STUDIES ON AFRICAN FRESHWATER BIVALVES

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PREFACE

African freshwater bivalves are today a neglected animal group, perhaps as a result of the fact that there are no species of economic or medical importance. While there is a plentiful amount of literature on the subject, most of it is outdated. African freshwater bivalves show great variation in morphology and this, coupled with the relatively few constant characters, has made it systematically a difficult group.

For almost a lifetime, Dr. Georg Mandahl-Barth has been interested in, and has worked with, this animal group, and through the years has established a large and very representative collection of African freshwater bivalves, which today is housed at the Danish Bilharziasis Laboratory. In the beginning of the 1980's Dr. Mandahl-Barth put his experience to paper in the shape of working documents prepared for DBL's younger staff members, and these notes were finally written up in 1982-85 (Unionidae, 1982, Mutelidae and Etheriidae, 1983, and Sphaeriidae and Corbiculidae, 1985). In recent years a great interest has been shown in these papers, for which reason we at DBL now have found it prudent to publish the manuscripts in the present form.

On behalf of DBL I should like to thank Dr. Mandahl-Barth for his very great work, which I am sure will be of immense value for many scientists. For me there is no doubt that Dr. Mandahl-Barth, with his vast experience and his knowledge of the problems within the systematics of African freshwater bivalves, is the only person today who has been able to write such a document.

I should also like to thank Dr. David Brown of the British Museum (Natural History) for his interest and promotion of the document. But most of all I should like to thank Dr. Thomas K. Kristensen for having edited the manuscripts and Mrs. Elaine Svenningsen for having translated Part II and typing the entire manuscript.

Finally it remains to be mentioned that Dr. Mandahl-Barth has also drawn all the detailed illustrations.

Dr. Flemming Frandsen
Director, Doctor of Science

INTRODUCTION

The present paper, "STUDIES ON AFRICAN FRESHWATER BIVALVES", is the result of thirty years'studies. As is the case all over the world, the majority of the species of these animals belong to the two superfamilies Unionacea and Sphaeriacea, and only a part of the former is treated here, viz. the Unionidae and, if one wants to maintain it as a distinct family, the Margaritiferidae. The study has comprised most of the known species, whether valid or not, and all the relevant literature. It was hoped that it would have resulted in an acceptable systematics, but, unfortunately, this is not the case. However, this disappointing result is in no way surprising, if the particular conditions affecting most freshwater organisms and certain traits in the biology of the unionids are taken into consideration.

It is a well-known fact that many hololimnic species are split up into a number of more or less different populations owing to the nature of their freshwater habitats. In particular, three aspects of this nature are of importance for the differentiation of populations. The first is that many inland waters are isolated, which often means that one population of a freshwater species can evolve in a certain direction without interbreeding with other populations. The second aspect is the wide variety of freshwater biotopes, which forces the animals (and plants) to adapt themselves to the conditions they find or to perish. These two aspects - isolation and variation - tend to result in the formation of species, but the third aspect of inland waters, their unstable nature and usually short duration, works in the opposite direction and will as a rule prevent the formation of new species, at least where molluscs are concerned, simply because the time available is insufficient. The result very often will be many more or less different populations of closely allied forms, which to a certain extent may be collected in subspecies, such as we know so well in several groups of freshwater snails and as we will meet again in the Sphaeriacea.

In the Unionacea the situation becomes still more complicated because of their manner of reproduction. No copulation takes place and it is quite accidental which male bivalve fertilizes

which female giving ample possibilities for cross-breeding between related forms. We should consider also their parasitic larval stage on fish, during which the young can be carried far away from the place where their parents live. Very little is known of the parasitic stage of the African Unionacea, but we must assume that they all have such a stage and there is no reason to disregard the significance it must have for the dispersal of the bivalves. When the young bivalve has finished its parasitic life and drops to the bottom, it will not move much for the rest of its life. It is bound to stay where it is and must adapt itself to the conditions or die. Most unionids possess a great adaptability, which often finds expression in the shape of the shell. Such ecotypes are well known in European unionids, and they can have so different appearances that they have been regarded as different species. There is no reason to believe that the African species should be less adaptable.

Remarks on the figures

Very often, when using the literature, I have felt how difficult it can be to compare, for instance, a photograph of a right valve with a more or less naturalistic drawing of a left valve. In order to avoid such confusion I have endeavoured to prepare rather standardized drawings always of a left valve giving the shape as accurately as possible and the sculpture as clearly as necessary and nothing more. Whenever possible I have drawn a typical shell or a shell of particular interest, but in some cases when no adequate material was available, I have redrawn published figures. I have not found it expedient to include figures of the anatomy, because studies of the soft parts of many specimens of several species and forms have convinced me that anatomical details are of little value for the species taxonomy where unionids are concerned. The anatomical characters are subjected to a rather great variation, partly caused by nutritional and sexual conditions and partly by the shape of the shell. Figures are individually numbered in each of the chapters: Unionidae, Mutelidae and Sphaeriacea.

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PART I. SUPERFAMILY UNIONACEA

This superfamily comprises the majority of the larger true freshwater bivalves. As a rule they have the beaks placed before the middle of the shell. The hinge may be schizodont, anodont or with secondary tubercles, but never heterodont, and they have a parasitic larval stage, after which they spend their lives buried in the bottom with only the posterior end reaching up into the water. The superfamily consists of three families, all represented in Africa.

Key to the families of Unionacea

1. Free-living, equivalve bivalves 2

   Sessile, inequivalve bivalves with one of the valves cemented to rocks or other shells .....Etheriidae

2. Hinge usually with teeth, a supra-anal opening present and the larvae are glochidia .....Unionidae

   Hinge without teeth or with a secondary row of tubercles, a supra-anal opening absent and the larvae are much more transformed than the glochidia .....Mutelidae

A: UNIONIDAE

The Unionidae are characterized by the peculiar hinge, which usually is termed schizodont, but in fact it is rather transformed. A typical schizodont hinge is present only in the marine family Trigoniidae with many extinct and a few living species in Australian coastal waters. In this the anterior and the posterior teeth are very similar, and those of the left valve are cleft into two (fig. 1). How the unionid hinge has developed from this can be seen in some species with a short and heavy shell, for instance in Caelatura nyassaensis (fig. 2): the anterior teeth of trigoniids have evolved to the cardinal teeth and the posterior to the lateral teeth. It should be remembered that the cardinal teeth of the unionids are not homologous with the cardinal teeth of a heterodont hinge. In some thin-shelled unionids, for instance Anodonta, the hinge has become toothless.

As in other Unionacea, the eggs are stored and fertilized in the gills, where they also hatch to a special larval stage called the glochidium, which is parasitic on fish.

The family comprises nearly one hundred genera with the majority living in North America and Eastern Asia. From Africa nine are known and no less than seven of them are represented by a single species and only one of them, Caelatura, consists of several species. I include Margaritifera in the family, as I do not find it justifiable to separate this genus in a family of its own.

Key to the genera

1. Unionids from Africa except the north-western area 2

   Unionids from north-western Africa 7

2. Shell with the dorsal margin prolonged anteriorly and posteriorly (Lake Mweru).....Prisodontopsis

   Dorsal margin not prolonged 3

3. Hinge with well developed teeth 4

   Hinge without cardinal teeth and with feeble lateral teeth (Lake Tanganyika) 6

4. Not from Ethiopia. Glochidia without a strong hook on the basal margin of each valve (figs. 11-12) .....Caelatura

   Glochidia with a strong hook on the basal margins (fig. 13) 5

5. Unionid from southern Africa .....Cafferia

   Unionid from Ethiopia .....Unio

6. Shell long and very compressed .....Pseudospatha

   Shell shorter and inflated .....Brazzaea

7. Hinge without teeth .....Anodonta

   Hinge with teeth 8

8. Lateral teeth normally developed. Mantle borders coalescent between supra-anal and anal opening 9

   Upper lateral tooth of left valve vestigial. Supra-anal opening not separated from anal opening .....Margaritifera

9. Cardinal teeth rather thin and not forming a distinct angle to the hinge plate .....Unio

   Cardinal teeth very strong, forming an almost right angle to the hinge plate .....Psilunio

1. Genus Caelatura Conrad 1853

Nearly two hundred supposed species and subspecies have been described in former days and more than half of them by the devotées of the "Ecole nouvelle" in France, who claimed that differences in the three dimensions length, height and diameter between two bivalves made it necessary to separate them as

distinct species. Naturally, this idea resulted in a great number of "new" species established on young shells.

The first real revision of the African Caelaturae was published by Haas in 1936, and the number of species was drastically reduced, viz. to 38, but unfortunately, and probably because of insufficient material, Haas created a number of new genera and subgenera, which now seem superfluous, because the many intermediate forms make a demarcation of them impossible. Earlier I was inclined to accept Haas's species concepts, but since then I have had the opportunity of studying much additional material with the result that the number of species must be reduced further. It is especially a large material of the type species, C. aegyptiaca, that has shown that some of the previously supposed good taxonomic characters are not quite as good.

Figs. 20-30 show how great the variation can be in a single species in the same river system and are sufficient to make it clear that the shape of the shell is not an important character. The sculpture is not much better. Figs. 14-19 indicate the umbonal sculpture as it is present on very young shells. The figured sculptures look quite different, but the various patterns are not bound to the particular species, but can just as well be present on the other species. Furthermore, the extension of the sculpture varies considerably from one shell to another even within a single population, ranging from covering most of the valves to being restricted to the umbonal area or completely absent. Haas (1936) found it significant that the sculpture in some cases is restricted to a number of oblique ridges on the area, but this is not unusual and cannot be regarded as an important taxonomic character.

The hinge is not much more valuable as a taxonomic character on the species level. Figs. 3-9 show the range of variation in the development of the cardinal teeth of the right valve within the genus. Of particular interest are figs. 4-6 showing three different forms of C. aegyptiaca corresponding to fig. 22, 21 and 20, respectively. Also in other species or forms of Caelatura a similar variation may occur. In fact, it is a question of the solidity of the shell: a thin-shelled Caelatura has a hinge like fig. 4 and the more solid the valves become, the nearer the hinge

will come to fig. 9.

It will appear from the above that it is impossible, at least for the time being, to prepare a key to the species without using the locality or the geographical distribution as the most important character. Under these circumstances it seems better to treat the more or less valid species in a geographical arrangement and to indicate for each of them the possible or probable relationships to other species, and especially to aegyptiaca, which takes up a key position of the genus and because it has a much wider distribution than any other African unionid. Therefore, it is a good species to start with.

Species of the River Nile and West Africa

These two areas, the River Nile drainage and West Africa, have many species of freshwater animals in common. This apparently rather peculiar fact is due to the earlier connection between the Nile and Lake Chad through the Bahr el Gazal and the Chari River and from the ancient much larger Lake Chad to the River Niger system and further westwards. In this huge area two species of unionids occur.

Caelatura aegyptiaca (Cailliaud 1827) figs. 4-6 and 20-40

The common unionid of the River Nile system. It is very variable in shape and in the development of the hinge and sculpture, but most of the many different forms can be derived from three fundamental forms and intermediates are very common. It is an unsolved question whether these fundamental forms are entirely phenotypic, but it seems likely that also genetic factors are involved, because different forms can be found in the same locality. The three fundamental forms are:

1. The commonest form (fig. 21) was described by Cailliaud (1827) as Unio niloticus and is probably the basic form. It has a fairly strong shell and rather short cardinal teeth (fig. 5). A zigzag sculpture may be present on the beaks, but usually only in young specimens, in which also oblique ridges may be present on the area and the areola as shown on figs. 26 and 27. It is the

prevailing form in the main Nile and larger canals, but is also known from the White Nile. The type locality is Bahr Yussuf. From this form the two others may be derived.

2. The typical form, C. aegyptiaca s. str., (fig. 22) is more thin-shelled, has longer and slenderer cardinal teeth (fig. 4) and frequently an angle between the dorsal and the anterior margin. It is mainly found in slowly running or stagnant water with a soft, muddy bottom. The type locality is also Bahr Yussuf. Sometimes the dorsal margin becomes more oblique and the shell relatively higher. It was such a form Servain 1890 described as Pharaonia misraimica (fig. 23). The shells shown on figs. 24 and 28 may also belong in this company. Pharaonia was created by Bourguignat (1880), but as a nomen nudum.

3. The third fundamental form was described as Unio parreyssi by Philippi (1848) and as Unio rugifer by KÜster (1852). It has developed in the opposite direction to the typical form and has a stronger and lower shell (fig. 20) and much stronger cardinal teeth (fig. 6). Also the zigzag sculpture frequently is more pronounced in this form, which probably at least partly is an ecotype from more swiftly running water and hard bottom of sand or gravel. It is more common in the White Nile and the upper part of the main Nile and is unknown in the delta and the canals of Lower Egypt. The only safe record from the Blue Nile I am aware of refers also to this form, though it was described as Nodularia (Caelatura) sobaensis Preston 1914.

Pallary (1909, 1924) described a number of supposed species and varieties from Egypt, partly on young shells, and added a series of photographs of shells Bourguignat had named but fortunately never described. It is best to leave them in silence. In the following account the three fundamental forms will be used as references to indicate the type of shell shape and hinge in other species or forms and not as taxonomic units. The occurrence of C. aegyptiaca in Lake Albert will be dealt with in the section "Species of the Great Lakes", so now we will turn to the West African forms of aegyptiaca, the majority of which have been described as distinct species by French malacologists.

In the Chari river and its affluents C. aegyptiaca seems to be common. From the delta in Lake Chad we have a good series of a

large form (up to 65 mm in length) of the aegyptiaca-type (fig. 31). The younger shells are relatively higher and some of them still have the juvenile nodules on the beaks (fig. 32). It was on such a young shell from the Chari that Germain (1912) established his Unio (Nodularia) jourdyi, but since Morelet (1886) had described a Unio jourdyi from Tonkin, Germain (1912) changed the name of the "species" to jeanelli (fig. 39). Earlier, in 1907, he had described a couple of supposed new species from some affluents of the Chari, viz. Unio (Nodularia) chivoti, apparently a young shell of the nilotica-type, and Unio (Nodularia) bangoranensis, a small shell of the parreyssi-type (fig. 33). From the Logone river just before its junction with the Chari and from a smaller stream in that area we have some aegyptiaca of the nilotica-type, but with oblique ridges on the area and the areola. They seem to be inseparable from Unio gabonensis Küster 1862 (fig. 34), which perhaps represents a subspecies to which I shall return in the section "Central African species".

The forms of aegyptiaca occurring in Lake Chad (figs. 36-39) are characterized by their small size, usually not exceeding about 30 mm in length. They are rather variable in shape and it is not unusual that shells of the aegyptiaca-type have cardinal teeth of the nilotica-type or even of the parreyssi-type. The oldest name for this lake form is Unio (Grandidieria) tsadiana Martens 1903 and other names are Unio (Nodularia) lacoini Germain 1906 with var. chudeaui and Unio (Nodularia) nguigmiensis both Germain 1909. Lévèque 1974 refers the various forms to C. aegyptiaca, but their small sizes could justify that they be regarded as a distinct subspecies.

I have not seen many samples of unionids from West Africa proper, but those I have seen do not deviate much from similar samples from the Nile system, apart from their smaller sizes (figs. 41-44). As usual, French conchologists have described a number of "species" from the former French West Africa, but they all seem to represent forms or young shells of C. aegyptiaca. Nevertheless Jousseaume (1886) found it necessary to establish a new genus, Reneus, for four "new species", which in fact were young aegyptiaca of different ages. The oldest form from this part of Africa is Unio juliani Rang 1835 from Senegal, and Haas (1936) collected all

the West African forms but one under that name with the reservation that they might well be forms of aegyptiaca. However, Haas (1969) divided his earlier C. juliani into three species entirely for geographical reasons: C. juliani should now be restricted to the forms of the Senegal river with affluents, whereas those of the River Niger system were separated as C. decampsiana (Wattebled 1884) and the single form from Guinea as C. koehleri (Germain 1909), but still he emphasized their close relationships to aegyptiaca.

The only West African form Haas really regarded as distinctly different is Unio essoensis Chaper 1885 from the Ivory Coast, but in my opinion essoensis is a parallel to the Egyptian misraimica, a form of aegyptiaca. Unfortunately, the original figures of essoensis show only the interior sides of the valves, but I have reconstructed the outer side (fig. 40) and a comparison with fig. 23 of misraimica discloses the great similarity. The most remarkable aspect of essoensis is the size, length 75 mm, height 53 mm and diameter 35 mm, which is almost twice the usual size of a West African aegyptiaca, but it is very likely that the use of a dredge in West African rivers would bring more large specimens to light.

Binder (1958) identified another form of aegyptiaca from the Ivory Coast with C. mesafricana Pilsbry & Bequaert 1927 because of the presence of ridges on the area, and Daget (1961) followed him, but since such ridges are quite common in C. aegyptiaca and some other species of Caelatura, they have no great taxonomic value.

Caelatura teretiuscula (Philippi 1847) figs. 57-60

The only other unionid known from the Nile and from West Africa. It is very different from aegyptiaca with a much longer and lower shell, twice as long as high or longer. The type specimen from the White Nile is 44 x 17.5 x 15 mm, but larger specimens occur, for instance 54 x 25 x 20 mm. The hinge is rather of the parreyssi-type, but the upper (additional) cardinal tooth of the right valve is weaker and the lower relatively stronger. A particular sculpture is absent. It is known from the White Nile and the Main Nile right to the delta, but seems to be much rarer than aegyptiaca. In West Africa it is recorded from

Lake Chad, the Chari river system and from the White Volta with tributaries. Germain (1906) described the form from Lake Chad as a distinct species, Unio mutelaeformis with a var. chariensis from the Mamoun River, but it can hardly be regarded as a subspecies, unless the small size, up to 35 mm in length, of the rather few known specimens turns out to be constant. Unio (Nodularia) gaillardi Germain 1909 was established on a single shell in the Paris museum labelled "Senegal, Verreaux 1845". It differs from the typical teretiuscula by the higher posterior part of the shell (fig. 60). It is not impossible that it is an aberrant form of teretiuscula, but Haas (1936) found it very similar to a young Elliptio jayensis (Lea) from Florida. Future investigations must show whether C. teretiuscula occurs west of Ghana.

The species is the type of Nitia Pallary (1924) established as a subgenus of Caelatura, but Haas (1936) raised it to a genus. However, the status as a subgenus seems more reasonable, as will be shown below under C. acuminata.

Species of the Great Lakes

The larger bivalves of the Great Lakes, unionids as well as mutelids, are of considerable zoogeographical and taxonomic interest, both because of the uniformity in species composition and because of differences in evolution. The Unionacea of the northern lakes, i.e. Lakes Albert, Edward, Victoria and Turkana, are closely related to the species of the Nile, which is quite understandable since the fauna of the Nile must have come from these lakes, but it is difficult to understand why the species of the lakes do not reach the same sizes as their counterparts in the Nile. This is least obvious, though unmistakable, for the bivalves of Lake Albert, which has the most direct connection with the Nile, but very marked for the bivalves of Lakes Victoria and Turkana. It is also a fact that the unionids of the lakes often have a better developed sculpture than their nilotic relatives. Since smaller size and stronger sculpture seem to be connected with life in big lakes, the taxonomic significance of such characters should not be exaggerated. Of course, the bivalve

fauna of Lakes Tanganyika and Malawi is more specialized and comprises some interesting endemisms.

Caelatura aegyptiaca aegyptiaca (Cailliaud 1827) figs. 29-30

As mentioned above (page 9) this species occurs in Lake Albert, mainly in the nilotica-form, but also more aegyptiaca-like forms are known. For further information about aegyptiaca in Lake Albert see Mandahl-Barth (1954). Moreover, it is a question whether these apparently typical aegyptiaca in Lake Albert have been carried by fish from the Albert Nile or are an atypical form of the lacustrine subspecies bakeri treated below.

Caelatura aegyptiaca bakeri (Adams 1866) figs. 45-47 and 52

Earlier I regarded this, the common Caelatura of Lake Albert, as a distinct species because of the shorter and stronger cardinal teeth and especially because I believed that only the inner gills function as marsupium. An examination of a larger additional material has shown that bakeri can have cardinal teeth of the nilotica-type, though most specimens have teeth of the parreyssi-type, and more important, that all four gills can be marsupial also in bakeri. It was Bloomer (1932) who found that bakeri differed from the other Caelatura species by having only the inner gills marsupial, but he examined a single young specimen. Very few of the many specimens I collected in Lake Albert in February 1951 had eggs or glochidia in the gills, but as I found a few having eggs in the inner gills, I thought Bloomer's statement to be correct, but these few were also young. Since then I have examined many more collected by Cridland in other months and found that it is only the young specimens, probably those breeding for the first time, that use only the inner gills as marsupium. We will meet the same phenomenon in C. mweruensis and possibly it is the case for all Caelatura species, as I have seen it in C. hauttecoeuri as well. Of this latter species I have seen a full-grown specimen that had the inner gills filled with eggs, but only a few in the outer gills, perhaps indicating that an egg-producing Caelatura fills the inner gills first and then the outer gills. It is unknown how long a time the egg-laying lasts as well as the length of the time from egg-laying to when

the glochidia leave the mother bivalve.

The shape of the shell varies in the same way as in the nominate subspecies, but the sculpture is, as a rule, much more pronounced. In some cases it is impossible to decide whether a specimen is an aegyptiaca or a bakeri, but since the two forms are very closely related, a hybridization is very likely.

Caelatura aegyptiaca stuhlmanni (Martens 1897) figs. 48-51

In 1954 I wrote that perhaps stuhlmanni is merely a local race of bakeri in Lake Edward, but because of the scanty material available at that time I would not make a decision. In the same year Cridland collected more specimens in the Uganda part of Lake Edward, and an examination of this material convinced me that my supposition was correct, but since bakeri must be regarded as a subspecies of aegyptiaca, the same must be the case for stuhlmanni. It varies in the same way as bakeri, from which it differs by the stronger cardinal teeth. The maximum size is 51 x 33 x 20.5 mm, which is about the same as bakeri can reach, viz. 51 x 33 x 22 mm. The slender form of stuhlmanni (fig. 48) was described as Parreysia regis by Pilsbry & Bequaert (1927) and the higher form (fig. 50) as Unio ngesianus by von Martens (1897).

In South Bay of Lake Albert Cridland collected some specimens of Caelatura with a higher shell and more centrally placed beaks than normal for bakeri and stuhlmanni (fig. 51). It is impossible to decide to which subspecies they should be referred, but the cardinal teeth suggest stuhlmanni. They give the impression of being a river-form and might have come from the Wasa River or perhaps rather from the Semliki (Mandahl-Barth 1954 p. 129).

Caelatura acuminata (Adams 1866) figs. 54-56

This is the other unionid of Lake Albert. The type specimen is a young shell measuring 29 x 15 x 10 mm and the largest seen is 40 x 21 x 14.5 mm, thus shorter and relatively higher than C. teretiuscula from the Nile. Frequently it has the same zigzag sculpture as bakeri, but usually restricted to the umbonal area. The hinge is of the parreyssi-type. It is a difficult species as it is connected with bakeri by intermediates (figs. 52-53) and also with teretiuscula (fig. 56). Some of the supposed acuminata,

especially those with a pronounced sculpture, might be young bakeri with a slenderer shell than normal and the least bakeri-like could be a lake-form of teretiuscula, but they merge into each other. For the time being I find it best to regard acuminata as a distinct species endemic to Lake Albert and strangely enough not occurring in Lake Edward. However, it should not be ignored that a young specimen of the regis form of stuhlmanni is not unlike some forms of acuminata, but it grows to a larger size and, as a rule, the sculpture is not restricted to the umbonal area.

Caelatura hauttecoeuri (Bourguignat 1883) figs. 66-72

This, the common Caelatura of Lake Victoria, is certainly the most variable African freshwater clam and impossible to describe in such a manner that it can be separated from all other species. The shape of the shell varies from almost circular to long wedge-shaped, the sculpture from nil to strong zigzag ridges covering most of the valves, and the colour of the periostracum from light yellow to dark brown or almost black, sometimes green, unicoloured or with radial rays. The inner side of the valves may be white, yellow, pink, red or blueish. The cardinal teeth are usually of the parreyssi-type, but sometimes stronger and sometimes rather of the nilotica-type. Common to all the many forms is only the rather small size, 30-35 mm in length and not exceeding 42 mm, and, of course, that they live in Lake Victoria and the Victoria Nile.

It is probable that many of these forms are descended from more or less different populations isolated during the interpluvial periods and that they would have evolved to distinct species (corresponding to the Bellamya species of Lake Victoria) were it not for the casual fecundation and the passive dispersal of the larvae. In my earlier revision (1954) I regarded some of these forms as subspecies and I am still of the opinion that they are genetically different, because they hardly can be ecotypes, but they are so closely related that cross-breedings take place producing all sorts of hybrids. The rather large material collected after 1954 by my colleagues and myself mainly in the Mwanza area has not contributed to a better understanding of the

hauttecoeuri-complex than that I presented in 1954, to which I refer for further information with regard to the Lake Victoria forms. But a better material of C.h. kyogae Mandahl-Barth 1954 collected by Cridland at Kele (fig. 72) has disclosed that this subspecies rather is intermediate between hauttecoeuri and bakeri indicating a close relationship, wherefore also hauttecoeuri could be regarded as a subspecies of aegyptiaca. However, the many forms of hauttecoeuri make it more practical to regard it as a distinct species.

Unio (Grandidieria) rothschildi Neuville & Anthony 1906 (fig. 73) from Lake Turkana and known only as dead shells is hardly specifically different from hauttecoeuri, but may represent a local, probably extinct subspecies.

Caelatura alluaudi (Dautzenberg 1908) fig. 87

A poorly known species which only has been found a few times in the Kavirondo Gulf and in Buvuma Channel. It has a much thinner shell than hauttecoeuri and much more delicate cardinal teeth of the aegyptiaca-type. Haas (1936) listed it as a synonym of the ruellani form of hauttecoeuri (for which he established the subgenus Kalliphenga!), but since it occurs together with hauttecoeuri and no intermediates are known, it is in all probability a distinct species, but a remarkably rare one.

Caelatura cridlandi Mandahl-Barth 1954 fig. 86

The largest of the Caelatura species and the only one which cannot be confused with any other species. The type specimen is 76 x 42 x 23 mm and the largest seen 84.5 x 48.2 x 25 mm. It is the most thin-shelled Caelatura and in accordance with this the cardinal teeth (fig. 3) are even longer and slenderer than those of the aegyptiaca-type. They are almost as long as the lateral teeth. When originally described it was known only from the northern part of Lake Victoria, but since then a number have been collected in the southern part as well. Haas (1962) established for it a new subgenus, Zairiella. The name is owing to my tentative placing of the species in the subgenus Zairia Rochebrune 1886, which was incorrect, but the name is unfortunate as cridlandi has nothing to do with Zaire.

It is very strange that this remarkably large species has developed in Lake Victoria, because all other Unionacea of that lake are considerably smaller than their counterparts in Lake Albert and in the Nile, but, of course, cridlandi has no counterpart anywhere.

Caelatura monceti (Bourguignat 1883) figs. 61-64

This is the Lake Victoria member of the Nitia group or subgenus. It is rather similar to the typical form of acuminata, but distinctly smaller and has relatively stronger cardinal teeth, of which the lower in the right valve is longer and more prominent. Shells with a concave ventral margin are quite common and it was this form Bourguignat (1883) described as Unio lourdeli. It is a question whether monceti is a distinct species or a local form of acuminata (or of teretiuscula), but the shape of the cardinal teeth and the usually less inflated umbonal area justify the former possibility. The largest specimen seen has the following dimensions: 38 x 16 x 11.5 mm, but the usual length is only about 26 mm. It is common in Lake Victoria and the first part of the Victoria Nile.

Unio (Grandidieria) chefneuxi Neuville & Anthony 1906 from Lake Rudolph and probably extinct, seems to be conspecific with monceti. In the pluvial periods, when the East African lakes were much larger than today, there must have been a connection between Lake Victoria and Lake Rudolph.

As no unionids are known from the other lakes in the Eastern Rift Valley or from Lakes George and Kivu, we now come to the species of Lake Tanganyika. Altogether 75 "species" of Unionidae have been described from this lake and 62 of these by Bourguignat. They are now reduced to five referred to three different genera. Only those belonging to the Caelatura will be dealt with here. The two other genera, Brazzaea and Pseudospatha, will be dealth with later. No less than 47 species of Caelatura have been described from Lake Tanganyika and 38 of them by Bourguignat. Now it is generally agreed that only three or four of them are valid, and, in fact, these are not nearly as variable as the many synonyms could suggest. The number of supposed species says more

about Bourguignat than about the bivalves.

Caelatura horei (Smith 1880) figs. 80-81

This is one of the most puzzling species of Caelatura, because it seems to be so closely related to aegyptiaca that Leloup (1950) as a matter of course referred it to that species. However, I find it difficult to accept that a bivalve of the Nile should live unchanged in Lake Tanganyika and solely for this reason I regard horei as a distinct species, though I must admit that several specimens of it would be identified with aegyptiaca if the locality was unknown. However, horei also shows affinities to C. ratidota, a species of East African rivers, and it is just possible that it is a lake-form of this species.

The type specimen is a young shell measuring 25 x 16.5 x 9 mm. An average-sized shell is 53 x 35 x 26 mm, for instance, and the maximum length is about 75 mm. It varies in the same way as aegyptiaca, from a rather thin-shelled form of the aegyptiaca-type through a heavier form of the nilotica-type or even stronger. However, it is impossible to use any of the synonyms for these forms, because the 16 "species" established by Bourguignat 1885 and 1886 were described solely on the shape and dimensions of the shells. Since these forms hardly can be regarded as subspecies, it is superfluous to name them. A particular sculpture is not present in larger shells, but young shells have a faint zigzag sculpture similar to what can be present in young aegyptiaca. The most striking difference between horei and aegyptiaca is that very large specimens of the former have heavy shells and strong cardinal teeth, whereas very large aegyptiaca are, as a rule, rather thin-shelled and have long, slender hinge teeth.

Caelatura burtoni (Woodward 1859) figs. 74-77

The Tanganyika counterpart to bakeri and hauttecoeuri, but without doubt specifically distinct. A shell of average size measures 30 x 23 x 15 mm and the largest known 36 x 26.2 x 17.8 mm, thus shorter, higher and more inflated that hauttecoeuri and, if present, the sculpture is much more delicate and often varying in strength on the same valve in such a way that radial areas of

stronger sculpture alternate with areas of finer sculpture. The colour of the periostracum is usually a light yellow or greenish and the inner side of the valves is yellow, pink or darker reddish. The hinge is of the parreyssi-type or a little stronger and the cardinal teeth are often serrated,

Bourguignat (1885a) established the genus Grandidieria for this species and seven others. Later (1885c,d, 1888) he added further 15 species among these a G. hauttecoeuri (fig. 77) which should not be confused with C. hauttecoeuri (Bgt. 1883), the common Caelatura of Lake Victoria. Haas (1936 accepted Grandidieria as a subgenus of Caelatura. Furthermore, he regarded the form with a relatively long shell and no particular sculpture as a distinct species, C. tanganyicensis (Smith 1880), but as shown by Leloup (1950) it is impossible to separate any of the many forms, and they are all linked together by intermediates.

Caelatura ujijiensis (Crosse 1881) fig. 82

As I have not seen this species the following remarks are taken from the literature, mainly from Leloup (1950). It was described by Smith (1881) as Unio nyassaensis var. tanganyicensis with the type locality Lake Tanganyika at Ujiji, but since Smith (1880) had described a Unio tanganyicensis (the preceding species), Crosse changed the name. Leloup regarded it as conspecific with C. nyassaensis (Lea 1864), to which it undoubtedly is related, but in my opinion hardly to such a degree that it is justifiable to unite them. The Tanganyika species is less transformed than that of Lake Malawi and forms a link between this and the more normal Caelatura species. On the other hand, since so many of the molluscs of Lake Malawi have heavier shells than their relatives in other lakes, it is possible that ujijiensis represents a subspecies of nyassaensis.

The maximum size is 44 x 32 x 19 mm, but it is usually smaller, about 30 mm in length. The shell is heavier and the hinge stronger than in the preceding species. The hinge plate is more or less curved and the cardinal teeth deeply cleft. A zigzag sculpture may be present or not.

Haas (1936) created a new genus, Nyassunio, for this and the Malawi species, whereas Leloup resuscitated the old genus name

Parreysia Conrad 1853, but it appears clearly from Leloup's many figures that ujijiensis without difficulty can be accepted as a Caelatura.

Lake Malawi - as the other Great Lakes - harbours many different forms of unionids and 15 of them have been described as species. Haas (1936) correctly reduced the number to three, but referred each of them to a separate genus. Mandahl-Barth (1972) proved that all three belong to the genus Caelatura, but in fact only two of them are living in the lake. The third species, (C.mossambicensis) is living in some rivers flowing into the lake.

Caelatura hypsiprymna (Martens 1897) figs. 78-79

Superficially this species can look very much like some forms of hauttecoeuri from Lake Victoria, and Germain (1906) actually did refer such to hypsiprymna, but the shell is heavier and in accordance with this the hinge much stronger (fig. 7). However, if these characters are caused by some special factors in the lake, and this seems highly probable, then they have no taxonomic significance, and the conclusion must be that hypsiprymna is closely related to hauttecoeuri. On the other hand, some forms of hypsiprymna, viz. those with a rather long and strongly sculptured shell show affinities to Unio zambesiensis Preston, which probably is a form of C. kunenensis (Mousson). For further information and synonyms I refer to my 1972 publication.

Caelatura nyassaensis (Lea 1864) figs. 83-85

Also for this species I refer to my publication of 1972. The shell is more or less triangular in outlines and relatively heavier than in any other Caelatura species and consequently has a stronger hinge (figs. 2 and 9). The sculpture varies much from one shell to another, and some with a pronounced sculpture and less triangular outlines can be confused with hypsiprymna, but the stronger hinge is distinctive.

Haas (1936) established the genus Nyassunio for this species and ujijiensis, which is needless, as the heavier shell and stronger hinge cannot be regarded as characters of generic

significance, but it is still an open question whether the two really are specifically distinct or merely two subspecies of one species. In any case nyassaensis is closely related to the Tanganyika species, in contrast to hypsiprymna, which shows affinities to the Lake Victoria species, a fact emphasizing the complexity of the systematics of the African Unionidae.

East and South African Species outside the Great Lakes

As it appears from the above the Caelatura species of the Great Lakes are fairly well known. Unfortunately, the same is not the case with regard to the species of rivers and smaller lakes in East Africa, because very little material has been collected in such localities. In the southern part of Africa the situation is somewhat better, but far from being satisfactory. It is most likely that unionids occur in most or perhaps all the permanent rivers and probably also in some of the smaller lakes and ponds, but species are known only from very few of them. Of course, the reason is that very little dredging has been done in such localities, and without this collecting method unionids are difficult to obtain.

Caelatura ratidota (Charmes 1885) figs. 97-99

This is the first of five "species" Charmes described from the Kingani river near Bagamoyo, but none of them was figured. Haas (1936) examined the type specimens and came to the expectable result that all belong to one species and he gave sketches of their outlines. He also examined the type specimen of Unio ambifarius Martens 1897 from Dar es Salaam and found it is a young shell of the same species. Since then no material of this species seems to have been collected in Tanzanian rivers, but from the upper courses of the Athi river system near Nairobi, samples of what appears to be the same species have been collected. These findings seem to indicate a wide distribution in East African rivers.

The type specimen is 41 x 25 x 12 mm and the largest I collected in the Stony Athi measures 60 x 36.5 x 26.5 mm. The

beaks are rather prominent and the hinge is of the parreyssi-type. The sculpture on the younger shells consists of zigzag ridges on the beaks and oblique ridges on area and areola (fig. 10). On full-grown shells only traces of this sculpture are present.

Haas (1936) referred this species to the Indian genus Indonaia Prashad 1918 and thought it might well be a local form of the following species (C. mossambicensis). In 1962 he created a new genus Afronaia for this and a few other species and in 1969 he repeated the supposition that ratidota is a mere local form of mossambicensis. In my opinion it is a genuine species closely related to aegyptiaca and quite distinct from mossambicensis and the other species he placed in Afronaia, which I cannot accept, not even as a subgenus.

In 1961 I collected a good sample of a Caelatura in Malya fishponds south-east of Mwanza, which might belong to ratidota, but it cannot be excluded that it represents an undescribed species. The shell (figs. 100-101) is smaller and relatively shorter than that of ratidota, the dorsal margin is more oblique and the beaks are placed more anteriorly. The largest specimen is 41.5 x 27.5 x 21 mm, thus more inflated than a ratidota of equal size. As a fishpond is a rather unnatural habitat I prefer to regard these bivalves as a form of ratidota, also because the younger shells have a very similar sculpture.

Ten years earlier on the shore of the Victoria Nile at Fajao (below the Murchison's Falls) I had picked up some rather worn shells of a Caelatura (fig. 102). It is mentioned in my earlier revision (1954 p. 133) and depicted on fig. 68 b as C. hautte-coeuri subspecies? and that is how I still classify it. My reasons for referring to it here are that it is a river-form, and that it cannot be excluded that similar forms might occur in rivers flowing into Lake Victoria.

Caelatura mossambicensis (Martens 1860) figs. 92-96

The type specimen from the Zambesi at Tete is 41 x 24 x 17 mm and the largest seen (from Lake Kariba) is 50 x 30 x 20 mm. Considering it is a river species it is rather thin-shelled and compressed. The beaks are similar and less inflated than in the preceding species and there is no particular sculpture in the

typical form. In spite of the rather thin shell, the hinge is of the parreyssi-type. It is known from rivers in Mozambique, Malawi and Zimbabwe and possibly also in southern Tanzania and Zambia.

Haas (1936) misidentified a young hypsiprymna as the young of mossambicensis and for that reason he supposed a close relationship between the latter and C. kunenensis (Mousson) and separated Unio liederi Martens 1897, which in reality is a young mossambicensis. Woodward (in: Pain, Crowley & Woodward 1964) repeated Haas' mistake. The type locality for liederi is Mbamba Bay in Lake Malawi at the Tanzania-Mozambique border, but the shell von Martens figured on pl 7 fig. 19 is from the Rufidji river at Ulungu (Ulanga?).

South of the distribution area of the typical mossambicensis and partly overlapping it a slightly different form occurs (figs. 95-96). On the authority of Haas, Connolly (1925) described it as Indonaia framesi, and Haas (1962) selected this form as the type species for his new genus Afronaia. However, framesi can hardly be regarded as a distinct species, because the only real difference between it and the typical mossambicensis is that framesi usually has a more or less pronounced sculpture on area and areola. According to Haas framesi also has a lower shell and a more oblique dorsal margin, but this is not always the case. The framesi form is known from rivers in Zimbabwe, southern Mozambique, Natal and Transvaal and may be accepted as a geographical race. It can be confused with a young Cafferia caffra (Krauss) occurring in the same area, but Cafferia has a relatively longer and lower shell, stronger cardinal teeth and a different sculpture.

Caelatura choziensis (Preston 1910) figs. 88-91

The type specimen is a young shell 25 mm long and 16.2 mm high and the maximum size, according to Haas (1936), is 47.5 x 28 x 18 mm, but the average size is about 35 mm in length. It is a thin-shelled species with faintly developed sculpture and cardinal teeth rather of the parreyssi-type, but finer. Young shells frequently are yellowish with radiating green rays, full-grown usually brownish. The type locality is the Chozi river, an affluent of the Chambeshi river which flows into Lake Bangweulu,

where the species is common and occurs in various ecological forms. Haas (1936), who had collected a large material in the Bangweulu area, described the lake form as a new subspecies, bangweolica, but admitted that also specimens of the typical form live in the lake. He also regarded C. luapulaensis (Preston) as a subspecies of choziensis, probably because the Luapula forms the outflow of the lake. However, luapulaensis has a much heavier, strongly sculptured shell and can hardly be a mere river-form of choziensis, which itself, in its typical form, lives in a river.

Species of Central Africa

Under this heading I collect the species and forms of Caelatura occurring in Africa from Cameroun and the Central African Republic in the north to Namibia and Botswana in the south. With a few exceptions (e.g. Lake Mweru) these are river-forms, and although we have more material from rivers in this part of Africa than from East African rivers, it is not yet possible to prepare a satisfactory classification of the species, because of their great variation. A great number of supposed species have been described, without doubt too many, but even when the number is drastically reduced, it is still difficult or hardly even possible to delimit the individual species, because more or less intermediate forms are not rare. As it is necessary to take them in a certain order, we will begin with those with a poorly developed sculpture. The first species described from this part of Africa is Unio gabonensis KÜster, which together with allied forms may represent a subspecies of aegyptiaca.

Caelatura aegyptiaca gabonensis (KÜster 1862) figs. 34,103-105,110

The type specimen is about 38 x 23 x 18 mm and the locality is Gabon. I have not seen any Caelatura from that country, but some from Cameroun could be the same form, and as mentioned p. 9 they are in fact aegyptiaca, wherefore gabonensis must be regarded as a form of that species. On the other hand, gabonensis also shows affinities to a series of supposed species from Cabinda and Lower Zaire, mainly from the lower course of the River Congo. They are

all rather thin-shelled and accordingly with slender cardinal teeth of the aegyptiaca- or nilotica-type. The sculpture, if present, is restricted to area and areola.

For the time being and because of lack of sufficient material I prefer to regard gabonensis and allies as a subspecies of aegyptiaca and the forms with a more compressed shell and distinctly oblique dorsal margin as a distinct species, C. bourguignati, though admitting they are merging into each other. The gabonensis group correspond to Haas' subgenus Zairia, established by Rochebrune (1886) as a genus, and his genus Mesafra. Haas (1936) found it necessary to separate C. mesafricana Pilsbry & Bequaert 1927 (fig. 105) into this genus because of the sculpture consisting of oblique ridges on the area and because of the oblong shape already present in the juvenile shell, asserting that all Caelatura species have a short and rounded juvenile shell, but this is not the case and the sculpture is not different from that of several other Caelatura species. The type-locality of mesafricana is the Garamba river in the north-eastern corner of Zaire, and it is not surprising that it shows affinities to the bangoranensis form of aegyptiaca from the Central African Republic.

The other "species" I regard as forms of gabonensis are Unio aequatorius Morelet 1885 from Mayumbe (fig. 104), U. landanensis Schepman 1891 from Cabinda (fig. 110), U. subniger Preston 1909 altered to U. putzeysi Preston 1912 from Lower Congo, Zairia araneosa Rochebrune 1886 also from Lower Congo, and Caelatura stanleyvillensis Pilsbry & Bequaert 1927 from Kisangani (fig. 103). Zairia elegans Rochebrune 1886 (figs. 112-113) from Lower Congo seems to link this subspecies to the next species and I am very much in doubt about its placing.

Caelatura bourguignati (Rochebrune 1886) figs. 111 and 114-116

Described as a Pharaonia Bourguignat 1880 (nomen nudum) and differing from C. ae. gabonensis by the oblique dorsal margin, smaller beaks and more compressed shell. The typical form was not figured but judging from the original description it is similar to C. rotula Pilsbry & Bequaert 1927 (fig. 116) with a very oblique dorsal margin and high posterior part. More common is a lower

form, described by Dautzenberg (1890) as Unio stagnorum (fig. 114) with the variety C. s. bomae Pilsbry & Bequaert 1827 (fig. 111), and I think that also Zairia disciformis Rochebrune 1886 (fig. 115) belongs to this species. They are all known only from the Lower Congo.

Simpson (1900) selected stagnorum as type species for his subgenus Laevirostris of the otherwise South American genus Diplodon, and Pilsbry & Bequaert (1927) correctly transferred it to Caelatura, but I cannot see any reason for maintaining it. I can hardly explain why I prefer to regard bourguignati as a distinct species and not as a subspecies of aegyptiaca. I am afraid it is rather a question of feelings than a result of a valuation of taxonomic characters.

Caelatura briarti (Dautzenberg 1901) fig. 117

The type specimen is about 54 x 42 x 31 mm and it must be an error in the original description that the height is stated to be 74 mm. In the outline of the shell it has some resemblance with the typical form of the preceding species, but the shell is much more solid, the hinge stronger and more curved, and the sculpture on the area more pronounced. It is known from the Lualaba and Lufoi river, an affluent of the Lufira river.

Haas (1936) placed it in the subgenus Laevirostris and assumed that the rather heavy shell was caused by a life in running water, obviously forgetting that the water of the Lower Congo is running quite fast and there thin-shelled forms are found (see under C. aegyptiaca gabonensis).

Caelatura mweruensis (Smith 1908) figs. 118-119

The type specimen is 26 x 15 x 10.5 mm and the largest known 41 x 25 x 14.5 mm, thus a rather compressed form. The beaks are only slightly prominent, the hinge of the parreyssi-type, and sculpture is present usually only on young shells. Type locality: Lake Mweru.

Haas (1936) created a new subgenus, Mweruella, for this species alone, and Pain & Woodward (1968) found that only the medial part of the inner gills serves as marsupium and for this reason they not merely raised Mweruella to a genus, but established a new

subfamily. However, it was a young specimen, 13.5 mm long, they examined. In a full-grown specimen, 35 mm long, I found all four gills filled with eggs. Furthermore, Pain & Woodward described the sculpture as a radial plication, but in reality it is of the same zigzag pattern as in other Caelatura species which is evident in very young shells.

In the lower Luapula mweruensis is present in a more inflated form with more prominent beaks. Haas (1936) described this form as Mesafra mesafricana stappersi. The type specimen, measuring 40 x 22 x 17 mm, is rather similar to mesafricana, mentioned above under C. ae. gabonensis, and Mandahl-Barth (1968) thought it superfluous to maintain the subspecies. I still think so, but will no longer refer the Luapula form to mesafricana. Now I am convinced it is merely a river-form of mweruensis (fig. 106).

In the same paper Haas described a supposed new species, C. schoutedeni (fig. 107) for which he created a new subgenus Kistinaia because of the inflated shell. However, as I have already shown (Mandahl-Barth, 1968), the shell is not always very inflated, and such shells seem to be intermediary between schoutedani and mweruensis, wherefore I regard the former as a form of the latter, possibly representing an ecotype of stony bottom and rough water. Also Pain & Woodward (1968) have schoutedeni as a synonym of mweruensis. This form is known from Lake Mweru and, according to Haas, also from the Lower Luapula.

From this river I have a shell from Haas' original material of schoutedeni, but which cannot be this form. It is shown here in fig. 108, and I am unable to decide whether it is a young stappersi (see under C. mweruensis) or a young mweruensis, thus supporting my opinion that stappersi is a river-form of mweruensis. However, if the locality was unknown I would probably have identified it with a young choziensis. Without doubt, the two species, mweruensis and choziensis, are closely related.

Caelatura symoensi Mandahl-Barth 1968 (fig. 109) has a peculiar shell and especially an unusual hinge (Mandahl-Barth 1968 pl. III fig. 2). Now I doubt it is a valid species and think it might be a very aberrant form of mweruensis.

The following and last group of Caelatura comprises species from Central Africa with heavy and usually strongly sculptured shells.

Caelatura kipopoensis Mandahl-Barth 1968, figs. 134-135

The type specimen is 50.6 x 28.7 x 25.5 mm, thus considerably larger and more inflated than the stappersi form of mweruensis to which it seems related, but differing, besides by the dimensions, also by the strong sculpture. The type-locality is Kipopo fishpond and the Kipopo river just above the fishpond, near Lubumbashi. Specimens of the type lot have well developed accessory hinge teeth (Mandahl-Barth 1968 pl. III fig. 1), but the accessory lateral teeth are not present in all specimens of two additional lots collected by Malaisse in 1969 in the Luiswishi river and in Mukungwe irrigation canal.

The species has been confused with other species. The Parryesia mweruensis in Pilsbry & Bequaert (1927 p. 31 fig. 8) from Lubumbashi is certainly this species, and the same is the case with regard to the C. choziensis luapulaensis of Haas (1936 p. 5 fig. 2e) from the Dikulwe river. Thus all known localities are situated in Upper Shaba (Katanga).

Caelatura luapulaensis (Preston 1913) figs. 125-127

The type specimen, measuring 40.5 x 25 x 15 mm, is relatively longer and more compressed than usual for the species. The largest I have seen has the following dimensions: 36 x 26.5 x 21.2 mm. The hinge is of the parreyssi-type or somewhat stronger and the upper (accessory) cardinal tooth of the right valve usually reduced. The sculpture is very variable, but always coarse, and the colour of the periostracum dark brownish or almost black. It is characteristic that the ridges are glossy and the interspaces are dull. The type locality is the Luapula at the confluence with the Lukulu river (ubi) and it is known from the Lower Luapula and some of its tributaries, e.g. the Mansa river, where McCullough collected a good sample.

Caelatura kunenensis (Mousson 1887) figs. 128-133

Under this name I unite a number of "species" described from systems of the rivers Cunene, Okavango and Upper Zambesi. They are rather variable in shape and sculpture, but all have solid shells and strong hinges of the parreyssi-type, frequently with the lower cardinal tooth of the right valve split at the edge (fig. 8).

The type locality is the Cunene river, but I have not seen any Caelatura from that river. In the original description Mousson states the length to be 28 mm and the height to 25 mm, which must be an error, as he describes the shell as being lengthened and irregularly triangular and his fig. 10 on plate 12 shows an oval shell 38 mm long and 25 mm high. Haas (1936) presented a photograph of a paratype and the measurements of that are 37 x 25 x 19 mm. The sculpture is well developed on area and areola and might have been present on the eroded umbonal area. Germain (1920) described a Nodularia (Caelatura) ellenbergeri and Walker (1922) a Nodularia croninae, both from the Upper Zambesi at Lealui and probably forms of kunenensis. The same seems to be the case with Nodularia rohani Germain 1925 from the Lwankundu river, an affluent of the Okavango, the type of which measures 45 x 31 x 18 mm (fig. 131). In the Thamalakane river in the Okavango delta, Appleton collected a good sample in 1976 of fairly typical kunenensis (figs. 132-133) and the largest of these is no less than 49.2 x 33.2 x 23 mm.

It is with some reservation I include Unio zambesiensis Preston 1905 (figs. 128-130) from the Zambesi just above the Victoria Falls in C. kunenensis. It has a relatively longer shell and more pronounced sculpture. For geographical reasons it is most likely a form of kunenensis, but on the other hand some specimens from the Zambesi at Palm Island (about 13 km above the Victoria Falls) are rather similar to some forms of hypsiprymna from Lake Malawi and the Shire river. Unfortunately, no material of this form seems to have been collected in the Zambesi below the Victoria Falls.

Haas (1936) referred kunenensis (incl. zambesiensis) to Indonaia Prashad and in 1962 to his new subgenus Afronaia, which I am unable to accept.

Caelatura leopoldvillensis (Putzeys 1898) figs. 123-124

The type specimen is 45 x 30 x 19 mm, about the normal size for a full-grown specimen. The anterior part of the dorsal margin is very oblique and the hinge is of the parreyssi-type, but more curved. As a rule, the sculpture is well developed with zigzag ridges on the umbonal area and oblique ridges on area and areola. The type locality is Stanley Pool and the species is recorded from

several localities in Lower Zaire.

Caelatura graueri Haas 1927 is probably not a distinct species but a form, possible a geographical race, of leopoldvillensis, from which it differs by the less oblique anterior part of the dorsal margin and finer sculpture (fig. 122). The type locality is Ukaika Forest west of Lake Edward, and it is also known from the Lualaba and the Congo in the Kisangani area and from some of their tributaries. The biggest known specimen, 47.3 x 31.8 x 21.5 mm, was collected by Bennike in the Itumbe stream 6.5 km west of Yakusu.

Haas (1936) created a new subgenus, Rhytidonaia, for leopoldvillensis and graueri, which is superfluous as both have much in common with kunenensis.

Caelatura lobensis (Frierson 1913) figs. 120-121

Frierson (1913) described two species: Parreysia lobensis (or loboensis as the name is spelled on the plate) from the Lobo (or Lobé) river and P. nyangensis from the Nyang river, both in Cameroun. There were two specimens of the former and a single one of the latter, and no more seem to have been found since. Both possess a sculpture of coarse, elevated growth lines, more delicate in the typical form than in nyangensis. The shape of the shells is also somewhat different, but not to such a degree to exclude that they can be conspecific, and as long as only the type sets are known, I prefer to regard them as such.

Haas (1936) created a new genus, Afroparreysia, for the two forms regarding them as valid, but since especially nyangensis is not very different from a certain form of luapulaensis, the genus must be rejected.

2. Genus Cafferia Simpson 1900

It is a controversial question whether Cafferia shall be regarded as a distinct genus or as a subgenus of Unio. Personally, I never have found it important. My reason for regarding Cafferia as a genus is that its distribution area is far away from that of Unio and without any connection in earlier times. Fourteen

supposed species and some varieties have been referred to Cafferia, but in reality they are nothing but forms of one single species.

Cafferia caffra (Krauss 1848) figs. 136-139

The type specimen is, also for this species, a young shell measuring 50 x 26 x 17 mm. The largest I have seen is 102 x 48 x 32.5 mm. The shape of the shell and the hinge resemble those of some Unio species, but the sculpture (fig. 139) is different, though rather variable both in strength and in extension and sometimes the umbonal area is covered with wavy ridges. Many supposed species seem to be no more than local forms or individual variations and can hardly be accepted even as subspecies of C. caffra. There is no reason to enumerate them here apart from Unio silongweensis Preston 1913 because that name is spelled wrongly, as the type locality is Lilongwe, not Silongwe as Preston wrote.

C. caffra is widely distributed in southern Africa from Zimbabwe and southern Malawi (Lilongwe) to the Cape Province and being the only large and heavy unionid of that area it cannot be confused with any other species when full-grown, but as mentioned p. 21 there is slight possibility for confusing a young specimen with the framesi form of Caelatura mossambicensis.

3. Genus Unio Philipson 1788

This well-known palaearctic genus occurs in Africa in two widely separated areas: Ethiopia and North-West Africa. Two species are known from these areas, both are found in Ethiopia and one of them also in North-West Africa.

Unio abyssinicus Martens 1866 figs. 142-144 and 158

The type specimen is 70 x 43 x 32 mm, which seems to be the average size of a full-grown specimen. The beaks are large and rather inflated and the hinge strong to very strong. The anterior part of the dorsal margin is sloping. As a rule, there is no particular sculpture, but indistinct ridges may be present on the area. These are more distinct on very young shells (fig. 158)

which also can have a series of short ridges on the anterior part of the beaks, which in some cases also possess one or two minute nodules on the tip. Today abyssinicus is restricted to Lake Tana, but formerly it was also living in the Nile and in Faiyum, where it is known as a subfossil.

Unio elongatulus Pfeiffer 1825

The common Unio of southern Europe and parts of the Middle East. In Spain and southern France, where also U. pictorum (Linnaeus 1757) occurs, the two species merge into each other. It is a variable species of which more than 150 local forms have been described as species. Haas (1940) collected them into 22 subspecies, which hardly can be maintained. Two of them are living in Africa and they are not very different, but since they occupy two widely separated areas, it is quite practical to maintain just these.

Unio elongatulus dembeae (Sowerby 1865) figs. 140-141 and 159

The Ethiopian form, which differs from the preceding species by the usually thinner, more compressed shell, less prominent beaks, the straight dorsal margin and slenderer hinge. The young shell (fig. 159) is quite different in shape and has a better developed sculpture. It can grow to a larger size than those figured, e.g. 66 x 33 x 22 mm. It is known from Lake Tana, the Awash river and Lake Haussa in Ethiopia and is also recorded from Somalia, but without a more exact locality (U. erlangeri Kobelt 1909). Jickeli (1874) described the juvenile shell as U. aeneus, and Bourguignat (1885) habitually created five new "species".

Unio elongatulus durieui (Deshayes 1847) figs. 145-148

This is the North-west African form. It is very variable in shape, which has led to the description of several "species" strangely enough not by Bourguignat, but by Kobelt (1884, 1886) and others. Some of them have been confused with other species and without access to the type specimens or a large material, it is difficult to unravel the synonymy. A few examples are sufficient to show the difficulties. Deshayes (1847) described a U. ravoisieri and Bourguignat (1864 pl. 20 figs. 5-9) presented

excellent drawings of what he claimed to be the type (probably rather the typical form) and this is certainly a form of elongatulus, but Haas (1940) has it both as a form of U. pictorum and as a synonym of Psilunio littoralis fellmanni (Deshayes). He also regarded U. moreleti Deshayes 1847 as synonymous with that species, whereas Bourguignat's form of this name is an elongatulus. Bourguignat's U. pictorum from Algeria is also a form of elongatulus, and it was superfluous that Pallary (1936) described it as a new species, U. subpictorum. In the same paper Pallary added two new species which are quite normal elongatulus. I think we can establish that all true Unios in North-west Africa must be referred to U. elongatulus.

In North-west Africa elongatulus can be confused with P. littoralis, but the hinges (fig. 160 and 162) and the umbonal sculptures (fig. 169 and 161) are quite different.

4. Genus Psilunio Stefanescu 1896

This genus differs from Unio by the usually shorter and more compressed shell and stronger hinge with large cardinal teeth forming an almost right angle to the hinge plate, which has a distinct projection between the cardinal and the lateral teeth (fig. 162). Also the umbonal sculpture (fig. 161) is different. Earlier the genus was called Potamida Swainson 1840, but this name is now regarded as synonymous with Margaritifera Schumacher 1816. Germain (1911) introduced the name Rhombunio. The genus comprises one or perhaps two species distributed from Spain and southern France to Syria and Israel, thus occupying the same area as U. elongatulus including North-west Africa.

Psilunio littoralis (Lamarck 1801) figs. 149-151

The dimensions of a full-grown shell are for instance 70 x 43 x 23 mm, and to the characters given above may be added that the anterior part of the shell usually is short and that the ventral margin often is more or less concave.

About 70 "species" have been described and Haas (1940) collected them into seven subspecies, one of which is restricted

to North-west Africa. The oldest name for this is Unio fellmanni Deshayes 1847 and other supposed species were described by Bourguignat, Mousson and Pallary. However, the North-west African forms are hardly separable from the typical form occurring in Spain and France.

Besides Unio elongatulus, littoralis could be confused with Margaritifera auricularia (Spengler), which, however, has a longer shell and a reduced upper lateral tooth in the left valve.

5. Genus Margaritifera Schumacher 1816

This genus, also known as Margaritana Schumacher 1817, is usually separated in a family of its own, Margaritiferidae, because of some anatomical details: the gills do not form a diaphragma behind the foot and the mantle borders are not coalescent between the anal and the supra-anal opening, details which in my opinion are insufficiently significant to justify such a separation. In all other characters Margaritifera is a true unionid. The genus comprises a few species in the northern hemisphere, with two in Europe, one of which also occurs in a few streams in the northern part of Morocco.

Margaritifera auricularia (Spengler 1793) fig. 152

A full-grown shell is e.g. 105 x 50 x 33 mm. It is longer and relatively lower than the preceding species and the upper lateral tooth of the left valve is vestigial. Pallary (1918) described the Moroccan form as Margaritana marocana and figured it in 1920. Haas (1940) amended the name to maroccana and used it as a subspecific name, but added that the Moroccan form is very similar to the typical form living in France and Spain. Pallary (1927, 1928) added two further "species" also inseparable from the typical form.

6. Genus Anodonta Lamarck 1791

As is so well known, this genus differs from all the preceding genera by the complete absence of hinge teeth. It has a wide

distribution in the palearctic region including North-west Africa.

Anodonta cygnea (Linnaeus 1758)

The largest and most thin-shelled of the North-west African unionids and the only one without hinge teeth, which makes it impossible to confuse it with other species, wherefore a figure is superfluous. As usual French conchologists have described some of the local forms as distinct species, but they are quite normal cygnea.

7. Genus Prisodontopsis Tomlin 1928

This and the following two genera are all monotypic. The shell is of medium size, rather compressed and unique among African unionids in having the dorsal margin prolonged into an anterior and a posterior "wing". The cardinal teeth are long and low and there is one distinct lateral tooth in each valve and above this several lamellae. The supra-anal opening is very long, as long as the posterior wing. Simpson (1900) referred the single species to a new genus Pseudavicula, but that name was preoccupied and Tomlin created the name now valid. Modell (1942) established a new subfamily for the genus, but named it Pseudaviculinae and Pain & Woodward altered it to Prisodontopsinae. However, it is difficult to accept that it should be necessary.

Prisodontopsis johnstoni (Smith 1893) fig. 157

The dimensions including the wings are about 60 x 36 x 12.5 mm. The species is endemic to Lake Mweru and the Lower Luapula.

8. Genus Brazzaea Bourguignat 1885

The shell is thin, inflated and has a double ridge running from the beaks to the posterior end. The hinge is almost edentulous as only the posterior parts of the lateral teeth are present. Leloup (1950) established a new subfamily Brazzaeainae (should have been Brazzaeinae) for this genus alone, mainly because of some details in the structure of the gills.

Brazzaea anceyi Bourguignat 1885, fig. 153

The type specimen is 78 x 46 x 33 mm which is an average size for the species. Bourguignat described no less than 13 "species", all from Lake Tanganyika and all mere forms of anceyi.

9. Genus Pseudospatha Simpson 1900

The shell is long, thin and compressed with the low beaks placed near the anterior end. The hinge has a long and low cardinal tooth and a lateral tooth in each valve. Like Brazzaea it has been regarded as a mutelid, but since both possess hinge teeth, though reduced, and a supra-anal opening they must belong to the Unionidae. Smith (1880) described the first and only species as a Spatha, and Bourguignat (1883) established a new genus Burtonia (preoccupied) and added in the following years 11 new "species", a number augmented by Germain (1908) and Pilsbry & Bequaert (1927). Leloup (1950) created the subfamily Pseudospathinae, but referred it to the Mutelidae. Pain & Woodward (1968) correctly transferred it to the Unionidae, but why maintain it?

Pseudospatha tanganyicensis (Smith 1880) figs. 154-156

The type specimen is 90 x 43 x 15 mm and the maximum size about 120 mm in length. The rather variable species is endemic to Lake Tanganyika.

List of synonyms of African Unionidae mentioned in the text

A. The genus Caelatura:

acuminatus Adams 1866 (Unio) - C. acuminata
aegyptiacus Cailliaud 1827 (Unio) - C. aegyptiaca
aequatorius Morelet 1885 (Unio) - C. aegyptiaca gabonensis
alluaudi Dautzenberg 1908 (Unio) - C. alluaudi
ambifarius von Martens 1897 (Unio) - C. ratidota
araneosa Rochebrune 1886 (Zairia) - C. aegyptiaca gabonensis
bakeri Adams 1866 (Unio) - C. aegypriaca bakeri
bangoranensis Germain 1907 (Unio) - C. aegyptiaca
bomae Pilsbry & Bequaert 1927 (Caelatura) - C. bourguignati
bourguignati Rochebrune 1886 (Pharaonia) . C. bourguignati
briarti Dautzenberg 1901 (Unio) - C. briarti
burtoni Woodward 1859 (Unio) - C. burtoni
chariensis Germain 1906 (Unio) - C. teretiuscula
chefneuxi Neuville & Anthony 1906 (Unio) - C. monceti
chivoti Germain 1907 (Unio) - C. aegyptiaca
choziensis Preston 1910 (Unio) - C. choziensis
chudeaui Germain 1909 (Uhio) - C. aegyptiaca
cridlandi Mandahl-Barth 1954 (Caelatura) - C. cridlandi
croninae Walker 1922 (Nodularia) - C. kunenensis
decampsianus Wattebled 1884 (Unio) - C. aegyptiaca
disciformis Rochebrune 1886 (Zairia) - C. bourguignati
elegans Rochebrune 1886 (Zairia) - C. aegyptiaca gabonensis
ellenbergeri Germain 1920 (Nodularia) - C. kunenensis
essoensis Chaper 1885 (Unio) - C. aegyptiaca
framesi Connolly 1925 (Indonaia) - C. mossambicensis
gabonensis Küster 1862 (Unio) - C. aegyptiaca gabonensis
gaillardi Germain 1909 (Unio) - C. teretiuscula
graueri Haas 1927 (Caelatura) - C. leopoldvillensis graueri
hauttecoeuri Bourguignat 1883 (Unio) - C. hauttecoeuri
hauttecoeuri Bourguignat 1885 (Grandidieria) - C. burtoni
horei Smith 1880 (Unio) - C. horei
hypsiprymnus von Martens 1897 (Unio) - C. hypsiprymna
jeanelli Germain 1912 (Unio) - C. aegyptiaca

jourdyi Germain 1912 (Unio) - C. aegyptiaca
juliani Rang 1835 (Unio) - C. aegyptiaca
kipopoensis Mandahl-Barth 1968 (Caelatura) - C. kipopoensis
koehleri Germain 1909 (Unio) - C. aegyptiaca
kunenensis Mousson 1887 (Unio) - C. kunenensis
kyogae Mandahl-Barth 1954 (Caelatura) - C. hauttecoeuri
lacoini Germain 1906 (Unio) - C. aegyptiaca
landanensis Schepman 1891 (Unio) - C. aegyptiaca gabonensis
leopoldvillensis Putzeys 1898 (Unio) - C. leopoldvillensis
liederi von Martens 1897 (Unio) - C. mossambicensis
lobensis Frierson 1913 (Parreysia) - C. lobensis
lourdeli Bourguignat 1883 (Unio) - C. monceti
luapulaensis Preston 1913 (Unio) - C. luapulaensis
mesafricana Pilsbry & Bequaert 1927 (Caelatura) - C. aegyptiaca gabonensis
mesafricana Binder 1958 (Caelatura) - C. aegyptiaca
misraimica Servain 1890 (Pharaonia) - C. aegyptiaca
monceti Bourguignat 1883 (Unio) - C. monceti
mossambicensis von Martens 1860 (Unio) - C. mossambicensis
mutelaeformis Germain 1906 (Unio) - C. teretiuscula
mweruensis Smith 1908 (Unio) - C. mweruensis
ngesianus von Martens 1897 (Unio) - C. aegyptiaca stuhlmanni
nguigmiensis Germain 1909 (Unio) - C. aegyptiaca
niloticus Cailliaud 1827 (Unio) - C. aegyptiaca
nyangensis Frierson 1913 (Parreysia) - C. lobensis
nyassaensis Lea 1864 (Unio) - C. nyassaensis
nyassaensis Leloup 1950 (Parreysia) - C. ujijiensis
parreysi Philippi 1848 (Unio) - C. aegyptiaca
putzeysi Preston 1912 (Unio) - C. aegypriaca gabonensis
ratidota Charmes 1885 (Unio) - C. ratidota
regis Pilsbry & Bequaert 1927 (Parreysia) - C. aegyptiaca stuhlmanni
rohani Germain 1925 (Nodularia) - C. kunenensis
rothschildi Neuville & Anthony 1906 (Unio) - C. hauttecoeuri?
rotula Pilsbry & Bequaert 1927 (Caelatura) - C. bourguignati
rugifer Küster 1852 (Unio) - C. aegyptiaca
schoutedeni Haas 1936 (Caelatura) - C. mweruensis
sobaensis Preston 1914 (Nodularia) - C. aegyptiaca

stagnorum Daautzenberg 1890 (Unio) - C. bourguignati
stanleyvillensis Pilsbry & Bequaert 1927 (Caelatura) - C. aegyptiaca gabonensis
stappersi Haas 1936 (Mesafra) - C. mweruensis
stuhlmanni von Martens 1897 (Unio) - C. aegyptiaca stuhlmanni
subniger Preston 1901 (Unio) - C. aegyptiaca gabonensis
symoensis Mandahl-Barth 1968 (Caelatura) - C. mweruensis
tanganyicensis Smith 1880 (Unio) - C. burtoni
tanganyicensis Smith 1881 (Unio) - C. ujijiensis
teretiusculus Philippi 1847 (Unio) - C. teretiuscula
tsadiana von Martens 1903 (Unio) - C. aegyptiaca
ujijiensis Crosse 1881 (Unio) - C. ujijiensis
zambesiensis Preston 1905 (Unio) - C. kunenensis

B. Other genera:

abyssinicus von Martens 1897 (Unio) - Unio abyssinicus
aeneus Jickeli 1874 (Unio) - Unio elongatulus dembeae
anceyi Bourguignat 1885 (Brazzaea) - Brazzaea anceyi
auricularia Spengler 1793 (Unio) - Margaritifera auricularia
caffer Krauss 1848 (Unio) - Cafferia caffra
cygnea Linnaeus 1758 (Mytilus) - Anodonta cygnea
dembeae Sowerby 1865 (Unio) - Unio elongatulus dembeae
durieui Deshayes 1847 (Unio) - Unio elongatulus durieui
elongatulus Pfeifferi 1835 (Unio) - Unio elongatulus
erlangeri Kobelt 1909 (Unio) - Unio elongatulus dembeae
fellmanni Deshayes 1841 (Unio) - Psilunio littoralis
johnstoni Smith 1893 (Unio) - Prisodontopsis johnstoni
littoralis Lamarck 1801 (Unio) - Psilunio littoralis
marocana Pallary 1918 (Margaritana) - Marfaritifera auricularia
ravoisieri Deshayes 1847 (Unio) - Unio elongatulus durieui
subpictorum Pallary 1936 (Unio) - Unio elongatulus durieui
tanganyicensis Smith 1880 (Spatha) - Pseudospatha tanganyicensis

List of Figures

All figures are reproduced in 2/3 natural size except when a magnification is indicated

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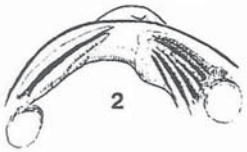
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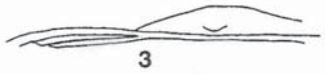
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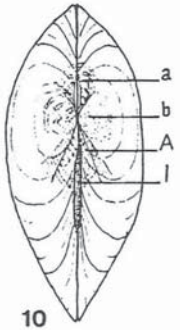

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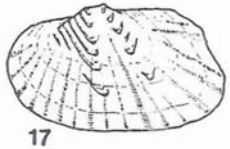
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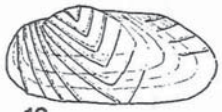
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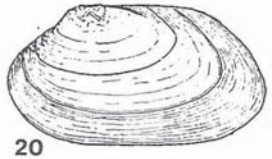
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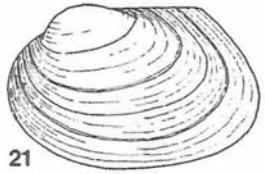
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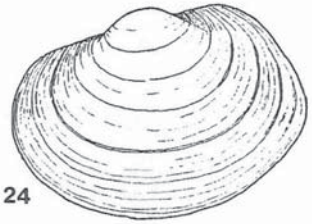
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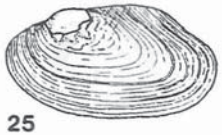
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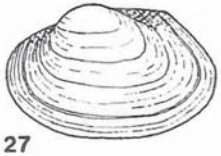
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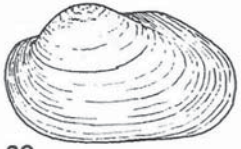
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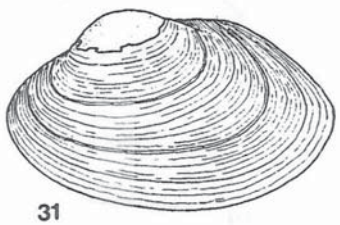
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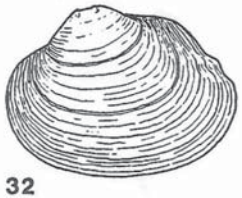
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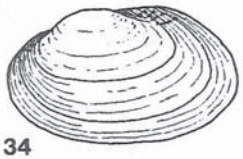
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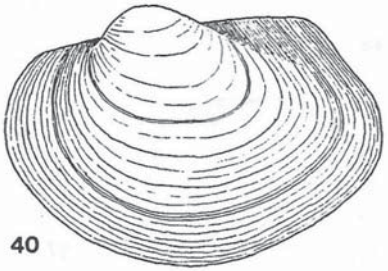
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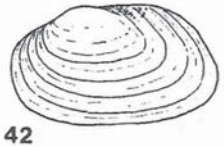
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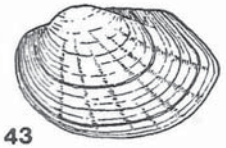
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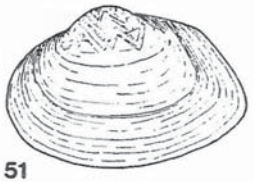
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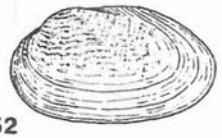
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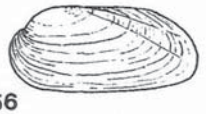
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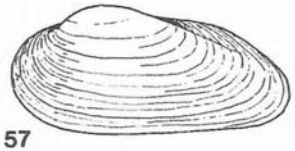
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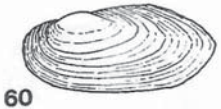
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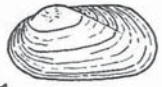
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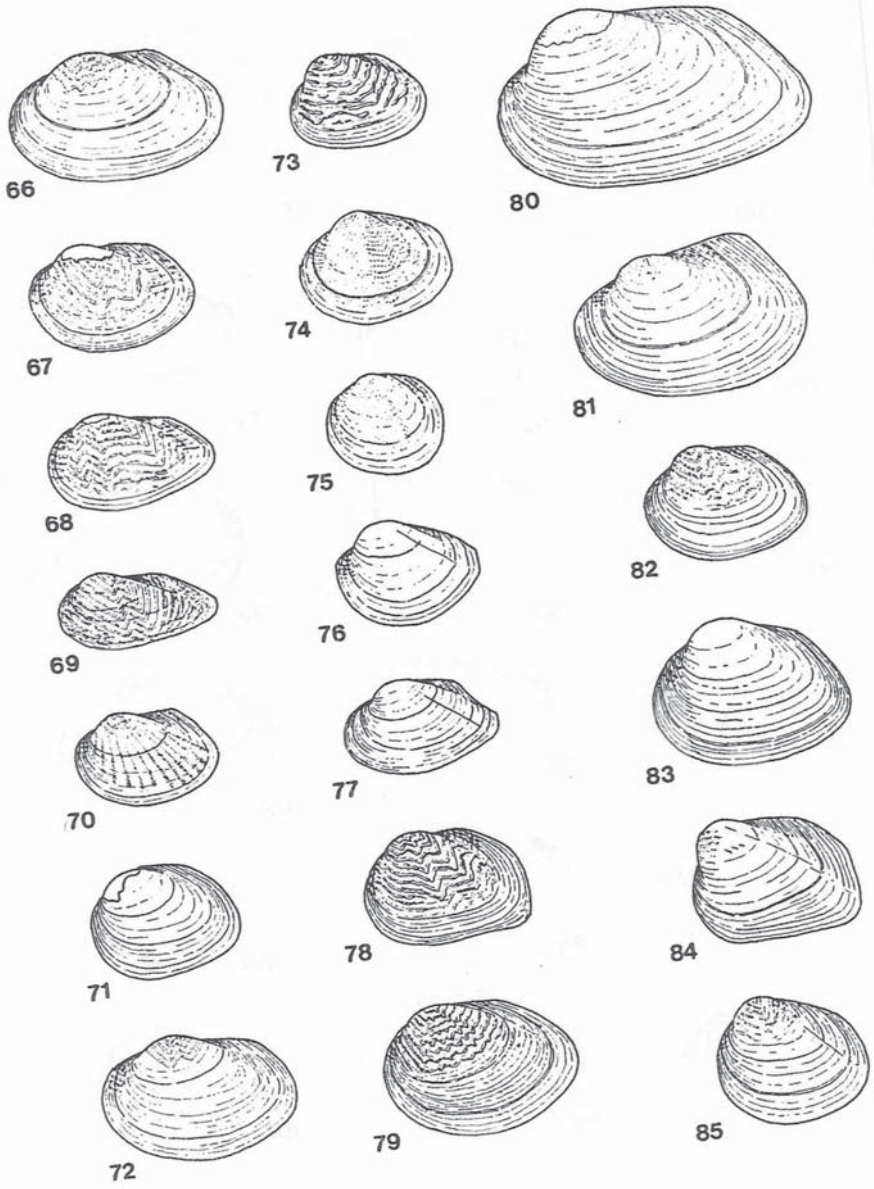
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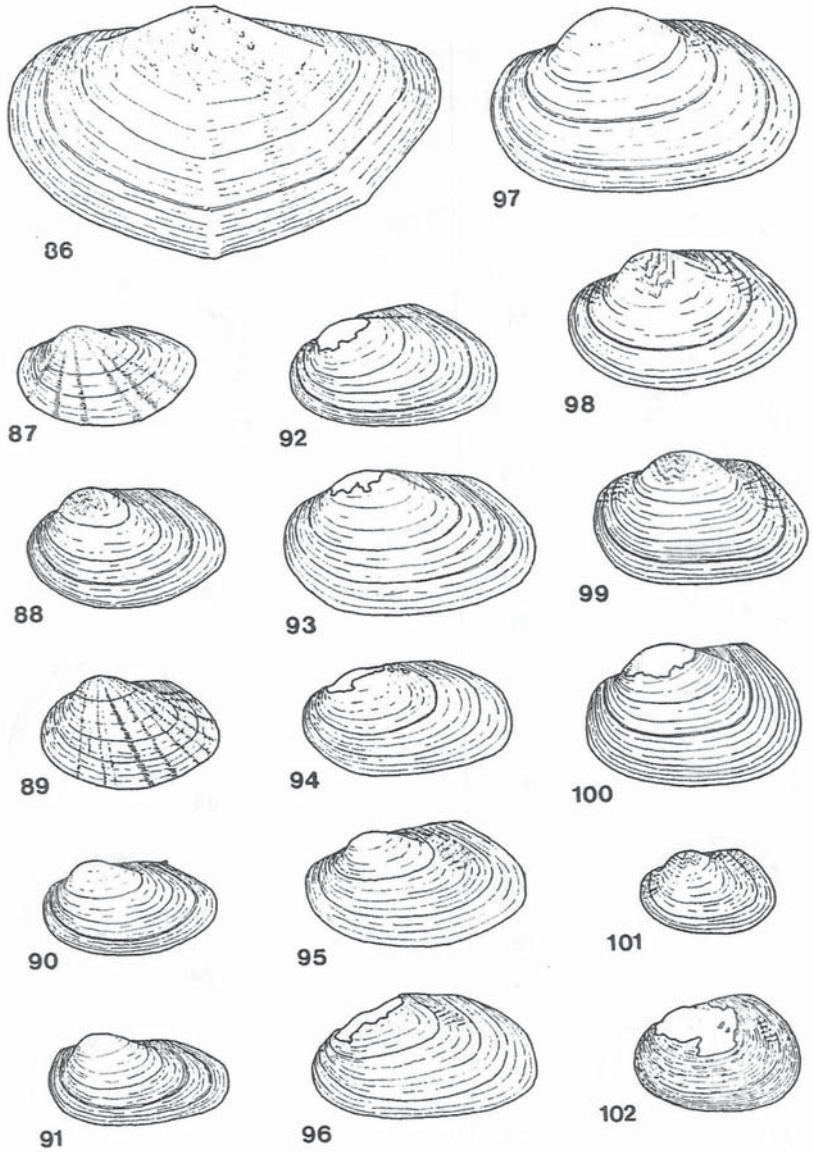
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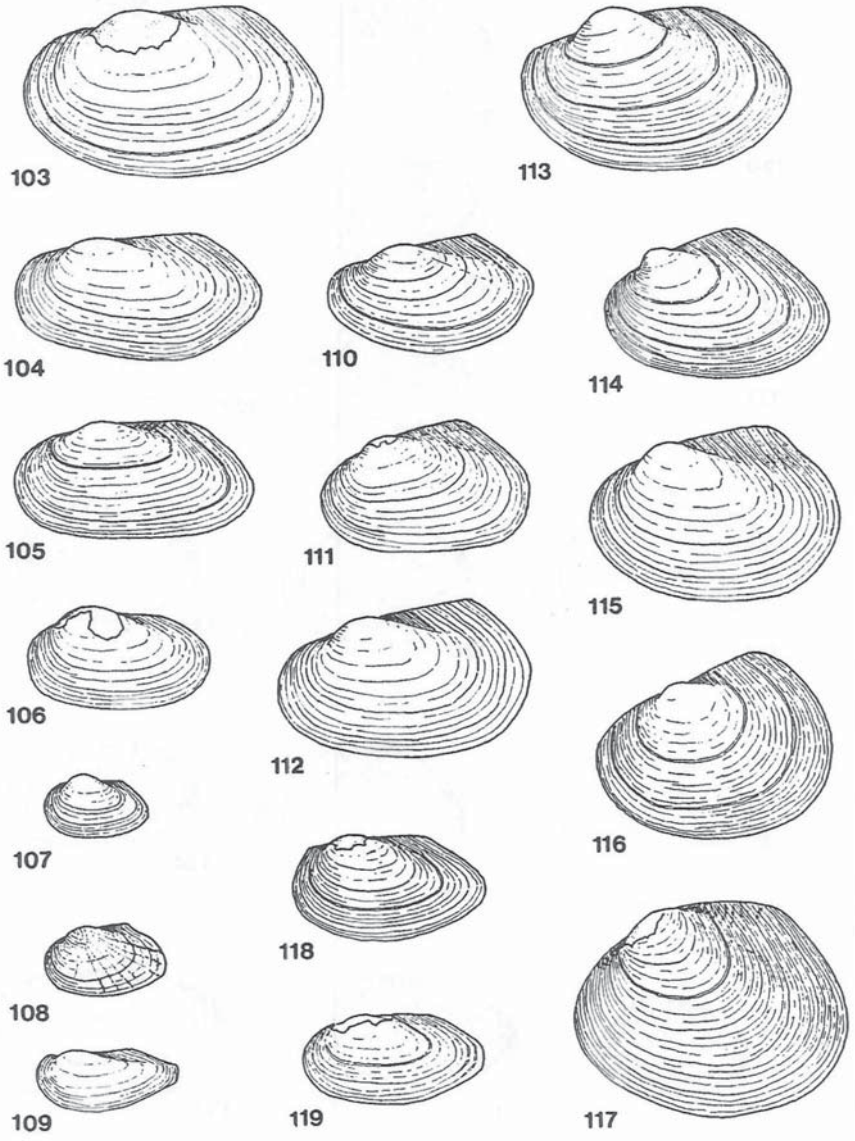
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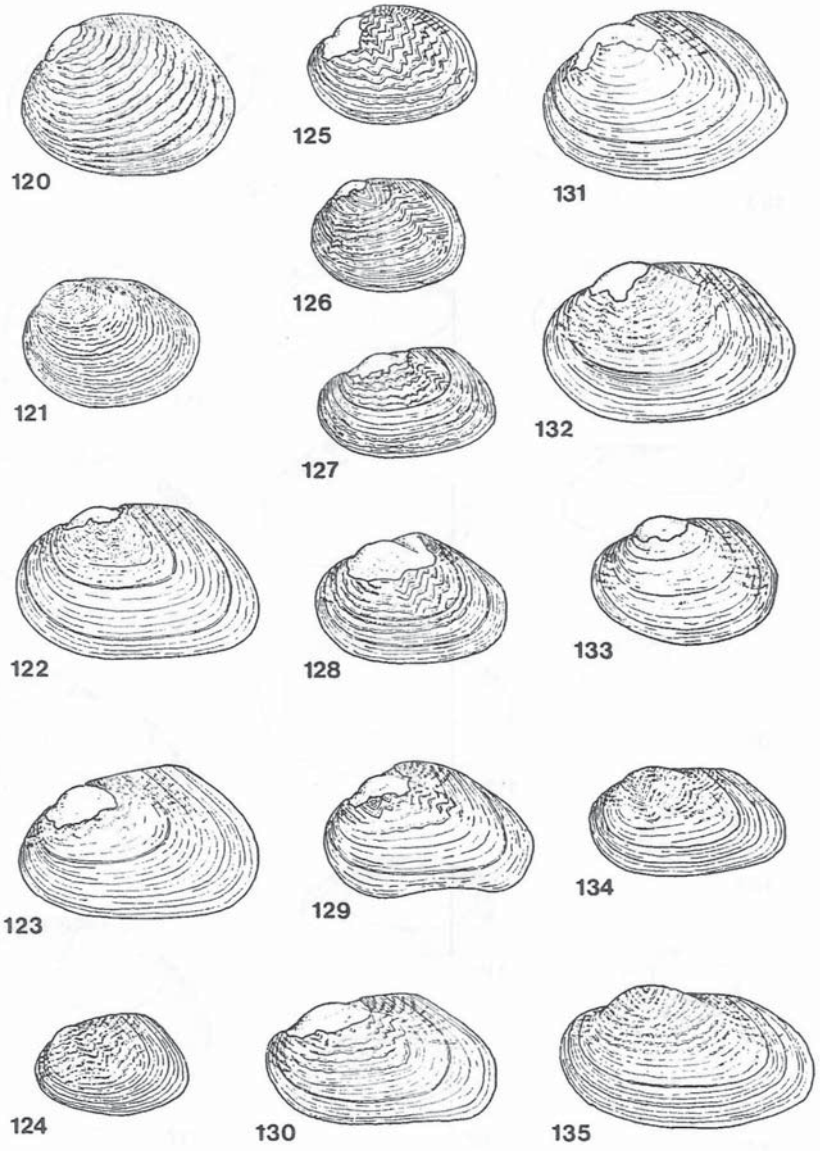
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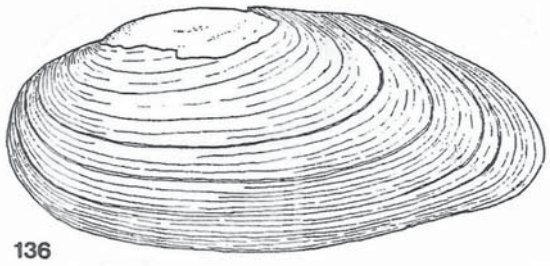
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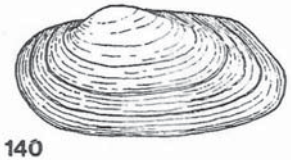
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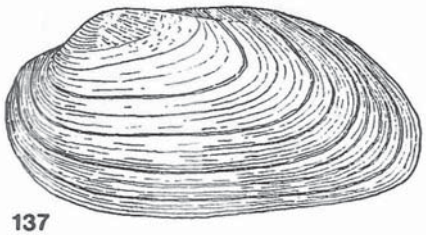
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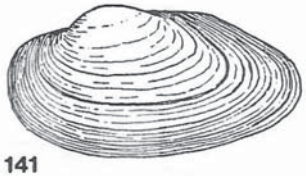
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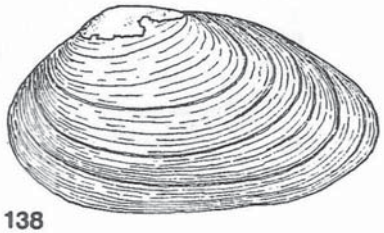
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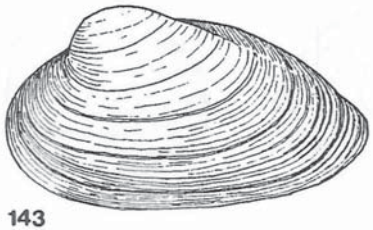
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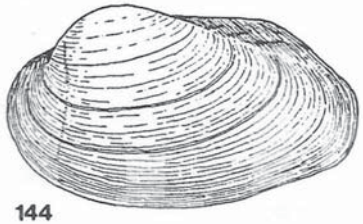
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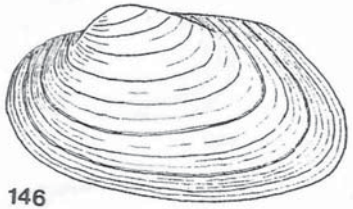
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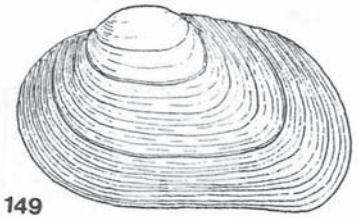
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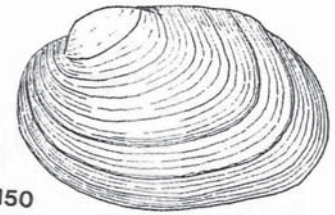
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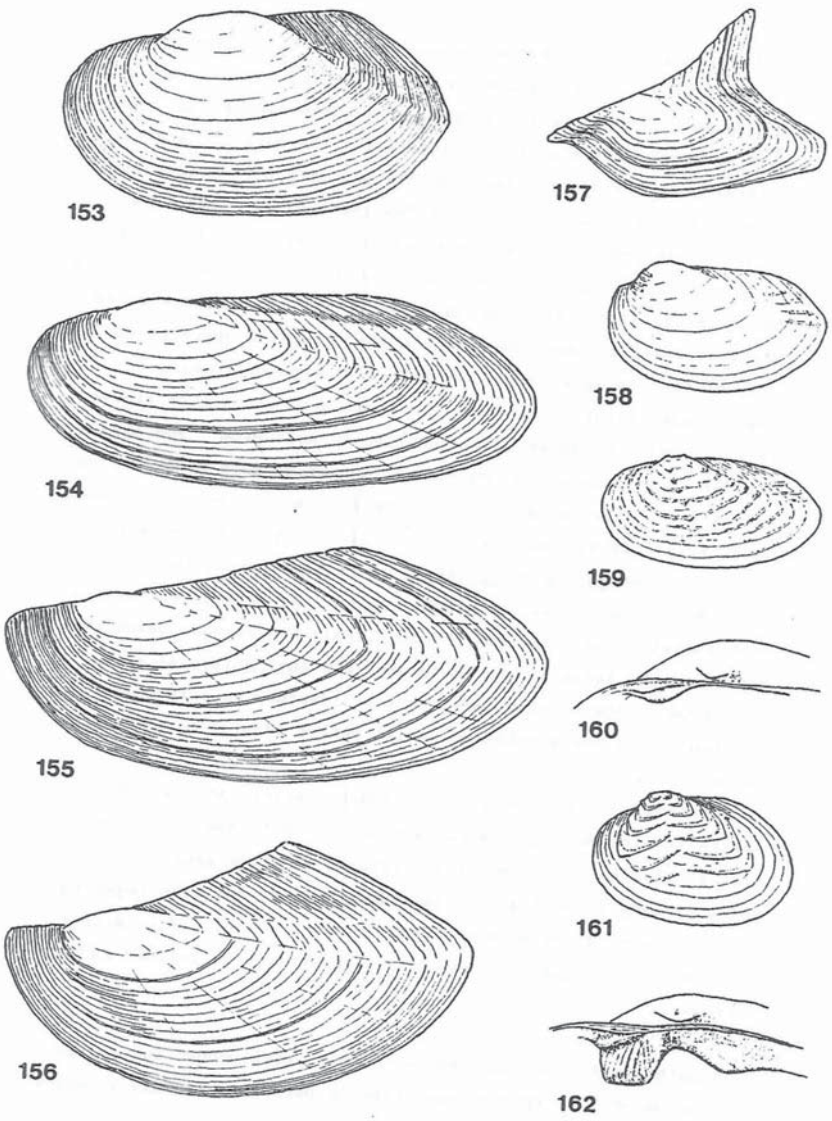

B: MUTELIDAE

Exteriorly a mutelid shell resembles that of a unionid and no distinctive external character exists, but, as a rule, the African species grow to a larger size and, with a few exceptions, they have no particular sculpture. Interiorly the lack of cardinal and lateral teeth is distinctive. In the majority of the species the hinge plates are smooth, but in a few these plates possess a series of secondary uniform, smaller or larger tubercles, and in such cases the hinge is termed pseudotaxodont. In the soft parts the mutelids differ from the unionids by the concrescence of the mantle borders between the anal and the branchial openings and in several species again below the branchial opening forming a praesiphonal suture. Furthermore a supra-anal opening is always absent. Only the inner gills function as marsupium. The eggs are smaller than those of the Unionidae, measuring only about 0.1 mm in diameter. The larval stage of the African species was unknown until Fryer (1961) published his excellent paper on the early development of Mutela bourguignati in Philos. Trans. roy. Soc. Lond. B. 711, vol. 244, to which I refer. He called the larva a "haustorial larva", but von Jhering (1891) had already described and named the larva of the South American Anodontites as a "lasidium". The mutelid larva must be regarded as a further development of the glochidium, still better adapted to the parasitic life.

The family is distributed over South America, Africa and Australia with most genera and species in South America. The African species may be naturally grouped in three genera, one of which by many malacologists, including myself, has been regarded as a subgenus of one of the others. I am now inclined to accept it as a distinct genus. These three genera can be defined as follows:

Aspatharia Bourguignat 1885 without a praesiphonal suture and with an umbonal sculpture consisting of parallel, broadly V-shaped ridges.

Spathopsis Simpson 1900 with a short praesiphonal suture and an umbonal sculpture consisting of concentric ridges.

Mutela Scopoli 1777 with a long praesiphonal suture and without a particular umbonal sculpture.

Besides these three genera some others have been referred to the Mutelidae. Brazzaea Bourguignat 1885 and Pseudospatha Simpson 1900 have been assigned to the family, but they are unionids and as such have been treated in Part A. The systematic position of the small Moncetia Bourguignat 1885 is somewhat uncertain, as the soft parts are unknown, but since the umbonal sculpture and the hinge agree with those of Spathopsis, it is here included in that genus. Rochebrune (1904) created two new genera: Arthropteron from Guinea and Mitriodon from Mali, of which the former hitherto has been accepted as a valid genus or subgenus, whereas the latter definitely was established on juvenile shells of Spathopsis. Germain (1908) examined the type of Arthropteron ouassouloui Rochebrune and suggested it is an abnormal shell of Brazzaea, which is impossible. Haas (1969) regards it as a distinct genus, and the problem of its systematic position is due to the fact that Rochebrune believed the anterior part of the shell to be the posterior! The peculiar feather-shaped structure he described as being behind the beaks is actually the groove between the dorsal margins of the two valves above the dilation of the left hinge plate in front of the beak and present in all Spathopsis with solid shells. The only unusual aspect is that this groove in Arthropteron is symmetrical, whereas normally it is more incurved on the left valve than on the right.

As the synonymy of the genera and subgenera of African Mutelidae is rather confusing, I shall attempt to unravel the history. The oldest name is Mutela Scopoli 1777 for Mytilus dubius Gmelin 1793, but in reality created for Adanson's "le Mutel" from 1757. Next comes Iridina Lamarck 1819 for his I. exotica, which however is a form of M. dubia. Conrad (1834) established his Pleiodon for his species P. macmurtrei, but this is a synonym of Mutela ovata (Swainson 1823). Lea (1838) introduced the name Spatha for Iridina nilotica Sowerby, but I. nilotica was actually described by Cailliaud. In the same year Lea created the name Platiris as a substitute for Iridina Lam. Swainson (1840) found it was I. nilotica that needed a new name and proposed Calliscapha.

During the following years right to 1927, when Pilsbry & Bequaert published their great work, the name Spatha was commonly used for the species belonging to Aspatharia and Spathopsis and sometimes also for some Mutela species, but after Bourguignat had started his confusing career several new names turned up, partly created by himself and partly because he introduced into France the very narrow concept of both species and genera. In 1879 he referred Iridina spekei Smith to a new genus, Cameronia, and in 1885 he created four new genera: the already mentioned Moncetia for his M. anceyi, Aspatharia for Margaritana vignouana Bernardi, Mutelina with the type species M. subdiaphana Bgt., which he forgot to describe, and Spathella for Spatha petersi Martens. Mutelina was much used by French conchologists mainly for the various forms and species of the Mutela rostrata group, and Spathella was used by the same people for the more thin shelled species, until Rochebrune & Germain (1904) discovered that Spathella Bgt. was preoccupied by Spathella Hall published one month earlier in 1885 than Bourguignat's name, and substituted it with Leptospatha, neglecting that Simpson (1900) had created the name Spathopsis for Anodonta guillaini Recluz or because Simpson regarded Spathopsis as a subgenus of the unionid genus Lamellidens from India, probably because he misunderstood the original description. Chelidonura Rochebrune 1886 and the substitute Chelidonopsis Ancey 1887 are mentioned under Mutela hirundo.

In order to complete the summary of the higher categories of African Mutelidae, it must be added that Modell (1964) divided them into five subfamilies: Dentaspathariinae for Prisodontopsis, which is a unionid, Aspathariinae for Aspatharia, with Arthropteron and Spathella as subgenera, and Pleidon, Spathopsinae for Spathopsis guillaini alone, Mutelinae for Mutela, Pseudospatha, which is a unionid, Chelidonopsis and Iridina, and Etheriinae, here treated as a family. He transferred Moncetia to the Unionidae. Modell's system is artificial and useless.

The three genera, here accepted as valid, are well defined and, as a rule, it is not difficult to place a mutelid shell in the right genus. Unfortunately, the same is not the case when the species are concerned. In fact, for the time being it is impossible to decide, how many species of mutelids we have in

Africa. The traditional morphological methods are insufficient for solving the problem. The reason is not so much lack of adequate material as lack of usable taxonomic characters, as these for most species are restricted to size, shape and thickness of the shells and these are of little value, except in some extreme cases. However, since a system is necessary, how insufficient it might be, we must try and get the best out of the possibilities. The previous attempts by Germain (1908), Simpson (1914), Pilsbry & Bequaert (1927) and Haas (1969) are of little help and especially the latter is very poor. Franc (1949) and Daget (1961, 1962 and 1964) dealing with the West African species give some useful information but as always is the case, when French malacologists are concerned, their species concepts are very narrow.

The following tentative classification of the African Mutelidae is based rather upon my species perception and my experience in African freshwater malacology than upon exact taxonomic characters. I admit it is by no means satisfactory, but I doubt it can be done much better until experimental methods are taken into use.

1. Genus Aspatharia Bourguignat 1885

The species belonging to this genus are characterized by the absence of a praesiphonal suture and by the umbonal sculpture consisting of parallel, broadly V-shaped ridges (fig. 8). Frequently only the posterior legs of the V's are present and sometimes there is no umbonal sculpture at all. This sculpture is seen easiest on juvenile shells as the umbonal area very often is eroded on older shells. In a few species the sculpture is extended over a larger part of the valves. Besides this sculpture some radiating striae consisting of very short lines parallel to the growth lines may be present, but they have no taxonomic value, as they can be present or absent in most species. The rather thin hinge plate is smooth and terminates posteriorly in a triangular sinulus. The type species of the genus is Anodonta vignouana Bernardi, which is a junior synonym of Anodonta rugifera Dunker, and not Anodonta chaiziana Rang as stated by Daget (1962).

The genus has a wide distribution in West Africa and Zaire and

a more scattered one in eastern Africa, where it is best represented in the southern part. About 32 species have been described and only five of these from eastern Africa. The number of species here regarded as valid is reduced to six. None of them exceeds 100 mm in length.

Aspatharia divaricata (Martens 1897) figs. 1-2

The type specimen, measuring 35 x 18 x 10 mm, was collected in the Simin river near the southeastern end of Lake Victoria and was, I believe, the only known specimen until Greenwood in 1952 dredged a single living specimen in the Buvuma Channel in the northern part of Lake Victoria from a depth of 60 feet (fig. 1). It is somewhat larger and relatively higher than the type, 40 x 23 x 12.5 mm. The inner gills contained a large number of small eggs. In 1954 Cridland found two fresh shells on the shore near Musoma, one measuring 43 x 25 x 14 mm and another relatively longer and slenderer: 48 x 24.5 x 14 mm (fig. 2). Both specimens show the influence of the sunlight, but in different ways. In the former the exposed valve is bleached, but in the latter it is not only bleached but has changed colour from dark olive green to a light brownish. The specimens mentioned above seem to be all that is known of this species apparently endemic to Lake Victoria. Records of this species from the former French Equatorial Africa and West Africa by Germain (1907) and Franc (1949) are due to misidentification of young, sculptured shells of other species. Franc advanced the theory that divaricata might be a young A. protchei or senegalensis, which is very unlikely. A. divaricata does not seem to be closely related to any of the other Aspatharia species and therefore undoubtedly valid. It is the only species of the genus restricted to East Africa.

Aspatharia rugifera (Dunker 1858) figs. 5-7

The type specimen is 64 x 32 x 25.5 mm and provided with a sculpture consisting of more or less strong ridges, divaricate on the posterior part of the shell and forming an irregular network on the rest of it. The shell is rather solid, with a slightly curved dorsal margin and a straight or slightly incurved ventral margin. The growth lines between the ridges are fine and closely

set providing the periostracum with a characteristic lustre, which discloses the species in cases where the sculpture is weak or absent.

Dunker described the species on a single shell he had received from Bernardi, who simultaneously described the species as Anodonta vignouana (a misprint for vignoniana). In both cases the type locality is the Como river in Gabon. According to Pilsbry & Bequaert (1927) Dunker's name has priority. Spatha corrugata Dautzenberg 1893 is the same species, but somewhat different because of the more strongly curved dorsal margin and weaker sculpture only present along the ridge on the posterior part of the shell. It measures 71 x 42 x 24 mm and was collected in the Niari river in the Congo Republic. In a stream called Seng near Ebolowa in southern Cameroun Ripert collected some specimens intermediate between rugifera and corrugata having the shape of the former and the sculpture of the latter (fig. 6). Walker (1910) described a Spatha kamerunensis from the Kribi river, also in south Cameroun, but nearer the coast than Ebolowa. The type specimen is 69 x 35.5 x 22 mm and has no particular sculpture apart from the fine, wavy lines parallel to the growth lines. Fig. 7 shows a shell collected by Ripert in a stream called Awon near Obala, just north of Yaoundé, which might be the same form, but it is larger, 92 x 46 x 30 mm, and has very little left of the sculpture. Spatha droueti var. roseotincta described by Dautzenberg (1921) from the Doumé river in southeast Cameroun might belong to the same form, but I have not seen it and it was not figured. Since, however, the shell from the Awon is not unlike some forms of A. droueti, known with certainty only from the Ivory Coast and Ghana, I think my suggestion is reasonable.

From the above it appears that the distribution of rugifera covers the southern part of Cameroun, Gabon and the Congo Republic. However, it must be wider, because Germain (1925) demonstrated the occurrence of the typical form in the Cunene river in southern Angola, but is has not been recorded from the interjacent area, unless the following species in reality is a form of rugifera, which I find unlikely, but with these bivalves one can never be sure.

Aspatharia semicorrugata (Preston 1909) figs. 3-4

The type is 87 mm long and 51.5 mm high, thus relatively higher than the preceding species, from which it also differs by the higher anterior part and the more posteriorly placed beaks. The sculpture is restricted to some, often indistinct, divaricate ridges between the beaks and the posterior end and a few radiating striae. Traces of fine, wavy lines may be present between the normal growth lines. Fresh shells are distinctly more glossy than those of the preceding species. The type locality is the Lower Congo. Aspatharia chapini, described by Pilsbry & Bequaert (1927) from the River Congo at Kinshasa, seems to be a younger shell than Preston's. The type specimen measures 77.5 x 41 x 28 mm.

It cannot be excluded that semicorrugata merely is a form of rugifera, but I have the impression they are specifically different.

Aspatharia droueti (Chaper 1885) figs. 8-10

The type specimen measures 78 x 43 x 28 mm, thus very near the same proportions as in the preceding species, but the dorsal margin is much more sloping anteriorly and no particular sculpture is present except on very young shells (fig. 8). The type locality is the Cania river in the Ivory Coast. McCullough collected it in some localities in Ghana (fig. 10).

It is possible that Spatha stuhlmanni var. comoeensis Germain 1908 from the Comoe river, Ivory Coast, belongs to this species, but the anterior dorsal margin is less sloping and on the whole it looks different. I am very much in doubt of its systematic position, as it seems to be intermediate between droueti and the chaiziana complex. This might indicate that droueti is not a distinct species, but an aberrant form of A. chaiziana, but judging from the rather scanty material of both species I have seen, I doubt this to be the case. At least, until more material is available, I prefer to regard droueti as a distinct species. Incidentally, it is a curious fact that droueti has attracted very little attention among French malacologists. The reason might be that Chaper was in opposition to Bourguignat.

Aspatharia dahomeyensis (Lea 1859) figs. 11-12

In 1859 Lea described two species, Anodonta dahomeyensis from Dahomey (now Benin) and A. senegalensis from Senegal, and in 1860 he brought figures of them. Undoubtedly, they are conspecific, as the only difference is the size. The type of dahomeyensis is 56 x 25.5 x 18 mm, whereas the type of the other is 86 x 38 x 28 mm. Both have the beaks placed rather posteriorly and consequently a relatively large anterior part of the shell. The dorsal margin is sloping, more so anteriorly, and the ventral margin is slightly concave. No particular sculpture is present.

Spatha complanata Jousseaume 1886, measuring only 46 x 23 x 12 mm, seems to be a younger shell of this species. The type locality is the River Niger at Fouladougou in Mali. Daget (1962), who regarded complanata and senegalensis as distinct species because of small differences in the juvenile shells, states the maximum length for complanata to be 91 mm. For dahomeyensis he gives the maximum length to be 99 mm and for senegalensis 84 mm. In the same paper he describes a supposed new species, Aspatharia nigeriensis, differing from dahomeyensis by the relatively higher shell, pink nacre instead of white, more glossy periostracum, and a more pointed posterior end. The maximum length is stated to be 89.5 mm. However, Daget did not select, describe and figure a type specimen and therefore the species is hardly valid, but this is not very important, because in all probability, it is just a form of dahomeyensis. The type locality is not indicated, but must be a small affluent to the River Niger at Bussa, now flooded after the construction of the Kaindji dam. As the same locality is given for dahomeyensis, the two "species" have probably been collected together. Fig. 12 shows a shell intermediate between dahomeyensis and nigeriensis. It is from Ghana. Thus the known distribution of dahomeyensis is West Africa from Senegal to western Nigeria. Records of the species in the Lake Chad area are due to misidentification of the following species.

Aspatharia pfeifferiana (Bernardi 1860) figs. 13-20

Under this name I unite a number of forms, originally described as species, from Central Africa. The beaks are placed more anteriorly than in the preceding species, but otherwise they can

be very much alike, and it is possible that pfeifferiana is rather a subspecies of dahomeyensis. If so, intermediates should occur in eastern Nigeria, but unfortunately, no Aspatharia has been described from that area. For the time being I prefer to regard pfeifferiana as a distinct species. It has a wide distribution from Chad to Zimbabwe and Ovamboland, but in East Africa proper it is only known from a single locality in Uganda.

In the typical pfeifferiana (fig. 13) the dorsal and the ventral margin are parallel and the height of the shell is slightly smaller than half the length, for instance 70 x 33 mm, and the diameter is about two thirds of the height. The type locality is Gabon, and typical specimens are known from Chad, Cameroun and, more locally, Zaire, but here as elsewhere the dorsal margin, as a rule, is slightly sloping.

The following "species" may be synonymous with pfeifferiana: Aspatharia dahomeyensis Lévèque 1974 from El Beid near Lake Chad. We have a good sample from that locality, kindly sent by Lévèque. Spatha decorsei Germain 1904 from Mamoun river (fig. 19) differs by the concave ventral margin. It is very similar to Spatha sinuata Martens 1883 (fig. 17) described from the Lubilash river in Shaba, which according to Pilsbry & Bequaert (1927) is the common form in eastern Zaire. Spatha stuhlmanni Martens 1897 (fig. 18) from Undussuma west of Lake Albert looks rather different, but judging from the shells of sinuata figured by Pilsbry & Bequaert (plate XXXV figs. 2-4) from Avakubi in the same area it is not a distinct species. This is supported by the single sample from Uganda, the Albert Nile at Pachwach, comprising both sinuata and stuhlmanni. Aspatharia flava Pilsbry & Bequaert (fig. 21) from Medje in the north-eastern part of Zaire might be an extraordinarily high form of stuhlmanni, but I have not seen it and dare not exclude the possibility that it is a distinct species.

Spathella protchei Rochebrune (fig. 14) was described on a shell from the River Congo at Mokaka (Mossaka?), but not figured until Pilsbry & Bequaert (1927) brought a photograph of a shell (pl. XXXIV fig. 1) which, however, is closer to the typical pfeifferiana than it should be according to Rochebrune's description. The shell presented here corresponds better with the

description. It was collected by Ripert in Lower Zaire.

Spatha cryptoradiata Putzeys 1898 (fig. 20) has oblique ridges on the posterior part of the shell, and I am in doubt of its correct systematic position, as it shows affinities to A. semicorrugata. Both have Stanley Pool (now Malebo Pool) as type locality. Pilsbry & Bequaert (1927) erroneously stated the type locality of cryptoradiata to be Loboy river in the Congo Republic and that was repeated by Haas (1969).

The following, evidently synonymous species are described from southeastern Africa: Anodon subreniformis Sowerby 1867 (fig. 15) with the type locality Lake Malawi, but probably from a river flowing into the lake, is relatively higher than the typical form and has a slightly concave ventral margin. I have not seen any shells belonging to the pfeifferiana complex from Lake Malawi, but the figured shell from the Hunyani river in Zimbabwe is close to Sowerby's species. Preston (1913) described three species, all assigned to the genus Mutela, though they definitely belong to Aspatharia. The species names are lukuluensis, sarae, and mathildae. His sarae from the Shire river is close to the typical pfeifferiana, mathildae (fig. 16) from the same river, is relatively higher like subreniformis, but with slightly convex ventral margin. His lukuluensis from the confluence of the Lukulu and Luapula rivers is similar to protchei.

In various papers French malacologists have recorded some of these forms from West Africa, very often based upon a single aberrant shell. Of course, these records should not be taken seriously.

Aspatharia chaiziana (Rang 1835) figs. 22-24

This, the last species of the genus, has caused much trouble, because it has been misunderstood by most malacologists, who assigned it to the genus Spathopsis and confused it with young specimens of that genus until Daget (1962) stated it to be an Aspatharia because of the absence of a praesiphonal suture, which for that matter Rang had already described. As a rule, the juvenile shell does not possess any particular umbonal sculpture, but in some cases V-shaped ridges are present. Haas (1929) brought a photograph of a young chaiziana with the typical

Aspatharia sculpture, but claimed it to be a juvenile Spathopsis wissmanni asserting that the sculpture was not a reliable character for the separation of Spathopsis from Aspatharia.

The type specimen is 67 mm long and 42 mm high and the locality is Gnédé in Senegal (fig. 24). It is recorded from several localities in West Africa from Senegal to Chad and northern Zaire, but it is certain that some of these records concern young Spathopsis rubens which, as a rule, have almost the same shape and the same pink or reddish nacre, but in such young specimens of rubens it is nearly always possible to see the concentric umbonal sculpture. However, the form described as Spatha mabillei by Jousseaume (1886) has a blueish white nacre and a relatively longer shell corresponding to fig. 23, which in fact has reddish nacre. It is from El Beid near Lake Chad and kindly forwarded by Dr. Lévèque, who (1974) regarded this form to be the typical form, whereas he identified the typical form, occurring in the same locality, with Bourguignat's bourguignati, which is a subspecies of Spathopsis wahlbergi (Krauss) restricted to Tanzania. Germain (1907) is responsible for this misunderstanding. Daget (1962) advanced the possibility that the typical mabillei with white nacre perhaps could be a form of dahomeyensis, but since this species sometimes has red nacre, I doubt that the colour of the nacre is an important taxonomic character in this group of bivalves. The following forms, described as species, are also referable to chaiziana.

Anodonta tawai Rang 1835 from Senegal was described on a juvenile shell. Spatha pangallensis Rochebrune 1882 from the Bakoy river, Mali, was not figured, but according to Daget it has the shape of mabillei and the nacre of chaiziana, though greenish in the umbonal cavity. Spatha rochebruni and tristis Jousseaume 1886, both from Senegal, are without doubt chaiziana and the latter is very close to the typical form, whereas the former (fig. 22) has the beaks placed more posteriorly. Spatha mabillei var. mamounensis Germain 1907 from the Mamoun river near the border between Chad and the Central African Republic might also be a form of chaiziana, and the same might be the case with regard to Spatha stuhlmanni var. comoeensis Germain 1908 from the Comoe river in the Ivory Coast (not to be confused with the Como river in Gabon),

but this is somewhat dubious as mentioned page 62.

2. Genus Spathopsis Simpson 1900

The type of the genus is Anodonta guillaini Recluz 1850, which I regard as a subspecies of S. wahlbergi (Krauss), and not Anodonta rubens as claimed by Daget (1961). The synonyms are dealt with page 58. It was Pilsbry & Bequaert (1927) who explained the differences between Aspatharia and Spathopsis and thereby established a safe base for the classification. They regarded Spathopsis as a subgenus of Aspatharia, but Daget (1961) gave it a generic rank, a conception I have adopted. Unfortunately, the two most important characters, the umbonal sculpture consisting of concentric ridges and the presence of a short praesiphonal suture, are difficult or impossible to observe on empty shells, which has led to some confusion as mentioned above under Aspatharia chaiziana. However, full-grown shells of most Spathopsis species have a relatively higher shell than most Aspathariae and they obtain a larger size, in most cases exceeding 100 mm in length. From the Mutelae of large size, they differ by the not gaping shells and the umbonal sculpture. The hinge plate is stronger terminating posteriorly in a more distinct sinulus and usually with a dilation on the left valve fitting under the hinge plate of the right valve. Above this part of the hinge the dorsal margins of the two valves do not meet, but form a rather long, in both ends tapering groove, which normally is widest on the left valve, but occasionally almost symetrical as in Arthropteron (see page 57). The early stages, including the eggs, are completely unknown.

The genus comprises six or seven species and some subspecies. It has a wide distribution in Africa from Senegal and Egypt to Transvaal and as opposed to the mainly fluviatile Aspatharia, the Spathopsis species are chiefly lacustrine, but they can also live in running water.

Spathopsis wahlbergi (Krauss 1848)

Under this name I collect a great number of forms, originally described as species, but as they are merging into each other,

they cannot be regarded as distinct species. However, it seems justifiable to group them in geographical races. As a rule, they have a relatively long and not very solid shell.

Spathopsis wahlbergi wahlbergi (Krauss 1848) figs. 25 and 30

The type specimen is about 115 x 59 x 35 mm, which is a fair size for a full-grown wahlbergi, but it can grow to a larger size. Spatha wahlbergi var. dorsalis Martens 1897 from near Tete in Mozambique measured 136 x 67 x 41 mm, perhaps the largest known specimen. It is characteristic for the nominate subspecies that the beaks are placed rather near to the anterior end and that the dorsal margin is straight and only slightly sloping. It is common in southern Africa from Natal and Transvaal to southern Tanzania. The type locality is the Aapies river in Transvaal.

Krauss described the species as an Iridina. Spatha natalensis Lea 1864 is a smaller shell (90 x 45 mm) from Natal. Spatha maitenguensis Sturany 1898 from the Maitengue river in Zimbabwe differs by the anterior dorsal margin being more sloping, though not as much as in the following subspecies. Spatha anceyi Ancey 1894 from Karonga at Lake Malawi has the posterior part of the shell relatively higher (98 x 52 mm). Simpson (1900) changed the name to Spatha lacustris, and Preston (1910) described the same shell as Spatha bertilloniana. Woodward (in Crowley, Pain and Woodward 1964) referred the same specimen to Spathopsis nyassaensis (Lea), but Ancey's detailed description and the figure correspond better with wahlbergi. Aspatharia (Spathopsis) wahlbergi Mandahl-Barth 1968 from Shaba is not this species, but Spathopsis dautzenbergi (Haas).

Spathopsis wahlbergi welwitschi (Morelet 1868) fig. 26

The type specimen, described as an Iridina, is from the Muria river in Angola and measures 90 x 48 mm. It differs from the nominate race by the still more anteriorly placed beaks and the strongly sloping anterior dorsal margin. The shell shown in fig. 26 from the Cunene river is not quite typical as the distinctive characters are less pronounced, and it is a question whether welwitschi can be maintained as a valid subspecies. More material from Angola is desirable.

Spathopsis wahlbergi bourguignati (Bourguignat 1885) figs. 28-29

In this subspecies I include the forms of wahlbergi from central and northern Tanzania described as species. Common to them is that the beaks are placed more posteriorly than in the nominate subspecies. The type specimen was collected on the southern shore of Lake Victoria. It was not figured, but the shell shown here (fig. 28) corresponds well with the description. It was picked up on the shore of Mwanza Bay and has the dimensions 83 x 45 x 25 mm. It is a far more typical bourguignati than that I figured in 1954 and which I doubt now really came from that area. It looks more like a wahlbergi s. str.

Bourguignat (1889) figured a smaller specimen of bourguignati from Bahi swamps west of Dodoma and described in the same paper two other species, Spathella spathuliformis from the Mogogo river in the same area and S. bloyeti from the Mkata river west of Morogoro. The three "species" are very similar apart from the sizes, but differences in any three dimensions were the most important specific characters according to Bourguignat.

Von Martens (1887) described a Spatha subaequilatera with the locality "Lake Victoria?", which is inseparable from bourguignati. In 1897 he is able to give some more precise localities: the Grummetti stream and the Simiyu river, both flowing into Lake Victoria from southeast. In the same excellent book he described a Spatha rotundata from a stream near Nyahua south-east of Tabora. It has a higher shell and a more convex ventral margin. The measurements are 92 x 58 x 30 mm. Sturany (1894) (in Baumann: Durch Massailand zur Nilquelle) described two species, which also may be forms of bourguignati, viz. Spatha baumanni (fig. 29) from the Grummetti stream, and S. martensi from the Ngoroine stream southeast of Musoma. The latter is the largest known specimen of this subspecies being 137 mm long and 77 mm high. We have a shell almost as large from the Duma river in Serengeti. The shell from Lake Kyoga shown in my 1954 publication as subaequilatera is rather a form of S. trapezia.

The records of bourguignati from Lake Chad by Germain (1907) and later by Lévèque (1974) do not belong to this subspecies, but probably to Aspatharia chaiziana. Crowley (1964) published a short paper on Aspatheria (sic!) bourguignati based upon shells

collected at Aruba Dam in Tsavo National Park, but evidently his shells belong to the form Pilsbry (1923) described as Spatha haasi, a synonym of S. wahlbergi guillaini.

Spathopsis wahlbergi hartmanni (Martens 1866) fig. 31

This supspecies can be very similar to the nominate one, but, as a rule, the dorsal margin is not sloping and almost parallel to the ventral and the shell is relatively lower, for instance 94 x 45.5 x 27 mm. The type locality is Birket Kura in Sennar, Sudan, and it is known also from northern Kenya, southern Ethiopia and other localities in the Sudan.

Spatha marnoi Jickeli 1874 from Bahr ez Zeraf, a tributary of the White Nile southwest of Malakal, is rather similar to the typical form, and Spathella fourtaui Pallary 1903 from the White Nile seems to be a younger shell of the same form, though with white not pink nacre, but perhaps it was bleached by the sunlight. From the Lake Rudolph area Rochebrune & Germain (1904) described two species, Spathella bozasi and S. brumpti, which also must be regarded as synonymous with hartmanni.

Spathopsis wahlbergi guillaini (Recluz 1850) figs. 33-34

Closely related to the preceding subspecies, but differing by the divaricate ridges on the posterior part of the shell. The type locality is the Denoq river near Brava, Somalia. The shell shown here in fig. 34 is from the Juba river at Bardera and represents the full-grown stage. It measures 128 x 66 x 40 mm and is unusually heavy for a wahlbergi weighing 125 g, which is twice the normal weight for a wahlbergi of that size.

Kobelt (1909) described a Spatha wahlberg var. bourguignati from Somalia? With a length of but 80 mm it is a young shell and if the locality is correct it must be a young guillaini, but if not it can also be a young hartmanni. Young shells of guillaini are inseparable from those of hartmanni, because the distinctive ridges are not present on shells less than 90 mm in length. Spatha haasi Pilsbry 1923 from the Boran land in Kenya is a synonym. I have collected similar shells in the small stream Maji ya Chumvi where it is crossed by the road from Voi to Mombasa, and they were quite normal in thickness. Aspatharia bourguignati Crowley 1964

(not of Bourguignat) from the Aruba Dam in Tsavo National Park is the same form. Thus the distribution of this subspecies seems to be southern Somalia and eastern Kenya.

Spathopsis wahlbergi tabula (Sowerby 1867) fig. 32

Sowerby's species, described in Conchologia Iconica 17, is from Sierra Leone, but was neglected until Haas (1936) resuscitated it as an older name for Spatha adansoni Jousseaume 1886, which name was commonly used and still is being used by French malacologists for the West African form here regarded as a subspecies of wahlbergi. The type of adansoni is 92 x 49 mm, thus relatively higher than hartmanni to which it is closely related, and this seems to be characteristic for the West African specimens. The largest specimen, according to Daget (1961), is that mentioned by Franc (1949) with a length of 105 mm.

Germain (1917) described a Spatha adansoni var. major measuring 110 x 60 mm, but in all probability this is a form of Spathopsis rubens, whereas his Spatha bourguignati var. major (1906) from Kanem, Chad, must be a tabula. Strangely enough, neither Franc nor Daget mentions Germain's two varieties major in their papers on the West African Mutelidae. Pain & Woodward (1962) and Haas (1969) include adansoni in the synonymy of S. rubens, where they also place Aspatharia chaiziana and other species. Such a mistake is only possible, if they have not seen a true tabula.

Spathopsis petersi (Martens 1860) figs. 45-46

A distinct species, smaller and lower than wahlbergi as the maximum size is about 72 x 30 x 18.5 mm and with parallel dorsal and ventral margins. This shape is present already in the juvenile shell (fig. 46). The type locality is the Zambesi river at Tete, Mozambique, and it is known also from Malawi, Zimbabwe and Transvaal.

Spatha modesta Lea 1864 from Mozambique is a synonym.

The following species of Spathopsis, the rubens group, generally have a relatively higher shell than those of the wahlbergi group, which is obvious already in the juvenile stage (compare figs. 30 and 48). As a rule, the shells are more solid,

often ponderous and with stronger hinge plates. The taxonomy of the species is not yet fully elucidated, and the correct systematic position of some of the many described "species" is still uncertain.

Spathopsis rubens (Lamarck 1819)

The type is fig. 1 on plate 201 in Encyclopédie Méthodique showing a shell 110 mm long and 74 mm high and the type locality is stated to be Senegal. The hinge plate (fig. 35) is longer and less strong than that of the following species, from which it also differs by the usually pink or red nacre, but that colour fades to white when a dead shell is exposed to sunlight. The periostracum is brown, not black as in wissmanni, and the shell is rarely as ponderous. A shell of rubens with the measurements 100 x 70 x 44 has a weight of 77 g whereas a wissmanni of 106 x 70 x 39 mm has a weight of 127 g. It seems natural to divide rubens into two subspecies: the nominate one living in West Africa and rubens arcuata inhabiting the River Nile system.

Spathopsis rubens rubens (Lamarck 1819) figs. 35-36

The shell is shorter and higher and has a more sloping anterior dorsal margin than the nilotic subspecies, but, of course, exceptions do occur in both subspecies. The maximum size, according to Daget (1961), is 133 x 93 mm, but shells exceeding 120 mm in length seem to be very rare. It is distributed from Senegal to Chad and possibly to and including Zaire, but I have not seen any specimen from that country and Pilsbry & Bequaert (1927) did not record it.

The following described forms may be synonyms of rubens s. str.: Anodon clappertoni Koenig 1826 from Nigeria, Anodonta splendens Cristofori & Jan 1832 without locality, Iridina solida Anton 1839 also without locality, Spatha baikii Adams 1866 from the River Niger, Spatha renei Jousseaume 1886 also from the Niger, Arthropteron ouassouloui Rochebrune 1904 from Ouassoulou, Guinea, and Mitriodon martini of same author and year from the Bafing river, an affluent of the Senegal river, Spatha rubens var. chudeaui and S. adansoni var. major both Germain 1907, respectively 1917, the former from Chad, the latter from Dahomey,

and Spatha renei var. compressa Germain 1908 from Bani river, Mali.

Spathopsis rubens arcuata (Cailliaud 1823) fig. 37

Differs from the nominate subspecies by the usually relatively longer shell and less sloping anterior dorsal margin. It also grows to a larger size, for instance 160 x 102 x 65 mm or 160 x 93 x 58 mm. The former is extraordinarily heavy weighing no less than 340 g! The latter has a more normal weight of 156 g. Both specimens were collected in the same pond near Giza, Egypt, and such large specimens occur mainly in stagnant or slowly running water as in the type locality, Bahr Yussuf, and other canals in Egypt. What size it can obtain in the Nile itself, I do not know. I have not seen any specimens from the main Nile and only a few from the White Nile. They are small, the largest measures only 73 x 42 x 27 mm (fig. 41), but there is no reason to believe that this should be the maximum size for the river form. It is referable to Spatha innesi Pallary 1903 from the White Nile.

Cailliaud (1823) described two species from Bahr Yussuf: Anodonta rubens and A. arcuta, a misprint for arcuata as pointed out already by Lea (1836). The latter was a smaller shell with incurved ventral margin as fig. 41. Anodonta anataria Cristofori & Jan 1832 from Egypt is a synonym. Spatha caillaudi Martens 1866 was introduced as a substitute for Cailliaud's rubens, but von Martens mispelled the name, it should have been cailliaudi. Spatha lepsii Jickeli 1874 from Upper Egypt is also a synonym. Aspatharia (Spathopsis) caillaudi Mandahl-Barth 1954 is not the same as von Martens' species, but rather a subspecies of Spathopsis trapezia (Martens).

Spathopsis wissmanni (Martens 1883) figs. 38-40

Related to rubens, with which it often has been united, but in my opinion it is a distinct species differing from the preceding by the shorter and stronger hinge plate (fig. 38), more ponderous shell, black periostracum and usually white nacre. Generally the shape of the shell is more regularly oval. The type specimen measured 138 x 91 mm and its locality is the Lubilash river in Shaba. It is widely distributed in West African rivers from

Senegal to Shaba and apparently also in Lake Tanganyika as Leloup's rubens seems to be this species.

In West Africa the species is better known as Spatha bellamyi Jousseaume 1886 (fig. 39), and although Franc (1949) proved that bellamyi is a synonym of wissmanni, Daget (1961) continued the use of the name bellamyi. Other probable synonyms are Mitriodon falemeensis and heudeloti Rochebrune 1904, both described on juvenile shells from tributaries of the Senegal river. Pilsbry & Bequaert (1927) were the first to emphasize the characteristic hinge plate of wissmanni, but nevertheless Haas (1929 and again 1936) claimed wissmanni to be a synonym of Aspatharia chaiziana, which he erroneously referred to Spathopsis. Leloup (1950), Pain & Woodward (1962), and Haas (1969) have all both wissmanni and chaiziana as synonyms of rubens, and the shell I presented on plate XI fig. 3 in my 1968 paper as rubens is actually a typical wissmanni.

Spathopsis dautzenbergi (Haas 1936) fig. 43

I am very much in doubt with regard to the systematic position of this species or form, which seems to be intermediate between wahlbergi and rubens. In my paper on the freshwater molluscs of Luapula-Bangweulu (1968) I referred it to wahlbergi, in spite of the size and weight of the shells I had at hand. The reason is that they did not agree very well with the type of dautzenbergi, which is only 82 x 47 x 32 mm, and my largest shell was 140 x 75 x 53 mm and had a weight of 165 g. The hinge plate is stronger than in rubens, but longer than that of wissmanni and relatively of the same length as in wahlbergi, with which it also agrees better in the shape of the shell than with either rubens or wissmanni. The colour of the nacre is not distinctive either, as the central part is light salmon-coloured and the marginal parts all the way round are blueish or greenish changing after the light. The periostracum is reddish brown. The type locality is the Chambeshi river in northern Zambia and other localities are the Luapula and some rivers in Shaba. It is possible that the large size of my specimens is due to the locality, Kipopo fish dam, but a single, rather worn valve from the Dikulwe river in Shaba is almost as large, 129.8 mm long, but the shell of that specimen has been less

inflated than those from Kipopo. It is possible that a larger material may prove it to be a local form of another species, but being unable to decide which one it could be, I prefer to maintain it as a distinct species.

Spathopsis nyassaensis (Lea 1864) fig. 47

The type specimen is a young shell, only 52 mm long, and the largest shell seen is 120 x 65 x 39 mm and weight 107 g. In the shape of the shell it is rather similar to S. wahlbergi welwitschi, but the hinge plate is shorter and stronger, intermediate between those of rubens and wissmanni, and the nacre resembles that of the preceding species. The anterior dorsal margin is strongly sloping and the shell is more compressed than in dautzenbergi, which nevertheless seems to be its nearest relative. Perhaps nyassaensis represents the lake form and dautzenbergi the river form of one and the same species?

Ancey (1894) described a Spathella kirki from the Shire river on semi-adult specimens, and a full-grown shell of the same lot was described by Preston (1910) as Spatha approximans. They do not differ much from the typical form. Spatha mwayana Preston 1913 from Lake Malawi at Mwaya is a young shell 70.7 mm long. Leloup (1950) records kirki from Lake Tanganyika, apparently correctly, but I have not seen any Spathopsis from that lake.

Spathopsis trapezia (Martens 1897)

Opposed to my opinion in 1954 I now regard this species as comprising two subspecies: the nominate one in Lake Victoria and another one in Lake Albert.

Spathopsis trapezia trapezia (Martens 1897) figs. 43-44

The type is 68 x 38 x 22 mm and that is near the maximum size. A somewhat shorter, more rounded form was described by von Martens as var. senilis. In the typical form the dorsal margin is almost straight and only slightly sloping, but shells with a curved dorsal margin, distinctly sloping anteriorly, are common. It is always rather thin-shelled with a narrow hinge plate. In rare cases the shell has preserved the shape of the juvenile shell (fig. 44) and it was such a one I in 1954 erroneously identified

with Spatha subaequilatera Martens. It was from Lake Kyoga, but since then I have seen more typical specimens from that swampy lake. The nominate subspecies is endemic to Lake Victoria and Lake Kyoga and the connecting Victoria Nile.

Spathopsis trapezia ovoidea nom. n. fig. 49

This is the form I in 1954 erroneously identified with Spatha caillaudi Martens, which, as shown above, is a synonym of Spathopsis rubens arcuata (Cailliaud). The type is the shell depicted in my book p. 150 fig. 79. The figure is slightly enlarged, the real size of that shell is 90 x 49.5 x 33.5 mm. It differs from the nominate subspecies by the larger size, more solid shell, stronger hinge plate and slightly more prominent beaks, which possibly is due to the fact that bivalves in Lake Albert very seldom have eroded beaks, opposite shells from Lake Victoria. Apparently, it is much more numerous in the southern part of Lake Albert than in the northern.

Naturally, I have considered the possibility, if not this subspecies could be a form of S. rubens arcuata, but I have come to the conclusion that it is more closely related to Lake Victoria's trapezia. However, I dare not exclude that both ovoidea and trapezia s. str. might be forms of rubens, mainly because the juvenile shells are very similar. Material from the Albert Nile and the southern Sudan is necessary for a solution of the problem, but until such is available, I prefer the present arrangement.

Spathopsis anceyi (Bourguignat 1885) fig. 27

Of this peculiar, small bivalve, endemic to Lake Tanganyika, only empty shells are known. I myself have not seen any, but judging from the drawings by Leloup (1950) fig. 47 of the umbonal sculpture and the hinge plate, it does not differ essentially from Spathopsis, but, of course, we do not know if a praesiphonal suture is present. Bourguignat established a new genus, Moncetia, for it and added in 1886 five further species, all individual variations of the same species, which usually has been named lavigeriana, but that name is from 1886. Simpson (1900) placed Moncetia as a subgenus of Spatha, and Pilsbry & Bequaert (1927) as

a subgenus of Aspatharia just like Spathopsis, but added (p. 413) that "the subgenus may prove superfluous". Nevertheless, Leloup maintains Moncetia as a separate genus.

3. Genus Mutela Scopoli 1777

In most species of this genus the shell is elongate and low, without any particular sculpture, and gaping in both ends. The hinge plate is smooth or provided with a series of mostly small, uniform tubercles. In a few species these tubercles are better developed (pseudotaxodont hinge). The praesiphonal suture is long. Because of the gaping shell the species are unable to stand a longer period without water.

The taxonomy of the genus is difficult. About 75 species have been described, all from Africa, and most of them by French conchologists with Bourguignat as the leader. The number definitely is too high, but to do as Haas (1969) and reduce it to four is to go too far. The following tentative classification seems acceptable to me, although it still contains some unsolved problems. The various genera, established for certain species or species groups, are mentioned in the introduction to the family.

Mutela rostrata (Rang 1835) figs. 50-54

The typical form is depicted fig. 50. It has an elongate, thin shell with almost parallel dorsal and ventral margin and usually greenish on the exterior side and bluish on the interior. Characteristic for it is the evenly rounded anterior end without an angle to the dorsal margin. A shell of fair size measures 79 x 28 x 17 mm. The type locality is Senegal, but the distribution covers Egypt and most of tropical Africa. Of course, such a wide distribution has caused an evolution of many local forms, often described as distinct species, but also quite typical populations have been described as new species just because their localities are far away from the type locality.

To the typical form I refer the following "species": Iridina caelestis Lea 1838 without locality, Mutelina legumen, tholloni and prasina Rochebrune 1886, all from the River Congo at Nganchu

(Gancini), Mutelina aegyptiaca Pallary 1924 from Egypt, Mutela langi Pilsbry & Bequaert 1927 from the River Congo at Zambi, and Mutela carrei Schwetz and Dartevelle 1948 from the Luapula (not carrei Putzeys).

Less typical, but quite common, is a form with a more oblique dorsal margin and consequently a higher posterior part (fig. 51). It was named Mutelina mabilli by Rochebrune (1886), who also described a Mutelina paludicola from the same locality, the River Congo at Nganchu, differing only by the smaller size (apart from the diameter stated to be 812 mm, obviously a printer's error). Mutelina falemeensis Germain 1907 (fig. 52) has a still more oblique dorsal margin, but in the same part of Chevalier's book of travel on p. 571 Germain showed, how all these forms are connected to each other, which did not prevent him from treating them as distinct species.

Less common is a form with the beaks placed more anteriorly and with the posterior end of the shell prolonged (fig. 54). It was described as Mutelina joubini by Germain (1904) on a shell from Upper Oubangui and later recorded from the River Niger by Franc (1949) and Daget (1964), who states the maximum length to be 134 mm, which might be due to a confusion with M. dubia. I find it likely that the prolongation of the shell is caused by certain ecological factors, for instance mud depositing. Mutela iris Pilsbry & Bequaert 1927 from Lake Kabamba, Shaba (fig. 53) seems to be intermediate between rostrata and joubini.

Mutela carrei (Putzeys 1898) figs. 55-56

Differs from the preceding species only by the sharp ridge running from the beak to the posterior end. The type specimen is 72 x 24 x 12.5 mm and was collected in Malebo Pool (formerly Stanley Pool). It has a more pointed end and slightly more curved ventral margin than the shell depicted (fig. 55). From the same locality Germain (1908) described a Chelidonopsis roubaudi (fig. 56), which is very similar apart from the less sharp ridge and less pointed posterior end.

Probably carrei is a valid species forming a link between the normal rostrata and the peculiar M. hirundo (Martens).

Mutela franci Daget 1964 fig. 57

It was described as Mutela carrei? by Franc (1949) and named by Daget. The type specimen is 75 x 32 x 21 mm, thus considerably more inflated than carrei. According to Daget the maximum length is 93 mm. The beaks are larger and the anterior end more rounded than in carrei. In colour and texture of the shell it agrees with rostrata. The type locality is the River Niger at Gourao, and it is collected in other parts of the Middle Niger.

It seems to be a valid species, but the fact that carinate Mutelae with the same thin shell and colour as rostrata have evolved independently in the Congo and in the Niger calls for reflections. Are they mere river forms of rostrata evolved under certain ecological conditions or are they distinct species? I regret that, because of lack of material, I must leave the question open.

Mutela hirundo (Martens 1881) figs. 58-59

This peculiar mutelid was described by von Martens on a not full-grown shell, 100 mm long, from the Kwango river in Zaire. The full-grown was described by Rochebrune (1886) from the River Congo at Nganchu (Gancini) as Chelidonura arietina. The dimensions were stated to be 124 x 33 x 17 mm and 40 mm between the posterior ends, but these measurements do not fully agree with the drawings of the type. The young shell is rather similar to carrei, but the pointed anterior end with a ridge seems to be present in all stages. The posterior ridges, already present in the preceding species, form in this species an almost closed pipe and the area above the ridge is flattened and extended posteriorly. As the name Chelidonura was preoccupied, Ancey (1887) substituted it by Chelidonopsis, but hirundo is a Mutela as already von Martens meant. The species is recorded from several localities in the River Congo system.

Mutela alata (Lea 1864) figs. 60-62

This species comprises a series of probably ecological forms from Lake Malawi and the Shire river showing how a Mutela can change. I just touched the topic in my paper on Lake Malawi (1972) and shall treat it more detailed here. In Lake Malombe,

just south of Lake Malawi and connected with it by the Shire river, we have a large, rather low and thin-shelled form, depicted on plate 2 fig. 9 in my paper. It corresponds fairly well with Mutela cuneata Preston 1910 from the Shire, but is larger, 104 x 47 mm against 81 x 36 mm for cuneata. Ancey (1894) described a Mutela simpsoni from the same river measuring 72 x 35 mm, thus relatively higher. Fig. 60 shows a larger specimen of this form. Preston's Mutela opalescens (fig. 61) is not very different. In Lake Malawi itself we have a much higher form, viz. M. alata, the type of which is 78 x 46 mm and the largest seen 94 x 54 mm. The typical alata has a heavier shell than the other forms. The weights for the largest alata and the largest shell from Lake Malombe are respectively 42 and 25 g, but that is not surprising since so many of the freshwater molluscs in Lake Malawi have heavier shells than their relatives elsewhere.

Mutela hargeri (Smith 1908) figs. 63-64

The species is divided into two subspecies, the nominate one (fig. 63) living in Lake Mweru and M. hargeri schomburgki Haas 1936 (fig. 64) from Lake Bangweulu. The differences in shape appear from the figures. Both have a thin, compressed shell, but apart from this they resemble M. alata and must be regarded as lake forms. Unfortunately, no Mutela corresponding with the cuneata form of alata is known from the Chambeshi river or the Luapula, but, of course, that does not necessarily mean that it does not exist. Strangely enough, it is only in these three southern lakes that Mutela has developed such high shells, in the other great lakes it has retained the usual elongate shape.

Mutela soleniformis Bourguignat 1885 fig. 68

A rather thin-shelled, large species (128 x 55 x 30 mm) endemic to Lake Tanganyika and known only as dead shells. It was first described by Smith (1881) as Iridina exotica Lamarck, which was a misidentification. As usual Bourguignat (1886) added six further "species" all based upon small individual variations. Leloup (1950) demonstrated the conformity between some of these forms, especially Bourguignat's moineti, and Mutela nilotica (Cailliaud), here regarded as a subspecies of Mutela dubia (Gmelin), perhaps a

parallel to the Caelatura aegyptiaca-horei problem mentioned on page 19.

Mutela bourguignati Bourguignat 1885 figs. 65-66

The common Mutela of Lake Victoria and the Victoria Nile. It is closely related to the Mutela dubia complex, but I think it represents a distinct species in the same way as Caelatura hauttecoeuri in relation to C. aegyptiaca. It is a rather small species, for instance 93 x 38 x 26.5 mm, which is larger than the type that measured only 55 mm in length but otherwise of the same proportions. The typical, elongate form (fig. 66) is not as common in Lake Victoria as the shorter and relatively higher form described as var. smithi by von Martens (1897) (fig. 65). A shell of this form of fair size has the following dimensions: 80 x 36 x 26 mm, but the largest bourguignati I have seen was a shell, 118 mm long and 50 mm high, I picked up on the shore at Mwanza. It is noteworthy that the hinge plate quite often has a series of small tubercles just behind the beaks, seldom, and then indistinctly, also in front of the beaks. Living specimens are rarely found, probably because they are too deeply buried in the bottom to be caught by the dredge.

Mutela alluaudi Germain 1909 fig. 67

Only a few specimens of this somewhat dubious species are known. The largest seen is 83 x 44 x 30 mm, but younger specimens seem to have a relatively lower shell, for instance 66 x 32 x 21 mm. In all known specimens the hinge plates are provided with small tubercles, best developed behind the beaks, but also present on the anterior part. It is known only from Lake Albert. In 1954 I wrote: "I cannot deny the possibility that M. alluaudi may be only an abnormally developed M. emini", a theory I now have abandoned, mainly because emini always has a smooth hinge plate. Now I find it more likely that alluaudi in reality is a form of bourguignati, which in the special conditions in Lake Albert obtains a shell exteriorly resembling that of emini. Perhaps its rarity is due to that, in reality, it is not a native of Lake Albert, but a stranger occasionally brought to the lake by fish having survived the passage through the Murchison Falls.

At this place it would have been natural to deal with the common Mutela of Lake Albert, but since I now regard M. emini as a form of M. nilotica, which is a subspecies of M. dubia, it is necessary to start with this.

Mutela dubia (Gmelin 1791)

In this species I unite a number of forms, originally described as species, with a distribution similar to that of Caelatura aegyptiaca, viz. from Senegal to Egypt and southwards to northern Zaire and Lake Albert. It is a large species with a maximum length of 176 mm (Franc 1949) and a usual length of about 140 mm for a full-grown shell. Common to the various forms is that the beaks are placed rather far posteriorly, at about one third or more of the length, and that the dorsal margin meets the anterior margin in a usually distinct angle. It seems justifiable to divide it into four geographical subspecies.

Mutela dubia dubia (Gmelin 1791) figs. 73-74

Fig. 73 shows the typical form and fig. 74 a common form with more oblique dorsal margin and lower anterior end. It is known as Mutela angustata (Sowerby 1868). The two forms can be found together and are connected by all intermediates. In these forms the hinge plates are smooth, but a series of smaller or larger tubercles may be present, mainly behind the beaks. When they are well developed such shells have been regarded as belonging to a distinct species and even genus, viz Iridina exotica Lamarck 1819 and sometimes to the genus Cameronia Bourguignat 1879, originally created for the Lake Tanganyika species with a pseudotaxodont hinge. Franc (1949) and Lévèque (1972) include exotica and other West African forms with denticulate hinge in the synonymy pf dubia. It concerns Iridina elongata Sowerby 1821, I. striata Swainson 1823, both without locality, and Pliodon hardeleti and tchadiensis Germain 1906, both from Lake Chad. Preston (1909) described a Mutela lhotelleriana from Gabon, which also might belong to this subspecies, but possibly to M. dubia garambae. Mutela chevalieri Germain 1904 from the Upper Oubangui seems to be based on a somewhat deformed shell.

M. dubia s. str. is distributed in West Africa from Senegal to Chad and the Central African Republic.

Mutela dubia nilotica (Cailliaud 1823) figs. 69-70

Unfortunately, it is impossible to indicate a constant taxonomic character by which this subspecies always can be separated from the nominate, but, as a rule, the anterior part is seldom as low as it often is in dubia s. str. and the hinge plates are never denticulate. However, since the nilotic form is so well known, and since the Lake Albert form and probably also the form occurring in northeastern Zaire have evolved from that rather than from the nominate subspecies, I prefer to maintain it as a separate subspecies admitting that the differences are insignificant. The type locality is Bahr Yussuf in Egypt, and it occurs throughout the River Nile system.

There are but few synonyms: Spatha (Mutela) plicata Martens 1866 and Mutela singularis Pallary 1924, the latter described on a young shell from the Mahmoudiya Canal in Lower Egypt.

Mutela dubia emini (Martens 1897) figs. 71-72

Smaller than nilotica and of a brighter brownish colour, usually darker on the anterior part, which frequently possesses some fine, radiating striae. The largest shell I have seen measures 135 x 51 x 40 mm, but shells exceeding 110 mm in length are not common. It is endemic to Lake Albert.

Mutela dubia garambae (Pilsbry & Bequaert 1927) fig. 75

It is with some hesitation I include this form in dubia, because it is more thin-shelled rather like rostrata, but in the shape, particularly in the form praetenuis Pilsbry & Bequaert, it is very similar to some forms of nilotica, but I am not so acquainted with it that I can make a final decision and will not exclude that it might represent a distinct species. Fig. 75 is a copy of the type specimen from the Garamba river in northeast Zaire. It is recorded from other rivers in the eastern Zaire including the Lualaba.

Mutela spekei (Woodward 1859) figs. 76-77

Possibly not a distinct species but a subspecies of M. dubia to which it undoubtedly is closely related, but to me it looks specifically different. It is very variable in the shape of the shell and in the development of the tubercles on the hinge plate (fig. 76). Leloup (1950) p. 109 fig. 50 shows the variation. Bourguignat (1885 and 1886) added no less than 26 "species", all individual or local variations of spekei, for which he in 1879 had created the genus Cameronia. The largest of Bourguignat's "species", Cameronia gigantea, is 176 mm long and 86 mm high. It is endemic to Lake Tanganyika.

Pain & Woodward (1964) maintained Cameronia as a subgenus, not of Mutela, but of Pleiodon Conrad 1834, established for the following species, and Haas (1969) retained Iridina for exotica Lamarck. However, the presence or absence of tubercles on the hinge plates can hardly be accepted as a significant taxonomic character in the Mutelae, and Iridina as well as Cameronia cannot even be regarded as subgenera. With regard to Conrad's Pleiodon the situation is somewhat difficult.

Mutela ovata (Swainson 1823) figs. 78-80

This is an enigmatic species, because we have very little information of its occurrence and until recently no specimens appear to have been collected since early in the last century. The oval shell is strong and only gaping a little at the anterior end. The hinge plates are more strongly denticulate than in any other mutelid, and the anterior part of the left plate is prominent as in Spathopsis.

Conrad (1834) described a Pleiodon macmurtrei, which evidently is identical with Swainson's ovata. The locality is Senegal according to Pain & Woodward (1964), but Liberia according to Haas (1969). Pain & Woodward have been informed that a specimen in the collections of the Museum of Comparative Zoology in Harvard is labelled "Cosumance river, near Sedhiou", which obviously is the Casamance river in Senegal. Sedhiou is a town about 170 km from the coast. In 1986 Dr. Karl-Otto Nagel collected a good number of this species in the Moyamba district of Sierra Leone. Bourguignat (1879) described four "new species" apparently on shells from old

cabinets, and Pain & Woodward a Pleiodon waterstoni (fig. 80) on two shells of unknown origin. They are most likely young ovata, but interesting because they have no tubercles on the anterior part of the hinge plates as in Mutela spekei. This supports my opinion that ovata is a Mutela, but perhaps Pleiodon should be maintained as a subgenus.

Appendix:

Mutela zambesiensis n.sp. figs. 81-82

The rather thin shell is long and low with very small beaks situated at about a quarter of the length. The anterior end is broadly rounded and the posterior end slightly more pointed. The dorsal margin is straight and somewhat sloping and with indistinct angles at the transition to the anterior and the posterior margin. By increasing size the dorsal margin becomes more sloping by which the greatest height of the shell moves closer to the posterior end. Periostracum is lighter or darker brownish and the nacre is pink or blueish.

The type is 85 mm long, 32 mm high and 17.5 mm in diameter and the type locality is the Zambesi river between Kariba and Chirundu. The type lot was collected by Mr. T. Farina in August 1964. Another sample of this species was collected by Dr. R. Jocqué, curator at the Musée de l'Afrique centrale, in October 1987 in the mud flats surrounding a small lake at Singalangwe, 15 km north of Kongola in the Caprivi Strip close to the Zambian border and 1 km from the Cuando river, a tributary of the Zambesi river. This sample comprises some larger shells, the largest of which has the following dimensions: 107 x 40 x 23 mm. It has a very dark brownish periostracum, but is strongly eroded.

Fig. 81 shows the type and fig. 82 shows an old shell from Singalangwe demonstrating the change of shell-form by increasing age.

It is with great reluctance I have described a new species of the genus Mutela already overburdened with so many superfluous names of supposed species, but as I have found it impossible to assign these shells to any of the accepted species, I could not see

any alternatives. This new species is of particular interest, because the younger shells show affinities to the rostrata group, whereas the older shells from the Caprivi Strip resemble some forms of M. dubia. More material, especially from the Upper Zambesi and the Cuando river is desirable for the establishment of its proper systematic position.

List of synonyms of African Mutelidae mentioned in the text

A. The Aspatharia

bourguignati Lévèque 1974 - A. chaiziana
chaiziana Rang 1835 (Anodonta) - A. chaiziana
chapini Pilsbry & Bequaert 1927 (Aspatharia) - A. semicorrugata
comoensis Germain 1908 (Spatha) - A. droueti
complanata Jousseaume 1886 (Spatha) - A. dahomeyensis
corrugata Dautzenberg 1893 (Spatha) - A. rugifera
cryptoradiata Putzeys 1898 (Spatha) - A. pfeifferiana?
dahomeyensis Lea 1859 (Anodonta) - A. dahomeyensis
dahomeyensis Lévèque 1974 (Aspatharia) - A. pfeifferiana
decorsei Germain 1904 (Spatha) - A. pfeifferiana
divariacata von Martens 1897 (Spatha) - A. divaricata
droueti Chaper 1885 (Spatha) - A. droueti
flava Pilsbry & Bequaert 1927 (Aspatharia) - A. pfeifferiana?
kamerunensis Walker 1910 (Spatha) - A. rugifera
lukuluensis Preston 1913 (Mutela) - A. pfeifferiana
mabillei Jousseaume 1886 (Spatha) - A. chaiziana
mamounensis Germain 1907 (Spatha) - A. chaiziana
mathildae Preston 1913 (Mutela) - A. pfeifferiana
nigeriensis Daget 1962 (Aspatharia) - A. dahomeyensis
pangallensis Rochebrune 1882 (Spatha) - A. chaiziana
pfeifferiana Bernardi 1860 (Margaritana) - A. pfeifferiana
protchei Rochebrune 1886 (Spathella) - A. pfeifferiana
rochebruni Jousseaume 1886 (Spatha) - A. chaiziana
roseotincta Dautzenberg 1921 (Spatha) - A. rugifera
rugifera Dunker 1858 (Anodonta) - A. rugifera
sarae Preston 1913 (Mutela) - A. pfeifferiana
semicorrugata Preston 1909 (Spatha) - A. semicorrugata
senegalensis Lea 1859 (Anodonta) - A. dahomeyensis
sinuata von Martens 1883 (Spatha) - A. pfeifferiana
stuhlmanni von Martens 1897 (Spatha) - A. pfeifferiana
subreniformis Sowerby 1867 (Anodon) - A. pfeifferiana
tawai Rang 1835 (Anodonta) - A. chaiziana

tristis Jousseaume 1886 (Spatha) - A. chaiziana
vignouana Bernardi 1859 (Margaritana) - A. rugifera

B. The Spathopsis

adansonii Jousseaume 1886 (Spatha) - S. wahlb. tabula
adansoni var. major Germain 1907 (Spatha) - S. r. rubens
anataria Cristofori & Jan 1832 (Anodonta) - S. r. arcuata
anceyi Bourguignat 1885 (Moncetia) - S. anceyi
anceyi Ancey 1894 (Spatha) - S. w. wahlbergi
approximans Preston 1910 (Spatha) - S. nyassaensis
arcuta Cailliaud 1823 (Anodonta) - S. r. arcuata
baikii Adams 1866 (Spatha) - S. r. rubens
baumanni Sturany 1894 (Spatha) - S- w. bourguignati
bellamyi Jousseaume 1886 (Spatha) - S. wissmanni
bertilloniana Preston 1910 (Spatha) - S. w. wahlbergi
bloyeti Bourguignat 1889 (Spathella) - S. w. bourguignati
bourguignati Bourguignat 1885 (Spathella) - S. w. bourguignati
bourguignati Crowley 1964 (Aspatheria) - S. w. guillaini
bourguignati Germain 1907 (Spatha) - A. chaiziana
bozasi Rochebrune & Germain 1904 (Spathella) - S. w. hartmanni
brumpti Rochebrune & Germain 1904 (Spathella) - S. w. hartmanni
caillaudi von Martens 1866 (Spatha) - S. r. arcuata
caillaudi Mandahl-Barth 1954 (Aspatharia) - S. t. ovoidea
chudeaui Germain 1907 (Spatha) - S. r. rubens
clappertoni Koenig 1826 (Anodon) - S. r. rubens
compressa Germain 1908 (Spatha) - S. r. rubens
dautzenbergi Haas 1936 (Aspatharia) - S. dautzenbergi
dorsalis von Martens 1897 (Spatha) - S. w. wahlbergi
falemeensis Rochebrune 1904 (Mitriodon) - S. wissmanni
fourtaui Pallary 1903 (Spathella) - S. w. hartmanni
guillaini Recluz 1850 (Anodonta) - S. w. guillaini
haasi Pilsbry 1923 (Spatha) - S. w. guillaini
hartmanni von Martens 1866 (Spatha) - S. w. hartmanni
heudeloti Rochebrune 1904 (Mitriodon) - S. wissmanni
kirki Ancey 1894 (Spathella) - S. nyassaensis
lacustris Simpson 1900 (Spatha) - S. w. wahlbergi

lepsii Jickeli 1874 (Spatha) - S. r. arcuata
maitenguensis Sturany 1898 (Spatha) - S. w. wahlbergi
marnoi Jickeli 1874 (Spatha) - S. w. hartmanni
martensi Sturany 1894 (Spatha) - S. w. bourguignati
martini Rochebrune 1904 (Mitriodon) - S. r. rubens
modesta Lea 1864 (Spatha) - S. petersi
mwayana Preston 1913 (Spatha) - S. nyassaensis
natalensis Lea 1864 (Spatha) - S. w. wahlbergi
nyassaensis Lea 1864 (Spatha) - S. nyassaensis
ouassouloui Rochebrune 1904 (Arthropteron) - S. r. rubens
petersi von Martens 1860 (Spatha) - S. petersi
renei Jousseaume 1886 (Spatha) - S. r. rubens
rotundata von Martens 1897 (Spatha) - S. w. bourguignati
rubens Lamarck 1819 (Anodonta) - S. r. rubens
rubens Cailliaud 1823 (Anodonta) - S. r. arcuata
rubens Mandahl-Barth 1968 (Aspatharia) - S. wissmanni
solida Anton 1839 (Iridina) - S. r. rubens
spathuliformis Bourguignat 1889 (Spathella) - S. w. bourguignati
splendens Cristofori & Jan 1832 (Anodonta) - S. r. rubens
subaequilatera von Martens 1887 (Spatha) - S. w. bourguignati
subaequilatera Mandahl-Barth 1954 (Aspatharia) - S. trapezia
tabula Sowerby 1867 (Anodon) - S. w. tabula
trapezia von Martens 1897 (Spatha) - S. t. trapezia
wahlbergi Krauss 1848 (Iridina) - S. w. wahlbergi
wahlbergi Mandahl-Barth 1968 (Aspatharia) - S. dautzenbergi
welwitschi Morelet 1868 (Iridina) - S. w. welwitschi
wissmanni von Martens 1883 (Spatha) - S. wissmanni

C. The Mutela

aegyptiaca Pallary 1924 (Mutelina) - M. rostrata
alata Lea 1864 (Spatha) - M. alata
alluaudi Germain 1909 (Mutela) - M. alluaudi
angustata Sowerby 1868 (Mutela) - M. d. dubia
arietina Rochebrune 1886 (Chelidonura) - M. hirundo
bourguignati Bourguignat 1885 (Mutela) - M. bourguignati
caelestis Lea 1838 (Iridina) - M. rostrata

carrei Putzeys 1898 (Burtonia) - M. carrei
carrei Schwetz & Dartevelle 1948 (Mutela) - M. rostrata
carrei Franc 1949 (Mutela) - M. franci
chevalieri Germain 1904 (Mutela) - M. d. dubia
cuneata Preston 1910 (Mutela) - M. alata
dubia Gmelin 1791 (Mytilus) - M. d. dubia
elongata Sowerby 1821 (Iridina) - M. d. dubia
emini von Martens 1897 (Mutela) - M. d. emini
exotica Lamarck 1819 (Iridina) - M. d. dubia
exotica Smith 1881 (Iridina) - M. soleniformis
falemeensis Germain 1907 (Mutelina) - M. rostrata
franci Daget 1964 (Mutela) - M. franci
garambae Pilsbry & Bequaert 1927 (Mutela) - M. d. garambae
gigantea Bourguignat 1886 (Cameronia) - M. spekei
hargeri Smith 1908 (Mutela) - M. h. hargeri
hardeleti Germain 1906 (Pliodon) - M. d. dubia
hirundo von Martens 1881 (Spatha) - M. hirundo
iris Pilsbry & Bequaert 1927 (Mutela) - M. rostrata
joubini Germain 1804 (Mutelina) - M. rostrata
langi Pilsbry & Bequaert 1927 (Mutela) - M. rostrata
legumen Rochebrune 1886 (Mutelina) - M. rostrata
mabilli Rochebrune 1886 (Mutelina) - M. rostrata
macmurtrei Conrad 1834 (Pleiodon) - M. ovata
nilotica Cailliaud 1823 (Iridina) - M. d. nilotica
opalescens Preston 1910 (Mutela) - M. alata
ovata Swainson 1823 (Iridina) - M. ovata
paludicola Rochebrune 1886 (Mutelina) - M. rostrata
plicata von Martens 1866 (Spatha) - M. d. nilotica
praetenius Pilsbry & Bequaert 1927 (Mutela) - M. d. garambae
prasina Rochebrune 1886 (Mutelina) - M. rostrata
rostrata Rang 1835 (Iridina) - M. rostrata
roubaudi Germain 1908 (Chelidonopsis) - M. carrei
schomburgki Haas 1936 (Mutela) - M. h. schomburgki
simpsoni Ancey 1894 (Mutela) - M. alata
singularis Pallary 1924 (Mutela) - M. d. nilotica
soleniformis Bourguignat 1885 (Mutela) - M. soleniformis
spekei Woodward 1859 (Iridina) - M. spekei
striata Swainson 1823 (Iridina) - M. d. dubia

tchadiensis Germain 1906 (Pliodon) - M. d. dubia
tholloni Rochebrune 1886 (Mutelina) - M. rostrata
waterstoni Pain & Woodward 1964 (Pliodon) - M. ovata
zambesiensis Mandahl-Barth (Mutela) - M. zambesiensis

List of Figures

All figures are in 2/3 natural size except when a magnification is indicated

Figure:

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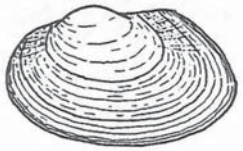

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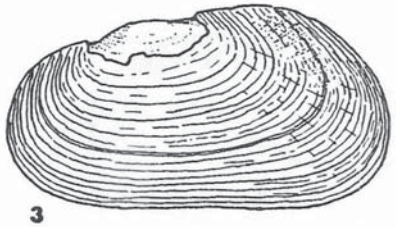

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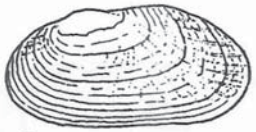

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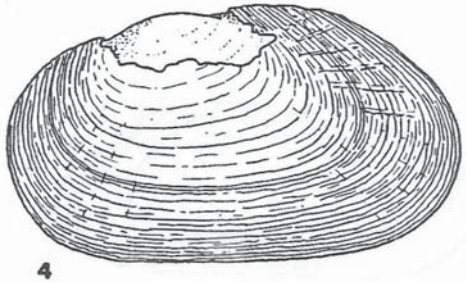

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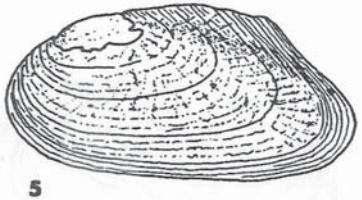

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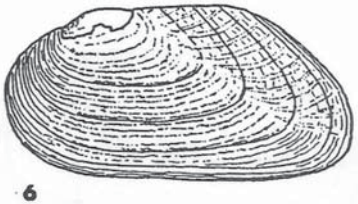

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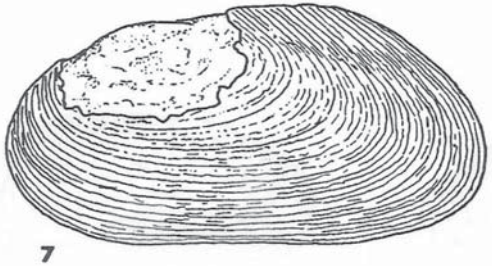

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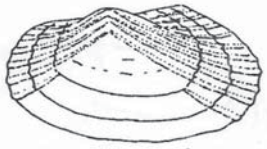

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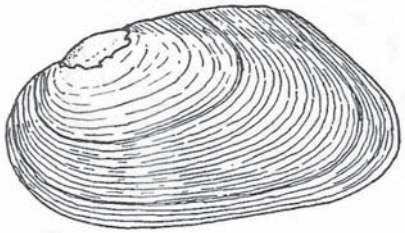

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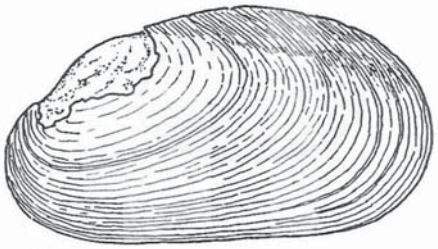

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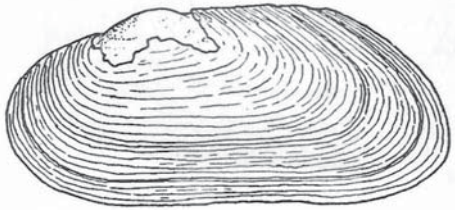

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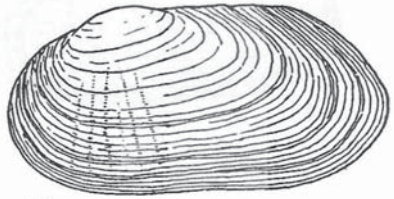

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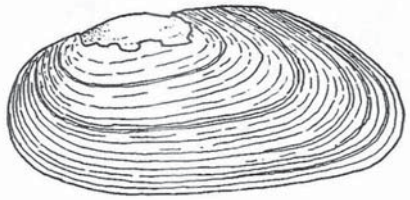

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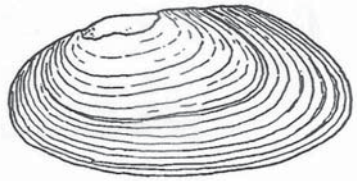

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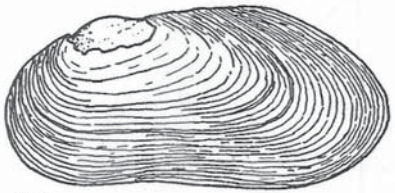

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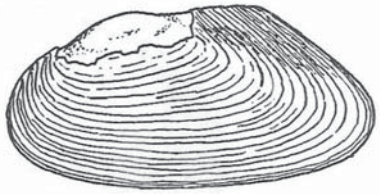

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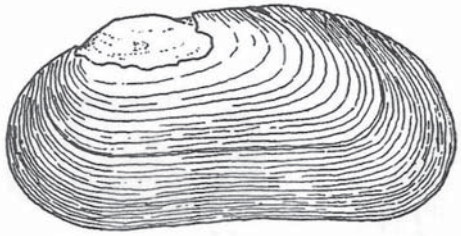

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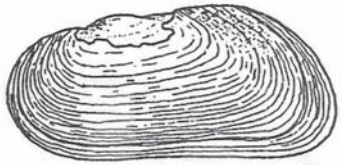

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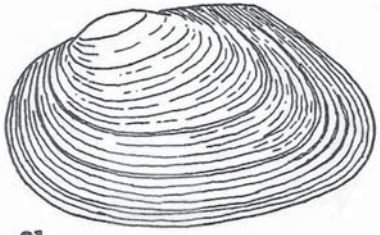

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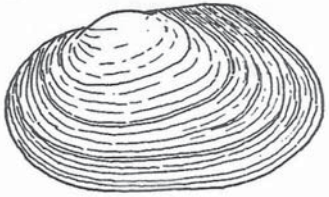

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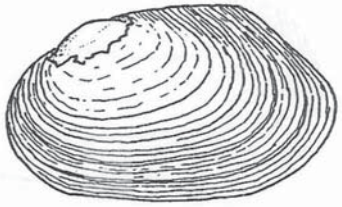

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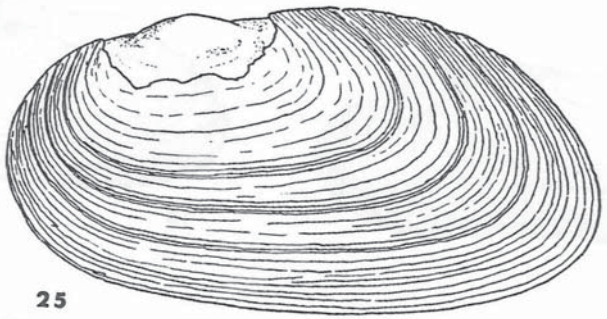

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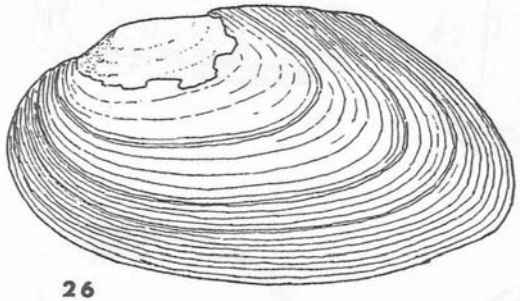

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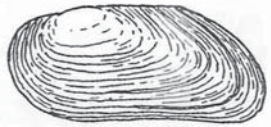

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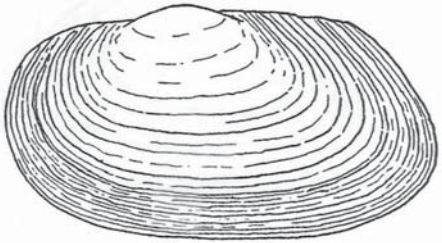

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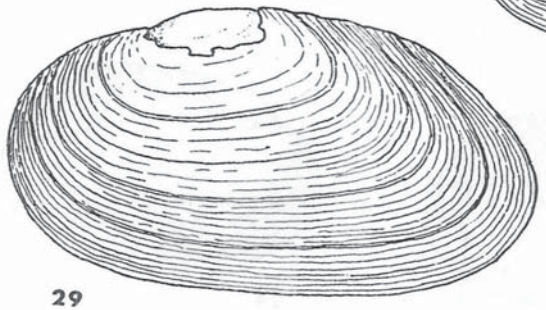

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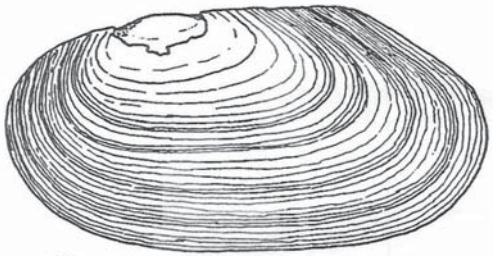

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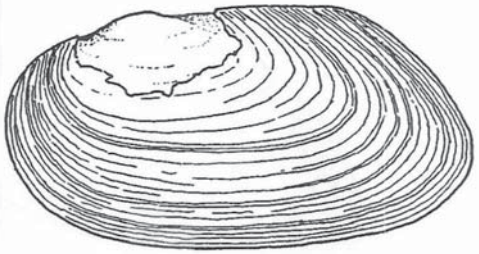

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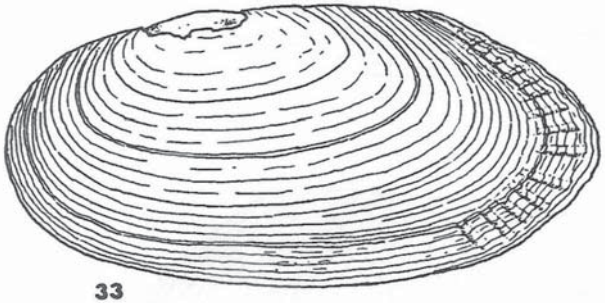

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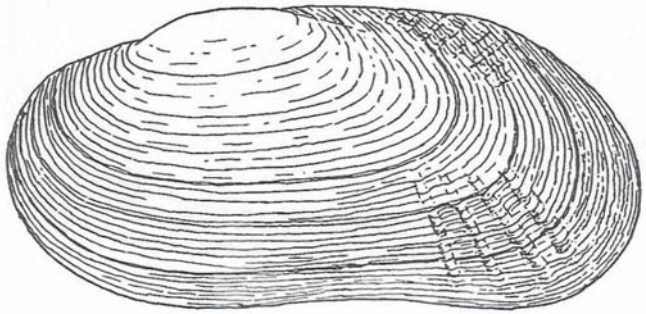

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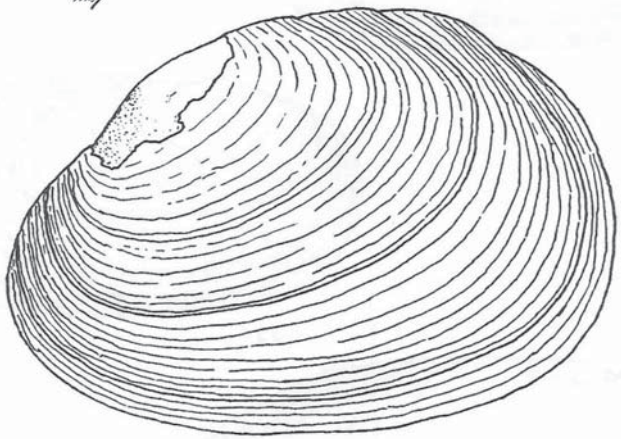

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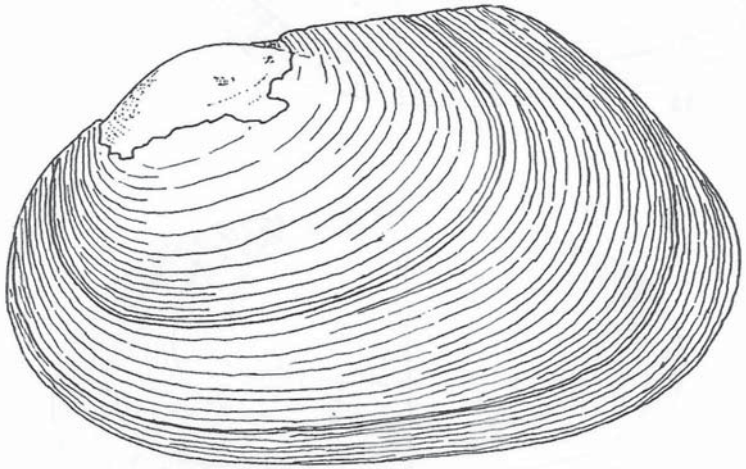

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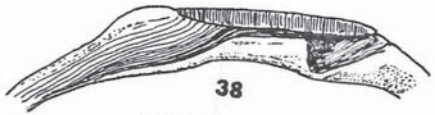

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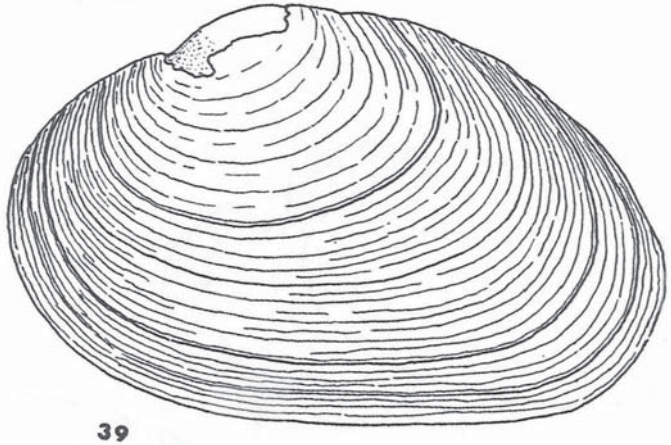

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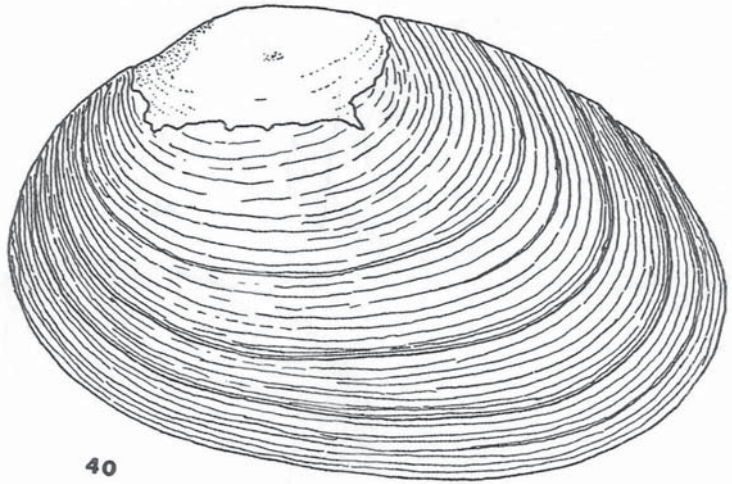

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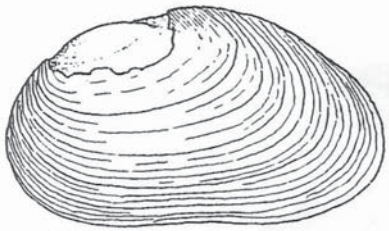

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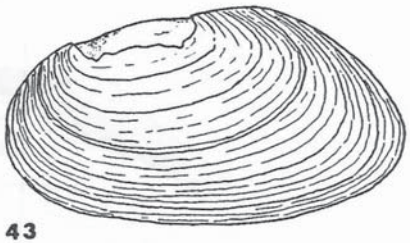

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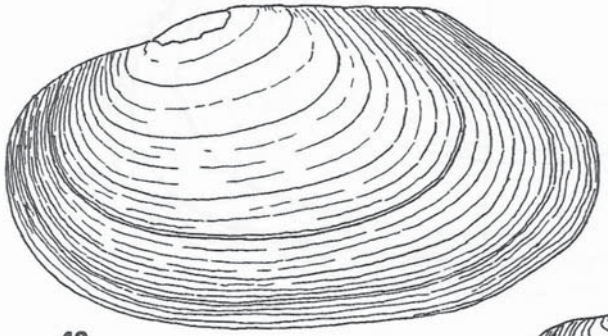

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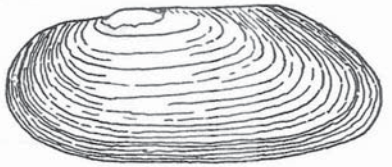

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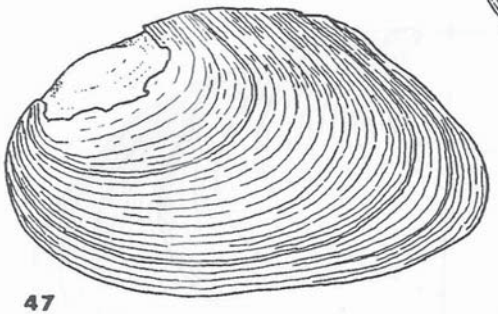

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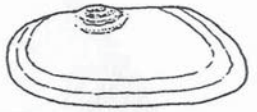

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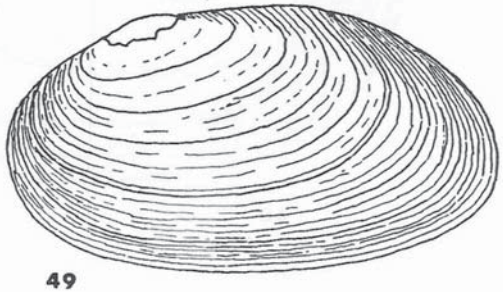

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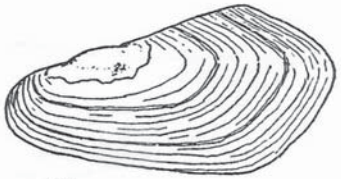

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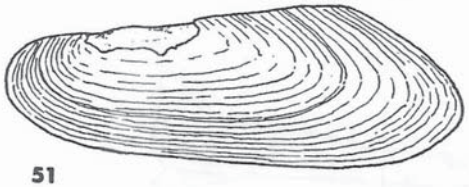

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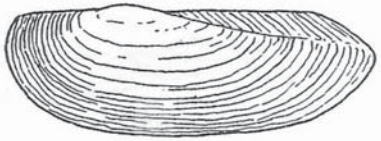

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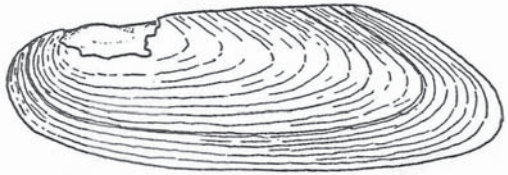

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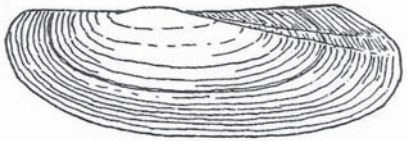

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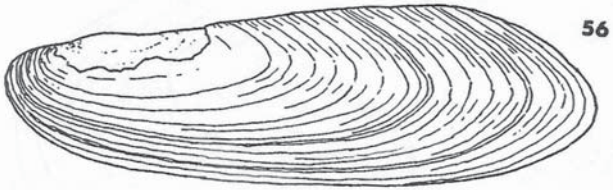

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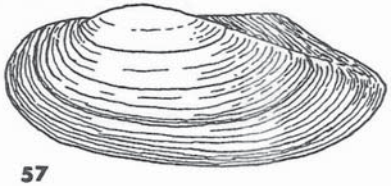

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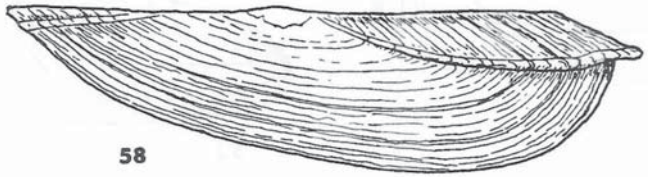

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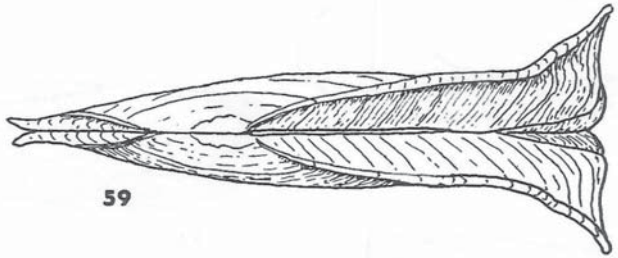

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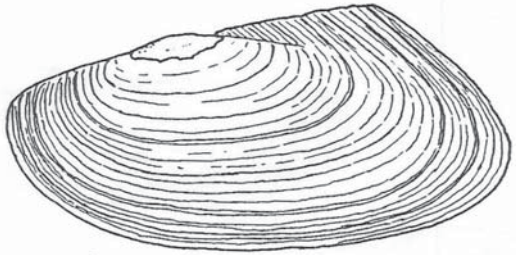

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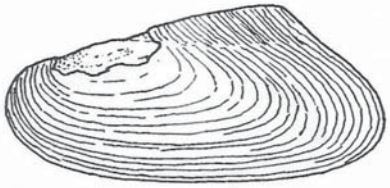

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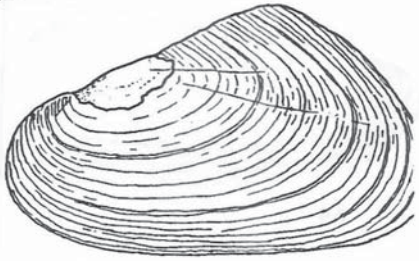

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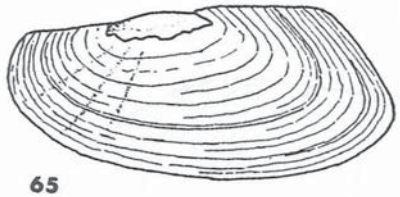

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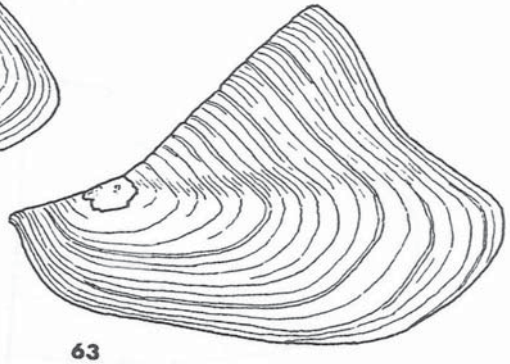

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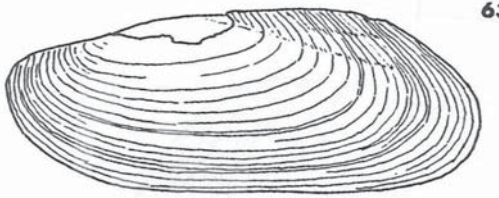

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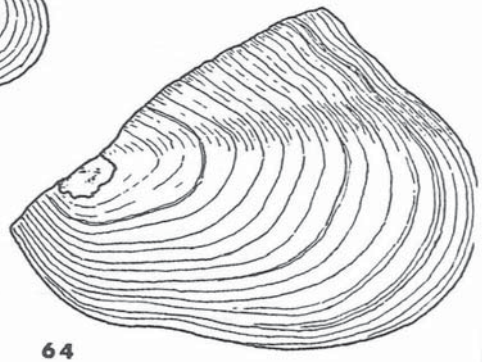

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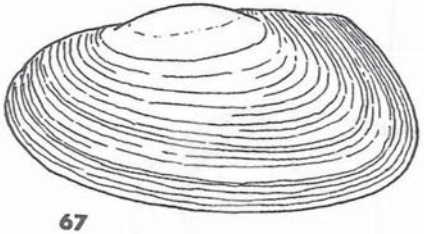

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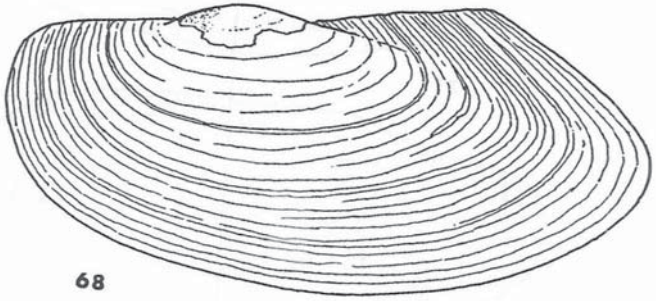

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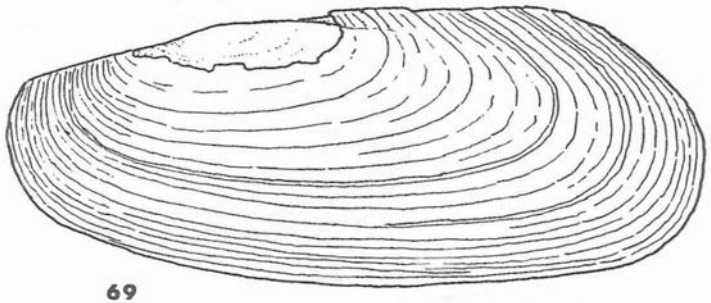

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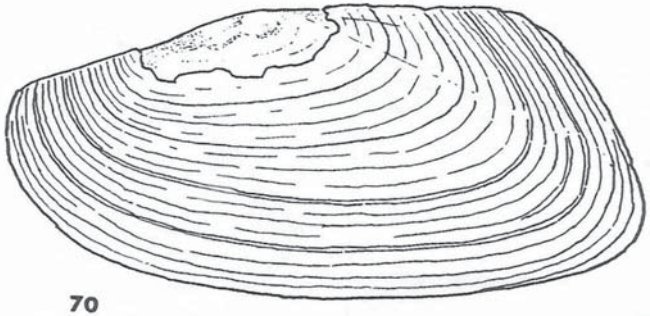

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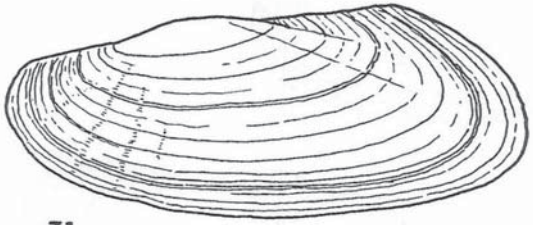

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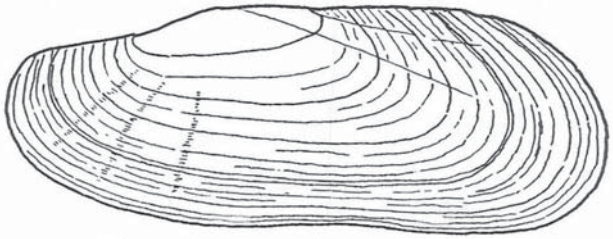

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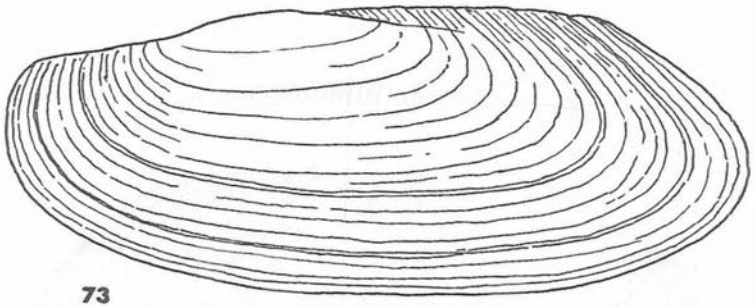

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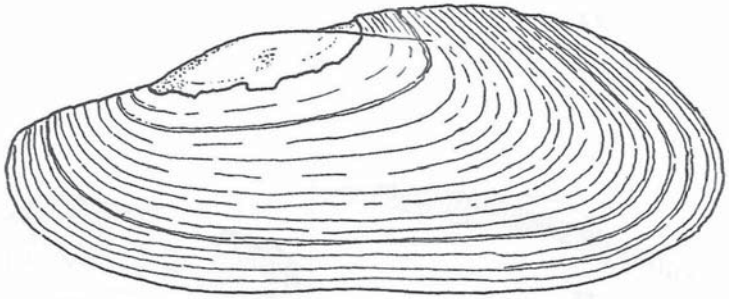

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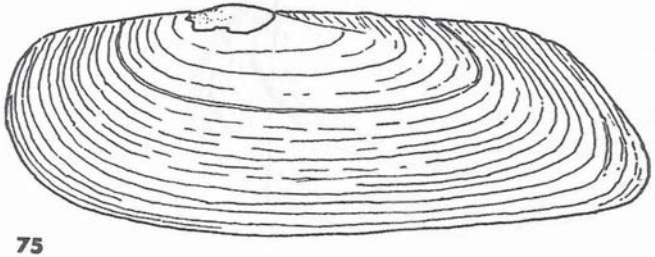

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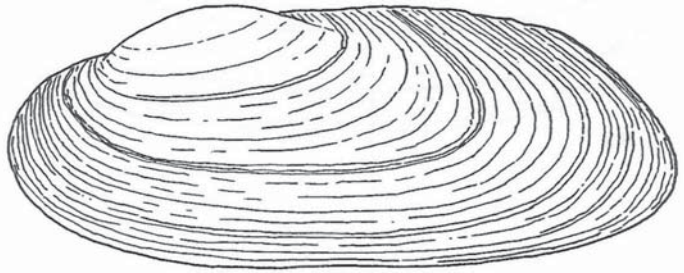

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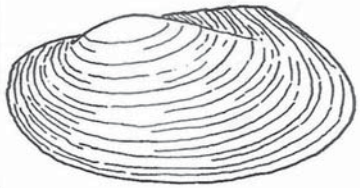

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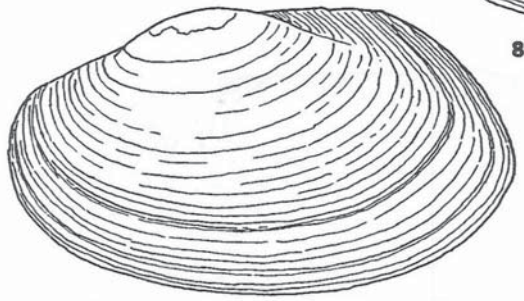

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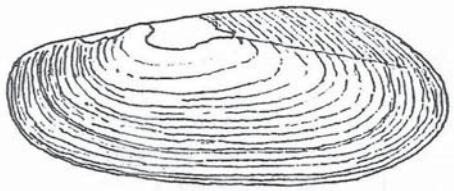

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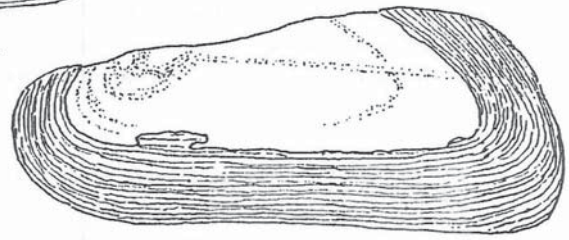

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C: ETHERIIDAE

A small family of sessile, oyster-like bivalves with irregular shells. It comprises three genera, one in India, one in South America and Etheria in Africa. Earlier I included Etheria (and the two other genera) in the Mutelidae, but now I have accepted the distinct family, already proposed by Swainson (1840).

Genus Etheria Lamarck 1807

About twenty supposed species have been described, but now it generally is agreed that they all are forms of a single species, for which the oldest name is Etheria elliptica Lamarck being the first of four species described by Lamarck (1807) and all with the erroneous locality "Indian Ocean". Oken (1818) correctly altered the name to Aetheria and that spelling was used by most authors until 1927, when Pilsbry & Bequaert resuscitated the original spelling. The name may seem odd, as there is certainly not anything ethereal or heavenly about a river-oyster, but the Greek word "aitheria" can also mean airy, and it must be in this sense that Lamarck used the allusion to the loose structure of the lower shell. Férussac (1823) was the first to state the African origin of Etheria, when he described E. cailliaudi from the Blue Nile.

Etheria differs from all other African freshwater bivalves by the irregular shell, usually with one of the valves cemented to a rock, another shell or other firm substratum, and taking shape from it. The lower valve, sometimes the left and sometimes the right, is of a looser, often lamellous structure and, as a rule, thicker than the upper valve. The beak and the hinge plate of the upper valve protrude over those of the lower. The shape of the shell varies from almost hemispherical to very elongate, and in some cases the upper valve is provided with long, hollow, tube-like projections. As in the Mutelidae only the inner gills are marsupial. The eggs are very small, only about 0.05 mm in diameter, but the further development is unknown. Perhaps the small eggs indicate that Etheria has a free-swimming larval stage. The preferred habitats of Etheria are exposed rocky shores of

great lakes and fast running rivers, and it seems to like rapids, cataracts and even waterfalls. It is incomprehensible how the small larvae are able to get a foothold in such localities. Evidently the great number of eggs is necessary for securing that a few larvae will get a chance to survive.

Etheria elliptica Larmarck 1807

Since the species cannot be confused with any other African freshwater bivalve and also because it has no constant shape, I have found it superfluous to depict it. In Anthony's monograph in Ann. Soc. roy. Zool. Mal. Belg. XLI, 1907 several forms are figured.

The distribution covers tropical Africa and Madagascar.

PART II. SUPERFAMILY SPHAERIACEA

This superfamily comprises the genuine freshwater bivalves with a heterodont hinge. The inner gills function as marsupium. The superfamily is distributed all over the world and consists of two families, Corbiculidae and Sphaeriidae, which are quite different, and there can never be any doubt whether a given bivalve belongs to the one or the other of these families. Thiele (1934) considers a third family, Cyrenoididae as belonging to the Sphaeriacea, but with reservations. The family consists only of the genus Cyrenoida Joannis 1835 with a very few estuarine species in West Africa. This genus does not belong to the Sphaeriacea, but rather to the otherwise marine superfamily Lucinacea.

A: CORBICULIDAE

A brief description of the family is given by Mandahl-Barth (1954 p. 157). In Africa the family is only represented by the genus Corbicula itself, since Soleilletia Bourguignat 1885, which has been placed in this family, has turned out to be subfossil shells of a marine bivalve, Caecella Gray, which is still found in the Red Sea, and which belongs to the family Mesodesmatidae (Van Damme 1984 p. 97).

Corbicula Mühlfeld 1811

This genus is also described by Mandahl-Barth (1954 p. 157). Since I wrote it, I have had the opportunity to examine a larger amount of material from other parts of Africa, and I have come to the conclusion that the many supposed species which have been described from Africa can be gathered together in two species, of which the one is very variable.

As a rule it is not easy to obtain live Corbicula, since they are found buried in clay at the bottom. One has to pull the dredge very slowly, going deeply into the bottom, but then it also becomes quickly full and works as a very effective anchor!

Operating the dredge in a normal manner usually results only in empty shells.

Haas (1936) believed that the African species could be divided into two groups, one with a smooth ligament plate, the other with a crenulated ligament plate. However, this is not correct. In all of them the ligament plate is simply more or less uneven.

1. Corbicula fluminalis (Müller 1774) figs. 1-5

The type locality is the Euphrates river and the type specimen is rounded triangular, slightly higher than long and with a strong concentric sculpture. Müller gives the dimensions in lines, which expressed in millimetres become 26.4 in length and 28.6 in height. The type specimen, which is preserved in the Zoological Museum, University of Copenhagen, is pictured by Kennard & Woodward (1926) pl. 9 fig. 4.

The typical high form is rare in Africa where it is only common in Lake Tana, and it has lived in the prehistorical lake in El Faiyum. In addition a few examples are known from the White Nile and certain other places. Figs. 1 and 2 show two examples from Lake Tana and the typical form is just in between these two. Fig. 1 is an intermediary to the form described by Cailliaud (1827) under the name Cyrena consobrina, which is more regularly oval and longer than high. The type locality is "Lower Egypt" and it is the common form in the Nile. A shell with a good size measures 27 x 24 x 17 mm and the largest I have seen (from Luxor) is 36.4 x 31.2 x 22.3 mm. Consobrina can hardly be considered as a geographical race, since it is also found in Lake Tana and is connected to the typical form through gradual transitions. Larger fresh shells are blue on the inner side, darkest between the pallial line and the basal margin while young shells as a rule have 1-3 wedge-shaped blue spots. Philippi (1846) used such young shells to describe Cyrena radiata (type locality the White Nile), a name which has been commonly used for the forms in the great lakes; the name, however, cannot be used because of Hanley's Cyrena radiata, which is from 1844, even though this species is now considered to belong to the genus Polymesoda.

The known distribution of C. fluminalis and consobrina in Africa stretches from Egypt and Ethiopia to Senegal and southwards

to northern Tanzania and Lower Zaire. Over the years a large number of supposed species have been described on young specimens, more or less diverging forms or simply on shells from a new area. The following species may be considered as synonyms: Cyrena pusilla Philippi 1856, Upper Nile; Cyrena africana var. albida Krauss 1848, Upper Nile; Corbicula difficilis Prime 1864, northern Africa?; C. delessertiana Prime 1870, Giza; C. zelebori Jickeli 1874, Suez; C. heuglini Clessin 1879, Lake Tana; C. senegalensis and meridionalis Clessin 1879, Senegal? (the existence here was first confirmed in 1961 when Daget mentions a young specimen under the name C. africana from the upper flow of the Gambia River); C. alba Clessin 1879, White Nile; C. jickeli Clessin 1879, Cairo; C. nilotica Clessin 1879, Blue Nile; C. soleilleti, callipyga and gravieriana Bourguignat 1885, all from the Awash River, Ethiopia; C. artini Pallary 1902, White Nile; C. doufilei Rochebrune & Germain 1904, White Nile at Dufile; C. kynganica, subtruncata, aegyptiaca, degousei and cameroni "Bourguignat" Germain 1906, all from the Kyngani River at Bagamoyo. After having illustrated and described those "species" named by Bourguignat but not described, Germain concludes that they are synonymous with consobrina!; C. fischeri Germain 1907, Mamun River, Chad; C. gabonensis Preston 1909, Gabon (fig. 5). The type specimen of the latter stands as a transitional form between fluminalis and consobrina, but we have more consobrina-like examples from Cameroun and Lower Zaire.

The most peculiar form of fluminalis is found in Lake Tchad (fig. 10). Von Martens described it in 1903 under the name Corbicula tsadiana and Germain (1905) as C. lacoini. The difference between the two, which Germain considered important, is that tsadiana is slightly longer than high (13 x 12 x 9 mm) while lacoini is a little higher than long (10.5 x 12 x 8 mm); larger examples do occur, up to approximately 15 mm in length. The shell is shiny, often without or almost without, concentric ribs and normally of a clear yellow colour. It appears so different from the typical fluminalis that it would be natural to consider it a distinct species, if it were not for the fact that it is connected with that form through gradual transitions, and more normal, consobrina-like forms are also found in the lake. The consobrina form is the predominant one in the Chari River Delta, but

intermediaries to tsadiana also exist. Despite this, however, I find tsadiana so divergent that I must consider it as a local race of fluminalis. C. tchadiensis Germain 1916 also belongs here.

The Corbicula forms in the great East African lakes are difficult to place because they seem to be more closely related among themselves than to fluminalis or africana Krauss 1848 from the southern part of Africa. Von Martens (1879) assigns the form in Lake Victoria to Philippi's radiata which, however, is only a young specimen of consobrina. Connolly (1939) considers the lake forms to be identical with africana and this point of view was adopted by Mandahl-Barth (1954), although with reservations. The material which I have had the opportunity to examine since then, has led me to conclude that the lake forms as well as africana are races of fluminalis. Contributing to my change of opinion is the fact that Cridland in 1956 collected some Corbicula shells near the mouth of the Nzoia River in Lake Victoria which quite resemble consobrina, and that he later found some in Zimbabwe which just as rightly can be assigned to consobrina as to africana. The following subspecies can presumably be defended:

C. fluminalis cunningtoni (Smith 1906) (fig. 6) from Lake Victoria is described more explicity by Mandahl-Barth (1954); let me add here that it can attain a larger size: 19 x 16 x 9.6 mm. The form I described in 1954 under the name C. africana albertiana (fig. 8) is certainly just an ecological form conditioned by the greater depth at which it lives. Pilsbry & Bequaerts C. radiata edwardi (1927) (fig. 7) from Lake Edward is not very different from certain forms of cunningtoni and perhaps ought not to be maintained.

C. fluminalis tanganyicensis (Crosse 1881) (fig. 9) from Lake Tanganyika is a small form (11 x 10 x 7.2 mm) almost without concentric sculpture and with a more triangular shape than the other lake forms. Leloup (1950) called it C. fluminalis, but it is likely more correct to consider it as a special subspecies. Unfortunately I have not seen any Corbicula from Lake Tanganyika.

Smith (1881) described it under the name Cyrena (Corbicula) radiata var. and the same year Crosse added tanganyicensis as a variety name. Bourguignat changed the name to Corbicula

tanganikana in 1885, Mabille (1901) described a C. foai and Germain (1906) attempted to revive Bourguignat's two manuscript names C. lavigeriana and jouberti.

C. fluminalis africana (Krauss 1848) fig. 11

The type specimen is 15 x 13 x 8 mm and comes from the Gauritz river in the Cape Province. It is thus smaller than the consobrina form and as a rule is more regularly ovate in contour and the sculpture most frequently finer with more closely placed concentric ribs. However, it can be somewhat larger, e.g. 17 x 14.8 x 9.5 mm and the sculpture is not always so evident as in the type specimen. The colour varies as with the lake forms, from yellow to almost black. Its distribution stretches from Malawi and Shaba down to the Cape.

Some populations in Zimbabwe (Mandahl-Barth 1968, pl. V fig. 12) and Shaba (Pilsbry & Bequaert 1927, fig. 71a-c) have a more triangular shell and can just as well be classed with the northern forms, for which reason I now consider africana as a race of fluminalis.

Haas (1936) separates the South African Corbicula into two species, which he designates C. fluminalis natalensis (Clessin 1879) and C. albida albida (Krauss 1848), but the latter is undoubtedly C. astartina Martens 1860, whereas the one he calls astartina is africana. In the figure text for natalensis (pl. 2 fig. 5) there are a few mistakes which can appear confusing. Haas calls it C. fluminensis natalensis and the shell is purported to be of natural size, but is actually one and a half times enlarged.

The following "species" must be considered as synonyms: C. kirkii Prime 1864 from Mozambique; Cyrena (Corbicula) radiata Smith 1877 from Lake Malawi; C. oliphantensis Craven 1880 from Transvaal and C. nyassana Bourguignat 1889, which is a new name for Smith's radiata.

2. C. astartina Martens 1860 fig. 12.

The paper with the original description was published in January 1860, but the accompanying plate is dated 1859. Unfortunately the description and the illustration do not

correspond, which has led to an amount of confusion that was first cleared up by Connolly (1939). The species becomes larger than africana, e.g. 22.7 x 17.3 x 11.9 mm and proportionately longer, and the sculpture consists of stronger and more separated concentric ribs than in any form of fluminalis. The colour as a rule is yellowish in young shells and dark olive in full-grown ones.

The type locality is Zambesi at Tete and it is known from some localities in Zimbabwe, Transvaal, Zambia and Shaba, but it must have a broader distribution in Zaire because Ripert collected some young typical shells in the little Funa river in Lower Zaire. C. radiata "oval form" in Pilsbry & Bequaert fig. 71 d-f from Kashiobwe in Shaba is astartina. The same is the case with C. albida albida and albida rosini in Haas (1936) and C. rosini in my 1968 Bangweulu publication.

B: SPHAERIIDAE

The family is described more extensively by Mandahl-Barth (1954). It consists of four genera, of which three are represented in Africa; the fourth, Byssanodonta d'Orbigny 1846 is restricted to South America, and the African species which have been assigned to this genus, belong to the genus Eupera Bourguignat 1854.

1. Genus Sphaerium Scopoli 1777

A more detailed description of the genus is found in my 1954 publication where I made much of showing that the sphaeria from tropical Africa constitute a particular subgenus because of the shape of the right cardinal tooth, but this does not hold true. The majority of the African species are quite variable and therefore difficult to define, and since many of them can be subdivided into geographical races, the question of species becomes difficult, as will be seen from the following summary.

1. Sphaerium lacustre (Müller 1774) figs. 22-23

The type locality is Frederiksdal, Denmark, but the species is also found in Algeria and Morocco, from where we have some specimens. The northwest African form was described by Temple Prime (1859) as S. ddingoli and by Bourguignat (1864) as S. ovale, but they differ very little from lacustre from North Zealand. The species is known by its thin shell, slender hinge and small, but prominent beaks. A good-sized shell measures 9.3 x 7.6 x 4.4 mm. The species has a holarctic distribution.

2. Sphaerium hartmanni (Jickeli 1874)

Under this name I have gathered together a number of forms originally described as species, but since there are transitions among them I now consider them as subspecies. Common for them all is the quite thin shell, which, however, is not nearly as brittle as in the previous species, and the narrow hinge plate which is enlarged in the middle to make room for the small cardinal tooth. The lateral teeth are short and slender, and the ligament is relatively long. As a rule the beaks are placed clearly in front of the middle of the shell. Presumably the following forms can be upheld as geographical races.

a. S. h. hartmanni (Jickeli 1874) figs. 15-16

The type locality is Nubia. A medium-sized shell measures 9.2 x 6.8 x 4.2 and the largest I have seen 12.1 x 9.9 x 5.6 mm. As a rule there is no angle between the dorsal margin and anterior margin. The colour is usually light greyish with a lighter peripheral zone. It is the common Sphaerium in Egypt and is also known from Ethiopia and northern Sudan.

S. teilhardi and S. pharaonum Pallary 1909 are synonyms.

b. S. h. courteti (Germain 1904) figs. 17-18

The type locality is the Bangoran river in the Central African Republic near the border to Chad. It was not depicted in the original description, but in 1907 Germain gave a more thorough description accompanied by a photograph of a shell which therefore must be considered as type specimen. Germain gives the maximum

size as 15 x 12 x 7.25 mm and we have examples of a similar size. In other words it can be larger than the nominate race, from which it also differs by the fact that the dorsal margin is less sloping and often possesses an angle between the dorsal and the anterior margin; but the character which Germain found so important, the crenulated anterior lateral teeth, cannot be upheld, since this has been found in only a few specimens, and the majority have smooth lateral teeth. Crenulated lateral teeth can also be found in other African sphaeria. Germain found this character so important, that he established a subgenus in 1909, Serratisphaerium, which, however, cannot be upheld.

The race has a wide distribution in West Africa from Chad to Gambia and southwards to Lower Zaire. We have a sample from Cameroun with yellowish shells. The colour is otherwise a rather dark greyish brown.

c. S. h. naivashaense (Preston 1912) figs. 19-20

The type locality is Lake Naivasha in Kenya and it is known from a number of other localities in Kenya, Uganda and northern Tanzania. It deviates from the nominate form by the relatively longer, stronger and darker shell. It also reaches a larger size, for example 14.2 x 12.7 x 7.2 mm.

d. S. h. bangweolicum Haas 1936, fig. 21.

The type locality is Nsombe Channel, Lake Bangweulu and the type specimen is 10 x 8 x 4.5 mm, but it can be as large as 12.3 x 9.6 x 6.3 mm. It is closely related to the preceding race, but differs from it by the smaller beaks. It is common in Lake Bangweulu and is also known from some localities in northern Zambia and in Shaba, but it most certainly has a wider distribution.

3. Sphaerium victoriae Smith 1906.

It is very similar to hartmanni and is possibly not specifically different, but since it also can be divided into a number of races, it is most practical to regard it as a distinct species. It differs from hartmanni by the beaks, which as a rule

are placed in the middle, and especially by the stronger lateral teeth, of which the anterior ones curl in under the edge of the hinge plate and into the umbonal cavity (fig. 25). The various races are treated by Mandahl-Barth (1954).

a. S. v. victoriae Smith 1906, figs. 24-25.

The type locality is the harbour of Bukoba, and as a rule the size is approximately 12 x 9 x 6.5 mm, but it can be larger: 14.3 x 11.1 x 6.4 mm. Often the shell has fine, radial lines. It is widespread, but not especially common, in Lake Victoria, where it can be found from close to the shore and to a depth of at least 20 m. It is also known from the Victoria Nile and some of those rivers which flow into Lake Victoria.

S. congener Preston 1912 from "between Entebbe and Mbarara" is most likely a synonym.

b. S. v. albertianum Mandahl-Barth 1954, fig. 26

The type locality is Lake Albert at Butiaba and the size is often around 10 x 7.5 x 5 mm, but it can be somewhat larger. It deviates from the nominate form by the thinner, more compressed shell and less prominent beaks. It is common in Lake Albert in shallower water.

c. S. v. lacuum Mandahl-Barth 1954, fig. 27

It deviates from the preceding, which it resembles closely, by the more angular posterior end, and as a rule, somewhat stronger shell and hinge. It has often also stronger growth lines. The type locality is the northeasterly part of Lake Edward at a depth of a few meters. It is also known from Kazinga channel, Lake Albert, where it is found at greater depths, and from the Albert Nile, as far north as Nimule. It is strange that it is found in shallow water in Lake Edward and in deep water in Lake Albert.

d. S. v. mohasicum (Thiele 1911) fig. 28

The type locality is Lake Mohasi in Rwanda. It deviates from the preceding races by the relatively higher and more compressed shell and smaller beaks. The hinge is also more delicate. It is known only from various lakes in southwestern Uganda and Rwanda.

4. Sphaerium bequaerti (Dautzenberg & Germain 1914) fig. 29, 32-33

It was described on a single, juvenile specimen from the Luapula river at Kasenga, and strangely enough as an Eupera, probably because the shell had some rust coloured spots, which however must be explained by ferruginous deposits, as I have seen in other sphaeria. The full-grown bequaerti is consistent with Pilsbry & Bequaert's S. stuhlmanni, which is not that species though, for which reason Haas (1936) renamed it to S. hartmanni congicum, but it is not a form of hartmanni. S. bequaerti must be considered the correct name, unless that species in Ethiopia which Jickeli (1874) called S. capense and which Bourguignat renamed subcapense is the same species, since the latter is from 1883. The sphaeria I have seen from Ethiopia have all been hartmanni, and it is impossible from Jickeli's figures to determine with certainty what his capense actually is.

The shell is not so compressed as in hartmanni and the hinge is somewhat stronger, especially at the lateral teeth, of which the posterior are not so far from the cardinal tooth. It deviates from stuhlmanni, which it resembles, by the position of the beaks which are placed in front of the middle and by the more delicate hinge. It varies quite a bit in size: 11.2 x 8.8 x 6.4 or 12.7 x 9.8 x 8.0 mm. In some localities bequaerti resembles stuhlmanni and in others, capense, and therefore one cannot rule out the possibility that all three are actually the same species. This is an ideal case for electrophoretic study.

Bequaerti is very widely distributed, stretching from Zambia and Tanzania through Zaire to Ghana, although there are areas in between where it is not yet known.

5. Sphaerium capense (Krauss 1848) figs. 30-31

The type locality is the Knysna River in the Cape Province. The type is 8 x 7 x 5.5 mm, but often larger, for example 10.7 x 9.2 x 7.2 mm, with a relatively larger diameter than the other species. In addition, the beaks are often placed slightly behind the middle and relatively large, and the posterior end is often more angular. The hinge is quite delicate and similar to that of bequaerti.

The species is distributed in southern Africa from Zambia and Zimbabwe to the Cape and is also found on Madagascar, since S. madagascariense Tristram 1863 is probably the same species.

6. Sphaerium incomitatum (Kuiper 1966) figs. 34-35

Described with reservations as a Pisidium, because the beaks are placed clearly behind the middle and Kuiper was only able to study young specimens. The largest measured only 5.3 mm in length. The type locality is Lake McIlwaine outside Harare in Zimbabwe, where Cridland later collected a large amount of material, which proved that the species can be much larger, up to 12.3 x 9.9 x 7.0 mm, but the majority are 10-11 mm long. The hinge is very similar to that in capense, but the shell is normally not so inflated. The beaks are smaller and the posterior less angular, as a rule evenly rounded, and because of the position of the beaks, shorter.

The species is distributed in Zimbabwe and is also known from a few localities in Zambia and Shaba.

7. Sphaerium stuhlmanni Martens 1897 figs. 36-37

The type locality is Lake Victoria at Busisi, but it is a species which has given reason to misunderstanding because von Martens' description and illustration do not correspond (as is the case with Corbicula astartina). His figure 8 on plate 7 undoubtedly shows the species which Smith described in 1892 as S. nyanzae, but his description just as undoubtedly is based on another species. Von Martens also misunderstood Smith's nyanzae, since he considered the then undescribed victoriae as this species. Considering that von Martens was exceptional in describing molluscs and did not draw them himself, I feel that one ought to have most faith in the descriptions.

S. stuhlmanni is described more explicitly by Mandahl-Barth (1954) and I have nothing more to add other than that I consider the few specimens which we retrieved with the dredge from Lake Edward to belong to the following species.

8. Sphaerium regularis (Mandahl-Barth 1954) figs. 38-39

Described as a subspecies of the above, but since intermediary forms do not seem to occur, I prefer to consider it as a distinct species. Concerning the difference between it and stuhlmanni, I refer to Mandahl-Barth 1954, p. 169.

9. Sphaerium nyanzae Smith 1892

The most thick shelled of the African Sphaeria and the one with the strongest hinge. It is known only from Lake Victoria, where it is found in two forms, which, when they are typically developed, are so different that they would unconditionally be considered as different species. However, intermediary forms are found and it is often impossible to determine whether a population belongs to the one or the other form. They are both treated thoroughly by Mandahl-Barth (1954) and I can only add that as far as I know, it is the only Sphaerium which can have radial bands.

a. S. n. nyanzae Smith 1892 figs. 40-41

I refer to Mandahl-Barth 1954, p. 169.

b. S. n. alluaudi (Dautzenberg 1908) fig. 42

Because of the radial bands Dautzenberg felt it necessary to establish a special genus, Pseudocorbicula, but it is not necessary. See Mandahl-Barth 1954, p. 170.

2. Genus Pisidium C. Pfeiffer 1821

The type species is Tellina amnica Müller 1774, which is regrettable, since amnicum differs from all the other pisidia in its size, up to 13-14 mm in length and from the majority of pisidia in its strong, concentric sculpture. The majority of the pisidia are less than 5 mm in length and the small size contributes to the difficulty of identifying them. A description of the genus can be found in Mandahl-Barth (1954) and the African species have been treated excellently by Kuiper (1966) for which reason I shall be brief here.

In the pisidia, the ligament is normally hidden by the edge of the dorsal margin, but in certain species (here the first four) it is outwardly visible. For these, Kuiper (1962) established the subgenus Afropisidium. Odhner (1921) established the subgenus Neopisidium for those species where the outer (posterior) gills have disappeared. However, some of the African species belong to both subgenera, for which reason I find it most practical to ignore them.

Pisidia are found both in lakes and rivers and in small water bodies, as a rule in the upper layer of the bottom. In Africa they do not seem to occur in such numbers as in Europe, perhaps only ostensibly, as owing to their poor size they will often slip through the mesh in the nets which are usually used in Africa.

1. Pisidium pirothi Jickeli 1881, figs. 43 and 61

The type locality is Harasa in eastern Sudan, and the size is approximately 3.5 mm in length. The most important characteristics are the outwardly visible ligament and the clear concentric sculpture, which can be finer or more rough. In the latter case it can be easily confused with the South African P. costulosum, in which the ligament is covered. P. victoriae Mandahl-Barth 1954 is a thin shelled form from Lake Victoria. The species is the most common of the African pisidia and the one with the widest distbituion, in that it is known from a number of localities from Egypt to South Africa and westwards to Mali. P. casertanum var. alexandrina Pallary 1909, P. clarckeanum var. exilis Favre 1943 and P. lepus Kuiper 1957 are synonyms.

2. Pisidium giraudi Bourguignat 1885 figs. 60 and 62

The type locality is Lake Tanganyika to which it is endemic. It can be approximately 3 mm long and rather variable in form, but is always recognized by the outwardly visible ligament and by the fact that the lateral teeth, especially the anterior teeth, are staggered in relation to each other in the right valve.

P. hermosum Bourguignat 1888 is the same species.

3. Pisidium fistulosum Mandahl-Barth 1954 figs. 44 and 63-64

The type locality is Lake Victoria at Bugaia Island at a depth of 64 meters. The length is 2.5 mm. It is known by the rather thick shell almost without sculpture, but with many small pores, and the outwardly visible ligament. The species is only known from Lake Victoria and at depths of more than 30 m.

4. Pisidium reticulatum Kuiper 1966 figs. 45 and 65

The type locality is Nosi-Be in Madagascar, but it has also been found in Zimbabwe and in the southerly part of Lake Malawi. It is separated easily from all other pisidia by its reticulate sculpture. The ligament is outwardly visible, while in all the following species it is hidden.

5. Pisidium amnicum (Müller 1774) figs. 13-14

The type locality is Frederiksdal, Denmark. With a shell length of 10 mm or more, it is the largest Pisidium-species, and the size combined with the strong concentric sculpture makes it easily recognizable. It is mentioned by Morelet (1853) from Algeria, but positive finds in Africa occurred first in 1955, when Brandt found it in the basin in front of the museum in Cairo, where it most certainly had been introduced, since it is otherwise not known from Egypt. Quite rightly, von Martens (1866) described a P. amnicum elongatum from the lower Nile, but it was a euphyllopod. Finally in 1972 Kuiper was able to report a sure find at Ifrana, Morocco.

6. Pisidium langleyanum Melville & Ponsonby 1891 figs. 46 and 66

The type locality is Port Elizabeth in the Cape Province. The length of the shell is about 3 mm, but sometimes a little longer. It is recognized by the rounded triangular shape and the relatively larger beaks, which are placed way in the back. It is known from many localities in South Africa and from Lake Bangweulu.

7. Pisidium kenianum Preston 1911, figs. 47 and 70

The type locality is someplace between Rumuruti and Mount Kenya. The shell length is up to 4.8 mm. Smaller specimens can resemble langleyanum very much, but the beaks are not placed so far back and are not so prominent. However, these are not characteristics which can exclude that kenianum in reality is a northern race of langleyanum. Sphaerium kigeziense Preston 1912 and Pisidium katangense Pilsbry & Bequaert 1927 are synonyms, but it says something about the distribution which stretches from Ethiopia to Zambia and Shaba.

8. Pisidium viridarium Kuiper 1956 figs. 50 and 73

The type locality is the Karura River northwest of Nairobi. The shell reaches the same size as the preceding species but as a rule is a little more regularly ovate and there is normally a small nodule in front of the upper posterior lateral tooth in the right valve. According to Kuiper it is distributed from Ethiopia to South Africa, but it is not always easy to distinguish from the preceding species with which it often occurs, and when this is the case there is only the small nodule in front of p_3 which is different. Some of the specimens we have from Uganda caused difficulties for Kuiper. At one time he borrowed all my pisidium material from Africa and came to the conclusion, that some of them which I had identified as kigeziense (kenianum) are actually viridarium. This applied to those from Lake Lutoto and from Mbarara, while he was uncertain about some from the rivers Kibimba and Sezibwa (Kuiper 1966, page 32, where he mentions the localities named as being in Kenya). Can it be excluded that kenianum sometimes has the small nodule and therefore becomes viridarium?

In his work, p. 38, Kuiper (1966) makes much of explaining how vividarium and ovampicum can be differentiated in South Africa, which surprises me, for I cannot see how one can confuse them. His argumentation does not seem convincing and I tend to think the reason is that ovampicum sometimes can also have a small nodule in front of the upper posterior lateral tooth in the right valve. If this is correct, then viridarium is not found at all in South

Africa and its distribution is then the same as kenianum. The result is, therefore, that viridarium is a doubtful species.

9. Pisidium armillatum Kuiper 1966 figs. 48 and 67

The type locality is the Rongai river at an altitude of 2900 meters in Kenya. The shell can be up to 3 mm long and is easily recognizable by the concentric ribs on the beaks. It is a highland form which is only known from Mount Kenya and Mount Elgon and from a few localities in between.

10. Pisidium invenustum Kuiper 1966 figs. 49 and 71

The type locality is Mawenzi Tarn on Kilimanjaro at an altitude of 4800 meters and it is only known from there. It is a small, 3 mm long, not very characteristic species which resembles a small, young Sphaerium. I have not seen the species, but from the description I would not exclude that it is only a small form of montigenum which perhaps is not diffeent from ovampicum.

11. Pisidium ovampicum Ancey 1890 figs. 51 and 72

The type locality is Omambonde in Ovamboland. The shell, which is thin and brittle with low, almost centered beaks, is normally around 3 mm long, but sometimes somewhat larger. It also resembles very much a juvenile Sphaerium, but it differentiates by the poor size and as a rule the white shell. It is distributed in East Africa from Ethiopia to South Africa and in addition in Madagascar. In Uganda and Kenya it is found mostly in the mountains (Ruwenzori, Elgon and Kenya).

P. georgeanum Kuiper 1952 from the Cape Province is a synonym.

12. Pisidium montigenum Kuiper 1966 figs. 52 and 74

The type locality is Lake Hohnel, Mt. Kenya. It is of the same size as the preceding species but differs in its more square contour. Since it is usually found together with ovampicum on Mts. Kenya and Ruwenzori, it is doubtful if it should be

considered an independent species. It is not known from other localities.

13. Pisidium artifex Kuiper 1960 figs. 53 and 68-69

The type locality is Hall Tarn, Mt. Kenya. The shell, which can be about 2.5 mm long, has a diameter which is almost as large, in other words a very inflated shell. It is known only from the type locality.

14. Pisidium casertanum (Poli 1791) figs. 54 and 76

The type locality is Sicily. It is the largest of the small species, in that in Europe it can be up to 8.5 mm in length; the largest African specimen is, however, only 5.8 mm in length. The species is very variable, and smaller specimens are often difficult to identify, owing to the fact that casertanum is often identified by eliminating other species. It is presumed to be distributed in most parts of the world, but since indisputable taxonomic characters are missing, it is doubtful if this is correct. Kuiper (1966) mentions it from northwest Africa and large parts of eastern Africa from Ethiopia to South Africa as well as Madagascar, which is probably correct. However, it is thought-provoking that he writes nothing about how it can be distinguished from the other species.

P. ruwenzoriense Germain 1911 from Ruwenzori is a synonym.

15. Pisidium personatum Malm 1855 figs. 55 and 76

The type locality is in Sweden. In form it is very much like ovampicum, but it has a nodule in front of the posterior lateral teeth. The size is about 3.3 mm in length. It is definitely found in northwest Africa and likely in Libya, but that it is thought to exist in Uganda is probably doubtful. As in the case of viridarium, I am not sure of the taxonomic importance of the callosity in front of the posterior lateral teeth.

16. Pisidium nitidum Jenyns 1832

The type locality is in England. In form and size it resembles very much P. personatum, from which it can be differentiated by the shiny shell, which as a rule has 3-5 furrows around the beaks, and by the lack of a nodule in front of the posterior lateral teeth. It is a holarctic species which has also been found in Morocco (Kuiper 1972).

17. Pisidium milium Held 1836 figs. 56 and 79

The species, which is described from Germany, is recognized by the almost rectangular, inflated outline of the shell, which can be up to 3.3 mm long. It is distributed in North America and Europe, especially north of the Alps, but is probably also found in Algeria.

18. Pisidium subtruncatum Malm 1855 figs. 57 and 75

The type locality is in Sweden. The shell, which can be up to 4 mm in length, is recognizable by the fact that the beaks are placed very far back and since it is very inflated, it appears almost cylindrical; but it is quite variable and not always easy to recognize. Distribution is the same as the preceding species and it has been mentioned from Tangier and Algeria.

19. Pisidium harrisoni Kuiper 1964 figs. 58 and 77

The type locality is the Vaal river in Transvaal. The type specimen is 4.1 mm long, but it is a large specimen. The beaks are placed very far back and are less protruding than in subtruncatum, from which it also differs by the broad rounded anterior end. It is only known from the type locality.

20. Pisidium costulosum Connolly 1931 figs. 59 and 80

The type locality is the Rhenoster river near Rustfontein in the Orange Province. The shell, which can be up to 3 mm long, is recognized by its strong concentric sculpture. P. pirothi can have

almost as strong a sculpture, but it has an outwardly visible ligament. The species seems to be restricted to South Africa.

3. Genus Eupera Bourguignat 1854

Mandahl-Barth (1954) followed Thiele (1934) and called the genus Byssanodonta d'Orbigny 1846, but Klappenbach (1960) showed that there are two different genera, both occurring in South America, but only Eupera is represented in Africa. The type species is the South American E. moquiniana (Bourguignat), originally described as a Pisidium. For a description of the genus I refer to Mandahl-Barth (1954).

Pilsbry & Bequaert (1927) maintain that the Eupera species are found especially in cavities of the valves of Etheria but this is not correct. I have studied many Etheria shells but never found a single Eupera in them. All the Eupera I have seen have been free-living at the bottom or amongst vegetation just as with Sphaerium. Five or perhaps six species are known from Africa, but since three of them were first described by me, it cannot be excluded that there are more species.

1. Eupera ferruginea (Krauss 1848) figs. 81 and 82

The type locality is the Knysna river in the Cape Province. In 1854 Deshayes described a "Pisum" parasiticum from the upper Nile, which was thought to be species-different from ferruginea, for which reason east and north African Eupera often have been called parasitica, but it concerns the same species.

The shell is relatively longer than in the following species, with the dorsal and ventral margins almost parallel. A small cardinal tooth is present in both the right and left valve. A good specimen measures 7.5 x 5.0 x 3.2 mm.

The species is distributed throughout Africa south of the Sahara and is also known from Egypt and Ethiopia as well as Madagascar and Mauritius. It is natural that within such an extensive area it varies somewhat, but it is probably not possible to divide it into geographical races, even though some of the West

African populations appear rather divergent.

2. Eupera ovata (Mandahl-Barth 1954) fig. 83

The type locality is the westernmost of the two crater lakes at Fort Portal in Uganda. It differs from the preceding species by the shorter, almost ovate and thinner shell and very fine sculpture. A very tiny cardinal tooth is present in both valves. The size can be up to 6.0 x 4.5 x 3 mm.

The species has also been found at Buyende in Uganda, and in Zambia and Zimbabwe.

3. Eupera crassa (Mandahl-Barth 1954) fig. 84

The type locality is Lake Victoria near Dagusi Island, where we found it at a depth of 12-13 meters. It appears to be endemic and not common in the lake. It differs from the other species by the very solid shell and stronger hinge, which has a very small cardinal tooth only in the left valve; there is a small cavity at the same place in the right valve. The species, however, resembles more a small Caelatura than a Eupera, but it only reaches a length of 5.6 mm.

4. Eupera triangulum Mandahl-Barth 1973, fig. 86

The type locality, and only known locality, is the small Sebleni river on Zanzibar. The species is easily recognized by its size (8.8 x 6.6 x 5.0 mm) and the high, triangular shape. It also has only one very small cardinal tooth in the left valve.

5. Eupera sturanyi (Waagen 1905) fig. 85

Described as a new species and subgenus of Sphaerium (Clessinella) from Lower Zaire in a paper on the hinge of Etheria, unfortunately only with a drawing of the hinge, which shows that it is a Eupera. It was first found again in material collected by Bennike in Ngaliema Bay at Kinshasa in a single specimen, which somewhat fits with the poor description of sturanyi. It measures

4.0 x 3.2 x 2.0 mm and is angled in outline with an almost right angle between the dorsal margin and the posterior margin.

It resembles very much Pilsbry & Bequaert's E. mediafricana etheriarum from Faradje in eastern Zaire (Pilsbry & Bequaert 1927, fig. 80 d). The typical mediafricana is described from Kisangani, but I strongly doubt that it is specifically different from ferruginea, which it also resembles very much, according to Pilsbry & Bequaert. The most important difference seems to be that the diameter is larger than in Krauss' type specimen. In addition, it is difficult to judge how large the diameter is in mediafricana, since the two authors on the same page (p. 356) give the maximum as 65% and 76% of the length. Unfortunately we do not have any material of Eupera from the Kisangani area.

List of synonyms of African Sphaeriacea mentioned in the text

A. The genus Corbicula:

aegyptiaca (Bgt.) Germain 1906 (Corbicula) - C. fluminalis
africana Krauss 1848 (Cyrena) - C. fluminalis africana
africana Daget 1961 (Corbicula) - C. fluminalis juv.
alba Clessin 1879 (Corbicula) - C. fluminalis
albida Krauss 1848 (Cyrena) - C. fluminalis
albida Haas 1936 (Corbicula) - C. astartina
albertiana Mandahl-Barth 1954 (Corbicula) - C. fluminalis cunningtoni
astartina von Martens 1860 (Cyrena) - C. astartina
astartina Haas 1936 (Corbicula) - C. fluminalis africana
callipyga Bourguignat 1885 (Corbicula) - C. fluminalis
consobrina Cailliaud 1827 (Cyrena) - C. fluminalis
cunningtoni Smith 1906 (Corbicula) - C. fluminalis cunningtoni
degousei (Bgt.) Germain 1906 (Corbicula) - C. fluminalis
delessertiana Prime 1870 (Corbicula) - C. fluminalis
difficilis Prime 1864 (Corbicula) - C. fluminalis
doufilei Rochebrune & Germain 1904 (Corbicula) - C. fluminalis
edwardi Pilsbry & Bequaert 1927 (Corbicula) - C. fluminalis cunningtoni
fischeri Germain 1907 (Corbicula) - C. fluminalis
fluminalis Müller 1774 (Tellina) - C. fluminalis
foai Mabille 1901 (Corbicula) - C. fluminalis tanganyicensis
gabonensis Preston 1909 (Corbicula) - C. fluminalis
gravieriana Bourguignat 1885 (Corbicula) - C. fluminalis
heuglini Clessin 1879 (Corbicula) - C. fluminalis
jickeli Clessin 1879 (Corbicula) - C. fluminalis
jouberti (Bgt.) Germain 1906 (Corbicula) - C. fluminalis tanganyicensis
kirkii Prime 1864 (Corbicula) - C. fluminalis africana
kynganica (Bgt.) Germain 1906 (Corbicula) - C. fluminalis
lacoini Germain 1905 (Corbicula) - C. fluminalis tsadiana
lavigeriana (Bgt.) Germain 1906 (Corbicula) - C. fluminalis tanganyicensis

meridionalis Clessin 1879 (Corbicula) - C. fluminalis
natalensis Clessin 1879 (Corbicula) - C. fluminalis africana
nilotica Clessin 1879 (Corbicula) - C. fluminalis
nyassana Bourguignat 1889 (Corbicula) - C. fluminalis africana
oliphantensis Craven 1880 (Corbicula) - C. fluminalis africana
pusilla Philippi 1856 (Cyrena) - C. fluminalis juv.
radiata Philippi 1846 (Cyrena) - C. fluminalis juv.
radiata Smith 1877 (Cyrena) - C. fluminalis africana
radiata von Martens 1879 (Corbicula) - C. fluminalis cunningtoni
radiata "oval form" Pilsbry & Bequaert 1927 (Corbicula) - C. astartina
radiata var. Smith 1881 (Cyrena) - C. fluminalis tanganyicensis
rosini Haas 1936 (Corbicula) - C. astartina
senegalensis Clessin 1879 (Corbicula) - C. fluminalis
soleilleti Bourguignat 1885 (Corbicula) - C. fluminalis
subtruncata (Bgt.) Germain 1906 (Corbicula) - C. fluminalis
tanganikana Bourguignat 1885 (Corbicula) - C. fluminalis tanganyicensis
tanganyicensis Crosse 1881 (Corbicula) - C. fluminalis tanganyicensis
tchadiensis Germain 1916 (Corbicula) - C. fluminalis tsadiana
tsadiana von Martens 1903 (Corbicula) - C. fluminalis tsadiana
zelebori Jickeli 1874 (Corbicula) - C. fluminalis

B. The genus Sphaerium:

albertianum Mandahl-Barth 1954 (Sphaerium) - S. victoriae albertianum
alluaudi Dautzenberg 1908 (Pseudocorbicula) - S. nyanzae alluaudi
bangweolicum Haas 1936 (Sphaerium) - S. hartmanni bangweolicum
bequaerti Dautzenberg & Germain 1914 (Eupera) - S. bequaerti
capensis Krauss 1848 ((Cyclas) - S. capense
capensis Jickeli 1874 (Cyclas) - S. bequaerti?
congener Preston 1912 (Sphaerium) - S. v. victoriae
congicum Haas 1936 (Sphaerium) - S. bequaerti
courteti Germain 1904 (Sphaerium) - S. hartmanni courteti

ddingoli Prime 1859 (Cyclas) - S. lacustre
hartmanni Jickeli 1874 (Cyclas) - S. h. hartmanni
incomitatum Kuiper 1966 (Pisidium) - S. icomitatum
lacustris Müller 1774 (Tellina) - S. lacustre
lacuum Mandahl-Barth 1954 (Sphaerium) - S. victoriae lacuum
mohasicum Thiele 1911 (Sphaerium) - S. victoriae mohasicum
naivashaensis Preston 1912 (Sphaerium) - S. hartmanni naivashaense
nyanzae Smith 1892 (Sphaerium) - S. n. nyanzae
nyanzae von Martens 1897 (Sphaerium) - S. v. victoriae
ovale Bourguignat 1864 (Cyclas) - S. lacustre
pharaonum Pallary 1909 (Sphaerium) - S. h. hartmanni
regularis Mandahl-Barth 1954 (Sphaerium) - S. regularis
stuhlmanni von Martens 1897 (Sphaerium) - S. stuhlmanni
stuhlmanni Pilsbry & Bequaert 1927 (Sphaerium) - S. bequaerti
subcapense Bourguignat 1883 (Sphaerium) - S. bequaerti?
teilhardi Pallary 1909 (Sphaerium) - S. h. hartmanni
victoriae Smith 1906 (Sphaerium) - S. v. victoriae

C. The genus Pisidium:

alexandrina Pallary 1909 (Pisidium) - P. pirothi
amnica Müller 1774 (Tellina) - P. amnicum
armillatum Kuiper 1966 (Pisidium) - P. armillatum
artifex Kuiper 1960 (Pisidium) - P. artifex
casertanum Poli 1791 (Cardium) - P. casertanum
costulosum Connolly 1931 (Pisidium) - P. costulosum
costulosum Haas 1936 (Pisidium) - P. pirothi
exilis Favre 1943 (Pisidium) - P. pirothi
fistulosum Mandahl-Barth 1954 (Pisidium) - P. fistulosum
georgeanum Kuiper 1952 (Pisidium) - P. ovampicum
giraudi Bourguignat 1885 (Pisidium) - P. giraudi
harrisoni Kuiper 1964 (Pisidium) - P. harrisoni
hermosum Bourguignat 1888 (Pisidium) - P. giraudi
invenustum Kuiper 1966 (Pisidium) - P. invenustum
katangense Pilsbry & Bequaert 1927 (Pisidium) - P. kenianum
kenianum Preston 1911 (Pisidium) - P. kenianum

kigeziense Preston 1912 (Sphaerium) - P. kenianum
langleyanum Melville & Ponsonby 1891 (Pisidium) - P. langleyanuum
lepus Kuiper 1957 (Pisidium) - P. pirothi
milium Held 1836 (Pisidium) - P. milium
montigenum Kuiper 1966 (Pisidium) - P. montigenum
nitidum Jenyns 1832 (Pisidium) - P. mitidum
ovampicum Ancey 1890 (Pisidium) - P. ovampicum
personatum Malm 1855 (Pisidium) - P. personatum
pirothi Jickeli 1881 (Pisidium) - P. pirothi
reticulatum Kuiper 1966 (Pisidium) - P. reticulatum
ruwenzoriense Germain 1911 (Pisidium) - P. casertanum
subtruncatum Malm 1855 (Pisidium) - P. subtruncatum
victoriae Mandahl-Barth 1954 (Pisidium) - P. pirothi
viridarium Kuiper 1956 (Pisidium) - P. viridarium

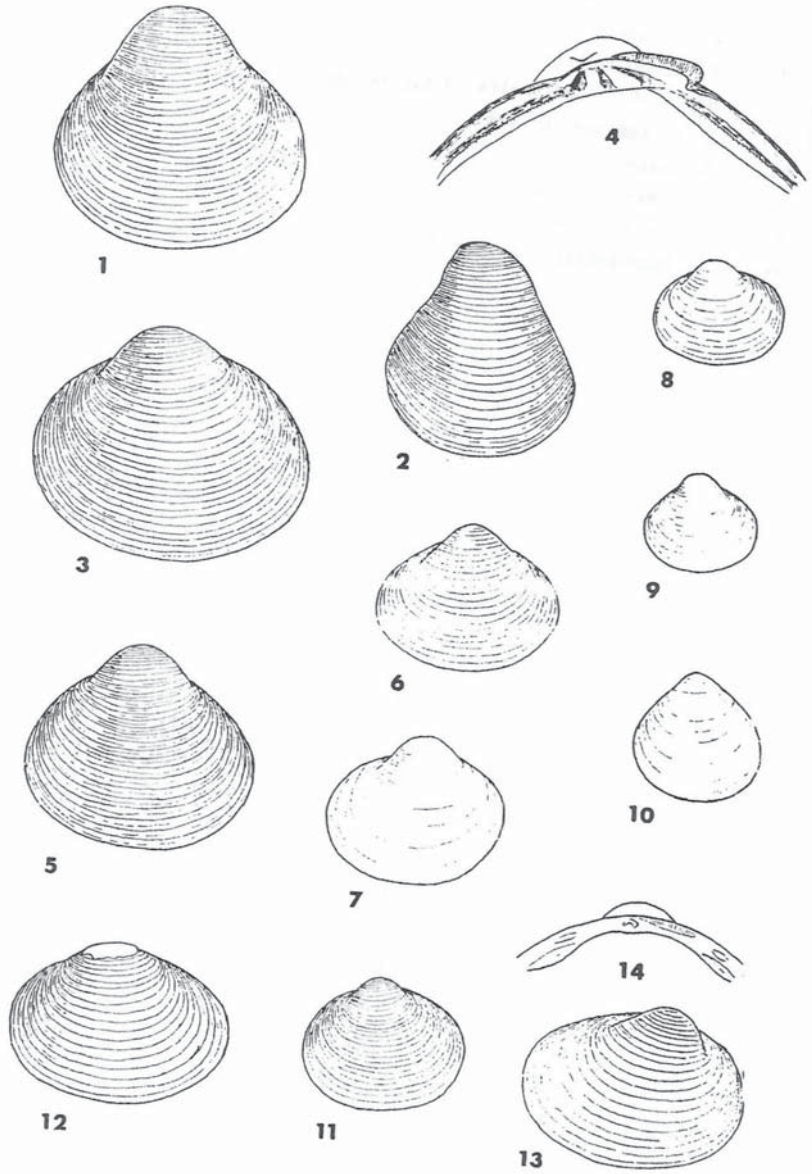
D. The genus Eupera:

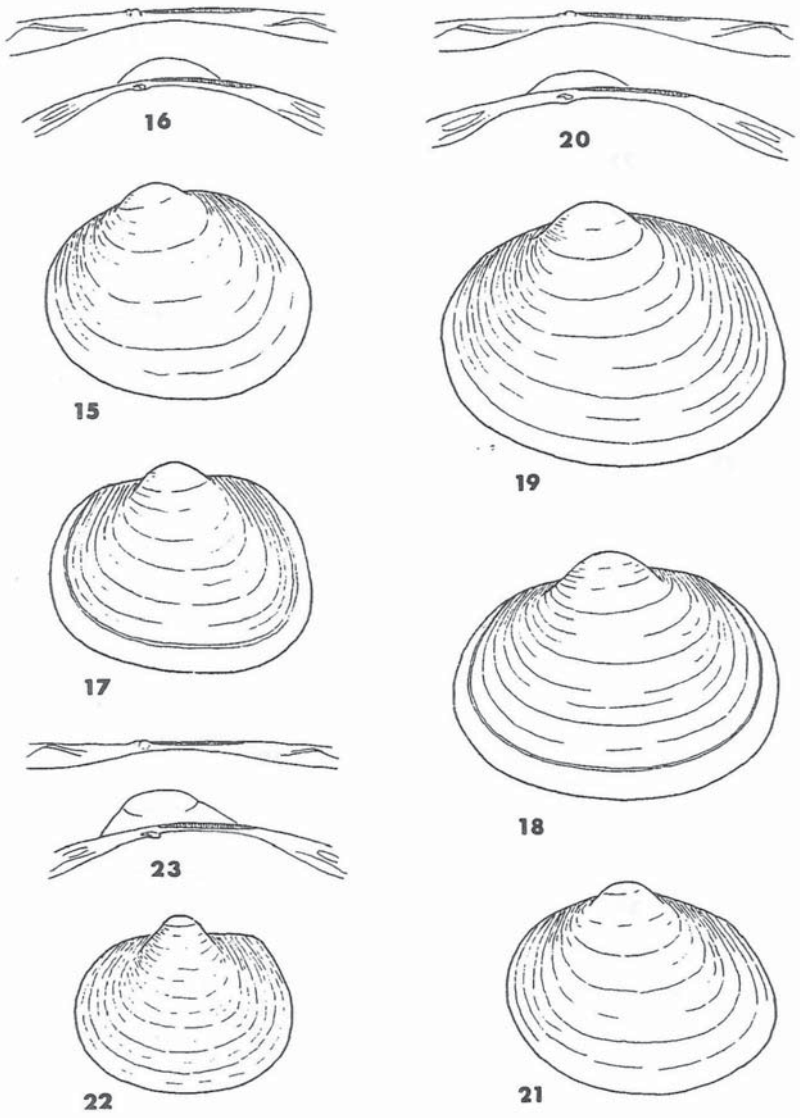
crassa Mandahl-Barth 1954 (Byssanodonta) - E. crassa
etheriarum Pilsbry & Bequaert 1927 (Eupera) - E. sturanyi?
ferruginea Krauss 1848 (Cyclas) - E. ferruginea
mediafricana Pilsbry & Bequaert 1927 (Eupera) - E. ferruginea?
ovata Mandahl-Barth 1954 (Byssanodonta) - E. ovata
parasiticum Deshayes 1854 (Pisum) - E. ferruginea
sturanyi Waagen 1905 (Sphaerium) - E. sturanyi
triangulum Mandahl-Barth 1973 (Eupera) - E. triangulum

List of Figures

All shells which are drawn from the side, show the left valve
Figures are in 2/3 natural size except when a
magnification is indicated

Figure:

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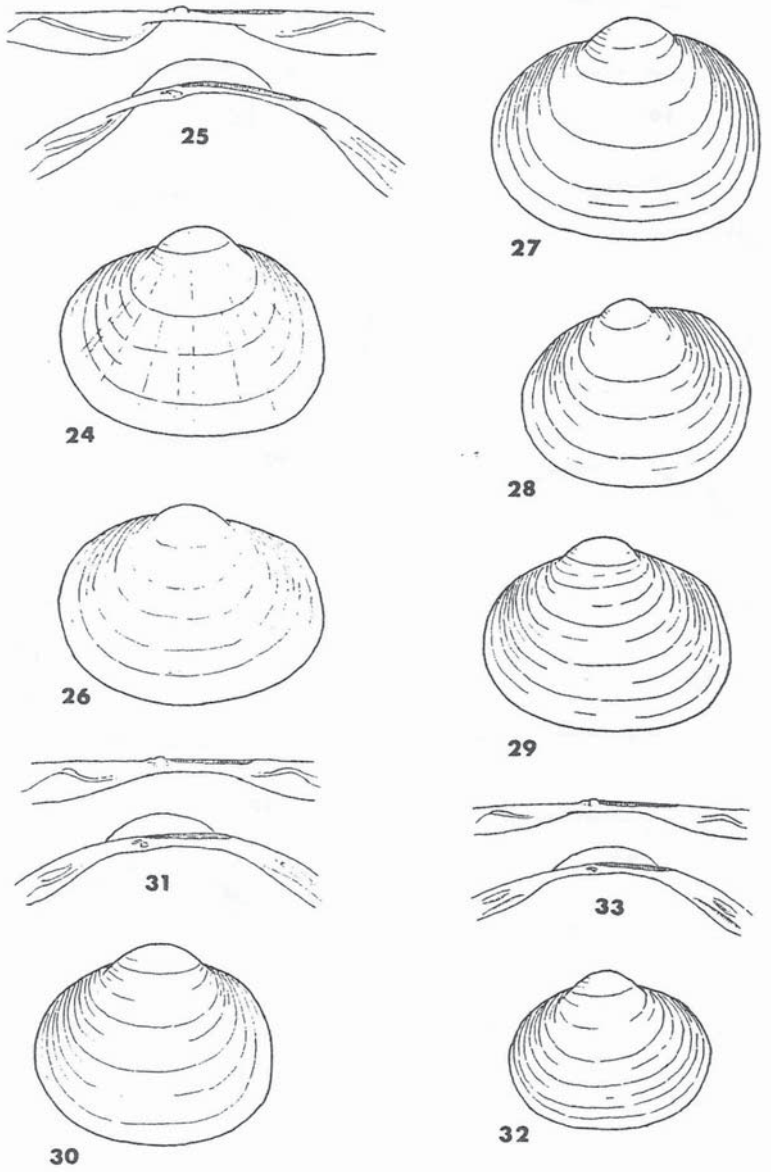
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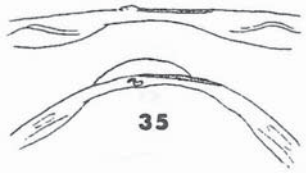

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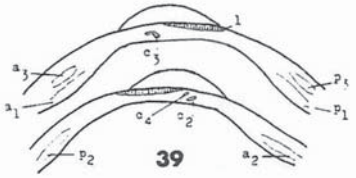

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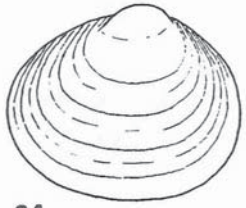

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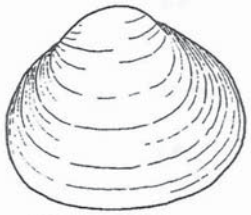

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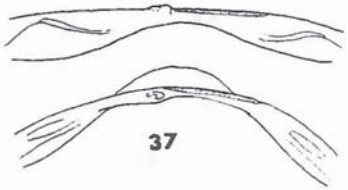

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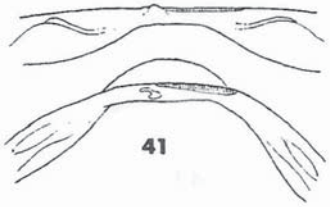

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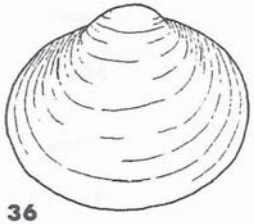

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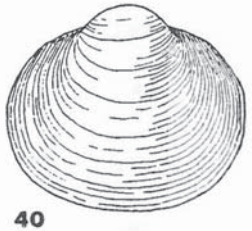

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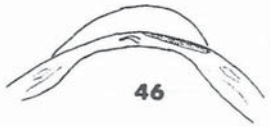

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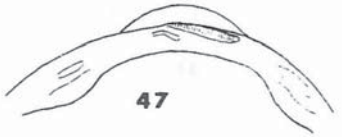

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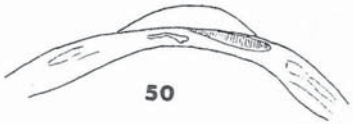

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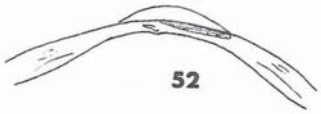

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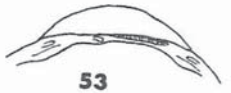

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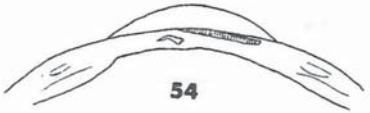

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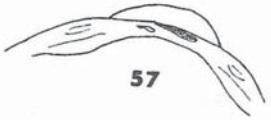

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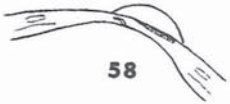

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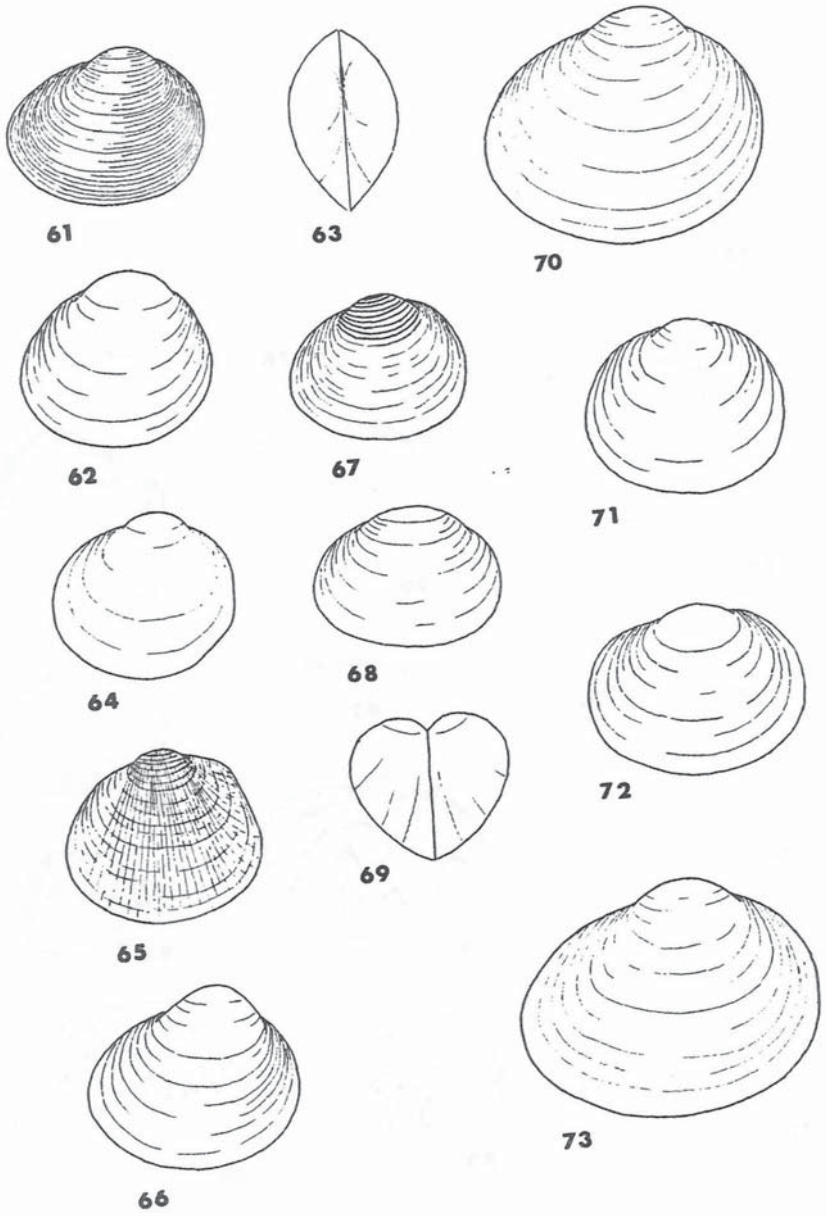
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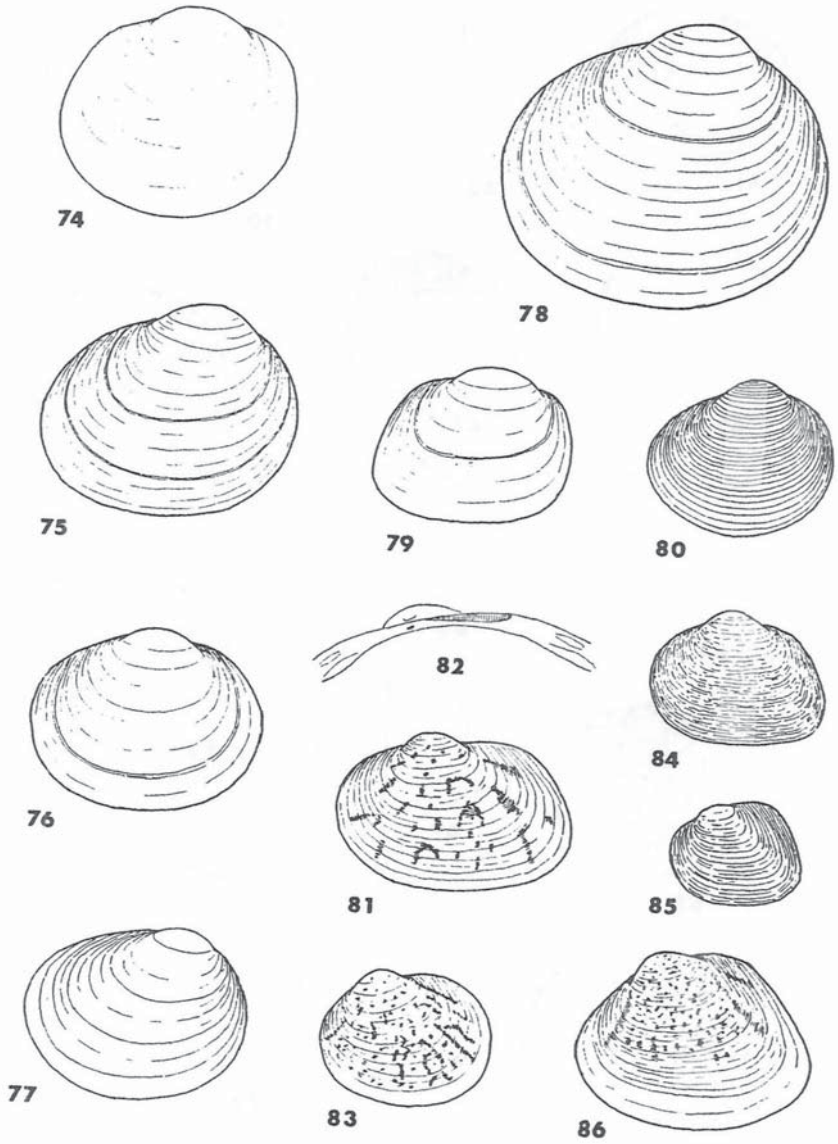
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