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INTERMEDIATE HOSTS OF SCHISTOSOMA

African Biomphalaria and Bulinus : I*

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SYNOPSIS

This study is an attempt to classify all described species of African *Biomphalaria* and *Bulinus*. It is based upon the author's examination of a great number of specimens collected from many parts of Africa. The variations attributable to age, environment and genetic factors which may be noted in the taxonomic characters are discussed, and some new species and subspecies are established. For each recognized species and subspecies the author states the distinguishing characters, indicates the geographical distribution, and gives a list of synonyms.

All descriptions of shells and of the anatomical structure of the snails, as also the locality-distribution of all forms,[a] are based entirely upon a personal examination of the snails; the literature has been consulted only with the purpose of finding the proper names for the various forms which had been found to be distinguishable by anatomical and conchological examination. As the study progressed, it became evident that no satisfactory results could be obtained so long as the variability of the various systematic characters was still unknown; a great number of specimens were therefore dissected and the variations of the systematically important organs were examined. In all forms for which sufficient material was available, series of specimens of different sizes (ages) from the same population were examined in order to clear up the variations attributable to the age of the snail. Moreover, full-grown specimens of as many populations of each form as possible were dissected, so that the variations of the same organ in different populations could be studied. In all about 5000 specimens from 683 different populations were examined.

Introduction

The discrimination of species among snails, and especially freshwater snails, is generally an intricate matter and is sometimes possible only when a large amount of material is available for a thorough statistical treatment

* This is the first part of a study on the known and suspect African snail intermediate hosts of Schistosoma; the second part, to be published in a forthcoming number of the *Bulletin*, will deal with the genus *Bulinus*.

[a] The term " form " is used here not as a taxonomic unit, but as a neutral term covering species as well as all lower taxonomic categories.

of the various characters. Only in investigations concerning snails from smaller, limited areas does the existence of clear-cut species appear to be evident; as soon as the investigation is extended to snails from larger areas or, as in the present case, from an entire continent, the distinction of the various species from one another will be found extremely puzzling. This is due to several causes which may be briefly elucidated as follows.

As is generally known, a species consists of a greater or smaller number of populations of more or less different appearance resulting from genetical and environmental factors. Characteristics caused by environment may often be very striking, but are of no importance for species discrimination, whereas genetic differences, which are the decisive classifying features, are in many cases far less distinct. Unfortunately, it is impossible to set up definite rules as to how great a genetic difference may be tolerated among the various populations within one and the same species. The general rule which states that if unlimited, voluntary interbreeding takes place the individuals must belong to the same species, and if interbreeding does not take place they are of different species, cannot be applied as a definite criterion when dealing with the basommatophores. There are two reasons for this. On the one hand, the basommatophores are able to breed without previous copulation; even if copulation has occurred it may have been of no importance because no fertilization has taken place. On the other hand, it seems that two forms in one locality may occur as different species while in another locality they appear to be races of one and the same species. Cross-breeding experiments performed in the laboratory, therefore, are of only very limited value, whereas investigations in the field as to which kinds may occur together without interbreeding and which may form transitional stages when occurring together, are of the greatest importance for the valuation of the taxonomic position of each particular form.

On account of their very limited possibilities for active dispersal, snails tend to form populations genetically deviating from each other to a greater or lesser degree. The longer the period of isolation, the greater is the likelihood of the formation of a local race, deviating genetically from the typical form of the species in regard to both the shape of the shell and the internal organs. Such populations of planorbids are found in great numbers everywhere in Africa, isolated for periods of very varying duration, and hence deviating from the original forms to very varying degrees.

On the other hand, freshwater snails are by no means devoid of possibilities of passive dispersal over land. This may happen by the aid either of man or of birds, by the flooding of areas, or by the changing of riverbeds. Such passive dispersal means that different populations sometimes become mixed together, and under such conditions transitional stages will be of frequent occurrence.

Among the freshwater snails of Africa, as well as of most parts of the world, there are thus long series of genetically more or less different

populations, the determination of which, as far as family and genus are concerned, is easy, but the finer discrimination into species and subspecies is extremely intricate, and the result may often be rather artificial. Moreover, its validity will always depend on the amount of material available and on the experience of the respective malacologist with these genera. Further, the number of species into which a genus is divided will naturally depend upon the malacologist's more or less narrow conception of the definition of species, together with his valuation of the taxonomic characters. The worker who lays most stress on, for instance, certain features in the structure of the genital organs is apt to reach a different conclusion as regards definition of species and their limitations from the one who, for example, pays more attention to the characters of the radula.

The circumstances, however, are still more intricate, because other factors obscure the characters, thereby obstructing determination of the species.

All snails, but particularly freshwater snails, are influenced by their environment. This especially holds for the shaping of the shell, which, since it grows with the animal and consists mainly of lime, depends for its development upon both feeding conditions and the amount of lime in the water. Roughly speaking, in waters rich in lime, where food conditions are good, the shells become large and solid, and in waters poor in lime they become thin and fragile. Several other factors may play a role in influencing the ecophenotype, and these, together with the genetic differences, result in the well-known fact that it is hardly possible to find two separate localities with quite identical populations of the same species of freshwater snail.

Age likewise influences the appearance of snails. Most of the basommatophores reach sexual maturity long before growth has finished, and it requires a considerable amount of experience to be able to decide whether a snail has reached its final form, or whether it is still in a juvenile and unfinished stage. This point may be of the utmost importance, because not only the shape of the shell, but also the structure of the genital organs, as well as of the radula, are subject to changes with progressive age.

An animal group in which the systematic relations are as difficult to unravel as with the African Planorbidae naturally also offers ample scope for incongruity in nomenclature. According to the International Rules of Nomenclature, only the oldest name in use for the respective species has validity. Even when this rule is strictly maintained, the result may none the less appear as a discrepancy between malacologists who are otherwise in agreement on the systematics, but who have different conceptions of species. If, for instance, one malacologist considers four forms, A, B, C, and D, as distinct species, while another recognizes them to be four subspecies of one and the same species, the first will naturally name them A, B, C, and D, while the other will name them Aa, Ab, Ac, and Ad, or, if he does

not go into details on the respective subspecies, merely A. This is common practice in malacology, but for the uninitiated it undeniably seems illogical. Discrepancies of nomenclature, however, may just as well be due to different interpretations of the original description (or of the " type-specimen "). During the second half of the nineteenth century a great number of " species " of African planorbids were established—far more indeed than was reasonable. This resulted partly from the narrow conceptions of species prevalent at that time, but chiefly from lack of understanding of the variability of the different species. With a single exception, all the original descriptions concern the shell only and are so brief that they are now quite insufficient.

The specimen upon which the description was based (the type-specimen) is in most cases preserved, which may be of great help for identification. Unfortunately, the type-specimen is very often of a deviating form, or is a young, not full-grown, and frequently also " dead ", more or less corroded, shell. Further, since the determination of planorbids from shell characters alone is, as a rule, impossible, the value of the type-specimens of snails is considerably less than in most other animal groups. If possible, it is of course valuable to study snails collected in the same locality as the type-specimen, but this often proves to be impossible, because the type-locality either is given too inexactly (for example, " Ethiopia " or " Lake Victoria ") or may later have been destroyed.

THE FAMILY PLANORBIDAE

The Planorbidae are aquatic pulmonates with a flat, discoid, lens-shaped, or higher ovate to turreted shell. The animal is sinistral, that is, the genital openings and the anus are situated on the left side, but in most of the flat-shelled forms the shell appears to be dextral, because it is carried inverted, so that the side representing the spire (apical side) in other families is the lower side of the planorbid shell and the upper side is umbilical. The ovate and turreted shells are all sinistral.

All planorbids have subulate tentacles, a secondary gill (pseudobranch) on the left side of the mantle border, and a radula most often with a bicuspid central tooth, tricuspid lateral teeth, and marginal teeth with the endocone divided into several small cusps, a single mesocone, and a single or divided ectocone. The blood is red, with dissolved haemoglobin.

The African Planorbidae may be arranged into two subfamilies, the Planorbinae and the Bulininae, easily recognizable by the shape of the shells and by some anatomical features. The Planorbinae have a discoid or lens-shaped shell, a pseudobranch forming a simple lobe, a prostate gland consisting of a series of glandular tubes along the spermaduct, and a copu-

latory organ which is not completely introverted when not in use. The Bulininae have an ovate or turreted shell, a folded pseudobranch, a compact prostate gland, and a copulatory organ (" ultrapenis ") which is completely introverted when not in use. The African Planorbinae comprise the medically important genus *Biomphalaria* and a few other genera consisting of smaller species, probably of no medical importance; the Bulininae are represented by only one genus, *Bulinus*, in Africa. Further information on the Planorbidae may be found in Baker [3] and in Hubendick.[7]

The Genus Biomphalaria Preston

This genus comprises all the larger African planorbid snails with a discoid shell, except the similar *Planorbarius metidjensis* (Forbes) (= *Pl. dufourii* Graells) from the western part of North Africa. In all other parts of Africa a planorbid shell of more than 2.5 mm high will be a *Biomphalaria.*

Shell

The shell is ultradextral, orbicular, and biconcave, and forms a disc of varying height with a diameter of between 7 mm and 22 mm. The number of whorls varies between 3½ and almost 7. When few whorls are present they increase rapidly in width, while with a greater number of whorls they become more closely coiled and their width increases more slowly. The whorls may be rounded or more or less angular with an obtuse angle on the upper side which frequently disappears towards the aperture, and a usually more pronounced angle on the under side. This angle is in some forms placed near the sutures, in others almost in the middle of the under side of the whorls. The aperture is rounded or slightly angular in correspondence with the shape of the ultimate whorl, and is usually placed in the same plane as the remainder of the shell, but sometimes the last part of the ultimate whorl is bent downwards. The umbilicus, that is, the concavity on the under side of the shell, is in some forms very wide and shallow, in others narrow and deeper. As mentioned above, the umbilicus of *Biomphalaria* shells corresponds not with the umbilicus of other shells, but with the spire.

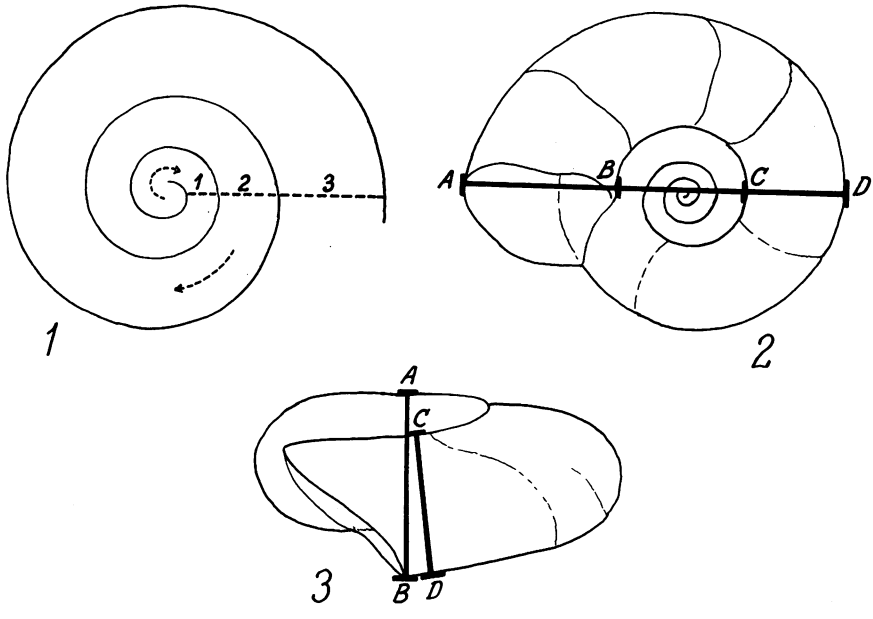
The shell is a lighter or darker brownish horn-colour, sometimes almost white, in other cases more reddish and very often concealed by a grey or black coating. The sculpture of the shell comprises curved, transversely arranged growth lines, sometimes crossed by faint spiral lines. On the under side of the whorls the spiral sculpture may be especially distinct.

As there are different ways of stating the dimensions of shells it will be suitable to explain the measurements used in this paper.

The number of whorls are counted in the way shown in Fig. 1. The stippled arrows show the direction of counting, and the stippled lines the

limits of each whorl. Thus 1, 2, and 3 indicate the end of the first, second and third whorl respectively. In *Biomphalaria* it is usually easier to count the whorls on the under side of the shell, since the first whorls are not as deeply sunken on this side as they are on the upper side. The diameter of the shell taken is its greatest diameter (the line A-D in Fig. 1(2)). The diameter of the umbilicus is to be understood as the greatest distance between the sutures on the under side of the shell, and not the distance between the angles (Fig. 1(2) B-C). The height of the shell is the largest dimension parallel to the axis (A-B in Fig. 1(3)). In most Biomphalariae this will be the same as the height of the last whorl, and for the sake of comparison it seems wiser to measure the height of the last whorl in all forms. This measure should be taken at a right angle to the longitudinal direction of the whorl, as shown in Fig. 1(3), C-D.

FIG. 1. SHELL DIMENSIONS



Immature specimens, particularly the very small ones, have a relatively higher shell than adults. In most forms a shell with a diameter of 3 mm has a height of about 2 mm (60%-66% of the diameter). In full-grown shells the height varies between 24% in *sudanica* and 36% in *pfeifferi*. The lake forms (*choanomphala*, *smithi*, etc.) have a still higher shell, the height being 42%-55% of the diameter.

The diameter of the umbilicus depends largely on the height of the shell. The higher the whorls are, the narrower is the umbilicus. That means that the umbilicus of immature shells is relatively narrower than is the case in adult specimens of the same form. In *pfeifferi*, for example, the umbilicus is 15% of the diameter in very small specimens and about 30% in full-grown ones; in *sudanica* the same proportions are 27% and 40%. The accompanying diagrams (see Fig. 2-4) show the relations between the diameter of the shell and its height and the diameter of the umbilicus in some *Biomphalaria* forms. It will be seen that in very small shells (2-4 mm in diameter) the proportions are almost the same for all forms. This is why it is so difficult to identify immature specimens.

Very rarely, and only in certain forms (*pfeifferi*, *rüppellii*, *gaudi*, *alexandrina*) immature shells may have developed lamellae in the aperture. The number of lamellae varies, but when fully developed six are present: a large one on the middle of the inner wall, a much smaller one below this, and four on the outer wall, the lowermost being placed more transversely than the others. The diameter of the shells with lamellae is usually between 5 mm and 7 mm, but a few specimens with fully developed lamellae measured 10-12 mm. The probably extinct *tchadiensis* which, typically, is lamellate is about the same size. Nothing is known of the significance of these lamellae, which can hardly be very important as they are so scarce. Lamellate shells of *Biomphalaria* were, in the past, erroneously referred to the North American genus *Planorbula* Haldemann.

Soft anatomy [a]

The general topography of the organs is shown in Fig. 5.[b]

The pallial organs. These are situated on the inner wall of the mantle and consist of the lung, the kidney, and the heart. To these may be added the rectum and the pseudo-branch. These organs seem to have little systematic value in *Biomphalaria* as they are very uniform in the various types except for their length, which is greatest in forms with a multispiral shell, such as *sudanica*, and smallest in forms with few whorls (*stanleyi*, *choanomphala*, etc.). The ridge along the rectum and the ridge between the rectum and the kidney are always present, but the third ridge, on the ventral surface of the kidney, commonly found in Planorbidae, is only present as faint traces and in few specimens. In contradistinction to *Bulinus*, this renal ridge has no systematic value in *Biomphalaria* because, when it is found, it occurs in very few specimens among many with no such ridge. The length of the pallial organs, especially the kidney, also depends upon the method of preservation; in very contracted animals they appear much shorter than in those which are fully extended.

[a] The anatomy of some *Biomphalaria* is described more or less fully by Watson (in Connolly [8]), Pilsbry,[10] Ranson,[12, 13] Ranson & Cherbonnier,[14] Abdel Malek,[1, 2] and Hubendick.[7]

[b] Fig. 5–17 were prepared with the aid of a camera lucida.

FIG. 2. RATIO OF DIAMETER OF SHELL TO HEIGHT OF SHELL (A) AND DIAMETER OF SHELL TO DIAMETER OF UMBILICUS (B) IN SOME PFEIFFERI FORMS

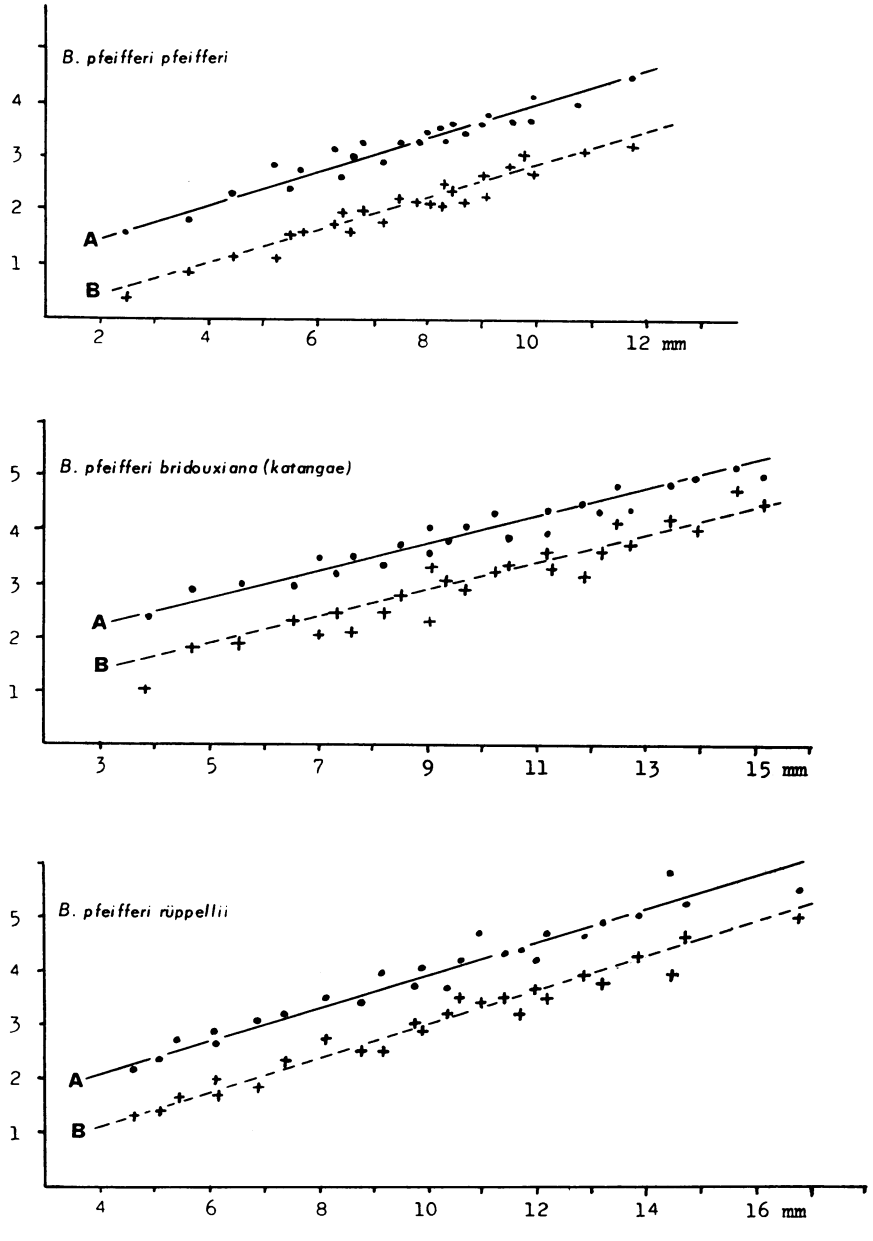


FIG. 3. RATIO OF DIAMETER OF SHELL TO HEIGHT OF SHELL (A) AND DIAMETER OF SHELL TO DIAMETER OF UMBILICUS (B) IN SOME CHOANOMPHALA FORMS

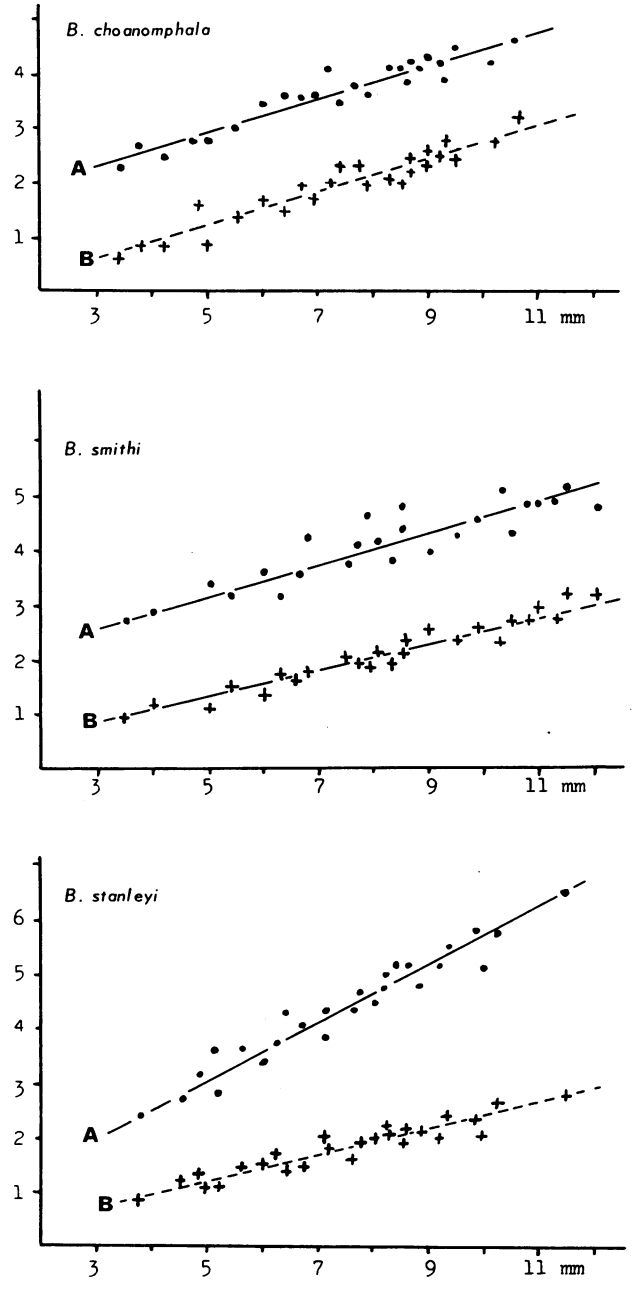


FIG. 4. RATIO OF DIAMETER OF SHELL TO HEIGHT OF SHELL (A) AND DIAMETER OF SHELL TO DIAMETER OF UMBILICUS (B) IN B. ALEXANDRINA ALEXANDRINA AND B. SUDANICA SUDANICA

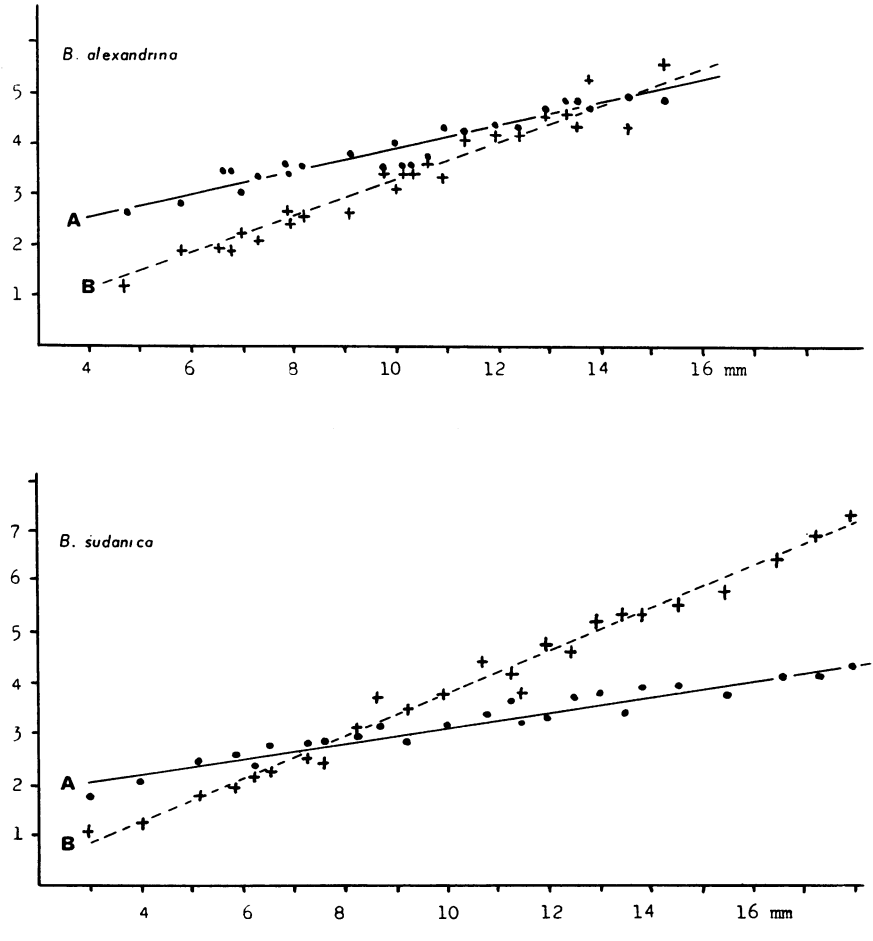
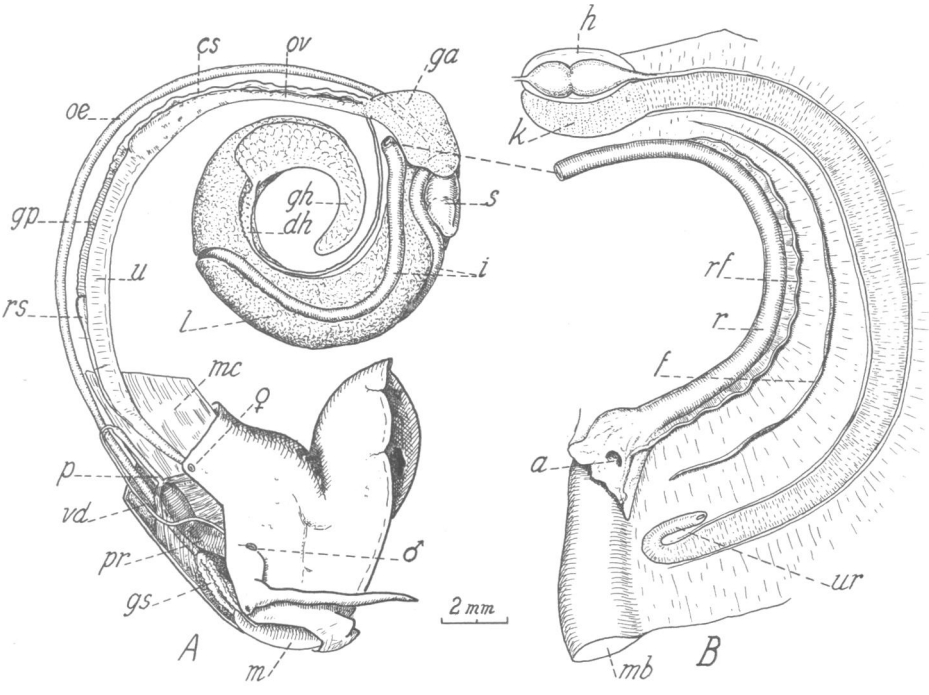


FIG. 5. GENERAL TOPOGRAPHY OF ORGANS OF B. PFEIFFERI PFEIFFERI

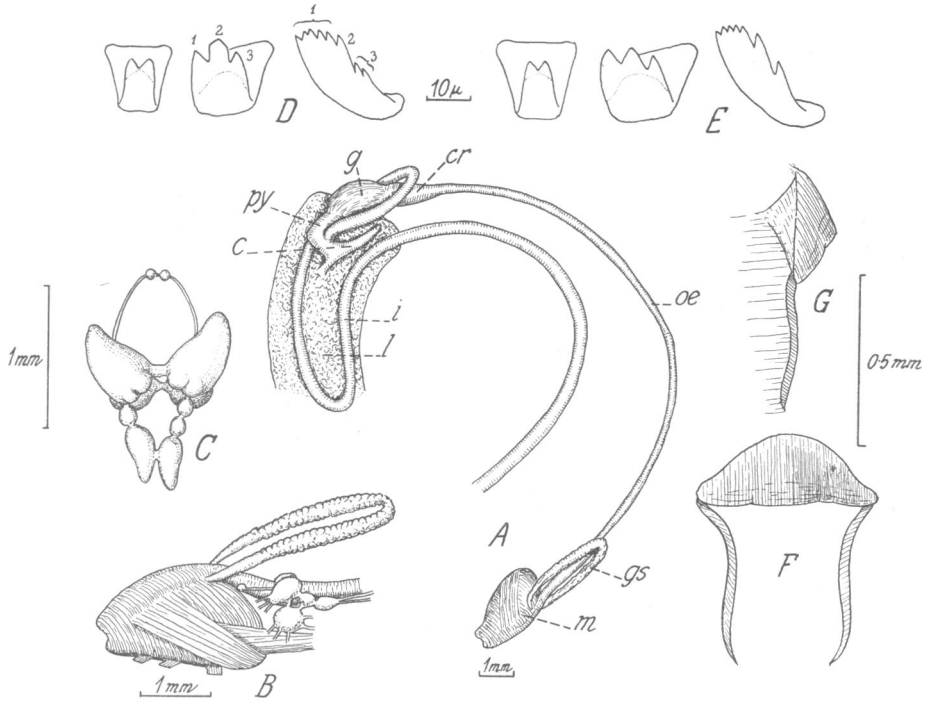


A = digestive and genital organs
B = pallial organs

a = anus
cs = spermaduct
dh = hermaphrodite duct
f = fold between rectum and kidney
ga = albumen gland
gh = ovotestis
gp = prostate gland
gs = salivary glands
h = pericardium with heart
i = intestine
k = kidney
l = liver
m = buccal mass
mb = mantle border
mc = columellar muscle
oe = oesophagus
ov = oviduct
p = vergic sheath
pr = preputium
r = rectum
rf = rectal fold
rs = receptaculum seminis
s = stomach
u = uterus
ur = ureter
vd = vas deferens
♀ = female opening
♂ = male opening

The digestive organs. These (see Fig. 6) are very similar to those found in other Planorbidae. They consist of the pear-shaped buccal mass containing the jaw, the radula, and the openings of the salivary glands, the long oesophagus, the stomach with the crop, the gizzard, and the pylorus —the latter with a caecum or stylotheca—and the long intestine which bends around the stomach and runs backwards in a loop embedded in the liver or hepato-pancreas, and then forwards along the left side of the mantle, where it forms the rectum.

FIG. 6. DIGESTIVE ORGANS AND NERVOUS SYSTEM OF B. PFEIFFERI RHODESIENSIS



A = digestive organs
c = caecum
cr = crop
g = gizzard
gs = salivary glands
i = intestine
l = liver
m = buccal mass
oe = oesophagus
py = pylorus

B = buccal mass, showing position of central nervous system
C = ganglia of nervous system
D = central tooth, first lateral tooth, and a marginal tooth of a form with arrowhead-shaped mesocones: 1 = endocone, 2 = mesocone, 3 = ectocone
E = central tooth, first lateral tooth, and a marginal tooth of a form with triangular mesocones
F = the jaw, front view
G = the jaw, lateral view

The jaw (Fig. 6 (F,G)) is of the type common in Planorbidae, consisting of a large, vertically striate superior part and two slender lateral parts. The colour of the jaw varies from an almost yellow light-brown to a rather dark brownish horn.

The radula (Fig. 6 (D, E)) is situated in the buccal mass as a membraneous plate on the upper side of which numerous small teeth are placed in transverse and longitudinal rows. Each transverse row has in the middle a central tooth and, symmetrically arranged on both sides of this, a number of lateral and marginal teeth. The shape and the development of the teeth are of systematic value, while the number of lateral and marginal teeth

depends on the age and size of the animal. A young snail has teeth of almost the same size as, but fewer in number than, the full-grown specimen.[a] The number of teeth in a single transverse row varies in full-grown *Biomphalaria* between 39 and 59.

The central tooth, as is usual in the Planorbidae, is somewhat smaller than the adjoining lateral teeth and is always provided with two cusps. The basal plate is much broader posteriorly than in front, with somewhat projecting posterior corners.

The lateral teeth have three main cusps: the endocone, the mesocone, and the ectocone. The ectocone is usually more separated from the mesocone than is the endocone. The mesocone is in most forms simply triangular, but some normally have arrowhead-shaped mesocones. Laterally the endocones become divided into two or more cusps. This division takes place usually from tooth No. 9 or 10, but sometimes from tooth No. 7, or even No. 5. The mesocones and the ectocones remain single on the lateral teeth. The basal plates have the shape of an oblique parallelogram with the posterior lateral angle somewhat prolonged.

The marginal teeth are long and obliquely placed. The endocones are usually divided into 3-6 small cusps; the mesocones remain single and are often distinctly larger than the cusps of the endocones; the ectocones are in some forms single, in others divided into 2, 3, or 4 minute cusps.

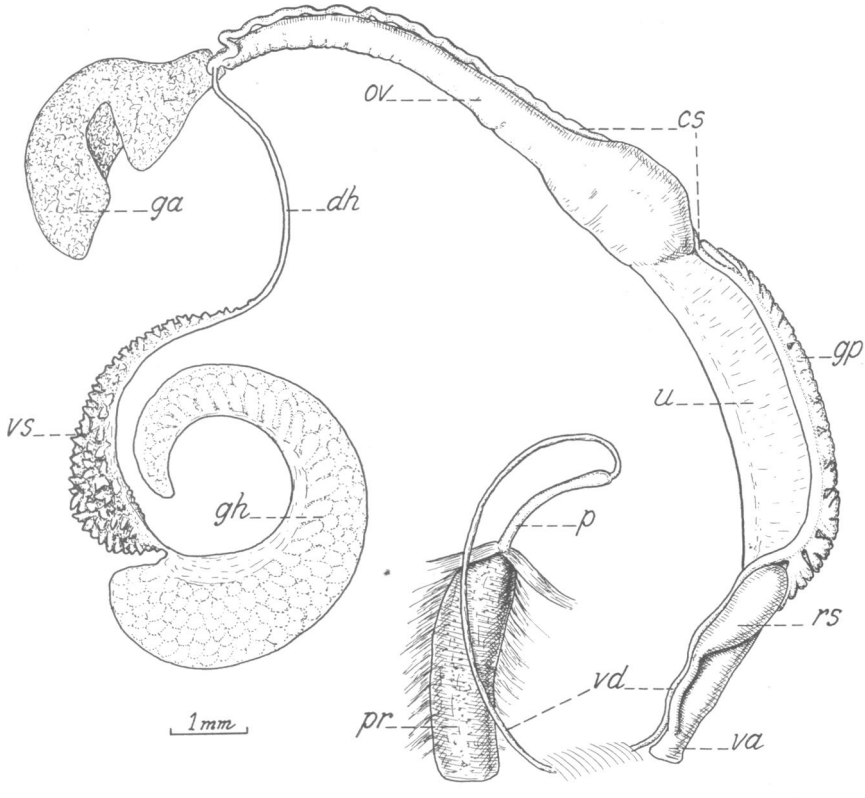
It is not unusual to find deviations from the normal, either in that a form with normally single ectocones on the marginal teeth has a single longitudinal row with divided ectocones, or in that a single specimen among the marginal teeth differs from the scheme typical for the form concerned. Coalescent lateral or marginal teeth have also been observed.

The easiest way to prepare a radula for examination is to put the buccal mass into a 5% solution of potassium hydroxide. If the snail is fresh or preserved in alcohol, the soft parts will be dissolved in about 24 hours, and the radula can be transferred to a 5% solution of acetic acid where it is carefully cleaned, stained for a few minutes in haematoxylin, briefly washed in distilled water, and embedded in glycerol or—better—in glycerol jelly on a slide. It is important that the radula be placed with the teeth upwards and carefully stretched out before the cover-glass is put on. For its examination a microscope with a magnifying power of at least 500× is necessary.

The genital organs (see Fig. 7, 8). The hermaphrodite genital gland or ovotestis is rather large and consists of numerous follicles. It forms the innermost whorl of the visceral sac and is partly covered by the liver. The hermaphrodite or ovisperm duct (Fig. 8(A)) is long. The first section of it has several seminal vesicles, the size and number of which seem to depend

[a] Only the very young specimens have distinctly smaller teeth.

FIG. 7. GENITAL ORGANS OF B. PFEIFFERI PFEIFFERI: (I)



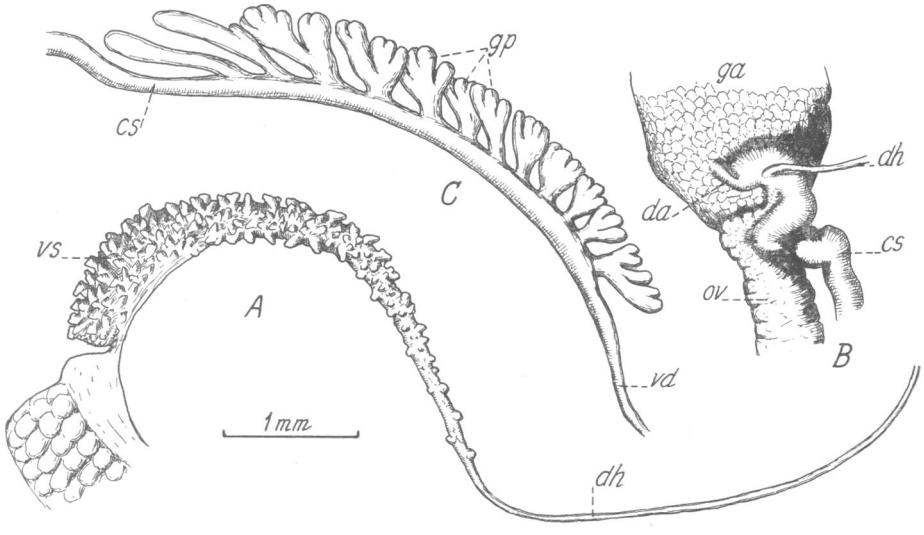
cs = spermaduct
dh = hermaphrodite duct
ga = albumen gland
gh = ovotestis
gp = prostate gland
ov = oviduct
p = vergic sheath
pr = preputium
rs = receptaculum seminis
u = uterus
va = vagina
vd = vas deferens
vs = seminal vesicles

on the sexual stage of the snail. The latter part of the ovisperm duct is a simple tube, terminating at the carrefour where the female and the male duct become separate.

The female part consists of the oviduct and the albumen gland which opens into the uppermost part of the carrefour (Fig. 8(B)) through a short duct. The gland itself is wrapped around the intestine, and its size depends on the sexual stage of the snail.

The upper part of the oviduct forms a more or less folded tube; the middle part is more voluminous, with thick walls rich in glandular cells; the distal part, the uterus, is a somewhat flattened tube. The length of the rather short, cylindrical vagina depends on the contraction of the snail;

FIG. 8. GENITAL ORGANS OF B. PFEIFFERI PFEIFFERI: (II)



A = hermaphrodite duct (dh) with seminal vesicles (vs)

B = carrefour
cs = spermaduct
da = albumen duct
dh = hermaphrodite duct
ga = albumen gland
ov = oviduct

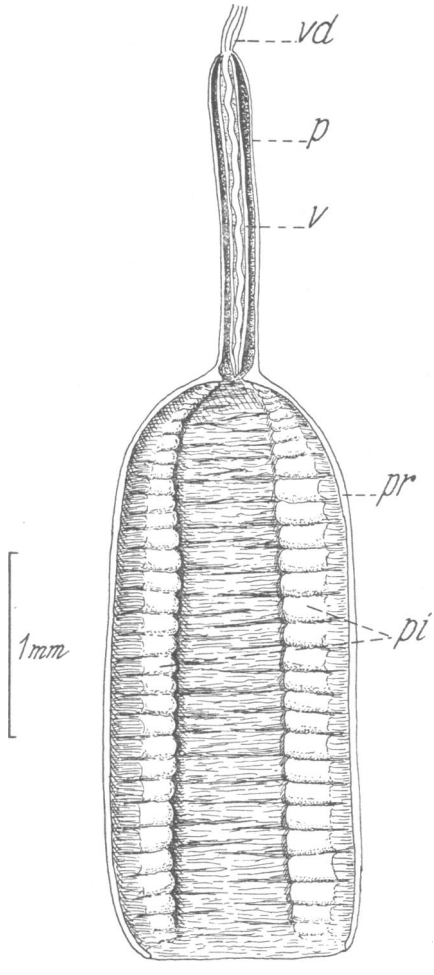
C = prostate gland (gp)
cs = spermaduct
vd = vas deferens

its opening is to be found on the left side of the animal under the mantle border. A more or less pedunculate receptaculum seminis or spermatheca enters the female duct at the junction between the vagina and the uterus. The size and shape of the spermatheca depends on whether it contains a spermatophore or not.

The male part, the spermaduct, is, in its first section, a long winding tube running along the oviduct. Its distal part is provided with a well-developed prostate gland (Fig. 8(C)) consisting of several branched tubes arranged in a single row and opening directly into the spermaduct. No separate prostate duct exists in *Biomphalaria*. The vas deferens is the male duct running from the distal end of the prostate to the copulatory organ. It is a long, winding, slender tube which at first follows the uterus and the vagina and is then hidden in the body wall from which it reappears near the base of the copulatory organ, running in a large bend backwards into the body cavity to open finally into the top of the copulatory organ.

The copulatory organ (see Fig. 9) consists above of a penial or vergic sheath surrounding the verge or penis proper which forms a longer or shorter, cylindrical and tapering tube containing a continuation of the vas deferens, which opens at the tip of the verge. The lower part of the copu-

FIG. 9. COPULATORY ORGAN OF B. PFEIFFERI PFEIFFERI



p = vergic sheath pr = preputium
pi = pilasters v = verge
vd = vas deferens

latory organ is a broader preputium, a muscular invagination from the surface of the body. It is provided with two longitudinal muscular ridges or pilasters. The male opening is situated just below and behind the left tentacle. The retractor muscles are attached at the junction between the vergic sheath and the preputium.

Among the soft parts, the copulatory organ and the radula are the characters of most value for systematization; since, however, they are rather delicate and tenuous, and subject to considerable individual and

local variability, a certain amount of practice in dissection under the microscope, and some experience in interpretation, are needed.

All parts of the genital organs tend to show great natural variation, apart from that caused by preservation methods. When the snail is contracted, the vagina and the uterus are much more contracted than the upper parts of the genital organs; the preputium, but not the vergic sheath, is also usually contracted in a contracted snail.

As the dimensions of the copulatory organ are considered to be a taxonomic character, it has been necessary to examine the influence of preservation on this organ. It was found that in 50 specimens of *alexandrina* the ratio of the length of vergic sheath to the length of preputium in contracted snails was 1.3-1.9 (average 1.62), but in fully extended specimens it was only 0.9-1.4 (average 1.14). The average ratios for 48 specimens of *sudanica* were 0.85 and 0.63 respectively. As really well-preserved snails were available only in a few forms, all the descriptions of the copulatory organ in the systematic part of this study are based upon contracted, full-grown specimens. It is important that only full-grown specimens are used because the ratio of the length of vergic sheath to the length of preputium depends on the age of the snail. In some forms this ratio is decidedly greater than 1, in others much less than 1, but in both cases we find that mature, though not full-grown, specimens often show a ratio near 1; the copulatory organ is thus of less value as a distinguishing character in young snails.

In most forms aberrant individuals have been found among populations of which other specimens examined showed copulatory organs of the normal size and shape. In forms belonging to the *pfeifferi* group it is not uncommon to find specimens with a longer vergic sheath than normal, or with the normal short vergic sheath, but with a verge longer than usual. In the Katanga form of *bridouxiana* particularly, such aberrations are common. Of 80 specimens 20 had a vergic sheath almost as long as the preputium and a verge slightly longer than the sheath. Of the remaining 60 specimens with the sheath much shorter than the preputium, 12 had a verge equal in length to the sheath, 37 a verge a little longer, and 11 a verge almost twice as long. Similar conditions are found in all other forms with a short vergic sheath, but the aberrant individuals are less frequent. In the forms belonging to the *alexandrina* group, which normally have a sheath distinctly longer than the preputium, individuals with a relatively shorter vergic sheath are fairly common in some populations, but very rare in others.

The variability of the other parts of the genital organs, especially of the hermaphrodite duct, the prostate gland, and the spermatheca, has also been examined with the hope that one or more of them would turn out to be useful in the systematics. All, however (as is clearly shown in Fig. 10-12), vary too much even within the same population to be of any taxonomic value.

FIG. 10. VARIATIONS IN THE SEMINAL VESICLES OF (A) B. PFEIFFERI PFEIFFERI AND (B) B. ALEXANDRINA ALEXANDRINA

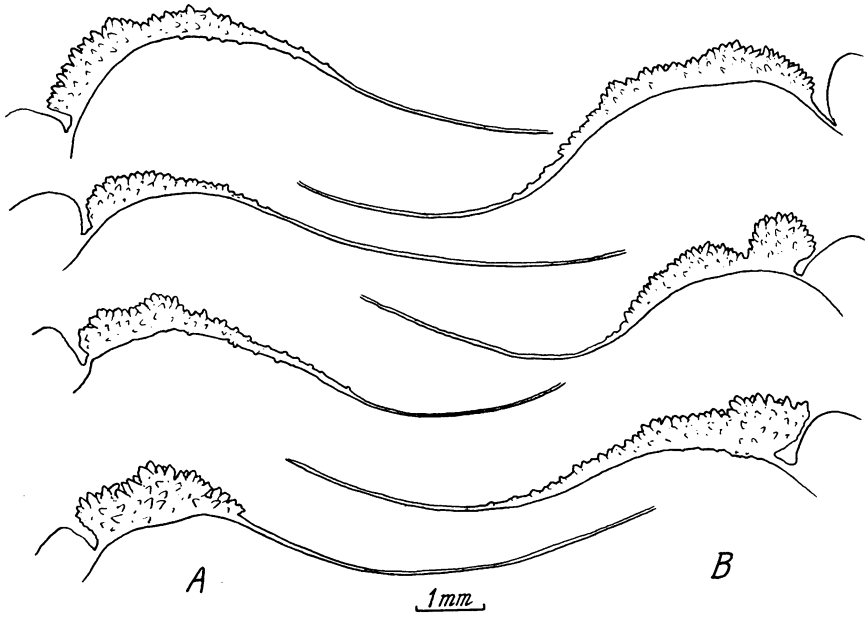


FIG. 11. VARIATIONS IN THE PROSTATE GLANDS OF (A) B. PFEIFFERI PFEIFFERI AND (B) B. ALEXANDRINA ALEXANDRINA

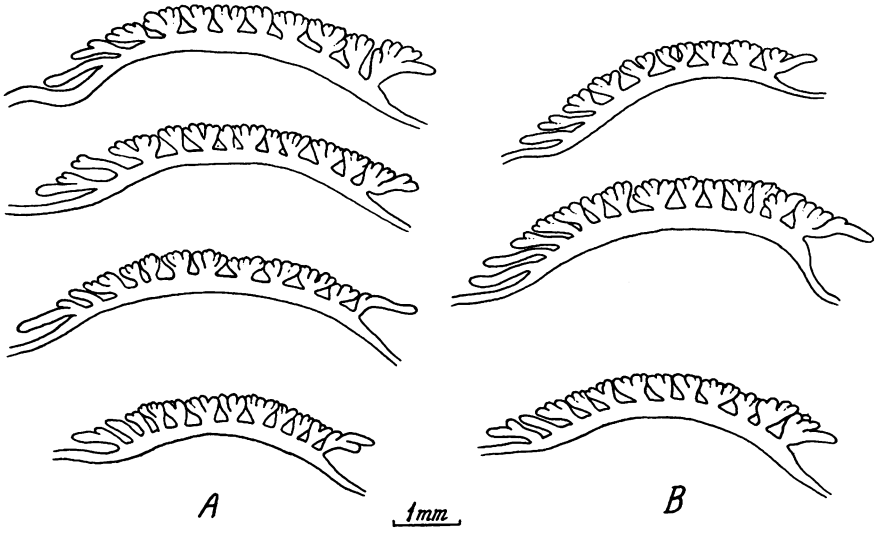
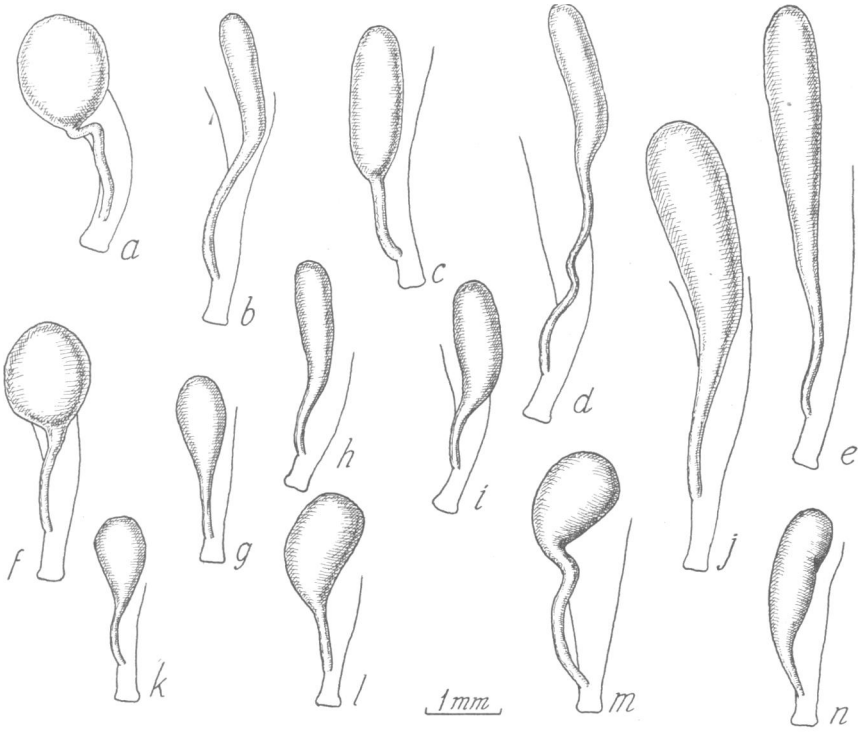


FIG. 12. VARIATIONS IN SIZE AND SHAPE OF RECEPTACULUM SEMINIS



a - e = *B. pfeifferi pfeifferi* k, l = *B. smithi*
f - j = *B. alexandrina alexandrina* m, n = *B. sudanica sudanica*

African Species and Subspecies of Biomphalaria

Until now about 50 species, 1 subspecies, and a number of varieties of the genus *Biomphalaria* have been named. Of these only 15 are recognized here as valid species or subspecies, the remainder being considered as their synonyms. Further, it has been necessary to establish one new species and three new subspecies, bringing the number of recognizable species and subspecies to 19.

From the shape of the shells and from certain anatomical structures it is possible to arrange these 19 forms of *Biomphalaria* into four groups:

(1) Pfeifferi *group*. The full-grown shell is usually less than 15 mm in diameter, with, at most, five whorls, which are convex or angular on both sides. The diameter of the shells is in most forms about two-and-a-half times the height of the last whorl. The diameter of the umbilicus is usually smaller than the height of the last whorl. The preputium, in contracted specimens, is long and cylindrical, in most forms longer than the vergic

sheath. The verge is as long as, or a little longer than, the sheath. The radula has triangular or arrowhead-shaped mesocones on the lateral teeth and single or divided ectocones on the marginal teeth.

This group comprises several forms and is represented in nearly all parts of Africa south of the Sahara.

(2) Choanomphala *group*. The shell is small, not exceeding 12 mm in diameter, and consists of only three-and-a-half to four-and-a-half angular whorls. The diameter of the shell is from two to two-and-a-half times the height of the last whorl and from four to five times the diameter of the narrow umbilicus. The copulatory organ has a sac-shaped or cylindrical preputium and a vergic sheath almost as long as the preputium. The verge is nearly equal in length to the sheath and often shows dilatation at the base. The mesocones on the lateral teeth are simply triangular, and the ectocones on the marginal teeth are single or bicuspid.

The group comprises few forms, which are restricted to certain of the great lakes.

(3) Alexandrina *group*. The shell is about 15 mm in diameter when full-grown, and consists of from five to five-and-a-half rounded or angular whorls. The relative height of the last whorl and the relative diameter of the umbilicus vary considerably within this group. The preputium is sac-shaped in contracted animals and shorter than the vergic sheath. The verge is almost as long as the sheath. The first lateral teeth have almost symmetrically arranged cusps of which the mesocones are arrowhead-shaped. The ectocones on the marginal teeth are divided into 2-4 cusps.

This group comprises few forms, which have a curiously isolated and restricted distribution.

(4) Sudanica *group*. The shell is large, up to 22 mm in diameter, and consists of from five-and-a-half to six-and-a-half closely coiled whorls which are flat or somewhat angular on the upper side and slightly angular on the under side. The diameter of the shell is from three to three-and-a-half times the height of the last whorl. The diameter of the umbilicus is, as a rule, decidedly greater than the greatest height of the last whorl. The preputium of contracted animals is sac-shaped and a little longer than the vergic sheath. The verge is nearly equal in length to the sheath. The lateral teeth have simply triangular mesocones, and the marginal teeth have single or divided ectocones.

This group, for which Thiele in his handbook [15] established a superfluous subgenus *Afroplanorbis*, comprises a West African and an East African species, each consisting of two subspecies.

It is very difficult to decide how many of the separable forms of *Biomphalaria* should be regarded as valid distinct species, because of the very small conchological and anatomical differences. In both respects almost every intermediate stage has been found, so that it seems reasonable to

collect them all into one species, as some authors have actually done. However, in nature some of them behave as separate species, for they have been found living in the same small place without interbreeding. In Lake Albert, for example, three forms (*stanleyi*, *sudanica*, and *elegans*) are widely distributed and have been found living together in a small area of some few square metres, but not a single intermediate specimen is known from that lake. In small streams near Banzyville in the Belgian Congo the late Dr Wanson collected a great number of *sudanica*, *rüppellii*, and *wansoni*, but not a single intermediate. In several localities two forms have been found in mixed populations, but apparently without hybrids. This is the case, for example, in Lake Edward (*sudanica* and *smithi*), Lake Victoria (*sudanica* and *choanomphala*, *choanomphala* and *rüppellii*), Lake Tanganyika (*bridouxiana* and *tanganyicensis*), and several dams in Uganda (*sudanica* and *rüppellii*). The forms which occur together without interbreeding must be regarded as belonging to different species.

Several of the forms seem to be good examples of subspecies. They are restricted to a certain area, and where the areas of two forms overlap intermediates are frequently found. This is the case for *sudanica* and *tanganyicensis*, *rüppellii* (including *adowensis*) and *nairobiensis*, *nairobiensis* and *bridouxiana*, *bridouxiana* and *pfeifferi*, and *bridouxiana* and *rhodesiensis*. From this it will be reasonable to consider *sudanica* and *tanganyicensis* as belonging to one species, and all the others as belonging to another. The following list shows the classification adopted here.

Pfeifferi group

B. pfeifferi pfeifferi (Krauss)
B. pfeifferi bridouxiana (Bourguignat)
B. pfeifferi rhodesiensis n. subsp.
B. pfeifferi nairobiensis (Dautzenberg)
B. pfeifferi rüppellii (Dunker)
B. pfeifferi gaudi (Ranson)
B. germaini (Ranson)

Choanomphala group

B. choanomphala choanomphala (Martens)
B. choanomphala elegans (Mandahl-Barth)
B. smithi Preston
B. stanleyi (Smith)

Alexandrina group

B. alexandrina alexandrina (Ehrenberg)
B. alexandrina wansoni n. subsp.
B. angulosa n. sp.
B. tchadiensis (Germain) ?

Sudanica group

B. camerunensis camerunensis (Boettger)
B. camerunensis manzadica n. subsp.
B. sudanica sudanica (Martens)
B. sudanica tanganyicensis (Smith)

The pfeifferi *group*

(1) *B. pfeifferi pfeifferi* (Krauss)

(see Plate I)

1848. *Planorbis pfeifferi* Krauss. Krauss, *Die südafrikanischen Mollusken*, Stuttgart, p. 83, plate 5, fig. 7. Type-locality: Umgeni River, Natal.

1882. *Planorbis madagascariensis* E. A. Smith. *Proc. zool. Soc. Lond.* p. 387, plate 22, fig. 20-22. Type-locality: Lake Itasy, Madagascar.

1893. *Planorbis bowkeri* Melvill and Ponsonby. *Ann. Mag. nat. Hist.* (6), **12**, 111, plate 3, fig. 19. Type-locality: northern Transvaal.

1910. *Planorbis hermanni* O. Boettger. *Abh. senckenb. naturf. Ges.* **32**, 452, plate 28, fig. 18 *a-c*. Type-locality: Okaputa pan, Damaraland.

The shell is of medium size, with from four-and-a-half to almost five regularly and rather rapidly increasing whorls separated by deep sutures. On the upper side the first two whorls are deeply sunken, and all whorls are rounded, except for the last third of the ultimate whorl of the adult shell, which is somewhat flattened. All whorls have on the under side an obtuse angle near the suture. The diameter of the rather shallow umbilicus is a little less than one-third of the diameter of the shell and about two-thirds of its height.

The mean measurements of 25 specimens from Transvaal are as follows—diameter of shell (D): 10.7 mm; height of last whorl (H): 4.2 mm; and diameter of umbilicus (U): 3.0 mm.

The mesocones of the lateral teeth are simply triangular or somewhat arrowhead-shaped; the ectocones of the marginal teeth are always single (see Fig. 13(a, b)). The vergic sheath is usually only about half the length of the large, cylindrical preputium, but sometimes longer. The verge is as a rule equal in length to the sheath, but in rare cases a trifle longer (see Fig. 14(b)).

Distribution: Madagascar and the southern part of Africa. The northern limit for the nominate race in Africa is approximately 15°-16° S.

B. pf. pfeifferi varies rather considerably with regard to the development of the last part of the ultimate whorl, which can be more or less sloping in front, or narrower and more rounded above. The relative size of the umbilicus also varies a little (from one-fourth to a little more than one-third of the diameter of the shell). The size is usually 10-12 mm in diameter, but in Southern Rhodesia it sometimes grows to 15 mm. In a few cases internal lamellae have been found in immature shells with a diameter of 5-7 mm.

In the northern part of its distribution *B. pf. pfeifferi* gradually merges into *B. pf. bridouxiana*. In the Rhodesias several populations of *Biomphalaria* could just as well be referred to *B. pf. bridouxiana* as to the nominate race.

"*Pl. madagascariensis*" is in all respects so similar to the nominate race that it seems unjustifiable to maintain it even as a subspecies. The only difference is that *madagascariensis* is perhaps on average a trifle larger. The mean measurements of 20 specimens from Ambositra are as follows—D: 11.9 mm; H: 4.6 mm; and U: 3.4 mm.

"*Pl. bowkeri*" seems to be an immature, typical *pfeifferi*.

"*Pl. hermanni*", known only as a fossil, is most likely a small form of *pfeifferi*.

Material examined: *Natal:* Durban. *Transvaal:* Kaapmuiden, Tzaneen, Nelspruit, Klein Lutaba. *Madagascar:* Ambositra. *Southern Rhodesia:* Salisbury, Umwindsi River, Triangle Sugar Estate. *Mozambique:* Lourenço Marques.

(2) *B. pfeifferi bridouxiana* (Bourguignat)
(see Plates II, III)

1888. *Planorbis bridouxianus* Bourguignat. Bourguignat, J. R., *Iconographie malacologique des animaux mollusques fluviatiles du lac Tanganika*, Corbeil, plate 1, fig. 9-12. 1890. *Ann. Sci. nat. (Zool.)* (7), **10**, 20, plate 1, fig. 9-12. Type-locality: the outlet of the small River Mahongolo in Lake Tanganyika near Kibanga.

1890. *Planorbis monceti* Bourguignat. *Ann. Sci. nat. (Zool.)* (7), **10**, 18. Type-locality: the western shore of Lake Tanganyika.

1934. *Biomphalaria rüppellii katangae* Haas. *Zool. Anz.* **107**, 223, fig. 3. Type-locality: a tributary of the River Mura near Panda, Katanga.

The shell is of medium size or larger, with five regularly increasing whorls which are rounded on the upper side and on the periphery, and bluntly angular near the sutures on the under side. The first whorls are deeply sunken above and only slightly below. The diameter of the shallow umbilicus is about one-third of the diameter of the shell and almost equal to its height.

The mean measurements of 18 specimens from Katanga are as follows—D: 11.9 mm; H: 4.3 mm; and U: 4.0 mm.

The mesocones of the lateral teeth are triangular or arrowhead-shaped; the ectocones of the marginal teeth are usually single but are sometimes (especially in larger specimens) divided into two or even three minute cusps (see Fig. 13(c, d, e)). In the copulatory organ the length of the vergic sheath is usually between half and two-thirds of the length of the preputium, which is long and cylindrical. The verge itself is usually somewhat longer than the sheath (see Fig. 14(e, f)).

B. pf. bridouxiana shows a great range of variation in both size and shape of shell and also, to a certain degree, in the anatomical characters. In reality it comprises a number of minor forms, but since it is impossible at present to decide whether these are geographical races or mere ecophenotypes it seems better to collect them all under the name *B. pf. bridouxiana*, and to give only a short description and a few remarks on the recognizable subdivisions.

The common form of *B. pf. bridouxiana* (Plate II, Fig. 4), which is described above, is identical with *B. rüppellii katangae* Haas and is certainly the central form from which all others belonging to the *pfeifferi* group have evolved. Unfortunately it is prohibited by the International Rules of Nomenclature to apply the name *katangae* Haas to the species or even to the subspecies, although it would be a great advantage if the names indicated the true relationships of the various forms. This form is widely distributed in the southern Belgian Congo, in Northern Rhodesia, and in the southern part of Tanganyika.

The form "*Planorbis bridouxianus*" was established on the basis of a "dead", immature shell from the River Mahongolo near its mouth. The adult shell (Plate II, Fig. 5) seems to be rather high with a broadly

concave upper side and a fairly wide, shallow umbilicus: its measurements are—D: 15.0 mm; H: 5.5 mm; and U: 5.8 mm. It is fairly common on the shores and in the marshes of Lake Tanganyika, as well as in several of the streams debouching in the lake.

A still higher form of *bridouxiana* (Plate III, Fig. 6) is found in one part of Lake Kivu (Bobandana Bay). The whorls are relatively higher and increase more rapidly in width, and the umbilicus is relatively narrower than in the Lake Tanganyika form. The mean measurements are—D: 13.8 mm; H: 5.9 mm; and U: 4.9 mm. In other parts of Lake Kivu a more normal *bridouxiana* is common.

From Katanga and westward a rather large and flat form (Plate III, Fig. 7), allied with the normal *bridouxiana*, seems to be fairly common, especially in streams and rivers. This form very much resembles " *Planorbis salinarum* " Morelet (1868, *Voyage du Dr Fr. Welwitsch dans les Royaumes d'Angola et de Benguela*, Paris, p. 85, plate 5, fig. 4) and is perhaps identical with it. It differs from all the other forms belonging to the *pfeifferi* group by the large, flat, and broadly umbilicated shell, the mean measurements of which are—D: 16.5 mm; H: 5.1 mm; and U: 5.7 mm. However, since no specimens from the type-locality, near Dungo, Angola, have been dissected hitherto, it is impossible to decide with certainty whether these flat forms are identical with *salinarum* or not. If they are, it would mean that the name *salinarum* Morelet, preceding by 20 years Bourguignat's *bridouxiana*, is the proper name for the subspecies, unless *salinarum* is revealed to be a distinct West African subspecies, the range of which overlaps with that of *bridouxiana* in the southern part of the Belgian Congo.

This does not, however, seem to be very probable, as another form of *Biomphalaria* is known from the Chibia district in Angola. It is a smaller type with a shell very much resembling that of the typical *pfeifferi* (D: 10.0 mm; H: 3.7 mm; and U: 3.0 mm) but the structure of the copulatory organ and the radula is as in *B. pf. rüppellii*, otherwise known only in eastern Africa. It is preferable to leave aside these Angolese forms until more material is available.

Material examined: *Northern Rhodesia:* Namwala, Ndola, Broken Hill, Lusaka, Mankolo, Kalungu River, Fort Jameson. *Angola:* Chibia. *Tanganyika Territory:* Tunduma. *Belgian Congo:* Lukonzolwa River, Sakania, Elisabethville, Keyberg, Kasimba River, Kisanga River, Lubilash River, Albertville, Lake Kivu, Lake Kirwa, Kabare.

(3) *B. pfeifferi rhodesiensis* n. subsp.
(see Plate IV, Fig. 9)

The shell is of medium size, consisting of five whorls rather slowly increasing in size and separated by a fairly deep suture; they are flattened above, and rounded at the periphery and below, but show a blunt angle near the suture. On both sides the first two whorls are deeply sunken.

In the rather wide umbilicus the angles on the earlier whorls project like ridges; the maximum size is about 14 mm in diameter.

The mean measurements of 11 specimens from Mazabuka are as follows—D: 12.7 mm; H: 4.1 mm; and U: 3.8 mm.

The mesocones of the lateral teeth are arrowhead-shaped, and the ectocones of the marginal teeth are single or divided into two or three minute cusps (see Fig. 13(f)). The length of the vergic sheath is about two-thirds of that of the long, cylindrical preputium. The verge is a trifle shorter than the sheath (see Fig. 14(a)).

Distribution: eastern part of Northern Rhodesia and Nyasaland (Dr P. L. Le Roux, personal communication).

Type-locality: Central Research Station, Mazabuka.

B. pf. rhodesiensis is a curious form. The shell resembles that of *B. sudanica* by the flatness of the upper side of the whorls, but has almost one whorl less at the same diameter and a much narrower umbilicus. Shells with irregular coiling are rather common. Intermediates between *B. pf. bridouxiana* and *B. pf. rhodesiensis* (see Plate III, Fig. 8) have been found at Tunduma, near the boundary between Northern Rhodesia and Tanganyika.

Material examined: *Northern Rhodesia:* Mazabuka, Mpika, Mumbwa, Fort Hill. *Tanganyika Territory:* Tunduma.

(4) *B. pfeifferi nairobiensis* (Dautzenberg)

(see Plate IV, Fig. 10, 11)

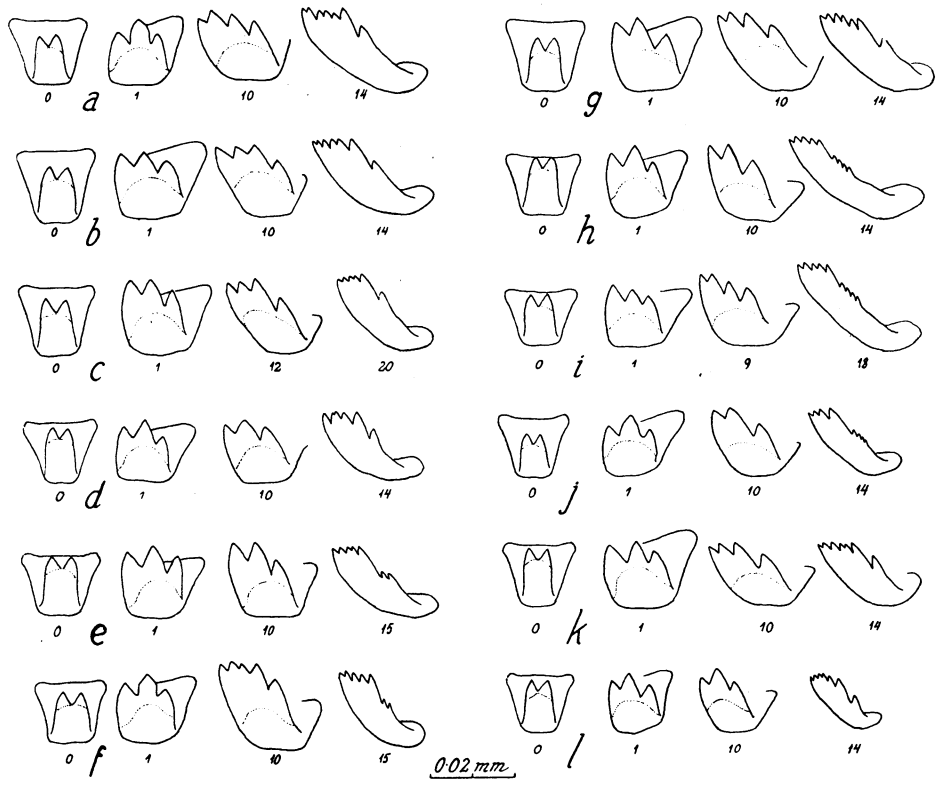
1908. *Planorbis nairobiensis* Dautzenberg. *J. Conchyliol.* **56**, 16, plate 2, fig. 1-3. Type-locality: Nairobi.

The shell is of rather small to medium size, consisting of from four to four-and-a-half regularly increasing, usually rounded whorls which have a blunt angle on the under side near the suture. The first two whorls on the upper side are deeply sunken. The diameter of the shallow umbilicus is, as a rule, a little less than one-third of the diameter of the shell and about three-fourths of the greatest height of the last whorl. The shell is often, but not always, a pale horn colour, but is frequently covered by a dark coating. The maximum size is about 15 mm in diameter.

The mean measurements of 11 specimens from Nairobi River are—D: 11.9 mm; H: 4.2 mm; and U: 3.8 mm. In most other localities this form is considerably smaller, for example, average measurements for 10 specimens from Ngudu (Tanganyika) were—D: 8.8 mm; H: 3.5 mm; and U: 2.5 mm.

The mesocones of the lateral teeth are simply triangular; the ectocones of the marginal teeth are usually bicuspid, but sometimes undivided (see Fig. 13(g)). Specimens from the Nairobi area have a rather long vergic

FIG. 13. RADULA TEETH OF THE PFEIFFERI GROUP



a = *pfeifferi*, Durban

b = *pfeifferi*, Salisbury

c = *bridouxiana*, Elisabethville

d = *bridouxiana*, Lake Kivu

e = *bridouxiana* (cf. *salinarum*), Kisanga River

f = *rhodesiensis*, Mazabuka

g = *nairobiensis*, Ngudu

h = *rüppellii*, Arua

i = *rüppellii* (*adowensis*), Jarvis Dam, Uganda

j = intermediate between *rüppellii* and *gaudi*, Jebel Marra

k = *gaudi*, Casamance River area

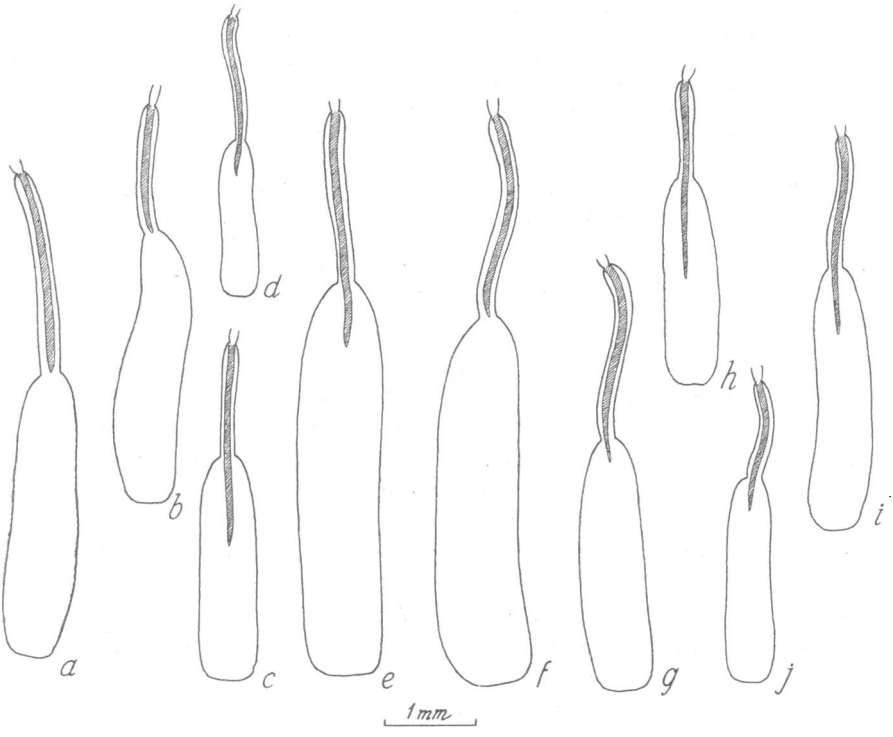
l = *germaini*, Tassili des Ajjer

sheath, about two-thirds of the length of the preputium, and the verge is only a little longer than the sheath (see Fig. 14(c, d)). In western Kenya and in Tanganyika the vergic sheath measures only half the length of the preputium, and the verge is almost twice as long as the sheath.

Distribution: southern Kenya and the northern part of Tanganyika; also a few in the eastern part of the Belgian Congo (Rutshuru).

B. pf. nairobiensis is a somewhat doubtful form. It looks very much like an immature specimen of the common form of *bridouxiana*, but is apparently full-grown. In anatomical structure the two are very similar,

FIG. 14. TYPICAL COPULATORY ORGANS OF CONTRACTED SNAILS OF THE PFEIFFERI GROUP



Diameter of shell given in mm

a = *rhodesiensis*, Mazabuka, 13 mm
b = *pfeifferi*, Durban, 12 mm
c = *nairobiensis*, Ngudu, 11 mm
d = *nairobiensis*, Teita Hills, Kenya, 11 mm
e = *bridouxiana*, Katanga, 15 mm
f = *bridouxiana*, Lake Kivu, 14 mm
g = *rüppellii*, Arua, 14 mm
h = *rüppellii* (*adowensis*), Aduwa, 12 mm
= intermediate between *rüppellii* and *gaudi*, Jebel Marra, 12 mm
= *gaudi*, Senegal, 9 mm

which suggests that *nairobiensis* should not be classed separately from *bridouxiana*; however, as long as no material from the central part of Tanganyika is available, it seems better to maintain *nairobiensis* as a distinct race. In the central part of Kenya intermediates between *nairobiensis* and *rüppellii* are common.

Material examined: *Tanganyika Territory:* Songea, Korogwe, Ngudu, Mbulu, Moshi, Arusha. *Kenya Colony:* Nairobi, Ngong Reserve, Kitui, Teita Hills, Kisumu, Akala, Nyando River, Embu, Mwea, Lake Jipe. *Belgian Congo:* Lodja.

(5) *B. pfeifferi rüppellii* (Dunker) (see Plate V, VI, VII)

1848. *Planorbis rüppellii* Dunker. *Proc. zool. Soc. Lond.* p. 42. Type-locality : Abyssinia.
1879. *Planorbis adowensis* Bourguignat. Bourguignat, J. R., *Description de diverses espèces terrestres et fluviatiles et de différents genres de mollusques de l'Egypte, de l'Abyssinie, de Zanzibar, du Sénégal et du centre de l'Afrique*, Paris, p. 11. Type-locality : Aduwa, Ethiopia.
1883. *Planorbis herbini* Bourguignat. *Ann. Sci. nat. (Zool.)* (6), **15**, 101, 127. Type-locality : Abyssinia.
1887. *Planorbis cecchii* Pollonera. *Boll. Lab. Mus. Zool. Anat. comp. Torino*, **2**, No. 34, p. 2. Type-locality : Cimbisi, Choa, Eritrea.
1898. *Planorbula boccardi* Pollonera. *Boll. Lab. Zool. Anat. comp. Torino*, **13**, No. 313, p. 11, fig. 22-25. Type-locality: Adi Ugri, Eritrea.
1904. *Planorbis bozasi* Rochebrune and Germain. *Bull. Mus. Hist. nat., Paris*, p. 141. Type-locality: Lake Shala, Ethiopia.

The shell is of medium size, with from four-and-a-half to a little more than five regularly increasing whorls separated by deep sutures. The whorls are rounded above, except for the last third of the ultimate one, which is usually somewhat flattened towards the aperture. The first two whorls are more deeply sunken on the upper side than on the under side. A more or less pronounced angle appears near the suture on the under side. The diameter of the rather shallow umbilicus is about one-third of the diameter of the shell, and almost equal to the height of the last whorl. The maximum diameter is about 17 mm, but the usual size is only about 13 mm.

The mean measurements of 12 specimens from Arua are as follows— D: 13.4 mm; H: 5.4 mm; and U: 4.8 mm.

The mesocones of the lateral teeth are triangular, while the ectocones of the marginal teeth are always divided into four small cusps (see Fig. 13 (h-j)). The vergic sheath is a trifle shorter than the cylindrical preputium. The verge is usually a little longer than the sheath. The copulatory organ is relatively of smaller size than in other races of *B. pfeifferi* (see Fig. 14 (g-i)).

Distribution: from Yemen and Eritrea to Tanganyika and the northern and eastern part of the Belgian Congo.

B. pf. rüppellii is the northernmost race of *B. pfeifferi*. It was described in the same year (1848) as *pfeifferi*, but it has been impossible to elucidate which of them has priority; as *pfeifferi*, however, is the more commonly used and known name, it may be accorded prior claim. The typical *rüppellii* from Ethiopia is a rather small shell, usually not exceeding 11 mm in diameter. In Uganda and Kenya it grows to a larger size, its maximum diameter being about 17 mm. Immature shells with a diameter of 5-7 mm occasionally possess lamellae inside the aperture (see Plate VI), arranged in exactly the same way as those found in young *pfeifferi*.

" *Planorbis adowensis* " Bourguignat is rather different from the typical *rüppellii* both in the shape of the shell and in the structure of the

copulatory organ. Most populations consist of either typical *rüppellii* or *adowensis*, but in some localities in the Sudan and Kenya mixed populations with all intermediates have been found. The distribution of the *adowensis* form is exactly the same as that of the typical *rüppellii*, so that they cannot justifiably be regarded as belonging to two different subspecies; nor can they be ecophenotypes when they are found in mixed populations and usually occur in the same kind of habitat. They can hardly be more than variations of one and the same subspecies. However, as the *adowensis* form is often strikingly different from the typical *rüppellii*, it is necessary to give a short description.

The shell is smaller, consisting of from four to four-and-a-half more rapidly increasing whorls, of which the last is usually more flattened toward the aperture. The contour of the shell is very often not regularly curved, but more or less angular. The umbilicus is narrower, and equals about one-fourth of the diameter of the shell and two-thirds of its height.

The mean measurements of 17 specimens from Jarvis Dam, Uganda, are as follows—D: 12.7 mm; H: 4.8 mm; and U: 3.4 mm, but usually smaller (specimens from Kakamega, Kenya are—D: 11.2 mm; H: 4.6 mm; and U: 2.5 mm).

The radula is exactly like that of *rüppellii*. The copulatory organ has a much shorter vergic sheath, measuring only about half the length of the preputium. The verge is twice as long as its sheath and reaches to the middle of the preputium.

"*Planorbis adowensis*" is a doubtful "species", because no type specimen nor original figure exists. Specimens from near Aduwa have been dissected.

"*Planorbis herbini*" was created by Bourguignat for the shell described and illustrated by Jickeli.[9] It is without doubt the *adowensis* form of *rüppellii*.

"*Planorbis cecchii*" is certainly an immature *rüppellii*, while "*Planorbula boccardi*" is an immature specimen of the *adowensis* form. "*Planorbis bozasi*" is inseparable from the typical *rüppellii*.

Material examined: *Eritrea:* Adi Ugri, between Aduwa and Adigrat, Asmara, Deca Mere, Fil-Fil, Mareb River. *Ethiopia:* Lake Tana, Akaki. *British Somaliland:* Tog Laferug. *Sudan:* Gezira, Wad Medani, Jebel Marra. *Kenya Colony:* Tebere, Kakamega, Marsabit, Mumias, Kasat River, Sukari Dam. *Uganda:* Lake Mutanda, Lake Bunyoni, Lake Nyabikede, Fort Portal, Jarvis Dam, Serere, Gulu, Arua. *Tanganyika Territory:* Mwanza. *Belgian Congo:* Lake Luhondo, Mongbwalu, Buta, Bunia, Beni, Bela, Butembo, Mobisio, Manguredjipa, Irumu, Penge, Banzyville.

(6) *B. pfeifferi gaudi* (Ranson)
(see Plate VIII)

1953. *Planorbis gaudi* Ranson. *Bull. Soc. Path. exot.* **46**, 804 (*nomen nudum*).

? 1864. *Planorbis duveyrieri* Deshayes. Duveyrier, H., *Exploration du Sahara — Les Touaregs du Nord*, Paris, p. 45, plate 3. Type-locality : Sahara, near Ghourd-Ma'ammer.

? 1864. *Planorbis aucapitainianus* Bourguignat. Bourguignat, J. R., *Mollusques terrestres et fluviatiles recueillis par M. Henri Duveyrier dans le Sahara.* In : Duveyrier, H., *Exploration du Sahara*, Paris, p. 24, plate 28, fig. 1-5. Type-locality : Sahara, near Ghourd-Ma'ammer.

The shell is small, with from four to four-and-a-half regularly increasing, rounded whorls which have a blunt angle near the suture on the under side. The first two whorls are deeply sunken on the upper side. The diameter of the shallow umbilicus is less than one-third of the diameter of the shell and slightly smaller than the height of the last whorl; the maximum diameter is 10.5 mm. The colour is usually a dark brownish-horn.

The mean measurements of 18 specimens from Gambia are as follows— D: 9.2 mm; H: 3.3 mm; and U: 2.8 mm.

The mesocones of the lateral teeth are simply triangular; the ectocones of the marginal teeth are single (see Fig. 13(k)). The copulatory organ has a vergic sheath, the length of which is about two-thirds of that of the cylindrical preputium. The verge is usually about one-third longer than the sheath (see Fig. 14(j)). In specimens from Liberia and Nigeria the vergic sheath is usually relatively longer with a verge of equal length.

Distribution: Senegal (type-locality: Rufisque), Gambia, Casamance River area, Liberia and Ghana. The eastern limit is not known, but in Jebel Marra (Darfur, Sudan) Dr D. J. Lewis has collected specimens which are intermediate between *gaudi* and *rüppellii*.

B. pf. gaudi is a West African parallel to the East African *B. pf. nairobiensis* and, like this, shows affinities to both *B. pf. rüppellii* and *B. pf. bridouxiana*. It is very probable that a more thorough examination of a larger amount of *Biomphalaria* material from the western and north-western parts of Africa will show that the name *gaudi* will be superseded by an older name. Germain has described a number of varieties belonging to what he named *Planorbis bridouxi* or *adowensis*, and one of these variety names may well be the proper name for this West African *Biomphalaria*, unless it is found not to differ essentially from the fossil "*Planorbis*" *duveyrieri* (= *aucapitainianus*) (see Plate VIII, Fig. 20) from the Sahara.

Material examined : *French West Africa:* Rufisque, Casamance River. *Gambia:* Kiti, Gambissar, Jakoroh. *Liberia:* Suakoko. *Ghana:* Chernsua River, Mampa Rive, Hu Stream.

(7) *B. germaini* (Ranson)
(see Plate IX, Fig. 21)

1953. *Planorbis germaini* Ranson. *Bull. Soc. Path. exot.* **46**, 805.

The name "*Planorbis germaini*" was given to the *Biomphalaria* from Lake Chad and from the Sahara, mentioned under various names by

Germain in a great number of papers. Through the kindness of Dr G. Ranson I have had the opportunity of examining a single specimen of his *germaini* from Tassili des Ajjer, and it differs remarkably from the foregoing both in the shape of the shell and in the structure of the radula (see Fig. 13 (l)). It belongs definitely to another form, possibly to another species, but since a single specimen is far from being enough for a sound valuation of a taxonomic unit within the genus *Biomphalaria*, I prefer to leave the final decision until more material is available. In my opinion this specimen from Tassili des Ajjer can hardly belong to the same form as the Lake Chad *Biomphalaria*, which does not differ essentially from *gaudi* with regard to the shell (see Plate VIII, Fig. 19). The soft anatomy of the Lake Chad form is still unknown.

A study of the Sahara forms of *Biomphalaria* will certainly be most interesting, as the few still living populations must be regarded as the last survivors from a time when the Sahara was no desert, and its lakes and rivers were filled with water giving favourable conditions for snail life. The scanty material available at the moment is far from being sufficient for such a study.

The choanomphala *group*

This group comprises a small number of characteristic high-shelled and narrow-umbilicated forms from Lakes Victoria, Kyoga, Albert, Edward and possibly also Kivu, and some of the smaller lakes in the neighbourhood of Lake Kivu. The systematic position of these lake forms is not yet quite clear. They seem to be closely allied, and have certainly evolved from the same species, but they cannot be regarded as subspecies of one species, because, when occurring together, they do not interbreed (*stanleyi* and *elegans* in Lake Albert).

To this group belong four main forms, *choanomphala*, *elegans*, *smithi*, and *stanleyi*. According to the anatomy, *choanomphala* is more nearly related to *elegans*, and *smithi* to *stanleyi*, than are the two pairs to each other. On the other hand, the differences in shell between *smithi* and *stanleyi* are greater than between *smithi* and *choanomphala*. For these reasons *choanomphala*, *smithi*, and *stanleyi* are here regarded as distinct species, and *elegans* as a subspecies of *choanomphala*.

(8) *B. choanomphala choanomphala* (Martens)

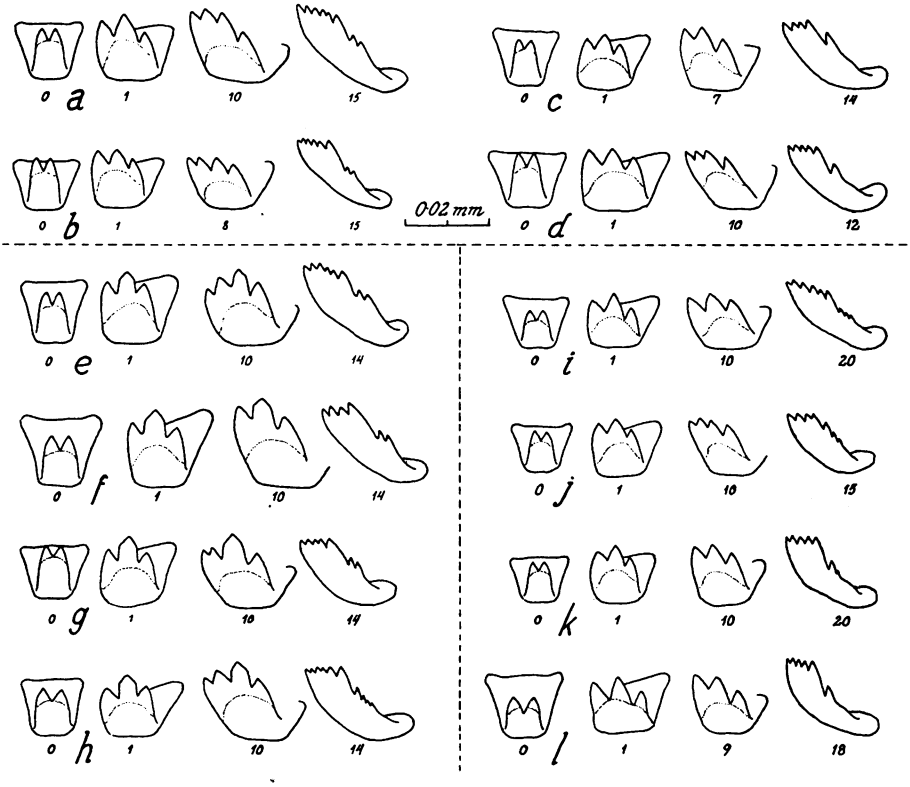
(see Plate IX, Fig. 22, 23)

1879. *Planorbis choanomphalus* Martens. *S. B. Ges. naturf. Fr. Berl.* p. 103. Type-locality: south-western shore of Lake Victoria.

1892. *Planorbis victoriae* E. A. Smith. *Ann. Mag. nat. Hist.* (6), **10**, 383. Type-locality: northern shore of Lake Victoria.

The shell is small and relatively high, with from three-and-a-half to four rapidly increasing whorls of which the last forms almost the entire

FIG. 15. RADULA TEETH



Choanomphala group

a = *choanomphala*, Jinja Bay

b = *elegans*, Butiaba

c = *smithi*, Lake Edward

d = *stanleyi*, Butiaba

Alexandrina group

e = *alexandrina*, north of Cairo

f = *alexandrina* ? Ghat

g = *wansoni*, Banzyville

h = *angulosa*, Lake Ngwasi

Sudanica group

i = *sudanica*, Nyenga, Uganda

j = intermediate between *sudanica* and *tanganyicensis*, Kavirondo Gulf

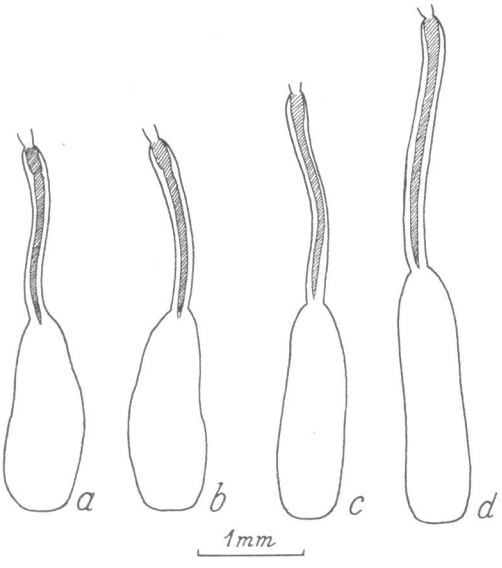
k = *tanganyicensis*, Albertville

l = *manzadica*, Manzadi

shell. The first whorls are rounded on the upper side, while the last is flattened above, angularly rounded on the outer side, and on the under side has an almost right-angled keel with flat sides, the inner of which is flush with the deep, funnel-shaped umbilicus. The basal keel or angle is placed medially on the whorls.

The mean measurements of 20 specimens from Dagusi Island are as follows—D: 7.2 mm; H: 3.2 mm; and U: 1.7 mm; those of 17 specimens from Mwanza are—D: 9.7 mm; H: 4.2 mm; and U: 2.5 mm.

FIG. 16. TYPICAL COPULATORY ORGANS OF CONTRACTED SNAILS OF THE CHOANOMPHALA GROUP



Diameter of shell given in mm

a = *choanomphala*, Jinja Bay, 10 mm
b = *elegans*, Butiaba, 9 mm
c = *stanleyi*, Butiaba, 9 mm
d = *smithi*, Lake Edward, 10 mm

The lateral teeth have triangular mesocones; the ectocones of the marginal teeth are bicuspid (see Fig. 15(a)). The vergic sheath is equal in length to the somewhat barrel-shaped preputium. The verge itself has a dilatation at the base and is equal in length to the sheath, or a little longer (see Fig. 16(a)).

Distribution: Lake Victoria, the Victoria Nile, and Lake Kyoga. In Lake Victoria this snail occurs from the shore and outwards to a depth of at least 40 feet (12 m).

B. ch. choanomphala varies considerably in both shape and size of shell. In Lake Victoria it is possible to distinguish between two forms which probably are only ecophenotypes, as the one is found in shallow water and the other at greater depth. The latter seems to be the typical form according to Martens' description. It is smaller and has more angular whorls. The Dagusi specimens, of which measurements are given above, belong to this form. The shallow-water form, "*Planorbis victoriae*" of Smith, has a bigger shell with more rounded whorls. The shells from Mwanza belong to this form.

Records of *B. choanomphala* from other African lakes (Lakes Albert, Edward, Kivu, and Tanganyika) show confusion with other forms. The erroneous identification of the high-shelled form of *B. pf. bridouxiana* of Lake Kivu in Pilsbry & Bequaert [11] is responsible for the later records of *choanomphala* in Lakes Kivu and Tanganyika.

Material examined: *Uganda:* Victoria Nile from Jinja to Bujagali, Lake Victoria at Jinja, Dagusi Island, Buvuma Channel, Entebbe, Sese Islands, Bukakata. *Kenya:* Kavirondo Gulf. *Tanganyika Territory:* Bukoba, Ilemera, Mwanza.

(9) *B. choanomphala elegans* (Mandahl-Barth)
(see Plate IX, Fig. 24)

1954. *Biomphalaria elegans* Mandahl-Barth. *Ann. mus. Congo Belge*, 8*vo*, **32**, 82, fig. 36*c*. Type-locality: Butiaba, eastern shore of Lake Albert.

The shell differs from that of the nominate race by the following characters. The first whorls have on the upper side a distinct angle which disappears towards the aperture. On the under side all the whorls have a pronounced angle running near the sutures. The concavities on both sides have regular, smooth sides. The sculpture, consisting of very fine growth lines, provides the shell with a silky lustre.

The mean measurements of 22 specimens from Butiaba are as follows—D: 7.8 mm; H: 3.4 mm; and U: 1.8 mm.

The radula and the copulatory organ are of the same structure as in the nominate race (see Fig. 15(b) and 16(b)).

Distribution: Lake Albert.

One *Biomphalaria* from Lake Kivu shows some resemblance with *B. ch. elegans*, but the shell is considerably bigger, having a diameter of up to at least 10 mm, and the angles on the whorls project like ridges in the concavities on both sides. A similar form is found in some of the lakes of Ruanda. More material is necessary before a final decision on the systematic position of these snails can be made.

Material examined: *Uganda:* Lake Albert at Tonya, Kibiro and Butiaba, Albert Nile at Liri and Packwach. *Belgian Congo:* Lake Albert and Lake Mohasi.

(10) *B. smithi* Preston
(see Plate X, Fig. 25)

1910. *Biomphalaria smithi* Preston. *Ann. Mag. nat. Hist.* (8), **6**, 535, plate 9, fig. 26-26a. Type-locality: Lake Edward.

The shell is of medium size, with from four to four-and-a-half rapidly increasing whorls. The last third of the ultimate whorl usually slopes downwards, often to such a degree that the upper edge of the aperture is attached to the penultimate whorl near its lower side. On the upper side the whorls are bluntly, and on the under side more pronouncedly, angular.

The basal angle is situated not near the suture, but closer to the middle of the whorl. The diameter of the narrow umbilicus (between the sutures) is about one-fourth of the diameter of the shell, and about half the height of the last whorl.

The mean measurements of 20 specimens from the north-eastern shore of Lake Edward are as follows—D: 11.7 mm; H: 4.9 mm; and U: 2.7 mm. The maximum diameter is about 13 mm.

The mesocones of the lateral teeth are simply triangular. The marginal teeth usually have an undivided ectocone, but sometimes a single or a few longitudinal rows of marginal teeth have bicuspid ectocones (see Fig. 15(c)). The copulatory organ is relatively long and slender. The vergic sheath is equal in length to the preputium or even a trifle longer. The verge is a little longer than the sheath, and in some specimens has slight dilatation at the base (see Fig. 16(d)).

Distribution: Lake Edward. It is not unlikely that *B. smithi* lives also in some crater lakes east of Lake Edward, because Mr C. C. Cridland has found some immature shells looking very much like young *smithi* in a crater lake near Kichwamba Hotel, south of the Kazinga Channel.

The usually sharp slope of the last whorl provides the shell of *smithi* with such a peculiar appearance that it seems to stand alone among the other *Biomphalariae*. This slope is not, however, a very important character, and in fact *smithi* is closely related to *stanleyi* and *choanomphala*. Immature shells with no deviation of the last whorl do not resemble the adults, but in these the deviation is sometimes not developed, in which case it may be difficult to separate *smithi* from *choanomphala* on the basis of the shells alone. Such specimens of *smithi* have also generally been identified with *choanomphala*.

Material examined: *Uganda:* Lake Edward, Mirambi Crater Lake. *Belgian Congo:* Lake Edward at Vitshumbi.

(11) *B. stanleyi* (Smith)
(see Plate X, Fig. 26, 27)

1888. *Planorbis stanleyi* E. A. Smith. *Proc. zool. Soc. Lond.* p. 55. Type-locality: Lake Albert.

The shell is of small to medium size, and relatively higher than in any other *Biomphalaria*. It consists of a little less than four whorls which on both sides bear a rounded angle projecting slightly into the concavities. The whorls are more high than wide. The diameter of the very narrow umbilicus is only one-fifth of the diameter of the shell and about two-fifths of the height of the last whorl.

The mean measurements of 14 specimens from Butiaba are as follows—D: 10.5 mm; H: 5.8 mm; and U: 2.2 mm. The maximum diameter is 11.6 mm.

The soft anatomy does not differ from that of *B. smithi* (see Fig. 15(d) and 16(c)).

Distribution: known only in Lake Albert.

Immature shells of *B. stanleyi* are relatively flatter, because it is the last whorl which gives the exceptionally high shell and aperture. It is the only *Biomphalaria* in which the diameter of the umbilicus increases at a lower rate than does the height during the growth of the shell. *Stanleyi* seems to differ too greatly from *smithi* in shell characters to be regarded as a subspecies, which otherwise would be plausible.

The many records in the literature of occurrences of *B. stanleyi* in lakes other than Lake Albert rest on confusion with other species. Germain's erroneous identification of *bridouxiana* with *stanleyi* (see Connolly [6]) is responsible for most such errors.

Material examined: *Uganda:* Lake Albert at Ndaga, Butiaba and Panyimur. *Belgian Congo:* Lake Albert at Blukwe.

The alexandrina *group*

This group comprises rather large *Biomphalariae* with a peculiar scattered distribution over the continent. They are characterized by the usually long vergic sheath—in contracted animals, exceeding the length of the preputium—and the arrowhead-shaped mesocones of the lateral teeth.

Three living forms which may be referred to two species are known, but it is very likely that the presumably extinct *B. tchadiensis* from Lake Chad also belongs to this group. It looks very much like an oversized immature *alexandrina.*

(12) *B. alexandrina alexandrina* (Ehrenberg)
(see Plate XI, XII)

1831. *Planorbis alexandrinus* Ehrenberg. Ehrenberg, C. G., *Symbolae Physicae seu Icones et Descriptiones Animalium Evertebratorum*, Berlin, vol. I, p. 18. Type-locality: the Nile Delta between Alexandria and Rosetta.

1838. *Planorbis boissyi*, Potiez and Michaud. Potiez, V. L. V. & Michaud, A. L. G., *Galerie des mollusques, ou catalogue méthodique, description et raisonné des mollusques et coquilles du Muséum de Douai*, Paris, vol. I, p. 208, plate 21, fig. 4-6. Type-locality: the Nile (not *Planorbis boissyi* Deshayes, 1837).

1874. *Planorbis paeteli* Jickeli. Jickeli, C. F., *Nova Acta Leop. Carol.* **37**, 212, plate 7, fig. 19. Type-locality: the Nile.[a]

The shell is rather large and consists of about five whorls, which as a rule are rounded on both sides except for the upper side of the last third of the ultimate whorl which is somewhat flattened. In some specimens a

[a] Bourguignat [4] and Innès [8] published a great number of " new species " from Egypt, all synonymous with *B. alexandrina.* It seems better to leave all these superfluous names in silence than to resuscitate them by giving references here.

blunt angle is present on the under side near the suture. The diameter of the shell is about three times the height of the last whorl. The umbilicus is open and wide, showing all the earlier whorls. Its diameter is usually equal to the height or a trifle greater.

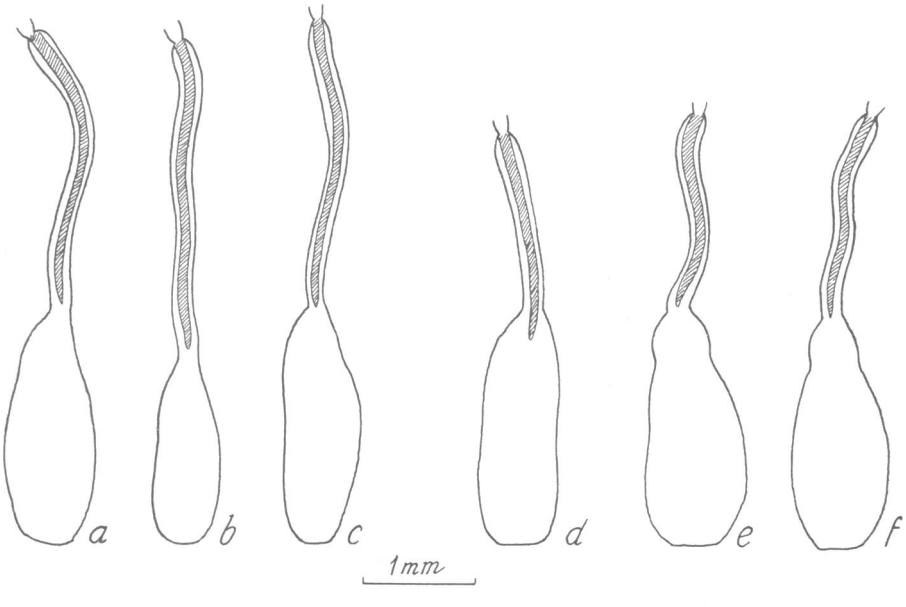
The mean measurements of 20 specimens from north of Cairo are as follows—D: 14.2 mm; H: 4.8 mm; and U: 5.0 mm. The maximum diameter is about 16 mm.

The lateral teeth are very characteristic, with an arrowhead-shaped mesocone and almost symmetrically placed endocones and ectocones. The ectocones of the marginal teeth are single or bicuspid (see Fig. 15(e)). In contracted animals the vergic sheath is about one-and-a-half times as long as the barrel-shaped preputium. The verge is equal in length to the preputium (see Fig. 17(a)).

Distribution: the Nile Delta.

B. a. alexandrina is commonly known as *B. boissyi* (Potiez & Michaud, 1838), but the name *alexandrina*, given by Ehrenberg, 1831, to the immature

FIG. 17. TYPICAL COPULATORY ORGANS OF CONTRACTED SNAILS OF THE ALEXANDRINA AND SUDANICA GROUPS



Diameter of shell given in mm

Alexandrina group
a = *alexandrina*, north of Cairo, 14 mm
b = *wansoni*, Banzyville, 14 mm
c = *angulosa*, Lake Ngwasi, 15 mm

Sudanica group
d = *manzadica*, Manzadi, 13 mm
e = *sudanica*, Nyenga, Uganda, 15 mm
f = *tanganyicensis*, Albertville, 16 mm

shell with internal lamellae, has priority, since it has been stated that young specimens of *boissyi* (5-7 mm in diameter) sometimes possess such lamellae. Besides, the name *boissyi* may not be used for the Egyptian species as it was given by Deshayes, 1837, to a fossil planorbid shell.

B. a. alexandrina shows a rather great range of variability both as regards shape and size of shell, and anatomical features. The typical *alexandrina* (see Plate XI, Fig. 29) with the long vergic sheath is apparently restricted to the coastal area of Egypt; it is of rather small size. The mean measurements of 10 specimens from Alexandria are as follows—D: 12.9 mm; H: 4.2 mm; and U: 4.7 mm. Southward, the shell tends to become bigger and the vergic sheath becomes relatively shorter, not exceeding the preputium in length (see Plate XII, Fig. 30). In some localities the shells are flatter, more widely umbilicated, and more closely coiled. The mean measurements of 10 such specimens from the Quesna area are as follows—D: 16.2 mm; H: 4.4 mm; and U: 6.3 mm. This form shows a great resemblance to *B. a. wansoni*, but differs from it by the much shorter vergic sheath, and also by the less pronounced arrowhead shape of the cusps on the lateral teeth of the radula. Future examination of a larger amount of material must decide whether it is desirable to regard this inland form as a distinct subspecies, in which case the name "*paeteli*" Jickeli is available.

By the kindness of Dr G. Ranson I have had the opportunity of examining a few specimens of a *Biomphalaria* from Ghat in Fezzan. They were not quite adult, although apparently mature. The shell (see Plate XII, Fig. 31) and copulatory organ were of the same type as those of *B. pf. rüppellii*, but the radula teeth (see Fig. 15(f)) were of the *alexandrina* type. Judging by other *Biomphalariae*, it is very likely that the copulatory organ in these is not fully developed, and that full-grown specimens will have a relatively longer vergic sheath. Additional material must be awaited before a final decision can be made.

Material examined: *Egypt:* Alexandria, Alexandria-Rosetta Road, Lake Mariut, Samahiya, Dessuq, Kafr Demera, Samahat Canal, Khadrawiya Canal, Khadrawat Canal, Batures, Beni Suef, Sanafir Canal, Gehabliya Canal. *Fezzan:* Ghat.

(13) *B. alexandrina wansoni* n. subsp.
(see Plate XIII, Fig. 32)

The shell is rather large, with about five regularly increasing whorls which are somewhat flattened on the upper side and evenly rounded on the under side. The diameter of the shell is more than three times the height of the ultimate whorl. The umbilicus is usually very shallow, with a diameter distinctly greater than the height.

The mean measurements of 20 specimens from Banzyville are—D: 15.0 mm; H: 4.4 mm; and U: 6.2 mm. The maximum diameter is about 17 mm.

The radula is as in the nominate race (see Fig. 15(g)). The copulatory organ has a still longer vergic sheath, about twice as long as the small, barrel-shaped preputium. The verge is equal in length to the sheath (see Fig. 17(b)).

Distribution: hitherto known only in the northernmost part of the Belgian Congo (type-locality: Banzyville), and in Ubangi-Shari.

This new subspecies was collected by the late Dr M. Wanson in streams in the neighbourhood of Banzyville. It differs from the nominate race by the flatter shell with more regularly increasing whorls and the relatively wider umbilicus, and further by the much longer vergic sheath.

Material examined: *Belgian Congo:* Banzyville.

(14) *B. angulosa* n. sp.
(see Plate XIII, Fig. 33)

The shell is rather large and high, with from four-and-a-half to five whorls which have a distinct angle on both sides. The angle on the upper side is placed almost in the middle of the whorls, while the basal angle is situated nearer to the sutures. The colour of the shell is a bright reddish-brown with a silky lustre caused by the regular and fine growth lines. The concavity on the upper side is deeper and more funnel-shaped than is the umbilicus, in which the angle of the earlier whorls projects as a ridge. The height of the last whorl is more than one-third of the diameter of the shell and is distinctly greater than the diameter of the umbilicus.

The mean measurements of two specimens from Lake Ngwasi (Tanganyika) are as follows—D: 15.0 mm; H: 5.5 mm; and U: 4.6 mm.

The lateral teeth have arrowhead-shaped mesocones and symmetrically arranged endocones and ectocones. The ectocones of the marginal teeth are divided into four cusps, the innermost of which is much bigger than the others (see Fig. 15(h)). The copulatory organ has a vergic sheath distinctly longer, as a rule, than the small, barrel-shaped preputium. The verge is a trifle shorter than the sheath (see Fig. 17(c)).

Distribution: hitherto known only from Lake Ngwasi in southern Tanganyika (type-locality), from Chambezi Wantipa in Northern Rhodesia, and from near Durban. These few findings indicate, perhaps, a wide distribution in south-east Africa.

In the appearance of the shell, *B. angulosa* shows some resemblance with *B. camerunensis*, the anatomy of which is unfortunately still unknown. In the soft parts *B. angulosa* is closely related with *B. alexandrina*, but the shell is so different that it seems more reasonable to regard it as a distinct species.

Material examined: *Tanganyika Territory:* Lake Ngwasi. *Northern Rhodesia:* Chambezi Wantipa. *Natal:* Durban.

(15) *B. tchadiensis* (Germain)
(see Plate XIV, Fig. 34)

1904. *Planorbula tchadiensis* Germain. *Bull. Mus. Hist. nat., Paris*, p. 468. Type-locality: Lake Chad in the Kouri archipelago.

The shell is rather small, consisting of almost five regularly increasing, rounded whorls which have a blunt angle on the under side near the sutures. Characteristic for this species is the strongly labiate and somewhat expanded aperture within which lamellae are often present. These lamellae correspond exactly to those sometimes found in immature shells of *B. alexandrina* and *pfeifferi*. The height of the last whorl is about one-third of the diameter of the shell. The diameter of the umbilicus is a little greater than the height.

The measurements of a big shell from Lake Chad are as follows—D: 10.1 mm; H: 3.3 mm; and U: 3.8 mm.

The appearance of the soft parts is unknown.

Distribution: Lake Chad.

Of this species only " dead " shells have been found, and it is very likely that it is extinct. It is not possible, therefore, to decide with certainty its systematic position, but it seems most reasonable to put it into the *alexandrina* group as it has the appearance of an oversized immature *B. alexandrina*.

Material examined: *French West Africa:* Lake Chad.

The sudanica *group*

This group comprises the largest of the *Biomphalariae* and consists of a West African and an East African species, each with two subspecies. Unfortunately, the nominate race of the West African species is known only from the shells of the type lot; thus it is not certain that it has been rightly classified. However, the form described here as a new subspecies of this species shows so great a resemblance in the shell with the presumed nominate race that it seems justifiable to arrange them in this way.

(16) *B. camerunensis camerunensis* (C. R. Boettger)

1941. *Australorbis camerunensis* Boettger. *Arch. Molluskenk.* **73**, 121. Type-locality: Mongonge, north-west of Mt Cameroon.

The shell is large, consisting of five-and-a-half rather slowly increasing whorls which are somewhat flattened on the upper side with a blunt angle above the periphery. The under side of the whorls is rounded and has a not very prominent angle near the suture. The height is a little more than one-third of the diameter of the shell. The diameter of the umbilicus, into which the angle on the earlier whorls projects like a ridge, is a little less than the height.

The measurements of the type specimen are as follows—D: 20.2 mm; H: 7.5 mm; and U: 6.5 mm.

Distribution: known only from the type-locality in the British Cameroons.

Hitherto it has been impossible to obtain material of this species. At the request of the author, Mr P. J. Moore of the Helminthiasis Research Scheme, Kumba, visited Mongonge in order to collect snails there, but without success as far as *Biomphalaria* is concerned. Mr Moore reports that Mongonge is now a deserted banana plantation, overrun by elephants, and that the only pool in the neighbourhood is two miles away. Neither snails nor water-plants were found in this pool.

(17) *B. camerunensis manzadica* n. subsp.
(see Plate XIV, Fig. 35)

The shell is rather large, with a little more than five regularly increasing whorls, which are flat on the upper side and have a very blunt angle above the rounded periphery. The under side of the whorls is flat between the periphery and the blunt angle near the suture. This angle projects like a ridge into the shallow umbilicus, the diameter of which is distinctly greater than the height of the last whorl. The diameter of the shell is three times as great as the height. The colour is a very dark brownish-horn.

The mean measurements of 14 specimens from Manzadi, Lower Congo, are as follows—D: 14.4 mm; H: 4.8 mm; and U: 5.8 mm. The maximum diameter is about 15.5 mm.

The central tooth and the first lateral teeth have widely separated triangular cusps. The ectocones of the marginal teeth are usually single, but sometimes bicuspid (see Fig. 15(1)). The vergic sheath is almost as long as the somewhat barrel-shaped preputium. The verge is, as a rule, a little longer than the sheath (see Fig. 17(d)).

Distribution: known only from a few localities in the Lower Congo. Type-locality: River N'Koko at Manzadi.

This new form was collected by the late Dr E. Dartevelle, of the Musée Royal du Congo Belge, who was generous enough to allow the author to publish the first description here.

Material examined: *Belgian Congo:* Manzadi, Zambi, Kimpese.

(18) *B. sudanica sudanica* (Martens)
(see Plate XV, Fig. 36)

1870. *Planorbis sudanicus* Martens. *Malak. Bl.* **17**, 35. Type-locality: Sudan, in the region of Bahr el Ghazal.

1904. *Planorbis tetragonostoma* Germain. *Bull. Mus. Hist. Nat., Paris*, p. 467.

The shell is large and flat, with up to a little more than six whorls, which are flat on the upper side, but separated by a fairly deep suture. The under side of the whorls is more convex with a rounded angle near the sutures. The umbilicus is very wide and shallow, occupying a little more than two-fifths of the diameter of the shell. The height of the last whorl is only about two-thirds of the diameter of the umbilicus and a little more than one-fourth of the diameter of the shell.

The mean measurements of 16 specimens from Nyenga, Uganda, are as follows—D: 15.1 mm; H: 4.2 mm; and U: 6.5 mm. The maximum diameter is about 18 mm.

The radula teeth are smaller than in other *Biomphalaria* species. The ectocones of the marginal teeth are single or more commonly divided into two or three small cusps (see Fig. 15(i, j)). The preputium is somewhat barrel-shaped and often has a constriction near its upper end. The sheath of the verge is a little shorter than the preputium and equal in length to the verge (see Fig. 17(e)).

Distribution: from southern Sudan and southward through Uganda and Kenya to the northern part of Tanganyika, and westward through the eastern and northern part of the Belgian Congo and the Ubangi-Shari to the Lake Chad region. Its main distribution lies north of the equator, but typical *sudanica* can also be found in Tanganyika, where otherwise *B. s. tanganyicensis* or intermediates between the two are prevalent.

B. s. sudanica is, as a rule, easily recognizable by the flat, widely umbilicate shell, consisting of a great number of slowly increasing whorls, but sometimes shells are found with a narrower umbilicus or with more rounded whorls. Such aberrations, however, are very often caused by irregular coiling.

Material examined: *Sudan:* Juba, Jonglei. *Uganda:* Nyenga, Kampala, Iganga, Kibimbe River, Bugondo, Akoli, Fajao, Lira, Butiaba, Kibiro, Packwach, Nimule; Lake Edward,[a] Lake Kikoronga, Kazinga Channel, Kichwamba, Lake Lutoto, Bujagali, Bugungu, Mbarara. *Belgian Congo:* Bunia, Doruma, Lake Edward.

(19) *B. sudanica tanganyicensis* (Smith)
(see Plate XV, Fig. 37)

1881. *Segmentina (Planorbula) alexandrina* var. *tanganyicensis* E. A. Smith. *Proc. zool. Soc. Lond.*, p. 294, plate 34, fig. 30-30b. Type-locality : Lake Tanganyika.

1888. *Planorbis tanganikanus* Bourguignat. Bourguignat, J. R., *Iconographie malacologique des animaux mollusques fluviatiles du lac Tanganika*, Corbeil, plate 1, fig. 16-17. 1890, *Ann. Sci. nat. (Zool.)* (7), **10**, 16, plate 1, fig. 16-17. Type-locality: Lake Tanganyika, near the outlet of the Lukuga River.

1888. *Planorbis lavigerianus* Bourguignat. Bourguignat, J. R., *Iconographie malacologique des animaux mollusques fluviatiles du lac Tanganika*, Corbeil, plate 1, fig. 5-8. 1890, *Ann. Sci. nat. (Zool.)* (7), **10**, 19, plate 1, fig. 5-8. Type locality: Lake Tanganyika, on the southern shore of the Ubuari Peninsula, near Kibanga.

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[a] In this and the following Uganda localities intermediates between *B. s. sudanica* and *B. s. tanganyicensis* are found.

The shell differs from that of the nominate race by the relatively greater height, narrower umbilicus, and more pronounced angle on the under side of the whorls. At the same size, it has half a whorl less than the typical form.

The mean measurements of 14 specimens from Albertville are as follows—D: 17.4 mm; H: 5.0 mm; and U: 6.8 mm. The maximum size is about 22 mm in diameter.

The anatomy does not differ from that of the nominate race (see Fig. 15(k) and 17(f)).

Distribution: Central Africa, mainly south of the equator; Uganda, the Belgian Congo; Tanganyika; and possibly also Northern Rhodesia.

Intermediates between *B. s. sudanica* and *B. s. tanganyicensis* are frequently found, especially in areas near the equator. Bourguignat's name *tanganikana* has been commonly used for this form, but an examination of the type-specimen of Smith's " var." *tanganyicensis* has shown that they belong to the same form. " *Planorbis lavigerianus* " seems to be an immature shell of this form.

Material examined: *Uganda.*[a] *Kenya Colony :* Kavirondo Gulf. *Tanganyika Territory :* Arusha, Mwanza. *Belgian Congo :* Usumbura, Albertville, Vitshumbi, Sasha River, Lake Kisale, Kongolo.

ACKNOWLEDGEMENTS

It is thanks to a rich supply of material from almost every part of Africa, made available by many kind friends in both Africa and Europe, that I have been able to base this study entirely upon a personal examination of the anatomical and conchological structure of the snails discussed. I therefore take great pleasure in expressing my warmest gratitude for the valuable help of: Dr E. T. Abdel Malek, Sudan; Dr W. Alves, Southern Rhodesia; Dr N. Ayad, Egypt; Dr E. Berry, U.S.A.; Dr E. Biocca, Italy; Mr V. Clarke, Southern Rhodesia ; Mr C. C. Cridland, Uganda; the late Dr E. Dartevelle, Belgium; Dr B. De Meillon, Union of South Africa; Dr B. O. L. Duke, Cameroons; Dr E. Barato Feio, Angola; Dr J. Gillet, Belgian Congo; Mrs A. Gismann, Egypt; Dr P. L. Le Roux, England; Dr D. J. Lewis, Sudan; Mr J. McClelland, England; Dr F. McCullough, formerly of the Gold Coast; Mr McMahon, Kenya; Mr J. P. Moore, Cameroons; Dr T. de Morais, Mozambique; Dr R. Paulian, Madagascar; Dr G. Ranson, France; Dr N. D. R. Schaafsma, formerly of Angola; Mr S. R. Smithers, Gambia; Dr B. Verdcourt, Kenya; the late Dr M. Wanson, Belgian Congo; Mr H. Watson, England; and Dr C. A. Wright, England.

RÉSUMÉ

L'auteur cherche à établir une classification de toutes les espèces de *Biomphalaria* et de *Bulinus* africains qui ont été décrites. Il a examiné à cette fin un grand nombre de spécimens recueillis dans de nombreuses régions de l'Afrique. Il analyse les variations imputables à l'âge, au milieu et aux facteurs génétiques qui peuvent être observées dans les caractères taxinomiques et il établit un certain nombre d'espèces et sous-espèces nouvelles. Pour chaque espèce et sous-espèce reconnue, l'auteur précise les caractères distinctifs, indique la distribution géographique et donne une liste de synonymes.

[a] See under *B. s. sudanica* on page 1143.

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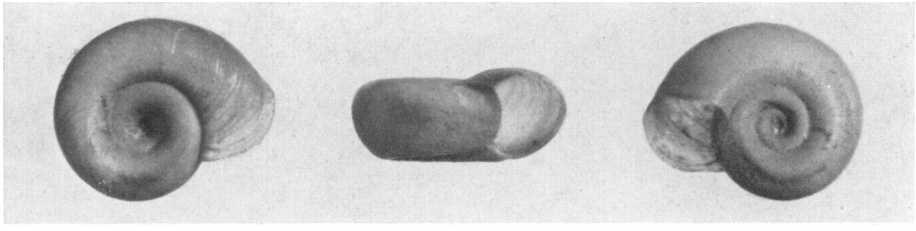
ILLUSTRATIONS *

* The magnification of Fig. 15 on Plate VI is × 18; that of all other photographs is × 3.

PLATE



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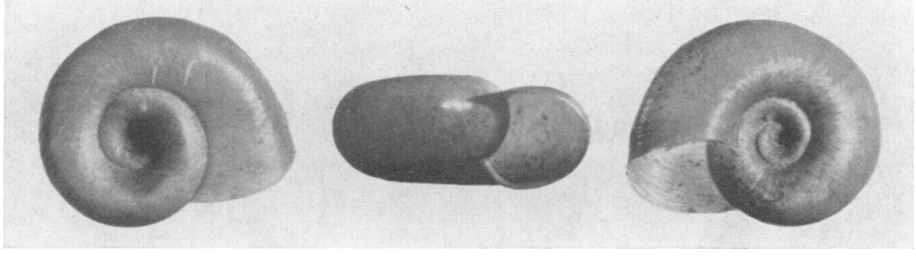

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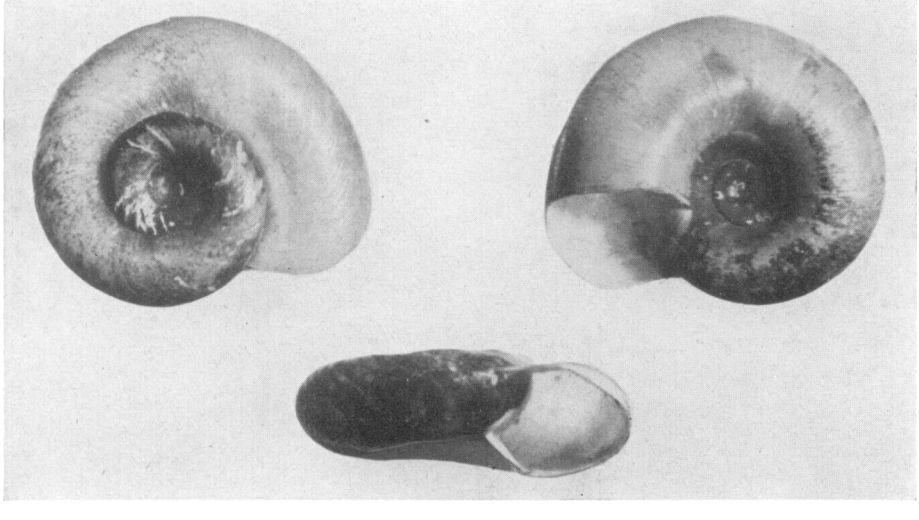

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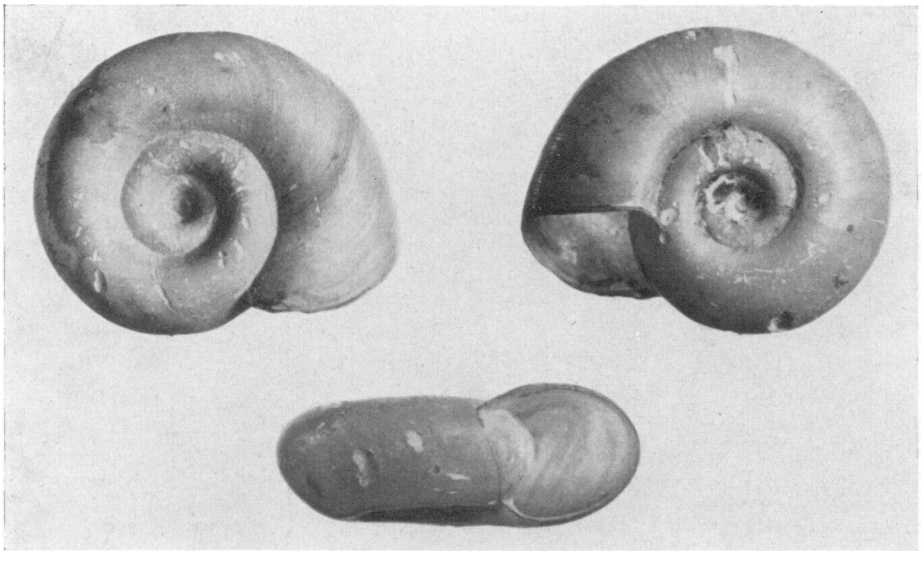
Fig. 1. *B. pfeifferi pfeifferi*, Umgeni River, Natal
Fig. 2. *B. pfeifferi pfeifferi*, Ambositra, Madagascar (= *madagascariensis* Smith)
Fig. 3. *B. pfeifferi pfeifferi*, Salisbury, Southern Rhodesia



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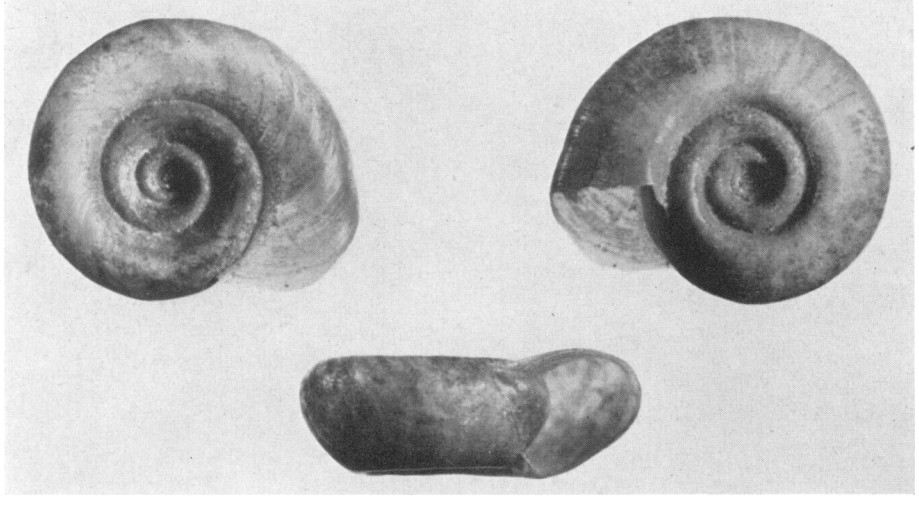

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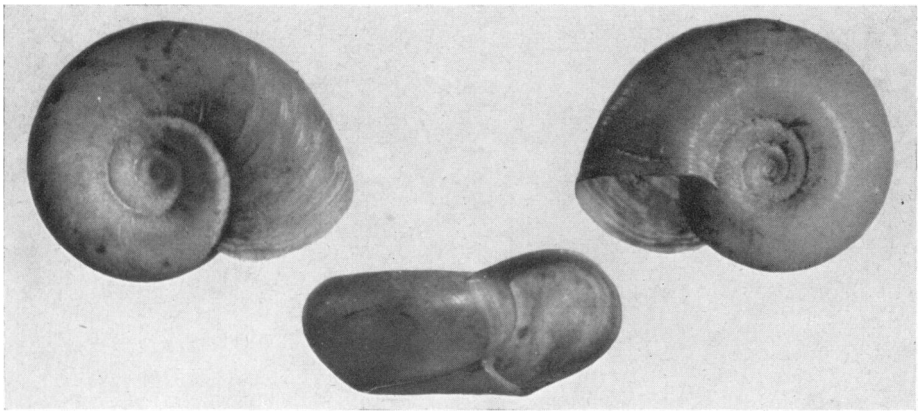
Fig. 4. *B. pfeifferi bridouxiana*, Kasimba River, Katanga (= *katangae* Haas)
Fig. 5. *B. pfeifferi bridouxiana*, Albertville, Lake Tanganyika



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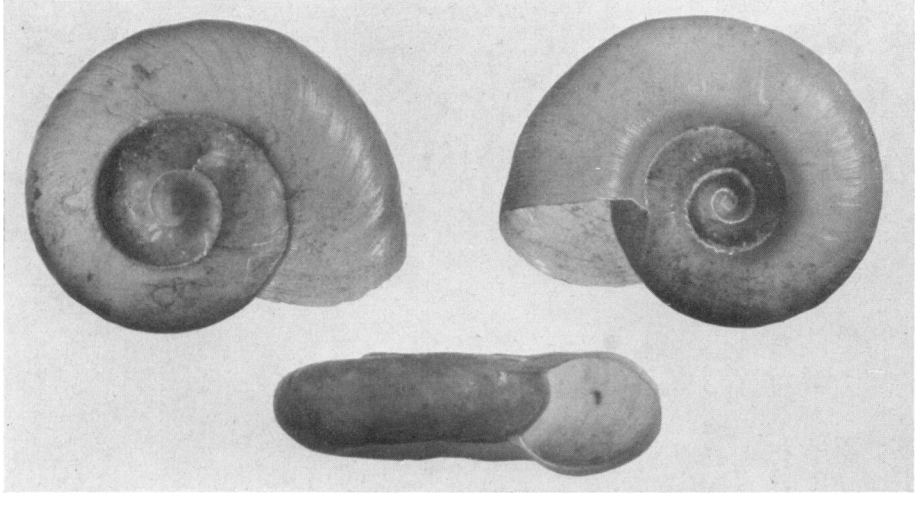

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Fig. 6. *B. pfeifferi bridouxiana*, Bobandana Bay, Lake Kivu
Fig. 7. *B. pfeifferi bridouxiana*, Kisanga River, Katanga (= *salinarum* Morelet?)
Fig. 8. Hybrid between *B. pfeifferi bridouxiana* and *rhodesiensis*? Tunduma, Tanganyika

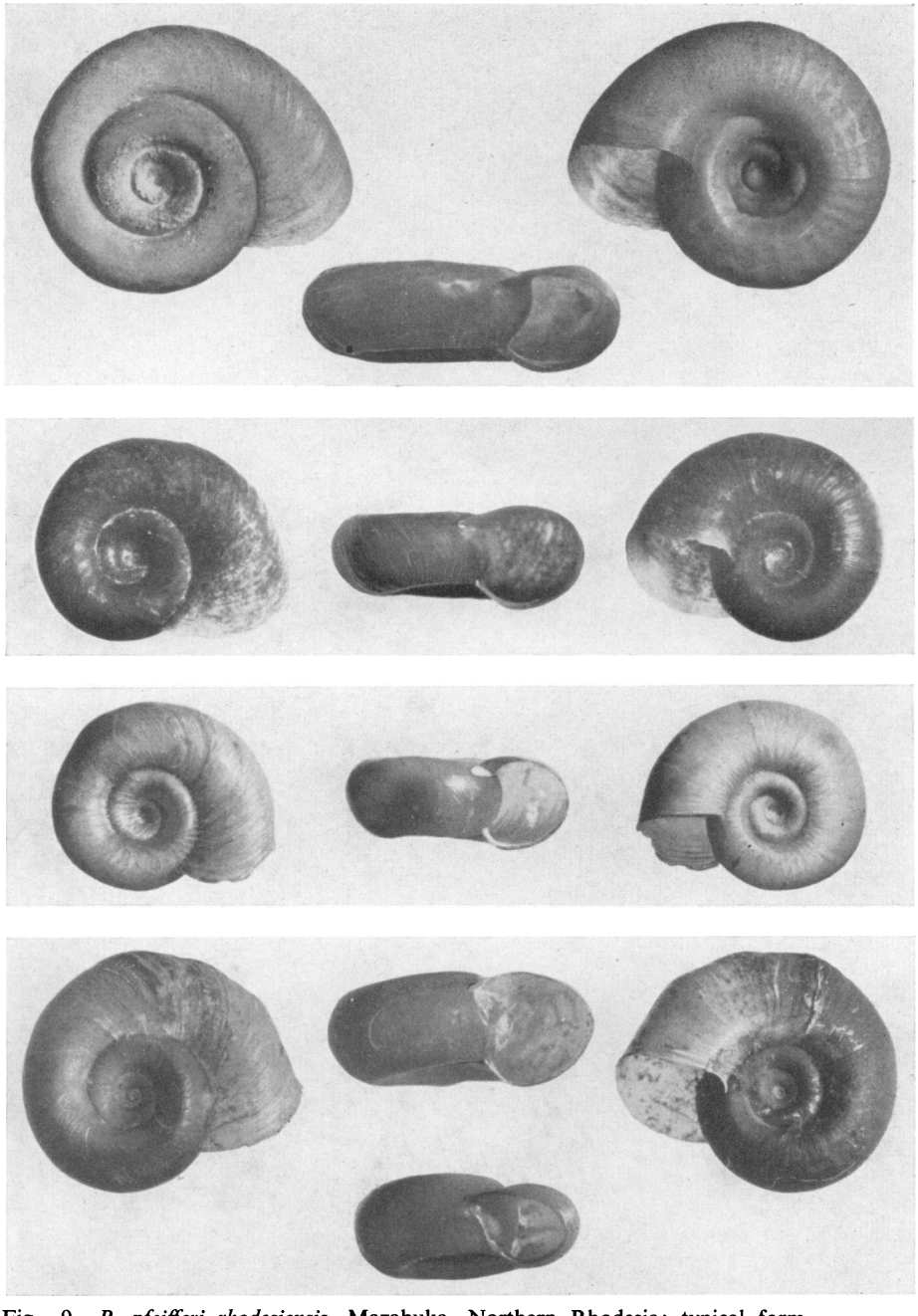

Fig. 9. *B. pfeifferi rhodesiensis*, Mazabuka, Northern Rhodesia; typical form
Fig. 10. *B. pfeifferi nairobiensis*, Nairobi River, Kenya
Fig. 11. *B. pfeifferi nairobiensis*, Ngudu, Tanganyika
Fig. 12. Hybrid between *B. pfeifferi nairobiensis* and *rüppellii* ? Athi River, Kenya. The lower centre shell shows internal lamellae.

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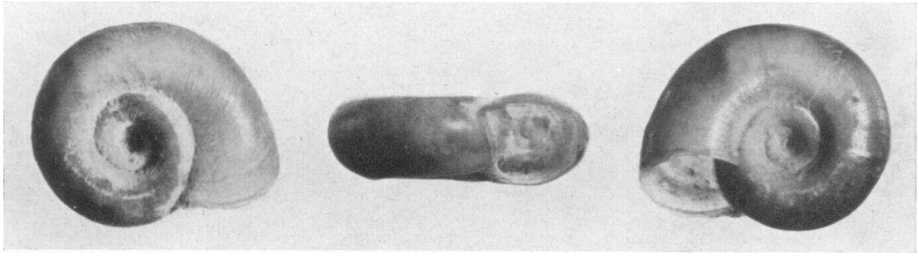

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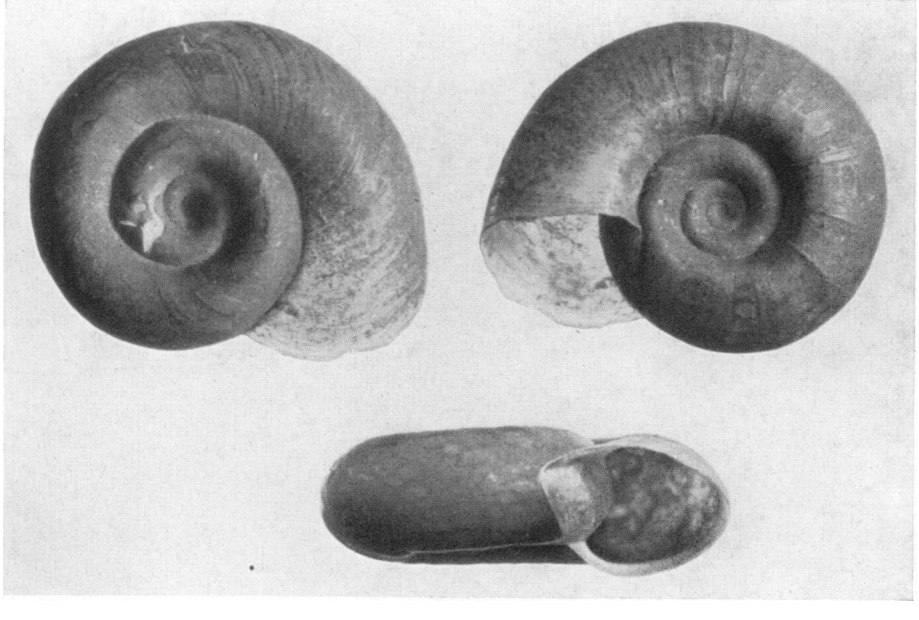

Fig. 13. *B. pfeifferi rüppellii*, Lake Tana, Ethiopia
Fig. 14. *B. pfeifferi rüppellii*, Arua, West Nile

PLATE VI

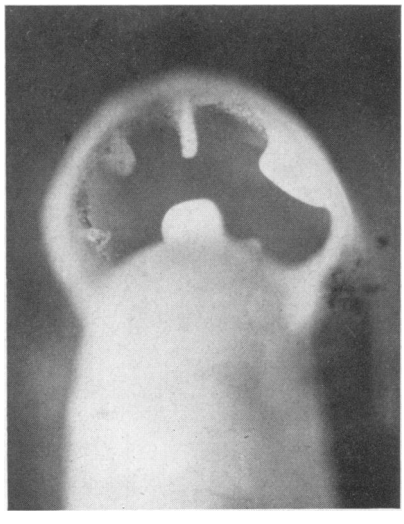

Fig. 15. *B. pfeifferi rüppellii*, Arua, West Nile; immature shell with internal lamellae

PLATE VII

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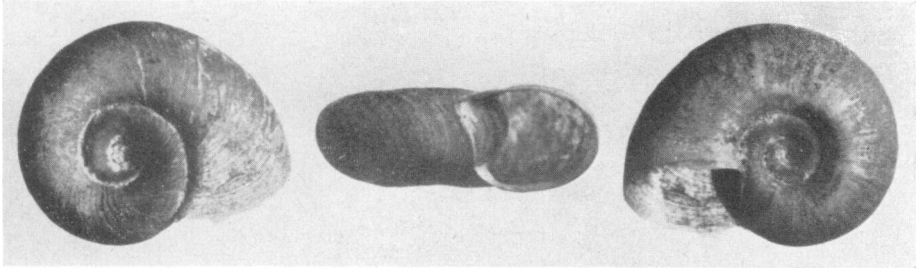

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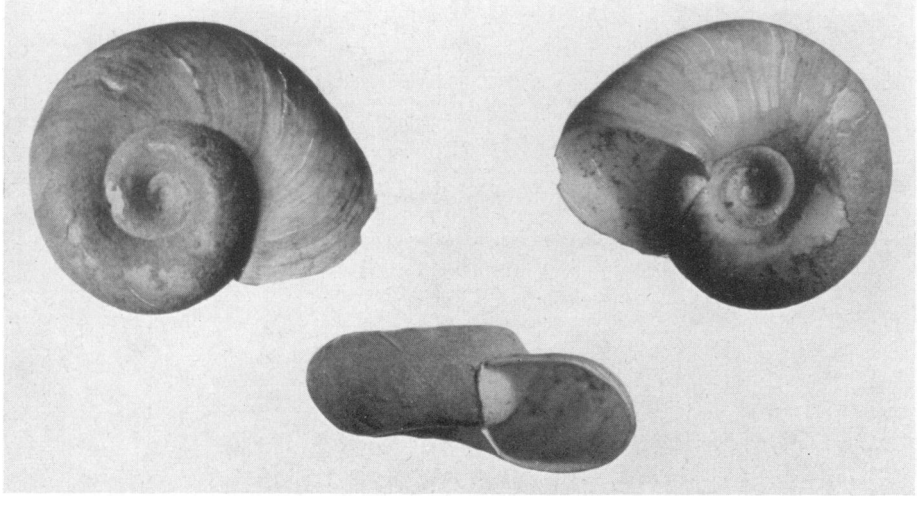

Fig. 16. *B. pfeifferi rüppellii*, Aduwa, Ethiopia (= *adowensis* Bourguignat)
Fig. 17. *B. pfeifferi rüppellii*, Jarvis Dam, Uganda (= *adowensis* Bourguignat)

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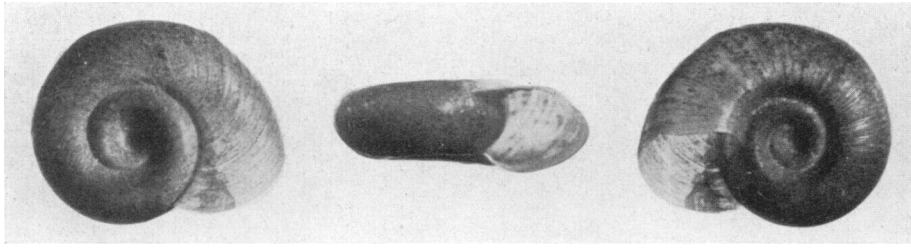

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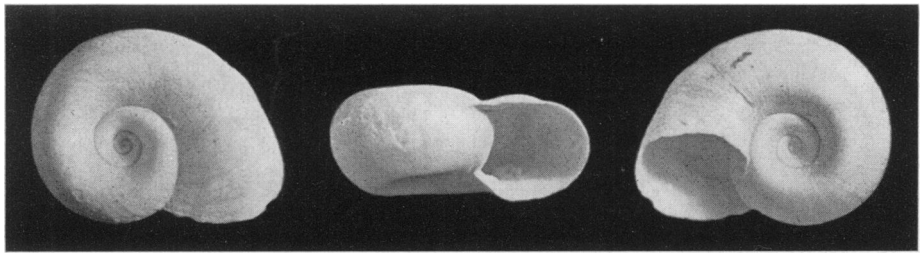

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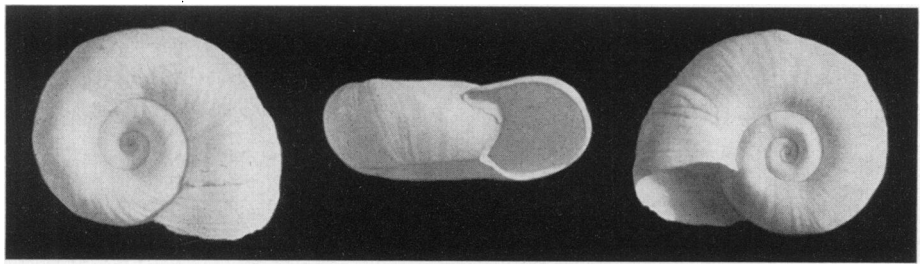
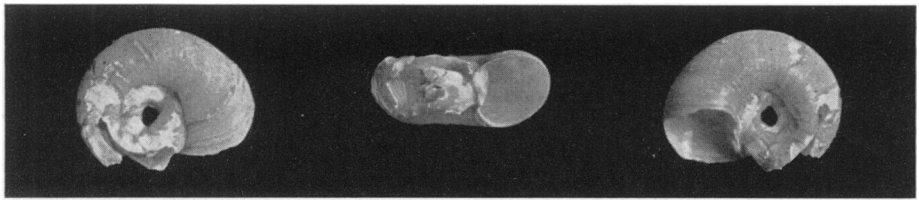


Fig. 18. *B. pfeifferi gaudi*, Casamance River area
Fig. 19. *B. pfeifferi gaudi* ? A fossil shell from Lake Chad
Fig. 20. *B. pfeifferi gaudi* ? A fossil shell from Tuat, Algerian Sahara (= *aucapitainianus* Bourguignat)

PLATE IX



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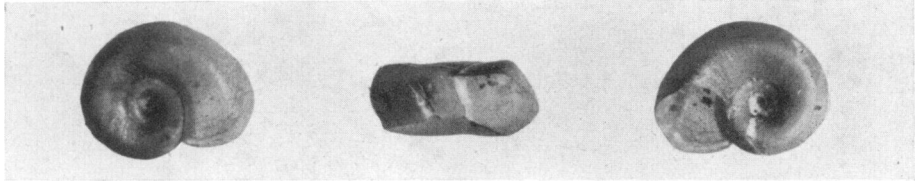

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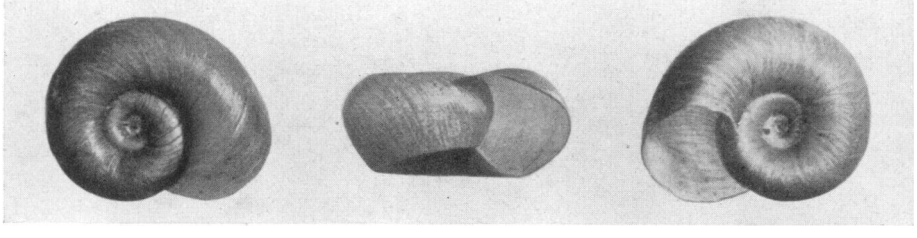

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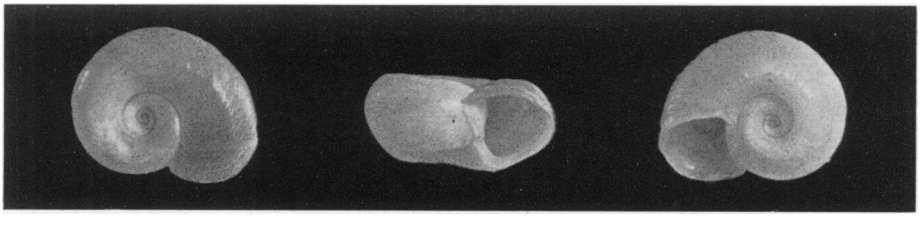

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Fig. 21. *B. germaini*, Tassili des Ajjer, Algerian Sahara
Fig. 22. *B. choanomphala choanomphala*, Dagusi Island, Lake Victoria; typical form
Fig. 23. *B. choanomphala choanomphala*, Entebbe, Lake Victoria (= *victoriae* Smith)
Fig. 24. *B. choanomphala elegans*, Butiaba, Lake Albert

PLATE X

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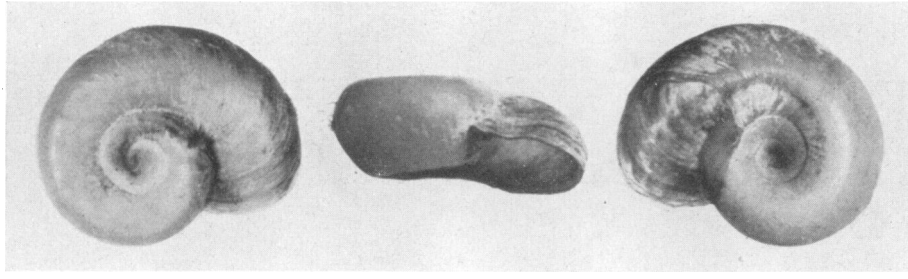

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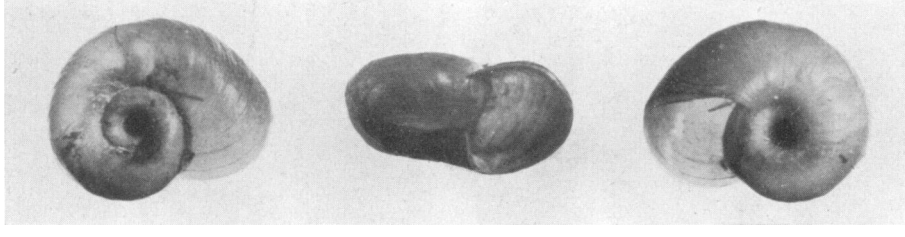

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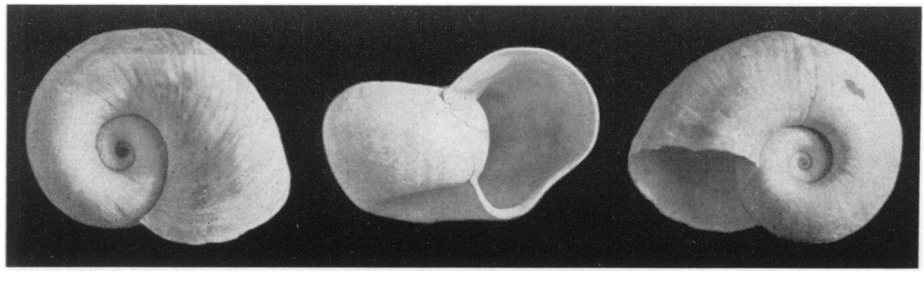

Fig. 25. *B. smithi*, Lake Edward, Uganda
Fig. 26. *B. stanleyi*, Butiaba, Lake Albert
Fig. 27. *B. stanleyi*, Butiaba, Lake Albert; a very big " dead " shell

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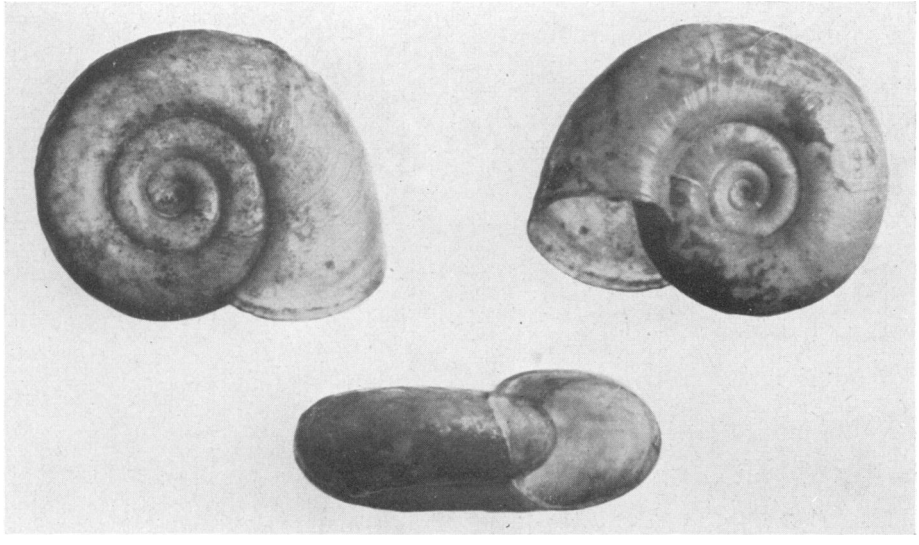

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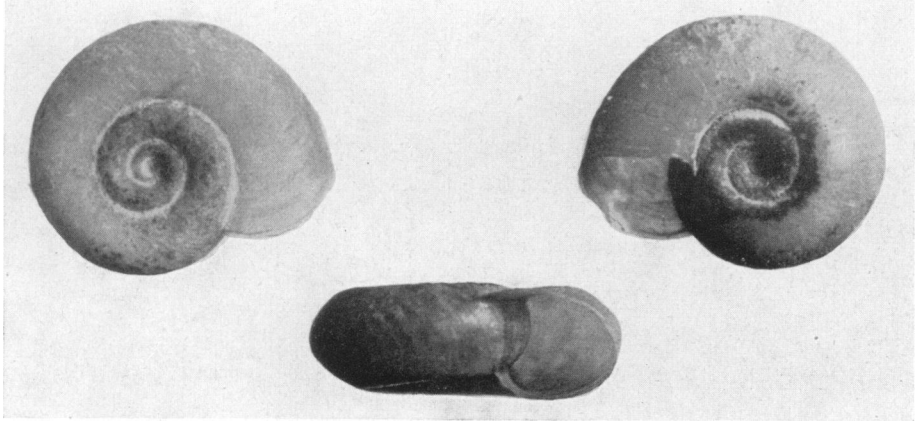

Fig. 28. *B. alexandrina alexandrina*, north of Cairo, Egypt
Fig. 29. *B. alexandrina alexandrina*, Alexandria; typical form

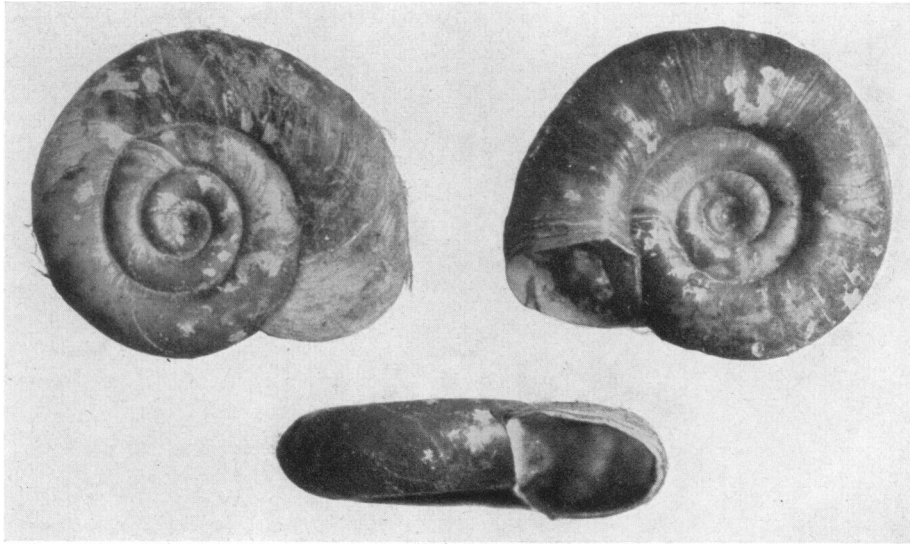

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Fig. 30. *B. alexandrina alexandrina* ? Quesna area, Egypt (= *paeteli* Jickeli)
Fig. 31. *B. alexandrina alexandrina* ? Ghat, Fezzan

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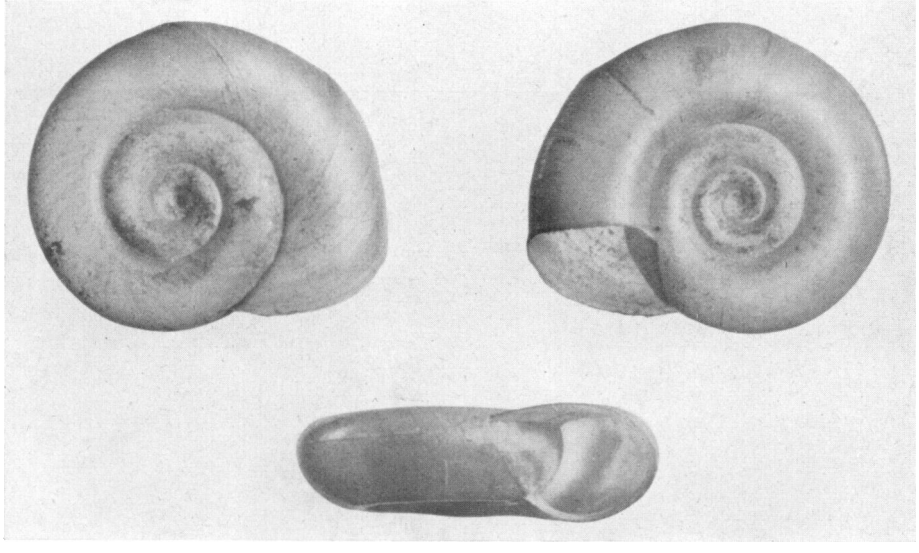

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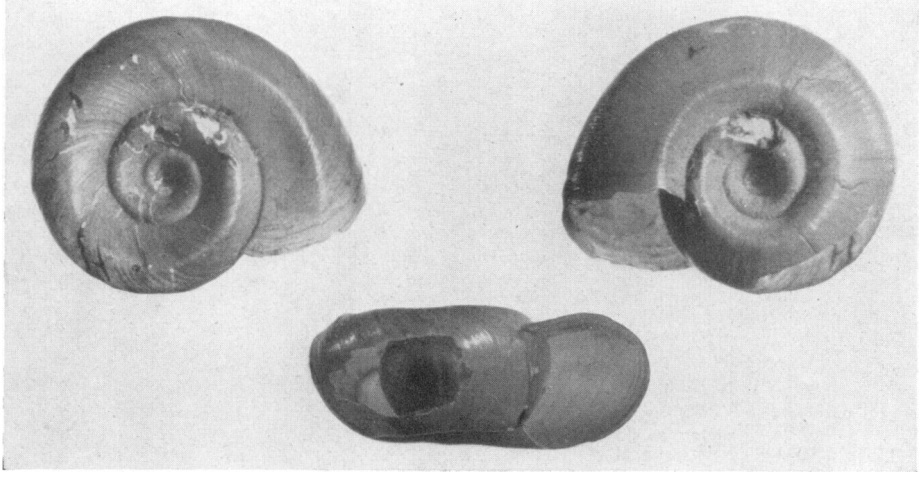
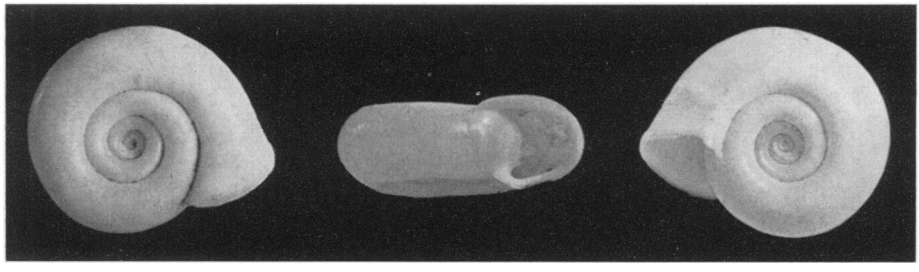


Fig. 32. *B. alexandrina wansoni*, Banzyville, Belgian Congo
Fig. 33. *B. angulosa*, Lake Ngwasi, Tanganyika



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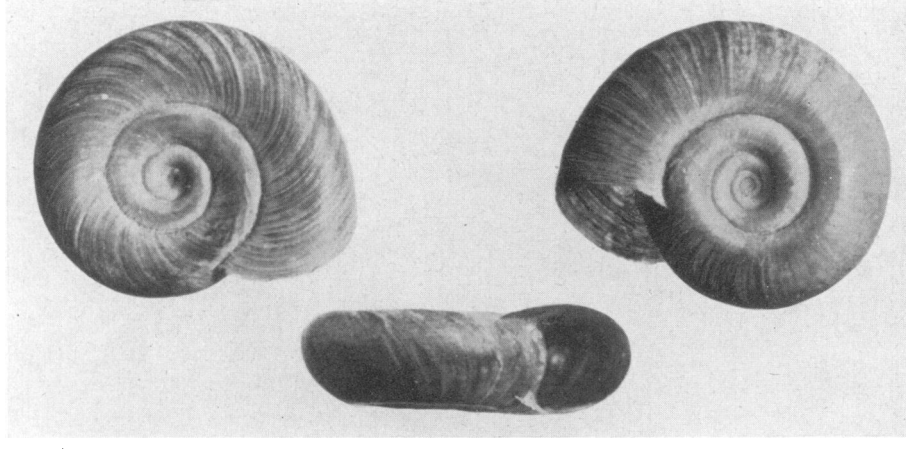

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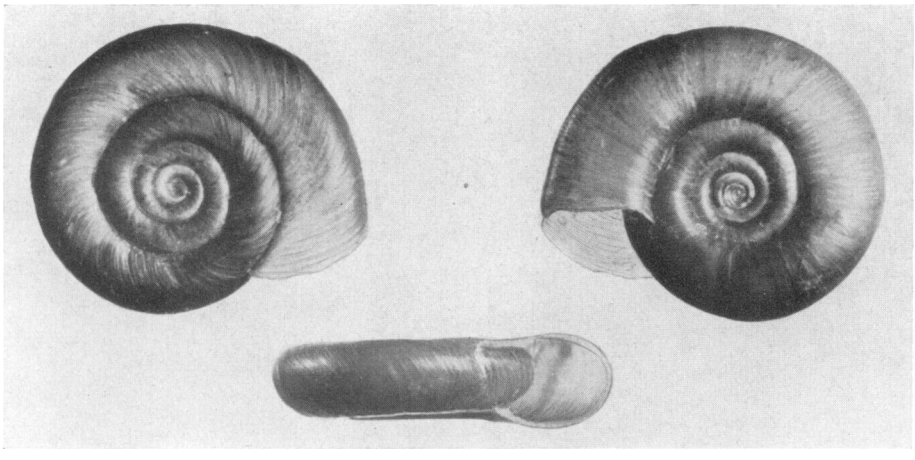
Fig. 34. *B. tchadiensis*, Lake Chad
Fig. 35. *B. camerunensis manzadica*, Manzadi, Belgian Congo



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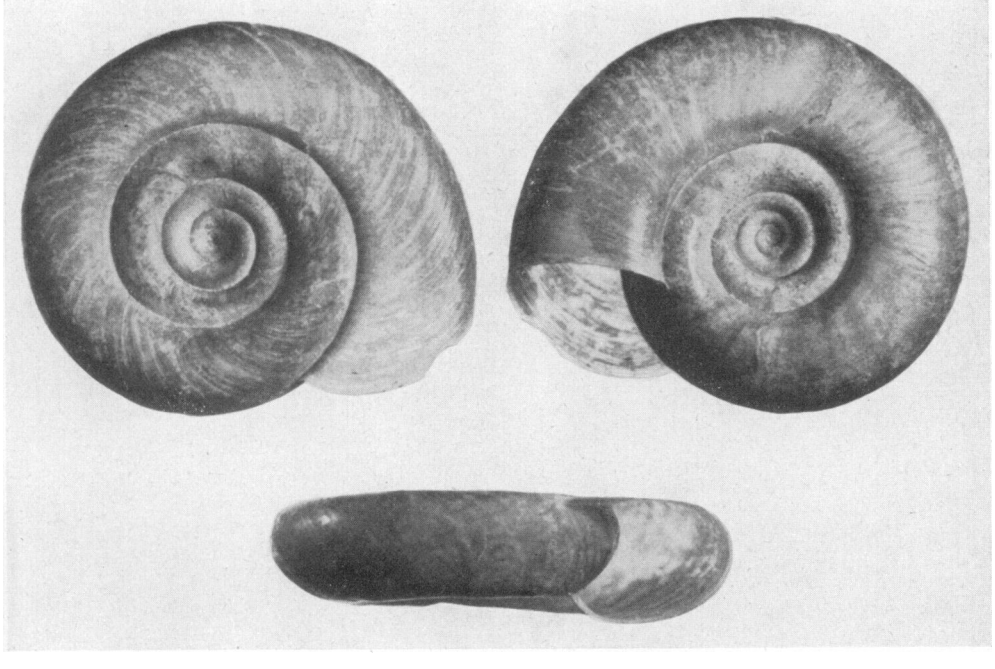

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Fig. 36. *B. sudanica sudanica*, Nyenga, Uganda
Fig. 37. *B. sudanica tanganyicensis*, Albertville, Lake Tanganyika