOLLUSK ASSEMBLAGES

Gabbiella shells and opercula were found in a number of shellbeds throughout the succession, as shown above. However, no single shell or operculum was found in any of the A-beds of the KBS Member (i.e., stromatolite beds). *Gabbiella* only occurs in C-beds (i.e., mollusk-dominated beds) or other shellbeds without any evidence of stromatolites. It is highly unlikely that this is due to taphonomic bias, as both shells and opercula of *Gabbiella* are not present in A-beds, whereas other mollusks still occur in high abundance (e.g., *Melanoides*, *Coelatura*, *Corbicula*). Therefore, it can be interpreted as an ecological signal: *Gabbiella* is not tolerant of the hypersaline environmental conditions of the stromatolite habitats; see Abell et al. (1982) and Lepre et al. (2007) for an interpretation of the stromatolite environments. The question is why *Gabbiella rosea* is present in Lake Turkana today despite the high alkalinity of the lake water. In this context Cohen (1986) mentioned that all modern mollusks of Lake Turkana are thin-shelled and stunted due to the alkaline water conditions, whereas the mollusks from the A-beds of the KBS Member look healthy with well-developed shells (Williamson, 1979; present study). More data on the geochemistry of the A-bed sediments and shells are necessary to reconstruct these environments, though. As *Gabbiella* is not the only mollusk lacking in the A-beds (e.g., *Bellamyia* is also absent), environmental differences are expected to be a very important driving force in the distribution of mollusks in the Koobi Fora Formation.

The relative abundance pattern of shells and opercula indicate the importance of the preservation potential of different hard parts for drawing paleobiological conclusions. Species diversity may be underestimated in some cases. The presence of opercula is an indicator that *Gabbiella* was present even if no shells are recorded. Only counting shells in this case would result in a reduced diversity. This has implications in particular for rare, fragile and small species with no opercula preserved, e.g.,

Bulinus truncatus, *Burnupia stuhlmanni* or planorbid species. The absence of these species from a certain sample or interval can not be considered an indicator of reduced diversity. They may simply not be preserved or retrievable in a given sample.

One other outcome of this study is that counting shells and opercula to estimate the abundance of mollusks is misleading. *Gabbiella rosea* is the only mollusk from the upper Burgi and KBS Members with preserved opercula. The corneous opercula of other mollusks (*Melanoides*, *Cleopatra*, etc.) are not preserved and cannot be included. For comparing relative abundances of mollusk species it is therefore not recommended to consider the *Gabbiella* opercula.

As shown above, a taphonomic bias of the mollusk assemblages is evident. More and further analyses are necessary to fully understand the extent of the bias and the implications for the paleobiological analysis and evolutionary scenarios of mollusks. This is also necessary to confirm or reject the assumptions of Williamson that life assemblages dominate over death assemblages in the upper Burgi and KBS Members of the Koobi Fora Formation.

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