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The Species of the Genus *Bulinus*, Intermediate Hosts of *Schistosoma**

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The conditions of snail life in African inland waters favour the evolution of microgeographical races while hindering the formation of new species, and the distinctions between many of the bulinid intermediate hosts of Schistosoma *are consequently blurred. In this paper the author comments on the distinguishing characters that have been established for the known* Bulinus *species and subspecies and summarizes the present knowledge of their distribution and importance as intermediate hosts. His work is based on the examination of over 1540 snail samples received at the WHO Snail Identification Centre in Charlottenlund, Denmark.*

During the past few years a great number of samples of *Bulinus* have been sent to the WHO Snail Identification Centre, Charlottenlund, Denmark, from many countries in Africa and the Near East. This material has considerably improved our knowledge of the distribution of the various *Bulinus* species, but has also shown, unfortunately, that several of the specific and subspecific characters are less constant and therefore less reliable than hitherto assumed. This unfortunate situation is in no way surprising, if the particular conditions affecting most freshwater organisms are taken into consideration, especially in combination with the peculiar hydrological conditions of Africa. It is necessary to keep these conditions in mind when dealing with African freshwater snails, otherwise it will be impossible to understand the complicated and rather unsatisfactory systematics of these animals.

It is a well-known fact, pointed out by Hubendick (1954, 1962), for instance, that many true freshwater species (" hololimnic " species, i.e., those that spend all their life in fresh water) 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—perhaps most—inland waters represent isolated habitats; the effect of this isolation is that one population of a freshwater species can evolve in a certain direction without its evolution being in any way affected by interbreeding with other populations of the same species. The second aspect is the wide range of variation of freshwater habitats, which forces the organisms to adapt themselves to the conditions they find or to perish. Such adaptation must not, of course, be conceived of as an adaptation of single individuals, but rather as an adaptation of the whole population in such a way that those individuals that are best fitted for life under the conditions that prevail will get most offspring, while the less well suited individuals will disappear.

These two aspects—isolation and variation—tend to result in the formation of new species, but the third aspect of inland waters—namely, their unstable nature and their usually short duration—works in the opposite direction and will as a rule prevent the formation of new species, at least where snails are concerned, simply because the time available is insufficient. In comparison with other animals, fish, for instance, snails seem to require a considerable length of time in order to evolve new species. A relatively young lake like Lake Victoria has a great number of endemic species of fishes, but very few endemic snail species. Only very ancient lakes (such as Lake Tanganyika) harbour a number of endemic snail species comparable with that of fishes. A remarkable and almost unique fact is the occurrence of an endemic *Bulinus* species in a small lake like

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Lake Mutanda in western Uganda. Beadle (1962) has published an interesting paper on speciation in the East African lakes, in which he emphasizes the importance of the great changes in size and volume of the lakes during geologically recent times. The changes are mainly due to variation in rainfall and to earth movements, and it is evident from the fact that several lakes and rivers in Africa have ceased to exist even within this century that such changes are still going on.

Thus, the conditions of snail life in African inland waters favour the evolution of microgeographical races but hinder the formation of new species. This is true both in general and for *Bulinus* species in particular in that very few of the latter can be characterized as " good " species, i.e., as showing clear-cut distinctions from allied species. In most cases the species are linked by intermediate forms, but usually these occur in limited areas only. Wright (1961) has correctly pointed out that such intermediates are to be expected in the centres of evolution of the species concerned. Tanganyika,[1] especially the north-eastern area, seems to be such an evolutionary centre both for *Physopsis* and for some *Bulinus sensu stricto*.

The following pages constitute a brief summary of our present knowledge of the distribution of all known species of *Bulinus*, with brief remarks on their distinguishing characters and their importance as intermediate hosts of *Schistosoma*. This summary is based on examination of 1543 samples.[2] At first glance this may seem to be fairly adequate material; in reality, it is much too scanty. *Bulinus* species are distributed over an area of some 34 million km^2, which only gives one sample of *Bulinus* for every 22 000 km^2; considering that 35 species and subspecies are recognized, it becomes evident that much more material must be collected and examined before there is any chance of reaching a satisfactory position.

The genus *Bulinus* is divided naturally into two subgenera: *Physopsis* and *Bulinus* s.s., the latter including the old subgenus *Pyrgophysa*.

SUBGENUS PHYSOPSIS

The subgenus *Physopsis* differs from *Bulinus* s.s. by the truncate columella, the ridge on the ventral side of the kidney, and by the interrupted spiral sculpture consisting of small nodules or a punctation on the upper whorls, not to be confused with the very delicate punctation which is present on the embryonic whorls of all *Bulinus* (Walter, 1962). These characters are not always present in all the individuals, but the microsculpture is the only one found lacking in all specimens of a population. A good distinguishing character in live specimens is the pointed " tail " of *Physopsis* and the blunter one of *Bulinus* s.s. The subgenus *Physopsis* is widely distributed in Africa south of the Sahara, and with a single exception all *Physopsis* are susceptible (in the terms of LeRoux, 1958) to *Schistosoma capense*.

Bulinus (Physopsis) africanus (Krauss) (Fig. 1 & 2)

Widely distributed in eastern Africa from Ethiopia to Natal and westwards to the eastern Congo (Leopoldville). Altogether 89 samples have been examined. Wright (1963b) records it from Angola, but those specimens are not very typical. The only reliable distinctive character between *B. africanus* and the other *Physopsis* species is the long and wide vergic sheath, almost twice as long and wide as the preputium, but specimens with a less characteristic copulatory organ are fairly common and difficult to separate from *B. globosus* or *B. nasutus*. The medical importance of this species is rather peculiar and not yet fully elucidated. The northern subspecies, *B. a. ovoideus* (Bourguignat), which is larger and has a coarser shell than the typical form, acts as intermediate host in Kenya (Teesdale, 1962), but not in Uganda (Cridland, 1955) and probably not in Tanganyika either (Webbe, 1962). The typical form, which is found from southern Tanganyika (Sturrock, 1964) southwards, is commonly accepted as an intermediate host of *S. capense*. Many reports of *B. africanus* acting as intermediate host in other parts of Africa are due to confusion with *B. globosus*.

Bulinus (Physopsis) globosus (Morelet) (Fig. 3)

In all 454 samples have been examined of this most common and widely distributed *Physopsis*. It is

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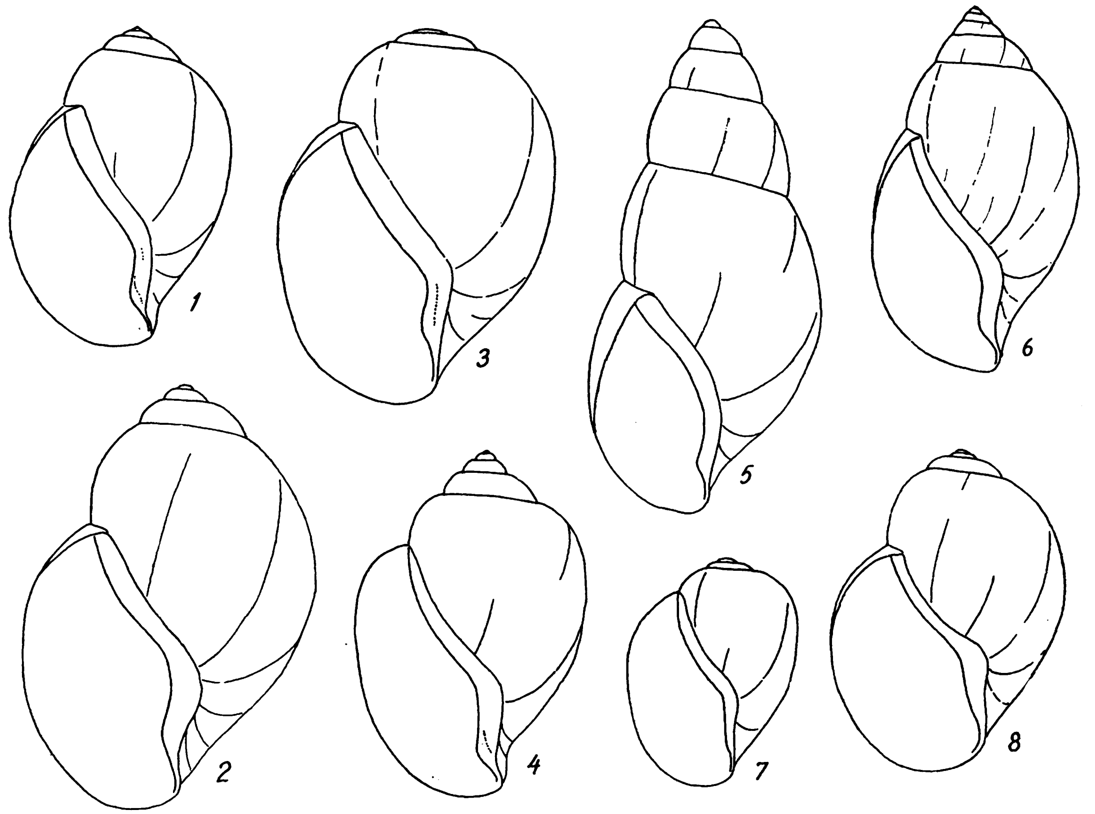
[1] The name Tanganyika, rather than Tanzania, is used in this paper for reasons of geographical precision.

[2] Each sample consists of from one to several hundred specimens, and altogether more than 10 000 snails have been examined.

FIG. 1-8. TYPICAL SHELLS OF *PHYSOPSIS*



1. ***B. africanus africanus*** **(Krauss), Natal. 2.** ***B. africanus ovoideus*** **(Bourguignat), Kenya. 3.** ***B. globosus*** **(Morelet), Angola, 4.** ***B. abyssinicus*** **(Martens), Somalia. 5.** ***B. nasutus productus*** **Mandahl-Barth, Uganda. 6.** ***B. nasutus nasutus*** **(Martens) Tanganyika. 7.** ***B. jousseaumei*** **(Dautzenberg), Gambia. 8.** ***B. ugandae*** **(Mandahl-Barth), Lake Victoria. All 3 × natural size.**

known from Gambia and all Africa south of the Sahara, except Ethiopia, Somalia and most of the Sudan. *B. globosus* is distinguishable from *B. africanus* by the short and narrow vergic sheath, distinctly shorter than the preputium, and from *B. nasutus* by the number of whorls, the shorter and more blunt spire and the microsculpture. It is possible to separate several local forms, sometimes rather distinct, but true geographical races do not seem to exist. *B. globosus* is the principal intermediate host of *S. capense* in western and southern Africa and also in some parts of eastern Africa, mainly in areas where *B. nasutus* is absent.

Bulinus (Physopsis) nasutus (Martens) (Fig. 5-6)

This species is known only from the former British East Africa, from where 76 samples have been examined. It differs from the other *Physopsis* by the usually conical, pointed spire, the larger number of whorls and the more pronounced microsculpture. The proportions of the copulatory organ are between those of *B. africanus* and those of *B. globosus*. It is divided into two subspecies: *B. n. nasutus* (Martens) and *B. n. productus* Mandahl-Barth. The former is known from south-eastern Kenya (Kitui and Digo) and southwards in the coastal district to Tunduru and westwards to Mbarali in the Southern Highlands of Tanganyika. The more long-spired *B. n. productus* is an inland form ranging from the Lango district of Uganda in the north to Shinyanga in Tanganyika in the south. Both subspecies are important intermediate snail hosts, probably more important in East Africa than *B. africanus* and *B. globosus* (Cridland, 1955, Webbe, 1963). In the

Tanga district of north-eastern Tanganyika it is often extremely difficult to distinguish between *B. nasutus*, *B. globosus* and *B. africanus*. The reason for this is probably that the evolutionary centre of all three species is to be found here.

Bulinus (Physopsis) abyssinicus (Martens) (Fig. 4)

Of this species 22 samples have been examined. It is known only from the southern part of Somalia, where it is probably responsible for the transmission of urinary bilharziasis (Maffi, 1959). The light-coloured shell, the shouldered whorls and the peculiar corrugated microsculpture are distinctive, but all three characters are not always present on the same shell.

Bulinus (Physopsis) jousseaumei (Dautzenberg) (Fig. 7)

Twelve samples of this West African species have been examined from Senegal, Gambia, Mali and the Congo (Brazzaville). The latter record is surprising as it seems to be outside the natural distribution of the species. The small size, almost obsolete truncation and frequently feeble microsculpture are distinctive. A form with very delicate spiral sculpture is known from Mauritania. Wright (1957) regards *B. jousseaumei* as a subspecies of *B. globosus* and in his 1961 paper (p. 229) he states that *B. jousseaumei* " is considered to be no more than a regional form of *B. globosus*, scarcely meriting even sub-specific status." Further, he believes (1957; p. 24) that " there is a well-marked cline grading from the typical *globosus* in the south to the small *jousseaumei* at the extreme northern limit of the range ". Three facts contradict this supposition: the distinctness of *B. jousseaumei*; the occurrence of true *B. globosus* of typical form and normal size in Gambia; and the fact that the cline does not exist at all as *B. globosus* from the northern limit (Gambia, Sierra Leone, Liberia, northern Ghana and Nigeria) attain the same shell length as do specimens from Congo (Leopoldville) and Angola. *B. jousseaumei* is a proved intermediate host in Gambia and Senegal (Smithers, 1956).

Bulinus (Physopsis) ugandae (Mandahl-Barth) (Fig. 8)

Twenty-five samples have been examined from Lake Victoria, Uganda, the Sudan and from Lake Marguerite in Ethiopia. The species has the same almost obsolete truncation of columella and very weak or completely lacking microsculpture as *B. jousseaumei*, but it reaches a larger size and has usually a more prominent spire. It is the only *Physopsis* not susceptible to *Schistosoma* (Cridland, 1955; African Conference on Bilharziasis, 1957).

SUBGENUS *BULINUS SENSU STRICTO*

The subgenus *Bulinus* s.s. comprises all *Bulinus* without truncate columella, renal ridge and interrupted spiral sculpture. The distribution of the subgenus covers the whole of Africa, the East African islands, the Near East and some Mediterranean countries. The species making up this subgenus can be placed in three groups.

THE *TROPICUS* GROUP

The *tropicus* group (Fig. 9-13), of which 162 samples have been examined, comprises *B. tropicus* (Krauss) and allied forms. The distinguishing characters between this and the *truncatus*-group are not too clear. The simply triangular mesocones of the lateral teeth are not quite as reliable as was earlier believed. In South Africa *B. tropicus* sometimes has slightly arrow-head-shaped mesocones as demonstrated by Stiglingh et al. (1962);[1] while *B. coulboisi* and *B. guernei*, for instance, have triangular mesocones. Further, aphallic specimens are very rare in *B. tropicus* and very common in the *truncatus* group. In most cases it is possible to separate the two groups on shell characters, but because of the very great variation it is difficult to describe the differences. It is most regrettable that no better distinguishing characters have been found, because probably no members of the *tropicus* group

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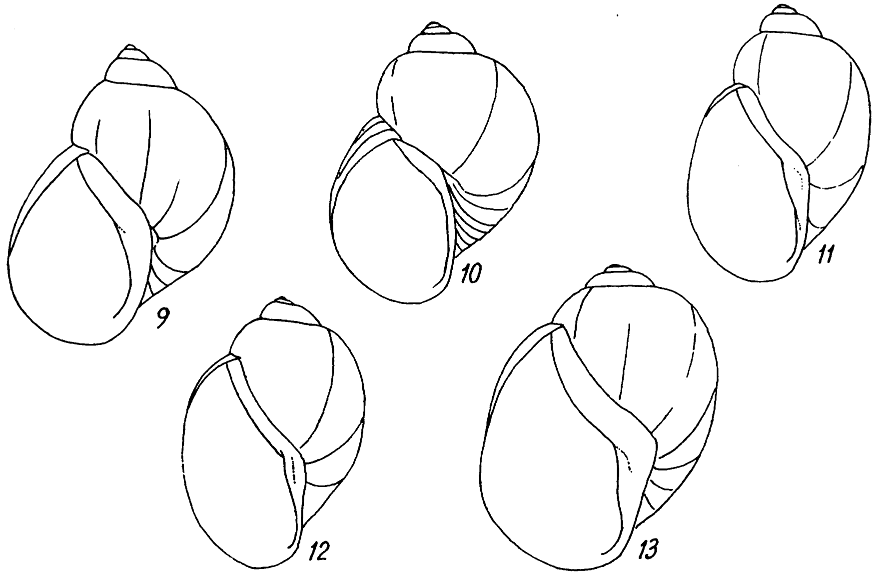
[1] The radula teeth delineated in Fig. 34 of this paper belong almost definitely to *B. natalensis*. Stiglingh et al. themselves also express some doubts about the identity of the specimen. Incidentally, it is rather astonishing that, on the basis of material consisting of only 9 South African samples, the authors can state (p. 93): " The mesocone is almost never simply triangular as is claimed by Mandahl-Barth (1956) ". In this connexion it is worth remembering that South African specimens of *Biomphalaria pfeifferi* also frequently possess arrow-head-shaped mesocones, although such are unknown in *B. pfeifferi* from other parts of Africa.

FIG. 9-13. TYPICAL SHELLS OF THE *TROPICUS* GROUP



9. *B. tropicus tropicus* (Krauss), Rhodesia. 10. *B. tropicus alluaudi* (Dautzenberg), Kenya. 11. *B. tropicus zanzebaricus* (Clessin), Tanganyika. 12. *B. tropicus toroensis* Mandahl-Barth, Uganda. 13. *B. liratus* (Tristram), Madagascar.
All 3 × natural size.

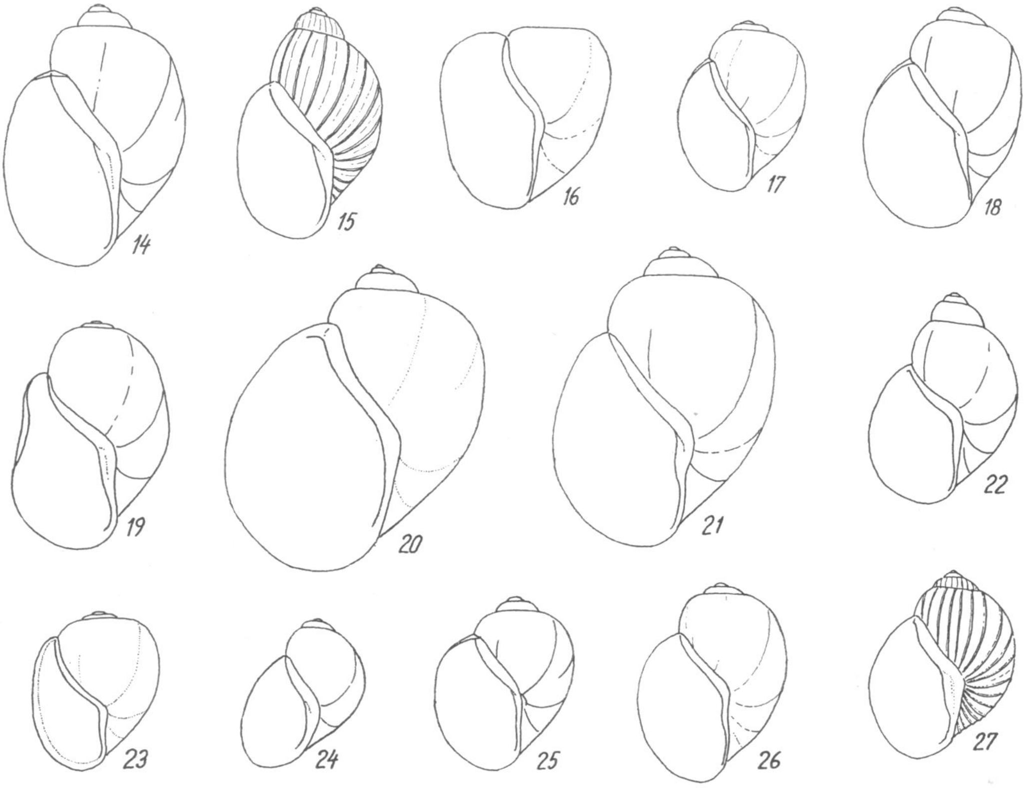
transmit human bilharziasis, while all members of the *truncatus* group must be regarded as potential vectors of at least *S. haematobium*. Teesdale (1962) has shown that *B. tropicus alluaudi* (Dautzenberg) in Kenya acts as intermediate host of *S. bovis*. This statement indicates that even the insusceptibility of *B. tropicus* to schistosomes is not a quite reliable character. *B. tropicus* comprises a great number of local forms in southern and eastern Africa. Some of these forms undoubtedly represent distinct subspecies, such as *B. t. alluaudi* (Dautzenberg), *B. t. zanzebaricus* (Clessin) and *B. t. toroensis* Mandahl-Barth, but a revision of the many other forms is badly needed. The *tropicus* group probably also comprises the Malagasy *B. liratus* (Tristram), which, however, shows some affinities to *B. natalensis*.

THE *TRUNCATUS* GROUP

The *truncatus* group also includes a great number of more or less different forms, some of which must be regarded as distinct species, others as subspecies, and the rest as local forms. In some cases, however, it is extremely difficult to decide whether a particular form should be regarded as a species, a subspecies or only an ecophenotypical form. The final decision can in many cases be reached only by laboratory experiments.

The many assumed species, mainly described in the previous century, from the Mediterranean countries, northern Africa and the Near East are usually regarded as belonging to one and the same species—*B. truncatus* (Audouin), sometimes incorrectly called *B. contortus* (Michaud). The true *B. contortus* from the Iberian peninsula and southern France is distinctly different from *B. truncatus* from Egypt and the Near East and must be regarded as a separate species. The remainder fall into two, not completely separated, groups—an eastern group, comprising the typical *truncatus* and allied forms in Eastern Africa; and a western group, including the West African forms and probably also the North-West African forms. The *Bulinus* of Sardinia and Sicily seems to represent an intermediate stage between the two groups. The main difference between these two groups is the size of the radula teeth. In the eastern group the first lateral teeth are about 25 μ long, while in the western group the same teeth are only about 15 μ long.

FIG. 14-27. TYPICAL SHELLS OF THE *TRUNCATUS* GROUP



14. *B. truncatus truncatus* (Audouin), Egypt. 15. *B. truncatus sericinus* (Jickeli), Ethiopia. 16. *B. truncatus trigonus* (Martens), Lake Victoria. 17. *B. truncatus rohlfsi* (Clessin), Chad. 18. *B. truncatus rivularis* (Philippi), Sardinia. 19. *B. mutandaensis* (Preston), Lake Mutanda, Uganda. 20. *B. truncatus* subsp.? Lake Awasa, Ethiopia. 21. *B. natalensis* (Küster), Tanganyika. 22. *B. contortus* (Michaud), Portugal. 23. *B. nyassanus* (Smith), Lake Nyasa. 24. *B. transversalis* (Martens), Lake Victoria. 25. *B. guernei* (Dautzenberg), Gambia. 26. *B. coulboisi* (Bourguignat), Lake Tanganyika. 27. *B. coulboisi* subsp.? Tanganyika.
All 3 × natural size.

The eastern group comprises the following three subspecies.

Bulinus (Bulinus) truncatus truncatus (Audouin) (Fig. 14)

This is the well-known intermediate host of *S. haematobium* in north-east Africa and the Near East. Altogether 46 samples originating from northern Uganda, the Sudan, Egypt, Israel, Lebanon, Iraq, and Iran have been examined. The synonymy of the African *B. truncatus* is given by Mandahl-Barth (1958; pp. 77-78). For the sake of completeness the probable Asian synonyms are listed below.

1831. *Physa brocchii* Ehrenberg. *Symbolae Physicae seu Icones et Descriptiones Animalium Evertebratorum*, Berlin, vol. I, p. 20. Type-locality: Beirut, Lebanon.

1841. *Physa guerini* Mittre. *Rev. Zool. Soc. Cuvier*, p. 68. Type-locality: " Levant ".

1874. *Physa brocchii* var. *approximans* Mousson. *J. Conchyliol.*, **22**, 41. Type-locality: " Mesopotamia ".

1874. *Physa lirata* Mousson. *J. Conchyliol.*, **22**, 43. Type-locality: Lower Mesopotamia. (Not *Physa lirata* Tristram).

1896. *Physa rollei* Kobelt. In: Rossmaessler, *Iconographie*, suppl. 1, p. 60, plate 19, fig. 6-8. Type-locality: Jaffa, Israel.

1900. *Physa moussoni* Ancey. *Nautilus*, **14**, 84. New name for *Physa lirata* Mousson.

1911. *Bullinus (Isidora) asiaticus* Germain. *Bull. Mus. Hist. nat. Paris*, p. 64. Type-locality: Syria.

1913. *Physa tiberiadensis* Preston. *J. Proc. Asiat. Soc. Beng.*, (2), **9**, 466, plate 27, fig. 2. Type-locality: Lake Tiberias at the Jordan River, Israel.

There seems no reason to regard any of the " species " listed above as distinct. Together they represent the range of variation of Asian *truncatus*, which is very similar to that found in Egyptian specimens. It is not known with certainty how far westwards in North Africa the typical *truncatus* reaches. It is possible that the *Bulinus* of Tunisia, Algeria and Morocco also belongs to *B. truncatus* s.s., but it seems more likely that it represents another subspecies. Unfortunately no material from these countries has been available for examination, and therefore a final decision cannot be made for the time being.

Bulinus (Bulinus) truncatus sericinus (Jickeli) (Fig. 15)

This subspecies replaces the nominate race in Ethiopia and is also recorded from Yemen and Aden (Wright, 1963a). In all, 21 Ethiopian samples have been examined. When typically developed, the shell is narrower than that of *B. t. truncatus* and costulate but in several of the Ethiopian lakes a more globose form without costulation occurs. The very aberrant form found in Lake Awasa (Fig. 20) differs so much from the other Ethiopian lake forms that it most likely represents a distinct subspecies or even species *B. t. sericinus* is the most probable intermediate host of *S. haematobium* in Ethiopia, but final proof is still lacking.

Bulinus (Bulinus) truncatus trigonus (Martens) (Fig. 16)

This is a southern representative of *B. truncatus*. It is restricted to Lake Victoria, Lake Edward and adjacent areas. Altogether 43 samples have been examined. When typically developed, the inversely conical shell with the flat spire is distinctive, but longer-spired shells occur and show the close relationship to the typical *truncatus*. It is not susceptible to *S. capense*, but probably to *S. haematobium*.

The following subspecies is intermediary between the eastern and the western group.

Bulinus (Bulinus) truncatus rivularis (Philippi) (Fig. 18)

1836. *Physa rivularis* Philippi. *Enum. Moll. Siciliae*, vol. I, p. 147, plate 9, fig. 1. Type-locality: Sicily.

1882. *Physa alessiana, aradae, bourguignati, cyanea,* and *oretana* Benoit. *Nuovo Catologo delle Conchiglie terrestri e fluviatili della Sicilia*, pp. 131-134. All described from Sicily.

1882. *Physa (Isidora) meneghiniana, saeprusana* and *tapparoniana* Paulucci. *Boll. Soc. malacol. ital.*, **8**, 319-322. All described from Sardinia.

As the many " species " listed above indicate, this subspecies is also very variable in shape of shell. It is a rather small form, usually not exceeding 10 mm in height of shell. The largest specimen seen is 11.7 mm high and 8.7 mm wide. It seems to be closely related to *B. t. truncatus*, but the radula teeth are smaller, measuring only 20 μ. Seven samples from Sardinia have been examined. It acts as intermediate host of *S. bovis* and has been experimentally infected with *S. haematobium* (African Conference on Bilharziasis, 1957).

The western group consists of the following subspecies.

Bulinus (Bulinus) truncatus rohlfsi (Clessin) (Fig. 17)

This subspecies is widely distributed in western Africa from Mauritania to Dar Fur and southwards through Ghana, Nigeria, the Central African Republic and the Congo (Leopoldville) to Angola. From the latter country it was first recorded by Wright (1963b). In all, 56 samples have been examined. All of these have a smaller and, as a rule, a more globose shell than the nominate subspecies, and the radula teeth are distinctly smaller. The first lateral teeth measure only 10 μ-15 μ. The mesocones of the lateral teeth are usually distinctly arrow-head-shaped, but in some samples from Mauritania they are more triangular and thus form intermediary stages between *B. t. rohlfsi* and *B. guernei*. *B. t. rohlfsi* acts as intermediate host of *S. haematobium* in Ghana (McCullough, 1956), and according to Wright (1963b) Angolese specimens are susceptible to *S. haematobium* as well.

The following three species are closely related to *B. truncatus* and have probably evolved from the eastern group of that species.

Bulinus (Bulinus) transversalis (Martens) (Fig. 24)

This species is known only from the northern shore of Lake Victoria and the first part of the Victoria Nile. Nine samples have been examined.

Bulinus (Bulinus) nyassanus (Smith) (Fig. 23)

Endemic to Lake Nyasa, whence five samples have been available for examination.

Bulinus (Bulinus) mutandaensis (Preston) (Fig. 19)

Endemic to Lake Mutanda in the Kigezi district of Uganda. Two samples have been examined.

All three species possess characteristic shells, and *B. mutandaensis* remarkably large radula teeth as well (Mandahl-Barth, 1958, 1960). Their status as intermediate hosts is not known, but they are probably susceptible to *S. haematobium.*

Four other species seem to be more closely related to the western group of *B. truncatus* in that their lateral teeth are less than 20 μ long and frequently have less arrow-head-shaped mesocones.

Bulinus (Bulinus) contortus (Michaud) (Fig. 22)

1829. *Physa contorta* Michaud. *Bull. Soc. linn. Bordeaux*, **3**, 268, fig. 15-16. Type-locality: Small rivers between Collioures and Port-Vendres, France.

1889. *Physa paulinoi* Locard. *Exchange*, **11**, 109. Type-locality: Coimbra, Portugal.

Only a single sample of this species, consisting of five specimens from Portugal, has been available for examination. They differ distinctly from *B. truncatus* by the lateral teeth being only 16 μ long and by the simply triangular, rather narrow and pointed mesocones, reminiscent of the teeth of *B. guernei.* Only two of the five specimens were euphallic, with a copulatory organ of the same proportions as in *B. truncatus.* Unfortunately, it has not been possible to compare the Portuguese specimens with material from the French type-locality, where it is extremely rare (Germain, 1931, p. 515). *B. contortus* is also recorded from the north-eastern part of Spain around Barcelona and Gerona (Graëlls, 1846, p. 11; Bofill & Haas, 1920, p. 573), but here also it seems to be scarce. In Portugal it was first recorded by Morelet (1845, p. 85), and according to Nobre (1930, p. 199) it is fairly common in the central province. It is noteworthy that it is not *B. contortus*, but *Planorbarius metidjensis* (Forbes) which is responsible for the transmission of urinary bilharziasis in Portugal, and also that *P. metidjensis* is not susceptible to *S. haematobium*, nor to *S. capense* (= " Rhodesian strain ") (African Conference on Bilharziasis, 1957). *Planorbarius* is not a near relative of *Bulinus*, in fact they belong to two different subfamilies of Planorbidae, and this, coupled with the information that *P. metidjensis* is not susceptible to the two African strains of schistosomes causing urinary bilharziasis, indicates perhaps that the Portuguese schistosomes are specifically different from *S. haematobium.* It is not yet known whether a *Bulinus* or *P. metidjensis* is responsible for the transmission of urinary bilharziasis in some parts of north-west Africa (J. Fraga de Azevedo—communication to WHO, 1956).

Bulinus (Bulinus) guernei (Dautzenberg) (Fig. 25)

Of this species, 12 samples from Mauritania, Senegal and Gambia have been examined. The shell has normally a rather prominent spire and convex whorls separated by deep sutures. Typically the lateral teeth have simply triangular mesocones, but in Mauritania specimens with more arrow-head-shaped mesocones have been found. Aphallic specimens are common. For these reasons it seems justifiable to transfer *B. guernei* to the *truncatus*-group; this suggested transfer is also supported by the fact that *B. guernei* acts as an intermediate host of *S. haematobium* (Smithers, 1956).

Bulinus (Bulinus) coulboisi (Bourguignat) (Fig. 26-27)

This species is known from East Africa and the eastern part of the Congo (Leopoldville). The examined material consists of 42 samples of rather different forms, and the taxonomic position of the species is somewhat uncertain. The typical form seems to be restricted to the lakes of the western Rift Valley and neighbouring territories. East of this area a curious, small, more *tropicus*-like form occurs, which possibly should be regarded as a subspecies of *B. coulboisi.* The shell has a more pointed spire and is frequently costulate. In the soft parts it is very similar to the typical *B. coulboisi*, and aphallic specimens are common. This form is known from a number of smaller lakes and dams in Northern and Central Tanganyika (Mitego, Nyambiti, Maswa, Ngudu, Nassa, and Bariadi in the Lake District, Kilimawe and Kisangara in the Tanga District, and Singida and Dodoma in Central Tanganyika). In some cases it is extremely difficult to separate *B. coulboisi* from certain forms of *B. tropicus*, and it will hardly be possible to improve the situation until the many forms of *B. tropicus* in Tanganyika are better understood. At least some of the forms, now collected in *B. coulboisi*, are susceptible to *S. haematobium* (African Conference on Bilharziasis, 1957).

Bulinus (Bulinus) natalensis (Küster) (Fig. 21)

Mandahl-Barth (1958) placed " *Physa* " *natalensis* as a synonym of *B. tropicus*, because at that time no typical specimens of *natalensis* had been examined. Since then much more material (44 samples) has come to hand, and it has become evident that *natalensis* is specifically distinct from *B. tropicus*. As some of the " species " listed as synonyms of *B. tropicus* s.l. in the papers cited above rightly belong to *natalensis*, its synonymy is given here.

1841. *Physa natalensis* " Krauss " Küster. Martini & Chemnitz, *Systematisches Conchylien-Cabinet*, Berlin, 2. Aufl., vol. I: **17**, 8, plate 1, fig. 12-14. Type-locality: Natal.

1866. *Physa angolensis* Morelet. *J. Conchyliol.*, **14**, 162. Type-locality: Duque de Braganza, Angola.

1866. *Physa welwitschi* Morelet. *J. Conchyliol.*, **14**, 162. Type-locality: near Bumbo River, Angola.

1873. *Physa algoensis* Sowerby. Reeve, L., *Conchologia iconica, or illustrations of the shells of molluscous animals*, London, **19**, plate 7, fig. 53. (Err. typ.)

1887. *Physa parietalis* Mousson. *J. Conchyliol.* **35**, 298, plate 12, fig. 8-8*a*. Type-locality: Ondangua, Ovamboland.

1903. *Physa zuluensis* Melvill & Ponsonby. *Ann. Mag. nat. Hist.*, (7), **12**, 606, plate 32, fig. 4. Type-locality: eastern Zululand.

When typically developed, the shell is very distinct. It is somewhat inflated, with rather low spire, twisted columella and fine spiral lines on the upper whorls. In its anatomy it agrees with *B. truncatus* s.s. and, like the latter, it is frequently aphallic. The radula teeth are distinctly smaller, the length of the first lateral teeth varying between 13 μ and 18 μ, and the mesocones are, as a rule, narrower than those of *truncatus*.

The mean measurements of 10 shells from a tributary of Gwebi River, Southern Rhodesia, are as follows: height of shell (H): 13.2 mm; diameter of shell (D): 9.6 mm; and height of aperture (A): 9.8 mm. The biggest shell has the following measurements: H: 15.1 mm; D: 10.6 mm; and A: 11.5 mm.

Like most other *Bulinus* species, *B. natalensis* is very variable in size and shape of shell, and in extreme cases it can be very difficult to distinguish it from certain forms of *B. tropicus*. *B. angolensis* as described and figured by Wright (1963b) must be referred to *B. natalensis*, and there seems no reason to retain it as a distinct subspecies. The two shells figured by Mandahl-Barth (1960, Plate I, B and C) represent two extremes of the variation of *B. natalensis*. Its status as intermediate host is not yet known.

Material examined: *Transvaal*: Nelspruit. *South-West Africa*: Ondangua, Okwambi. *Rhodesia*: Lake McIlwaine, Prince Edward Dam, Bromley Dam, Ngezi Dam, Musitkwe Dam, Mazoe Dam, Chindamora, tributary of Gwebi River, Dando River, Hunyani River, Ruwa River, Lake Kariba. *Zambia*: Chozi River, Mankoyo, Nkinde Pond. *Angola*: Lufinda. *Congo*: Kalambo, Ruzizi Plains. *Tanganyika*: Mantare, Kalenga, Iringa.

THE *FORSKALII* GROUP

The *forskalii* group comprises the remaining eight species of *Bulinus*. Most of the members of this group are characterized by long-spired shells and very small radula teeth.

Bulinus (Bulinus) reticulatus Mandahl-Barth (Fig. 29)

In all, 14 samples of this small species from Rhodesia, Tanganyika, Kenya and Aden have been examined. The small shell with shouldered whorls and open umbilicus makes this species easily recognizable. The form occurring in Aden has most peculiar radula teeth (Wright, 1963a, Fig. 8), so distinctly different from teeth of African specimens that the Aden form must be regarded as a distinct subspecies, for which I propose the name *B. reticulatus wrighti* n. subsp. The shell figured by Wright (1963a, plate 2, fig. 6) is selected as the type. The only other *Bulinus* with teeth of the same type is the *B. cernicus* of Mauritius, which is in other respects different. According to Wright (1963a, p. 267) *B. reticulatus* is a potential intermediate host of *S. haematobium* in the Aden Protectorate. Its status as intermediate host in Africa is not yet known.

Bulinis (Bulinus) camerunensis Mandahl-Barth (Fig. 28)

Known only from the type-locality in Cameroon from which two samples have been examined. The characteristic shell and exceedingly small radula teeth separate it from all other *Bulinus*. Its status as intermediate host is not known.

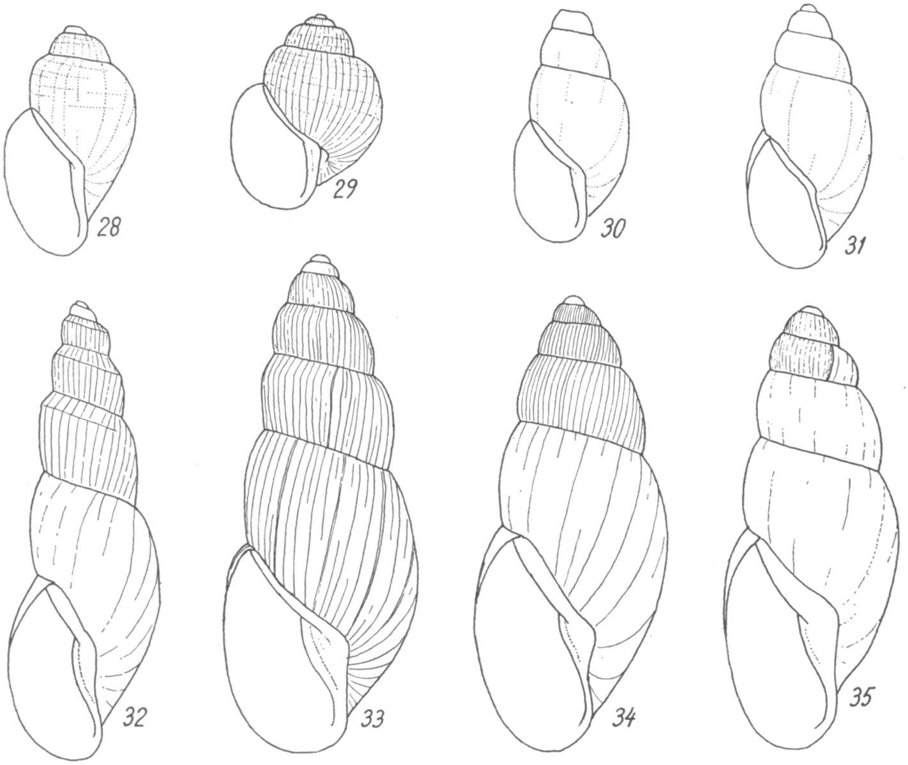
Bulinus (Bulinus) cernicus (Morelet) (Fig. 30)

This is endemic to Mauritius, where it acts as an intermediate host of *S. haematobium*. One sample, consisting of 19 specimens, has been available for examination. The small, ovate shell almost without microsculpture and the peculiar lateral teeth with an expanded mesocone are distinctive. In all specimens seen the spire is decollate.

Bulinus (Bulinus) beccarii (Paladilhe) (Fig. 31)

This is known only from Aden. It was tentatively put into the synonymy of *B. cernicus* by Mandahl-Barth (1958), but is undoubtedly specifically distinct (Wright, 1963a). It is closely related to *B. forskalii*, but has a smaller shell consisting of only 5.5 whorls

FIG. 28-35. TYPICAL SHELLS OF THE *FORSKALII* GROUP



28. *B. camerunensis* Mandahl-Barth, Cameroon. 29. *B. reticulatus* Mandahl-Barth, Tanganyika. 30. *B. cernicus* (Morelet), Mauritius. 31. *B. beccarii* (Paladilhe), Aden. 32. *B. forskalii* (Ehrenberg), Kenya. 33. *B. bavayi* (Dautzenberg), Madagascar. 34. *B. scalaris* (Dunker), Kenya. 35. *B. senegalensis* Müller. All 5.5 × natural size.

and does not have the shoulder angle or costulation of *B. forskalii*. A single sample has been examined. Wright (1963, p. 269) reports that it acts as an intermediate host of *S. haematobium*.

Bulinus (Bulinus) forskalii (Ehrenberg) (Fig. 32)

This common species is widely distributed in Africa from Mauritania, Egypt and Ethiopia southwards, and is also known from Madagascar. Altogether 366 samples have been examined. Like the other species of *Bulinus* with a wide distribution, *B. forskalii* also comprises a great number of local forms, some of which might be valid subspecies. The distinctive shoulder angle on the upper whorls is not always present; of the 366 samples examined 16 had no angle at all, and in 72 the angle was faint and difficult to observe. In such cases the small copulatory organ separates it from *B. scalaris*, and the size and the shape of the radula teeth from *B. senegalensis*. *B. forskalii* has been incriminated by various authors as an intermediate host of *S. haematobium*, but it seems to be of minor importance.

Bulinus (Bulinus) bavayi (Dautzenberg) (Fig. 33)

This species is endemic to the island of Madagascar, from which nine samples have been examined. It is closely related to *B. forskalii*, but probably is a distinct species, although no significant differences in the soft parts have been found. The shell is much wider than that of *B. forskalii*; for instance, it may be 14 mm high and 5.4 mm wide, while a Malagasy *B. forskalii* of the same height is only 3.8 mm wide. Further *B. bavayi* has a coarser and more irregular costulation on all the whorls, while in *B. forskalii* the costulation is more regular and, as a rule, restricted to the upper whorls. *B. bavayi* is a potential intermediate host of *S. haematobium* (or *S. capense*?) in the Malagasy Republic.

Bulinus (Bulinus) scalaris (Dunker) (Fig. 34)

This species is widely distributed, but seems to be rare, probably owing to its particular habitat—rainwater pools and other temporary bodies of water. Altogether 11 samples from Ethiopia, Kenya, Uganda, Congo and Zambia have been examined. Wright (1963b) records it from Angola. The very large copulatory organ is a good distinguishing character, which easily separates it from *B. forskalii* and *B. senegalensis*. Nothing is known regarding its status as intermediate host.

Bulinus (Bulinus) senegalensis (Müller) (Fig. 35)

The type-species of the genus *Bulinus* is known with certainty only from Senegal and Gambia, where it acts as an intermediate host of *S. haematobium* (Smithers, 1956). Ten samples from these countries have been examined. The relatively large radula teeth of the *truncatus* type are the only reliable distinguishing character between *B. senegalensis* and the other long-spired species of *Bulinus*, and records of its occurrence in Northern Nigeria, Niger, Chad, and the Sudan (Wright, 1959) must be viewed with some reservation until confirmed by an examination of the radula.

RÉSUMÉ

L'examen des *Bulinus* envoyés d'Afrique et du Proche-Orient au Centre OMS d'Identification des Mollusques, Charlottenlund, Danemark, a précisé nos connaissances de la répartition des différentes espèces, mais a montré aussi que certains caractères spécifiques et subspécifiques étaient moins constants et méritaient moins de crédit qu'il n'était admis.

Le sous-genre *Physopsis* diffère du sous-genre *Bulinus sensu stricto* par sa columelle tronquée, la crête sur la face ventrale du rein, les spires supérieures de sa coquille sculptées de petits nodules ou ponctuations discontinus. Les principaux caractères d'identification utilisés sont: la forme de la coquille, les organes copulatoires et le fourreau de la verge, le mésocone des dents de la radula.

L'auteur trouve insuffisant d'avoir examiné 1543 exemplaires pour résumer la connaissance actuelle des 35 espèces et sous-espèces de *Bulinus* qui se trouvent sur une aire de 34 millions de km^2. De meilleurs caractères distinctifs lui paraissent nécessaires, notamment entre les groupes *tropicus* et *truncatus* de *Bulinus* s.s.

Donnant pour chaque espèce la synonymie, les caractères distinctifs, la distribution, l'importance connue comme hôte intermédiaire, l'article détaille le tableau suivant du genre:

Bulinus (Physopsis) :

B. (Ph.) africanus, *B.(Ph.) globosus*, *B. (Ph.) nasutus*, *B. (Ph.) abyssinicus*, *B. (Ph.) jousseaumei*, *B. (Ph.) ugandae*, seul à n'être pas sensible à *Schistosoma capense*, dans ce groupe.

Bulinus sensu stricto :

Groupe *tropicus* qui comprend de nombreuses variétés locales dont certaines représentent certainement des sous-espèces distinctes, comme:

B. (B.) tropicus alluaudi, *B. (B.) tropicus zanzebaricus*, *B. (B.) tropicus toroensis.*

Groupe *truncatus* dont tous les membres peuvent être considérés comme des vecteurs possibles de *Schistosoma :*

B. (B.) truncatus truncatus, *B. (B.) truncatus sericinus*, *B. (B.) truncatus trigonus*, *B. (B.) truncatus rivularis*, *B. (B.) truncatus rohlfsi*, *B. (B.) transversalis*, *B. (B.) nyassanus*, *B. (B.) mutandaensis*, *B. (B.) contortus*, *B. (B.) guernei*, *B. (B.) coulboisi*, *B. (B.) natalensis.*

Groupe *forskalii* dont la plupart des membres sont caractérisés par des coquilles à spires allongées et de très petites dents de la radula:

B. (B.) reticulatus, *B. (B.) camerunensis*, *B. (B.) cernicus*, *B. (B.) beccarii*, *B. (B.) forskalii*, *B. (B.) bavayi*, *B. (B.) scalaris*, *B. (B.) senegalensis.*

Les conditions particulières de l'intérieur de l'Afrique favorisent l'apparition d'écophénotypes. L'isolement de nombreux gîtes permet à leurs populations d'évoluer dans un sens personnel, sans perdre pour cela l'interfécondité avec d'autres populations de la même espèce. Les grandes variations des habitats en eau fraîche provoquent la disparition des individus qui ne peuvent s'y adapter. Par ailleurs, la courte durée des collections d'eau s'oppose à la formation de nouveaux types. Les gastéropodes donnent de nouvelles espèces moins rapidement que les poissons par exemple. La région du Tanganyika, particulièrement dans sa partie nord-est, paraît un centre d'évolution active de *Physopsis* et de certains *Bulinus sensu stricto.*

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