

CONTRIBUTIONS TO THE MORPHOLOGY
OF BULINUS TROPICUS (KRAUSS)

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I. INTRODUCTION

The interest in Bulinus tropicus (Krauss) has, up till now, been centered mainly around the medical and veterinary importance of this species and consequently there have been few serious attempts at a thorough investigation of the morphology. Much has been written on the problem of the classification of the Planorbidae and although the crux of the matter is of course the intrinsic variability of these species, numerous other factors have played a part in bringing about the general confusion on this issue, which now exists. Probably the most important of these factors is that it was not initially realised by the taxonomists that they were dealing with an extremely variable species. Even when the variability was recognised the nature and causes thereof were not, indeed are not, properly understood. In certain instances a specimen may resemble one species in some respects and another species in others, so that it is almost impossible to ascertain to which species a particular specimen in reality belongs. Further confusion arose from the fact that the criteria used in species discrimination were not always well chosen. When the shell alone was used to identify a species it was usually viewed as a dead, isolated object and neither the anatomy of the snail producing the shell, nor the ecological factors influencing it, were taken into account. Finally there was the practice of sending snails for identification to overseas authorities who often applied different names to the various samples of the same species. In spite of Cawston's warnings that only confusion would arise as a result of giving too many

names, new names were freely applied, as is testified by the long, but by no means exhaustive, list of synonyms given in Connolly (1939). Schwetz (1952) suggests certain remedies for this unhealthy state of affairs and the main ideas are that there should be a sound biological approach to these problems and that ultimate proof of relationships should be obtained by carefully planned breeding experiments. That the latter is a feasible proposition is demonstrated by the fact that various bulinids bred by Cawston resulted in a uniform population.

Besides the taxonomic tangle of confusion on the specific level brief mention should also be made of some obscure relations on the subgeneric level. Wright (1957) considers B. hemprichii depressus Haas as a synonym of B. globosus (Morelet) while Mandahl-Barth (1956) maintains that the former species is a synonym of B. tropicus tropicus whereas Dr. van Eeden is of the opinion that both these authors might be at fault.

The snails act as vectors for the larval stages of certain trematode worms and, in certain localities, almost all the mature forms of a sample may be infected. The degree of infestation varies - it may be slight but is generally very heavy, especially in the region of the digestive gland and hermaphrodite gland into which the larvae may penetrate. Severe cases of infestation may result in the complete atrophy of the ovotestis and sporocysts and cercariae may even be found in the blood vessels of the gill, mantle collar and mantle.

Owing to the similarity of the larval forms, the identity of the parasite is often difficult to establish.

Owing to the similarity of the larval forms, the identity of the parasite is often difficult to establish. It appears that in B. tropicus the parasites are mostly amphistomes, non-mammalian schistosomes and, occasionally, chained echinostomes. In 1922 Porter reported that Schistosoma mansoni is harboured by B. tropicus and she later (1938) claimed to have infected a puppy with Schistosoma haematobium by using cercariae issuing from the same snail species. Cawston (1922), de Meillon (1948) and Alves (1956) could not find experimental support for these findings. In spite of this Mozley, as late as 1951, still regarded B. tropicus as dangerous to man. Although there may be a number of explanations for these conflicting results, faulty identification of the snails used might have been one of them, emphasizing the necessity of a greater knowledge of the actual and possible vector species.

B. tropicus often lives in close association with other organisms. Thus certain unidentified species of Collembola were occasionally encountered in the mantle cavity and even in the rectum. A more regular association seems to be that between B. tropicus and the oligochaete, Chaetogaster which lives commensally in the mantle cavity of the snail. This association was also reported by Bayer (1955).

As the aim of this paper is not purely taxonomical, an account is given of all the systems except the muscular system. Because live snails were obtainable only from a few localities, and also because of the limiting time factor, no breeding experiments were performed but an attempt is made to give a description of the snail

and its shell where possible taking into account the effects of environmental factors. Unfortunately it was not possible to pay the attention desired to the ecological aspect.

II. MATERIAL AND TECHNIQUE.

Most of the material used in this study was sent, for identification to this Institute by the staff of the Union Health Department as part of the anti-bilharziasis programme in the Transvaal. Snails were collected from the following localities which will, in the text, be referred to by the symbols indicated below.

<u>Locality</u>	<u>District</u>	<u>Province</u>
B-Beestekraal	Brits	Transvaal
S-Sanddrift	"	"
W-Wasgoedspruit	Potchefstroom	"
D-Municipal Dam	"	"
L-Native township	"	"
K-Kameeldrift	Brits	"
A-Kameeldrift (locus 2)	"	"
H-Shongwanstad	Potgietersrust	"
M-Middelburg	Middelburg	"
G-Grahamstown	Grahamstown	Cape Province

It is to be regretted that none of these collection sites represents the type locality which Krauss (1848 p.84) gives as "in flumine Lepenula (inter 25-26° lat. aust.)". This is subsequently designated as the Lepenula River (Pilsbry & Bequ., 1927; Porter, 1938; Connolly, 1939; Mandahl-Barth, 1956) which, according to Porter (1938), must be somewhere in the Western Transvaal. Virtually all attempts to trace this river failed, the only streams with more or less similar names being Lipalula, mentioned by Fuller (1932) and Lepelle, referred to by Baines (1877). The above localities were selected as snails collected from them resemble typical B. tropicus, and also because, apart from Grahamstown,

the localities are in the Transvaal. The number of specimens examined is as follows: - Beestekraal 42, Wasgoedspruit 56 and at least ten from each of the remaining localities.

The snails were narcotised and killed according to the method suggested by van Eeden (1958) which was found to give satisfactory results. In the case of long preserved specimens, removal from the shell was facilitated by dropping the snail into boiling water for a few seconds. In some instances the expansion of air in the upper whorls caused the expulsion of the snail from its shell. Dissection was done under water. The mantle was removed and with it, part of the floor of the mantle cavity, to include the proximal part of the rectal ridge. The mantle was then pinned down and the kidney and mantle ridges drawn to scale on graph paper, either by using a camera lucida or an eyepiece micrometer grid. Measurements were made from the drawings using an opisometer (rotameter). Radula preparations were mounted in CMC 10 (a Turttox product), and a number of these was drawn with the aid of a camera lucida. Wholemounds of 32 penes were made using the technique of van Eeden (1958). In the remaining specimens the preputium and penis sheath were measured using an eyepiece micrometer. The penis sheath was then opened and the penis and epiphallus unravelled, pinned to the bottom of the petri dish and measured. The shell, radula, penis and the rest of the soft parts of each snail were given a symbol and a letter to allow correlation of any peculiarities occurring, and to allow comparison of snails from different localities and of different sizes. Snail specimens from localities B and W were serially sectioned, usually

after having been fixed in formalin. To prevent the sand in the gizzard from damaging the microtome blade it is necessary to remove the sand or entire gizzard, as suggested by Carriker and Bilstad (1946). A few specimens from W were fixed in Bouin's fluid. Serial sections were made of entire snails and, occasionally, of isolated organs. Although a few slides were stained with Masson's, Mallory's triple stain proved to be more satisfactory.

III. SHELL.

Like many natural sciences today, conchology has passed through a qualitative, purely descriptive phase and is now placing emphasis on the quantitative aspect. A study of the shell alone is no longer regarded as a foundation on which to erect the structure of taxonomy (Schwetz, 1954), but it still has a part in that structure. In certain groups of snails the shell does not vary greatly within genera or species, and then provides a more dependable criterion for classification than in those snails in which the shell is subject to great variation, such as Bulinus species which are "notoriously polymorphic" (Cawston, 1938). Yet, even in this genus, the shell exhibits certain characters by which the various groups and species are distinguished and which necessitates some reference to it in any morphological account of B. tropicus.

The most complete descriptions of the shell are those given by Krauss (1848), Germain and Neveu-Lemaire (1926), Connolly (1931, 1939), Cawston (1938), Mozley (1939), Mandahl-Barth (1954, 1956) and Fraga de Azevedo (1957). These all lead one to the conclusion that there is no

single description of B. tropicus which will embrace all the diverse forms of this species and one has only to be confronted with a series of shells like those photographed by Mandahl-Barth (1956), or indeed my own series, most fully to realise this.

The indications of size given in the literature are generally not very useful. Boettger's (1910) data are based on a single specimen while from Mandahl-Barth (1954), Germain and Neveu-Lemaire (1926) and Mozley (1939) it is impossible to deduce whether the dimensions given are based on a few specimens or on one only. Krauss (1848) seems to have examined a number of shells while Fraga de Azevedo's mean, based on a too small sample of five shells, is also unreliable. With regard to the largest specimen Germain and Neveu-Lemaire (1926) record a shell 15 mm. long and 11 mm. broad, while Mandahl-Barth (1956) mentions one of 15.2 mm. long and 10.8 mm. broad. Cawston (1923) claims that snails at the Durban golf course grew to as much as 16 mm. in breadth.

From the descriptions by the above-mentioned authors the following may be noted. The shell is pointed ovate (Mandahl-Barth, 1954) somewhat obese (Connolly, 1939) and oval and bulging (Germain and Neveu-Lemaire, 1926). According to Stiles (1931) the name Bulinus is originally derived from ~~from~~ the Latin word bulla, meaning a bubble, an apt description of these rather fragile shells. The general appearance of the shell varies so much that three out of four authors emphasize this variability as a feature of the species.

The spire varies from slightly elevated (Mozley, 1939) to rather high, about half the length of the aperture (Mandahl-Barth, 1956).

Mozley (1939) notes that the shell consists of three whorls increasing rapidly while Krauss (1848) and Germain and Neveu-Lemaire (1926) found shells with as many as five whorls, but four to four and a half convex whorls is the usual number (Mandahl-Barth, 1954, 1956; Fraga de Azevedo, 1957). The sutures may be very deep (Mozley, 1939; Fraga de Azevedo, 1957), deep (Germain and Neveu-Lemaire, 1926), or fairly deep (Mandahl-Barth, 1954, 1956).

The colour of the shell is described as yellowish reddish, pale, shiny (Fraga de Azevedo, 1957), yellowish brown (Germain and Neveu-Lemaire, 1926), lighter or darker dull brownish (Mandahl-Barth, 1956) or pale or dark horny brown (Mandahl-Barth, 1954). According to Germain and Neveu-Lemaire (1926) the shell is rather solid while Mandahl-Barth (1954) and Mozley (1939) regard it as "rather thin walled" and "thin walled" respectively. The sculpturing may consist of minute regular growth lines (Mozley, 1939) or rather coarse growth lines (Mandahl-Barth, 1956), in either case closely set. Krauss (1848) records that striations on the last three whorls may, in juveniles, be covered by a thin membrane through which the costulations show. The nature of this membrane is not clear to me.

The aperture is oval (Germain and Neveu-Lemaire, 1926; Mozley, 1939; Fraga de Azevedo, 1957) and the labrum regularly curved (Mandahl-Barth, 1956) and simple (Krauss, 1848; Germain and Neveu-Lemaire, 1926; Fraga

de Azevedo). Krauss (1848) states that the labrum is joined to the body whorl by a clear white shiny lamella, which, according to Fraga de Azevedo (1957), is sometimes indistinguishable from the labrum. The columella is straight (Mandahl-Barth, 1954; Fraga de Azevedo, 1957) and according to Connolly (1931, 1939) it may also be slightly concave. The columellar margin is generally widely reflexed (Mandahl-Barth, 1956; Fraga de Azevedo, 1957) and may either cover the umbilicus which is open from below (Krauss, 1848), or may only partially cover the umbilicus (Mandahl-Barth, 1954). The umbilicus is described both as narrow (Germain and Neveu-Lemaire, 1926; Mandahl-Barth, 1956) and as broad and deep (Mozley, 1939; Fraga de Azevedo, 1957).

From the above summary the fact emerges that these descriptions differ so much that they are often completely inadequate in species discrimination and the need for reducing verbal descriptions, wherever possible, to concise mathematical terms becomes clear. Although statistics cannot, in taxonomy, play the decisive role which it does in experimental work, it is nevertheless indispensable in bringing out correlations, differences, indications of variability etc. In the present work the t -test and analysis of variance were not applied because the samples were collected by different people at different seasons. Bearing in mind that "it is the naturalist's original sin to pay more attention to very small, or extra large or otherwise exceptional specimens" (Boycott, 1928, p.28) my samples are most probably not random, and, except for those from localities W and B, are not large enough to compare classes of equal size, as was done by Schutte and van Eeden (1959a). It was moreover not possible to

compare data from modal classes since in some localities, e.g. K, there were no specimens large enough to fall in the modal class. In any case Table 1 reveals that there is so little difference between the mean of the modal class and the mean of the total sample that the latter has been used wherever it might be expected to throw light on some aspect of the shell or soft anatomy.

It has often been suggested and it has in some cases been demonstrated, among others by Simroth and Grimpe (1918), Baker (1928), Rotarides (1932), Wesenberg-Lund (1939), Boettger (1944), Hubendick (1951) and Schwetz (1954), that ecological factors influence the shell in a number of ways. Unfortunately the very factors known to be affected by ecological conditions are those most commonly employed in taxonomic discrimination, eg. size, shape, thickness of the shell, colour and sculpturing and my own observations can do no more than to underline the necessity of a closer investigation of the relation between ecological factors and conchological features.

Shells from nine localities were treated statistically to discover correlations of changes in ratios and also in shell form, and to find out which of these changes were dependent on increasing age of the snail.

With regard to size it seems to me important to know the maximum length attained by any shell in the population, the mode of the sample, which is often of more use than the mean, and also the size range of the sample. These data are represented in Fig. 1. The largest shell in my series is 13.3 mm. but the mode of all the localities combined is only 9.8 mm. (Fig. 2a). These figures cannot, however, be regarded as truly representative of B. tropicus as the irregularity of

the "normal curves" proves that the sampling was inadequate. The snails in sample K are all regarded as young because they have the same general facies as juveniles in sample W, and the average length is only 7.2 mm. As they come from the same locality as sample A and were collected on the same day the difference in size between the samples seems explicable only by assuming that the juveniles, in this case, occupied a particular part of the habitat, different from that occupied by the adults. This supposition is further strengthened by the fact that the juveniles of sample W are thickly covered with sediment, a condition rarely found in adults and this, too, indicates that the juveniles may live under conditions slightly different from the normal adult habitat. In this case they seem to prefer a more benthonic life.

Series K indicates that size, which must obviously be influenced by ecological factors affecting growth, has an important effect on the general shape of the shell. In young snails (type 1), such as sample K, the whorls overlap each other greatly resulting in the relatively large mouth aperture. The base of the columella is straight (Fig. 3a). In the mature forms two types of shell are distinguishable, depending on the tightness of the coiling of the whorls. In these older snails the whorls do not overlap as much as in the juveniles, so that the height of the aperture (AH) is relatively smaller when compared with the total length of the shell (L). This results in a higher value for the ratio L/AH (Table II). Type 2 is represented by sample W. These snails have tightly wound whorls which are generally not highly convex. The shell is elongated and the umbilicus narrow. Although types 1 and 2 differ in

details from figures 4 and 14 (Physa zuluensis M. & P. and Isidora compta M. & P.) of Melvill & Ponsonby (1903), type 1 agrees with their fig. 4, and type 2 with fig. 14 (See fig. 3a & b). Type 3 is represented by sample B. This last type has whorls which are more convex than in the former two, and not as tightly wound round the central axis, resulting in a more globose form with a wide umbilicus (Fig. 3c), it is often found that as the age of the snail increases, the shell assumes a more elongated form (Lais 1925, Franz 1928, Degner 1930 quoted from Neuhaus 1952).

That this is also true of B. tropicus is revealed by fig. 4a in which the ratio L/B (length/breadth) is plotted against L (length of the shell). This shows that with regard to this ratio, only shells of approximately equal length should be compared.

A few shells from each locality are ^{reproduced in fig. 3} ~~figured in Plate 3~~ to show the variation occurring in the series. The first few shells of each row are representative of the most "typical" shape occurring in the sample. With two possible exceptions the shape of the shell seems to be correlated with the habitat. As sample K consists of juveniles it is not clear into which type they would have developed, but the shape of type 2 represented by samples D, W, H, and type 3 represented by samples B, S, A, could very well be the result of reaction to running and stagnant water respectively. The globose type 3 is found in dams while type 2 is found in slow-flowing streams. These findings are in accordance with the view held by Sinroth & Crimpe (1918), Baker (1928) and other authors, that stream forms are more elongated than those living in stagnant water.

The two exceptions which do not fit into this picture are shells from locality L (pools) which show a "stream" shape, and shells from locality M (a stream), which show a "pool" shape. In the last mentioned case the habitat contained many waterplants and thus the flow of water may have been hindered to such an extent that the habitat in which the snails lived may in reality have been a "pool" habitat.

These conclusions are in conflict with the findings of Boettger (1944) working on various Lymnaea species. This author was primarily interested in the difference between lake forms in stagnant water, and those subject to wave action. Snails under the latter conditions were found to be short spired and obese, thus agreeing with what, in B. tropicus, seems to be the stagnant water form. Boettger also found that stream forms had rounded apertures, once more a character apparently correlated with a pool habitat in B. tropicus. These apparently conflicting results may, perhaps, be ascribed to the fact that the effects of running water or waves, on the snail, are probably not the same. These findings illustrate the need of detailed field studies which were not always possible in the present investigation as snails were sent to this Institute from various parts of the country.

The spire shape is rather characteristic in each of the samples, and as in Australian Bulinus species (Gabriel 1939, quoting Hedley, 1917) the length varies. Table III demonstrates that the ratio of shell length/spire (measured as indicated in fig 5a), varies enormously, both in the entire series and in each sample separately. In spite of this there is an obvious negative correlation (fig. 4b) in this ratio and the length of the shell, proving that the smaller forms have relatively shorter spires. Mandahl-

Barth (1956) gives the length of the spire as about half the height of the aperture. From Table I it can be seen that, in my series, the ratio of spire/height of aperture, excluding samples D and K which have unusually short spires, is 0.2, i.e. only about one fifth of the aperture height. This discrepancy between my own and Mandahl-Barth's (1956) values may in part be explained by the fact that different methods of measuring the spire were used. Since there is no standard method of measuring the spire, I considered the spire as the length of the shell minus the last complete whorl.

The angle of the spire, measured as shown in fig. 5b is too variable to be of any use in taxonomy. From Table III it is apparent that shell types with spires as different in shape and length as K and A have spire angles of almost the same magnitude, while the total range of the whole series is $58-134^{\circ}$.

Mozley's (1939) description of a shell of three whorls increasing rapidly was probably based on an immature specimen for in these the number of whorls is small and, as they greatly overlap each other they do increase rapidly. The whorls agree in shape with the descriptions given in the literature and a histogram of the number of whorls in my series is given in fig. 6

Hubendick (1951), working on Lymnaea pereger Müller, demonstrated that the thickness of the shell may be influenced by the surroundings. My series seems to support his view for shells from some localities are transparent and fragile while those from other localities are opaque and stout. The colour likewise varies from a brownish yellow in the former to a yellowish white or a white in the latter. The real colour of the shell

is of course often obscured by a coating of sediment which occurs sporadically. It is at times found only on the older whorls of the adult shell, is sometimes restricted to all the juveniles of a sample and in yet other cases only some of the juveniles may exhibit this feature. As a rule the shells are shiny only on the inside but in some cases also at the reflexed columellar margin.

The majority of shells in my series possess fine regular growth lines but a few are smooth while those from certain localities have pronounced narrow ridges which Boettger (1944) attributes to growth under exceptionally favourable conditions. In the Potchefstroom area snails were collected from three localities, viz. from a stream (W) known as Wasgoedspruit, from the Municipal dam (D) and from temporary pools at the native township (L). The shells from locality W are elongated and fairly smooth whereas those from localities D and L are more squat and have coarse striations or ridges although attention should also be focussed on the sporadic occurrence of smooth forms in a sculptured population. The sculpturing agrees with findings on "stream" and "pool" shaped shells and also with the observations on Viviparus costatus Qu. & G. (Haas, 1922), a species in which stream forms are smooth while the lake forms are sculptured. Only the rearing of a few generations of snails from the three Potchefstroom localities (as was done by Schwetz (1954a) with Bulinus coulboisi Bourguignat and B. truncatus Audouin) would demonstrate the role played by differing ecological conditions in the formation of the various shell types.

The varying aperture shapes in my series can be classified into three types coinciding with the three

Costulatus

general types of shell referred to above. (See fig. 3). Fig. 7 reveals that the ratio aperture height/aperture breadth does not change as the snail becomes older and fluctuates between 1.4 and 1.5 for all samples except the juveniles from locality K in which the ratio is 1.3. The graph plotted in fig. 8 which reflects the relation between shell length/aperture height plotted against the entire length of the shell shows a correlation, which means that as the snail becomes older the mouth aperture becomes relatively smaller. Two additional ratios which might prove to be of taxonomic value are (a) shell breadth/aperture breadth (B/AH) and (b) aperture height/shell breadth (AH/B). The corresponding data for my specimens of B. tropicus are tabulated in Table 9 IIIb. Both the ratios B/AH and AH/B are fairly constant, the low value for snails from locality K being due to the relatively large mouth aperture of immature forms. The ratio of MH/B shows the same degree of constancy. The shape of the aperture is partly determined by the shape of the columella which is usually straight, slightly concave or concave in the three shell types respectively. The columellar margin is broadly reflexed and its lower half is generally free and either covers the umbilicus which is narrow, as in type 2, or only partly covers the umbilicus which is wide and deep as in type 3. The callus is usually well developed and of the same colour as the rest of the shell. In sample L, however, it is transparent and indistinct while in sample H it is white and contrasts sharply with the dark shell.

In sample B the labrum sometimes meets the body whorl in a very rounded angle, the aperture margin being slightly expanded like a trumpet. This presumably

represents the condition described by Fraga de Azevedo (1957). This angle was measured by the method indicated in fig. 5c and was found to be surprisingly constant (see Table III) the mean varying by about one degree only in all localities except H in which the shells are large and elongated and the labrum is more depressed than usual thus producing a very streamlined shell.

A graph in which the number of whorls is plotted against the length of the shell is shown in fig. 10. The correlation revealed by this graph is only to be expected, for as the number of whorls increases the length of the shell must also increase. Because the length of the shell depends on so many factors, and is obviously not a reliable criterion for determining the age of the snail both the number of whorls and the length of the shell were plotted against the number of transverse rows of radular teeth (Fig. 11) which have already been proved by Hubendick, (1945); Schutte and van Eeden (1959) and myself (Fig. 11b) to increase with the age of the snail, to see which graph showed the closer correlation. In both cases the scatter was so great that the correlation was scarcely evident. This must partially be ascribed to the fact that there were not enough of the smaller shells.

To find a satisfactory criterion for determining the age of the snails, they should be reared from eggs, in the laboratory, under different conditions. Various organs should then be examined at intervals to ascertain which features alter with increasing age, and are least affected or unaffected by external factors.

IV. EXTERNAL ANATOMY AND MANTLE.

There is a great dearth of literature on the anatomy of B. tropicus, the only complete account that I was able to trace was that by Fraga de Azevedo (1957). I could not obtain the works of Buchner (1890); Pelseneer (1895); Sarasin and Sarasin (1898); Baker (1931) and Quick (1933, 1934) but the general descriptions of the morphology of the Planorbidae and various bulinids given by Watson (1925); Simroth (1928); Boettger (1944); Baker (1945); Hubendick (1946, 1947); Abdel-malek (1952) and Wright (1957) were consulted.

The animal is described as blue-grey (Fraga de Azevedo, 1957) and although this is true of preserved specimens, live animals are yellowish or reddish brown as a result of the haemoglobin in the blood. Living specimens of B. tropicus have small white flecks due to concretions in the tissue (Baker, 1945; Abdel-Malek, 1952). The tentacles are filiform and circular in cross section, though in his 1946 publication, Hubendick regards the tentacle as an outgrowth of the post-tenac^tular process, and the latter as the homologue of the disc-shaped tentacles of Lymnaeidae. Hubendick's (1947) figure of a cross section of the tentacle of B. africanus Krauss (Plate 2 fig. 8) differs from that of B. tropicus in being more solid. In the latter there is one central (C) and a number of peripheral cavities (P.C.) in the loose muscular tissue which is surrounded by a basement membrane (B.M.) supporting the external epithelium (E) (Fig. 12). The eyes are situated medially at the base of each tentacle and not at its outer side as mentioned by Mandahl-Barth (1954). Lateral processes occur at the base of the tentacle in

Bulininae, Planorbinae and Ancyliidae (Hubendick, 1947a).

In B. tropicus there are two unequally developed processes, the dorsal process (D.T.P.) being more prominent than the ventral one (V.T.P.) (Fig. 12). Between them they enclose a ciliated groove, thus creating a condition resembling that found in species of Miratesta and Protancylus (Simroth, 1928).

The gill (G) anal lobe (A.L.) and pneumostome (P.N.) are situated on the left hand side of the animal in the sharp angle formed by the junction of the labrum of the shell with the body whorl. The natural relations of the various structures are most readily understood by referring to fig. 13a . The pneumostome is large and bounded ventrally by a small lobe referred to as the inferior pallial lobe, mantle lobe or lower mantle lobe by Hubendick (1946, 1955) and as the pulmonary siphon by Watson (1925) and Baker (1945). The shape of the siphon varies constantly in a living animal where it is alternately produced and retracted to collect air from the surface and then to convey it to the mantle cavity. The rectum opens at the tip of the anal lobe which is flattened dorso-ventrally and lies medially to and slightly in front of the gill. This region agrees more closely with Watson's (1925) figure of Physopsis globosa (Morelet) than Hubendick's (1955) figure of B. tropicus. The gill is a U-shaped structure thrown into a number of large transverse folds alternately protruding on the dorsal and ventral surfaces. These could be called the primary folds of which there are 4 or 5 on each surface. Each of these primary folds consists of a number of smaller secondary folds running in the same direction so that the large surface area, the thin epithelium and large blood

spaces allow for the maximum oxygenation of the blood. As the mantle cavity of Bulinus is generally filled with air, an osphradium in its primitive position would be functionally useless in this species, where in fact it lies outside the mantle cavity on the collar, just median to the pneumostome, and not just within the opening of the mantle cavity as claimed by Hubendick (1947a). Moreover this organ is much smaller than the one figured on page 30 by this author and agrees better with his later description (1947b) and Lacaze-Duthier's figure of the asphradium of Planorbarius corneus Linné reproduced in Boettger (1944).

V. INTERNAL ANATOMY.

The mantle which only slightly overlaps the edge of the labrum of the shell has conspicuous black patches concentrated mostly over the kidney region. There is considerable unnecessary confusion with regard to the descriptions of organs of the mantle eg. Hubendick (1947b) and Schutte and van Eeden (1959a) as it is not always possible to determine whether the author is referring to the right hand side of the animal or the right of the dissection.

1. The renal system.

The kidney (fig. 14) is well developed and consists of a proximal saccular (S.K.) and a distal tubular portion (T.K.). The saccular part lies on the right hand side of the animal and posterior to the heart while the tubular part roughly follows the border of the mantle cavity, posteriorly and on the left hand side before being reflected laterally as the ureter (U) ~~which is~~

which is generally of the same thickness throughout. The distal dilatation shown in Plate XXII by Fraga de Azevedo (1957) is probably unusual. Misrepresentations easily occur when the author does not draw the figures himself, as in Plate XVII in which the sperm duct enters the prostate gland in the normal manner, but the vas deferens leaves the female system at the base of the spermatheca. In the snails I examined the saccular part is more distinct from the tubular part than appears to be the case in the figures by either Hubendick (1947a) or Mandahl-Barth (1956). The saccular portion possesses internal transverse ridges which are more pronounced in the tubular region where they form lamellae (L). The ureter is usually smooth internally but a few small ridges may occur. The internal ridges may be fairly large but are never solid. Each consists of only a single layer of epithelial cells (E) which sometimes appear to be a pseudostratified epithelium. A basement membrane is just visible and the two lamellae of each ridge are connected by fine, sparse connective tissue fibres among which numerous pigment cells may occur (fig.15). The whole structure is much less solid than that figured by Abdel-Malek (1952) for Helisoma corpulentum Say. Histologically the proximal region of the tubular portion of the kidney differs from the distal region. In the former the cells are large, almost globose, possessing conspicuous round bodies (U.C.) which apparently are subsequently set free into the lumen, as in certain Stylommatophora (Simroth 1928) while distally the cells are much smaller and narrower. I found no trace of a longitudinal muscle on the ventral surface of the kidney.

Hubendick (1955) contends that the measurement of organs is useless taxonomically as the size may be affected to a varying degree by different types of fixative. Although it is true that slight changes most probably do occur, and also that not all the snails are relaxed to the same degree I cannot but support Schutte and van Eeden (1959a) in their rejection of Hubendick's (1955) statement. The kidney (K) and ureter (U) were measured as described elsewhere and the ratio K/U calculated for 137 snails. Although the variation in each sample is great, the values ranging from 2.0 - 4.5 (fig. 1⁶) the different means show a fair degree of constancy. The mean for all the snails was 2.9 while the mean for 30 snails of 7.7 mm. and less, was 2.7 and for 25 snails of more than 10 mm. it was found to be 2.8. In other words there is a random variation of these three values which indicates that the ratio does not increase with age.

2. The mantle ridges.

A final feature of the mantle which is considered to be of systematic importance (Mandahl-Barth, 1954, 1956) is the ridges which occur on the ventral surface of the mantle and along the rectum. The confusion resulting from the nomenclature employed in describing these is dealt with in great detail by Schutte and van Eeden (1959a) and need not be recapitulated. Although I do not share these authors' criticism of Watson's (1925) use of the terms ridge and fold, I nevertheless adhere to their terminology to avoid further confusion. In B. tropicus there are only two ridges, the renal and the median rectal ridges being absent. A well developed lateral rectal ridge is described for the Planorbidae in general (Baker, 1945) for Physopsis globosa (Watson 1925) and various bulinids (Hubendick, 1955). In B.

tropicus this ridge originates as the flattened edge of the anal lobe (A.L.) and is continued posteriorly to end against the roof of the mantle cavity (M.C.R.), near to its posterior margin. At this point it meets the intermediate mantle ridge (I.M.R.) which runs anteriorly along the mantle between the rectum (R) and the kidney (K) to end near the thickened mantle collar (COL) (fig.14). The degree of development of this ridge is variable, especially that part near the mantle collar, but it is nevertheless always distinct. No cilia were seen on this ridge but this fact may perhaps be attributed to the prolonged preservation, because the material was a few years old when dissected. However, seeing that the top of the ridge is covered by a layer of columnar epithelium while the sides are clothed with cuboidal cells, I assume that the ridge is in reality ciliated, as it is in B. africanus (Hubendick, 1947a). The length of this ridge relative to that of the nephridium is used by Mandahl-Barth (1954,1956) for distinguishing certain Bulinus species from each other. This author records that the intermediate mantle ridge is much shorter than the kidney in the short spired Bulinus species (excluding Physopsis) (1956). Although I found this to be true the ridge in my own series of snails is longer than that figured by this author. The different means of the ratio length of kidney (excluding ureter)/intermediate mantle ridge, calculated separately for the nine samples studied, varies from 1.4 - 1.9 while the mean of all the localities and the mode are 1.6. In 1954 Mandahl-Barth expressed the opinion that the ridge extends posteriorly as far as the mantle edge while he subsequently (1956)

figures the ridge as ending between the rectum and kidney. In my series the former condition is always realised. The rectal ridge bears cilia, as in the case of the intermediate ridge, and epithelium of these ridges, the collar and the sole of the foot resemble Boettger's (1944) fig. 44.

3. The circulatory system.

The blood vessels of the mantle are depicted in fig.14. An account of these structures in the Planorbidae is given by Baker (1945) and Abdel-Malek (1952). The latter notes that the pulmonary vein (P.V.) supplies the gill (G), a statement I cannot comprehend since the blood in this vein should flow into the auricle (A) instead. From a dissection of B. tropicus it appears that the gill is drained by the renal vein (R.V.) which proceeds posteriorly between the kidney and the ureter (U). It seems logical to assume that blood from this vein flows through the large vessels of the kidney into the pulmonary vein (P.V.) so that it would be more true to say that the latter drains the gill. The blood containing corpuscles which become red in Mallory's stain passes from the pulmonary vein into the auricle and thence into the less delicate ventricle (V) which has internal muscle strands (MS.) resembling those found in Thiara granifera (Lamarck) (Abbott, 1952). From here the aorta (A.O.) supplies the structures indicated in fig.17. The heart is surrounded by a pericardium (PER) and the pericardial cavity is frequently filled with round white eggs (E). Although in this instance they are free from one another they are probably identical with the strings of unidentified spherical bodies mentioned by Schutte and van Eeden (1959b) in

Biomphalaria pfeifferi Krauss. Cross sections of these eggs are depicted in fig. 18.

V. INTERNAL ANATOMY.

1. Radula.

In this system attention is focussed on only those features which are of taxonomic importance. In the Planorbinae the jaw and the radula are taxonomically important (Baker, 1945) and the salivary glands are sometimes described. The jaw (J) of B. tropicus is described and figured by Hubendick (1947) and Fraga de Azevedo (1957). It forms the dorsal bar of the T-shaped mouth and, in specimens examined by me it differs markedly from that described by either of the authors mentioned (fig. 29). Hubendick (1947, 1955) states that the jaw of B. tropicus is weakly developed, without lateral lips (L.L.) I found it to be well developed in all the specimens examined. The dorsal horizontal portion is generally broader, dorso-ventrally, than indicated in Hubendick's figure (p. 30) and snails from all nine localities possess lateral lips. These are attached to the two extremities of the jaw and are folded behind the jaw to meet in the midline whence they descend vertically to form the upright portion of the mouth. Admittedly the lips may be poorly developed and they may even appear to be absent in cases where they are folded in by retraction of the buccal mass, as occurs in snails killed in boiling water. Fraga de Azevedo (1957) describes the jaw as biconvex, a shape assumed by none of the jaws of my series. The chitinous cross-piece described by the same author as overlapping the jaw dorsally was not encountered either.

During the examination of the radula attention was paid to the general proportions of the ribbon and to the size, shape and number of the teeth. The length/breadth ratio was found to be fairly constant, both for snails from different habitats and of different sizes (Table IV). That this constancy is of taxonomic importance has not yet been proved and the data are given merely to facilitate future comparative studies. That it may be of importance is indicated by the fact that in the case of B. pfeifferi this ratio was found to vary between 2.15 - 3.09. (Schutte and van Eeden, 1959a) whereas in B. tropicus it varies between 2.1 and 3.1.

Attention is mostly focussed on the teeth. These are arranged in regular rows, the transverse rows curving slightly forward as in Physopsis globosa (Watson 1925). When dealing with the Bulininae, Mandahl-Barth (1956) emphasized the importance of the relative size of the teeth and, in certain cases, the shape of the first lateral, while he apparently finds the shape of the marginals more important as a means to characterise the different species of the Planorbinae. In describing B. tropicus he refers to the radula merely by saying that the teeth are rather small. From the data in Table V it is seen that, considering their small size, the size of the teeth varies considerably. The discrepancy in the sizes of teeth may be partly accounted for by differences in the age of the snails for it is known that with increasing age the teeth change not only in chemical composition (Verdcourt, 1948), but also in size (Hubendick, 1955). That this is not the only factor concerned is suggested by the fact that although specimen B₄₁ is so much smaller than B₁₃, (Table V), teeth of

the former are still larger than those described by Connolly (1939) Mandahl-Barth (1956) or Fraga de Azevedo (1957).

When describing a tooth it is convenient to distinguish between the base (B) and the crown (CR.) a terminology employed in all the recent papers except that of Fraga de Azevedo (1957), who uses the word ectocone to indicate crown (Fig. 20a).

The teeth of B. tropicus follow the general pattern of the Planorbinae, viz. a bicuspid central, tricuspid laterals and elongated marginals in which the cusps are replaced by a variable number of denticles (Fig. 20b). As the teeth are very similar within this family verbal descriptions are insufficient to bring out the critical differences, and should be supplemented by figures. The figures given by many authors such as Cawston (1925) Hubendick (1947) and Fraga de Azevedo (1957) unfortunately leave much to be desired, a fact which makes a careful comparison of radulae difficult. Some figures are thickly drawn and indistinct, some are minute and finelined while in yet other instances the laterals and marginals are left unnumbered.

The centrals vary much in the shape of their cusps which may be broad and relatively far apart or narrow and more upright in position, while there may also be a small denticle between the two main cusps (Fig. 20c). In all the specimens of B. tropicus examined under oil immersion, the sides of the crown have a more or less fluted (F) appearance, although it may not always be very evident, a circumstance which probably explains why this feature, which also occurs in other types of tooth, has not yet, to my knowledge, been recorded in the literature.

The general proportions of the central are shown in fig. 20b although the tooth may be either a little more elongated or squat. The crown may also be relatively smaller when compared with the base and this always appears to be the case when the central is slightly out of focus on account of its having been pushed out of position by pressure on the coverslip. The shape of the base differs from that shown by Cawston (1925, 1926). Nowhere did I see the rounded corners of the broad ^eand of the base figured by this author. In some cases the base approaches the trapezoidal shape shown by Mandahl-Barth (1956) although it is usually more horned, like the figures by Connolly (1939) and Fraga de Azevedo (1957) and yet not quite like either.

The laterals are larger than the centrals and almost invariably have a tiny denticle at the base of the mesocone (ME), either on one side or both. The first lateral is a broad tooth, fluted medially while the cutting edges of the ecto- (EC) and endocones (EN) adjacent to the mesocone may be concave, straight or convex. (fig. 20b). The mesocone is almost never simply triangular as is claimed by Mandahl-Barth (1956). Usually the two sides converge slowly from the base and then suddenly slope more sharply towards the apex, the lateral side of the triangle being longer than the median (fig. 20b). In this respect they differ from that described and figured by Mandahl-Barth (1956) and yet by reason of the more acute apex of the cusp and the longer lateral side of the triangle they are usually distinct from the truncatus group. The radulae of snails from locality G (fig. 20d) are an exception to this in that they strongly resemble those of the truncatus group which

might indicate that either the Grahamstown specimens do not belong to the tropicus group at all, or that the shape of the mesocone does not constitute a reliable basis to distinguish between the tropicus and truncatus groups as claimed by Mandahl-Barth (1956). However it might perhaps be premature to suggest the latter explanation as indicated. The base of the tooth is relatively smaller than that of the centrals and the tooth is not like any figured in the literature. It approximates that shown by Mandahl-Barth (1956) but actually it is closest to Schutte and van Eeden's (1959a) figure of B. pfeifferi. Proceeding laterally in the radula the teeth become progressively more obliquely placed and the ectocone comes to lie lower than the endo- and mesocone. Gradually the last-mentioned two cusps are replaced by 5-9 denticles (D) while 1-4 denticles appear laterally at the base of the ectocone. At the same time the tooth becomes more elongated till it assumes the shape typical of a marginal (fig. 20c). There is no clarity or uniformity as to how the various authors distinguish between lateral and marginal teeth, and as the transition is so gradual and variable, I have for the sake of objectivity, regarded the first marginal tooth as a tooth in which the endo- and mesocone are represented by at least three denticles of approximately equal size or four denticles which may be of unequal size. In counting the teeth I therefore located the first marginal and then proceeded medially counting the teeth between this and the central, thus grouping the atypical laterals or so-called intermediate teeth of Schutte and van Eeden (1959a) and Fraga de Azevedo (1957) which, in B. tropicus, vary in number from 0-2, with the typical laterals. This procedure is also reflected in the radula formula. The distinction

between what is typically lateral, intermediate and typically marginals is not feasible in B. tropicus where the transition from the first to the last-mentioned is much more gradual than seems to be the case in B. pfeifferi.

The marginals are elongated and obliquely placed. The tooth is fluted medially and the denticles occasionally have bifid tips. The denticle which represents the mesocone of the lateral teeth is broader and higher than the other denticles. Sometimes it is evenly rounded laterally but more typically it is angular (fig. 20c). Lateral to the ectocone there are up to 5 small denticles which may increase in number so as to produce a serrated lateral margin. The crowns of the extreme marginals have reduced denticles and occasionally unicuspid marginals, similar to those described for B. pfeifferi (Schutte and van Eeden, 1959a) seem to occur. On close inspection, however, these mostly turn out to be ordinary marginals seen edge-on. The base of the marginal tooth is more elongated than any figured in current literature. Besides the teeth described above a variety of abnormally shaped teeth may occur throughout a longitudinal row but these are easily recognised as anomalies and merit no further attention.

Several authors have thus far given radula formulae for B. tropicus but these, unfortunately, are not always in concurrence with each other. Thus Connolly (1939) gives the formula as 1:8:22 x 90+n, and that given by Fraga de Azevedo (1957) is 1:25 x 121. Cawston (1925, 1926) gives no formula but sets the number of laterals at 8, which, excluding the central, seems to be the only figure common to the various formulae. The limitations of these formulae and the possible causes for the

different results have already been dealt with by Schutte and van Eeden (1959a) whose views are fully borne out by my investigation of B. tropicus. While 8 laterals seem to be a constant mean, the actual number varies from one radula to another, and even from one transverse row to the other. The number of marginals to a transverse row likewise oscillates greatly and, moreover, increases with the age of the snail. In B. tropicus the issue is further complicated by the fact that there is no satisfactory criterion for distinguishing between the various types of tooth. Finally the number of transverse rows reflected in the formula has been proved to increase with the age of the snail (Schutte and van Eeden, 1959a). Thus in B. tropicus the mean number of rows for snails having shells of 7.7 mm. and less is 113, whereas the mean number of rows for snails having shells larger than 10 mm. is 134. Bearing in mind the shortcomings of any such formula, I nevertheless offer one as it may, in certain respects, be useful. From my own investigations of 92 radulae from 9 localities and from a random selection of a few from each locality in which the relative numbers of teeth were counted, a representative formula for B. tropicus seems to be $1:6 + 2:24 \times 123$. In this formula the number 2 represents the intermediate teeth which are neither typically lateral nor typically marginal.

A final feature worthy of mention in this system is the salivary glands. They are very uniform in the Planorbidae (Baker, 1945) where they are long and cylindrical. Contrary to Hubendick's (1947) account of the condition in B. tropicus in which he states that the glands do not pass through the nerve ring, they do pass

through it, narrowing considerably as they do so and then becoming larger posteriorly. The end of the loop is attached to the oesophagus or body wall or both of these, and at this point receives a blood vessel. The glands are sausage shaped (Hubendick, 1955) and although they may sometimes have slight constrictions they are not moniliform as in the case of P. globosa (Watson, 1925). For the rest the description by this author is applicable to B. tropicus except for the fact that there is not much more of the gland behind the nerve ring than there is in front of it, the lengths being about equal. Histological detail of the gland is shown in fig. 21b . It appears that the structure is more or less the same throughout the length of the gland, except at the very thin part passing through the nerve ring, where the cells do not show signs of such active secretion as in the parts with larger cells.

2. Nervous system.

The nervous system is generally very reliable for comparative studies (Hubendick, 1955) and therefore attention will be focussed not only on the ganglia but also on their associated nerves. It was unfortunately not possible for me to study the reports of the nervous system in various Basommatophora as presented by Lacaze-Duthiers (1872), Pelseneer (1895), and Elo (1938) but accounts or short notes are also found in Watson (1925), Simroth (1928), Boettger (1944), Baker (1945) and Hubendick (1947a & b). Some of Pelseneer's figures are reproduced in Boettger (1944) and Simroth (1928) while the last-mentioned author also reproduces figures by Lacaze-Duthiers.

Hubendick (1947b) is of the opinion that, allowing for the differences resulting from being coiled sinistrally or dextrally, the nervous system of the Planorbidae shows a maximum agreement with that of the Lymnaeidae and Physidae. In these families the system consists of a concentrated ring of ganglia surrounding the oesophagus (fig. 22). Some disagreement exists concerning the naming of the three most posterior ganglia of the ring. Schutte and van Eeden (1959a) name the median one the visceral, and those on either side the parietals while Baker (1945) designates the median one as the abdominal and the two adjacent ganglia as the viscerals. The issue is further complicated by the fact that Boettger (1944) when referring to a figure by Pelseneer, uses the terms visceral and parietal for the median and lateral ganglia respectively while Simroth (1928) referring to the same figure, uses the terms abdominal (A.G.) and parietal (PA.G.). The term visceral is also used to include pleural, parietal and visceral ganglia by Simroth (1928) and parietal and visceral by Watson (1925) and Wright (1957). Until such time as the homology of these ganglia has been finally settled it seems best to adhere to the nomenclature most commonly used, viz. parietal and visceral.

The cerebral ganglia (C.G.) are the largest. Each is composed of a large dorsal and a smaller ventral lobe, though variations occur not only as regards the general shape of the ganglia which sometimes possess numerous small lobes, but also in the surface which may be quite smooth or have the appearance of a mulberry. These ganglia differ in a number of details from the generalised description for the Basommatophora given by Boettger (1944).

This author found seven cerebral nerves, originating in the following order from front to back: - n. opticus, n. staticus, n. tentacularis, n. fronto-labialis superior, n. Labialis medius, n. labialis minor, n. nuchalis. In the snails examined I recognised only six nerves which do not arise in the order mentioned by Boettger (1944). The first nerve to arise from the dorsal lobe is the stout tentacular (T.M) which proceeds to the base of the tentacle where it enters a ganglion which Simroth (1928) describes as the cup-shaped ganglion. In B. tropicus the ganglion does not surround a cup-shaped hollow, but a groove. The fine ocular arises just posterior to the tentacular nerve and agrees entirely with Simroth's description of it. An extremely delicate nerve originates at the posterior edge of this ganglion and innervates the statocyst (ST.) associated with each pedal ganglion. The inferior cerebral lobe also gives rise to three nerves. There are two labial nerves (L.N) the more slender anterior one of which branches in two. At the point of origin of the more posterior labial nerve, the penial nerve arises on the left side so that this ganglion has seven nerves. The last nerve is about as fine as the one supplying the statocyst and proceeds mediad to innervate the walls of the cephalic artery. Finally the cerebro-buccal connective arises from the inferior cerebral lobe on each side. The buccal ganglia are oval and relatively smaller than in B. (P.) globosus (Watson, 1925). The interbuccal connectives too are shorter than in that species where, according to Watson, they are of about the same length as the widest part of the ganglion. In fact, in B. tropicus the buccal ganglia may be contiguous. The

origin and distribution of the buccal nerves, however, agree with Watson's findings (fig. 23). The pleural ganglia (PL.G.) agree with Boettger's (1944) observations in being small and having no peripheral nerves.

The parietal ganglia are asymmetrical, the left being at least twice the size of the right. As in Boettger's (1944) description the right parietal ganglion has only one nerve. In B. tropicus it splits into two, the anterior branch innervating the anterior part of the collar and the other branch curving round to that part of the collar which overhangs the foot posteriorly. Boettger's descriptions of the left parietal and the visceral ganglia do not coincide with the condition obtaining in B. tropicus where the left parietal has three nerves. The largest of these corresponds with the single nerve of the right ganglion and has two main branches, one innervating the dorsal lip of the pneumostome and giving off a tiny branch to the ureter, while the more ventral branch supplies the osphradium and collar. The remaining two parietal nerves are very fine, the median one running backwards along the cephalic artery to supply the anterior body wall at the level of the base of the uterus, while the lateral nerve joins a branch from the stoutest and most posterior abdominal nerve, at the level of the collar.

The abdominal ganglion is the only ganglion which is single and it bears three nerves. The stoutest of these passed^s just posterior to the vagina, and then splits into two, the first branch supplying the median part of the gill, while the second branch supplies the collar posterior to the gill. In this respect it differs from all the descriptions in the literature where it is stated that the gill is supplied by the left parietal. The nerve just

antero-dorsal to it runs between the uterus and columellar muscle and sends small branches to both. It also has a very fine branch supplying the cephalic artery. The third nerve which is also very fine arises from the right side of the ganglion and supplies the right retractor muscle of the buccal mass.

The pedal ganglia are almost as large as the cerebral and agree with Boettger's (1944) account in having six nerves. Three of these are stout and innervate the anterior, median and posterior portions of the foot, while three more dorsal slender nerves supply the body wall, generally at the level of the lateral muscle bands. In addition to the ganglia already mentioned there is, situated posterior to the inter-pedal connective, a minute little ganglion which sends a few fibres to the foot. Conspicuous white statocysts (fig. 24) containing highly refractile crystals are placed posterodorsally on the pedal ganglia.

3. Reproductive system.

The value of the genital system in determining relationships and in discriminating between closely related species is universally recognised by present day malacologists and this approach has already been applied with some degree of success to some members of the family Planorbidae (Hubendick, 1947, 1955; Mandahl-Barth, 1954, 1956.). Although it is the gross morphology which is usually taken into account, Hubendick (1955) is of the opinion that the cytological and physiological differences, too, may be decisive. When, as is very often the case, the taxonomist is forced to deal with preserved material, the physiological differences cannot be assessed and he must rely on dissection and serial

sections. According to Hubendick (1955) the organs on which attention should be focussed in this connection are the penial complex and vas deferens in the male, and the vagina and spermatheca in the female system. Theoretically the vesiculae seminales and albumen gland are less reliable since they are subject to changes associated with development and the breeding cycle which in the bulinids seems to be discontinuous (Wright, 1957).

Although the literature at my disposal contains no reference to the histology of the hermaphrodite gland in B. tropicus this aspect is dealt with in the case of various other snails such as the Pulmonata generally (Simroth, 1928), the Basommatophora (Boettger, 1944), the Planorbidae (Abdel-Malek, 1952), B. contortus (Audouin) (Larambergue, 1939) and for B. jousseaumei (Dautzenberg) (Wright, 1957). The general morphology of the ovotestis of B. tropicus agrees with that of Physopsis globosa figured by Watson (1925), and with Abdel-Malek's (1952) description. The number of acini (AC) most commonly varies between 14 - 16 in the longest of the longitudinal rows, of which there are three to four at the widest part of the gland. Only the longest of the longitudinal rows extends as far as the apex of the organ. The acini are arranged with their narrow bases opening into the tubular common atrium (C.A.) which is continuous with the hermaphrodite duct. (H.D.).

As noted by Abdel-Malek (1952) the ovotestis is surrounded by a pigmented connective tissue layer which is most densely pigmented over the apices of the acini. The germinal epithelium lines only the basal portion of each acinus so that in this respect B. tropicus agrees with B. contortus (Larambergue, 1939) and B. jousseaumei

(Wright, 1957) but differs from both Planorbis planorbis (L.) where the germinal epithelium is restricted to the common atrium (Boettger, 1944) and Arianta arbustorum (L.) where this epithelium seems to be present in the apical portion of the acinus as well, (Simroth, 1928 fig. 205A). Like Larambergue (1939) I can see no differentiation of the ovotestis into male and female zones, the two kinds of sexual element occurring intermingled.

The ovocytes (OV) have double nucleoli (NI), a condition also occurring in species of Helix and Arion (Ancel and Lams, quoted from Simroth 1928). Each nucleolus consists of two apposed spherical bodies, one slightly smaller and staining more deeply than the other.

Simroth (1928) claims that as soon as the undifferentiated cells of the germinal epithelium (G.E.) become differentiated into male elements they leave the syncytium and complete their development in the lumen of the acinus. This is apparently supported by Abdel-Malek (1952) who mentions sperm bundles (S.B.) occurring free in the lumen in Helisoma trivolvis Say. My own impression is that in B. tropicus the sperms may either be free in the lumen or attached to Sertoli cells, a view also put forward by Wright (1957), although transverse sections through the basal part of the acinus reveal the basal cells (P.C.) attached to its walls, thus lending support to Boettger (1944) who maintains that the basal cells never float in the lumen. The spermatogonia (SG) spermatids (STD) and sperm (SP) cells are easily recognisable as such and present no noteworthy features.

The hermaphrodite duct (H.D.) is tubular both proximally, i.e. nearest to the ovotestis, and distally but has a middle region with closely arranged irregular

vesicles (V.S.) forming the vesiculae seminales which contain sperm. That part of the duct bearing the vesicles is convoluted so that the whole appears as a solid and rather wide structure. Where the hermaphrodite duct splits into the male and female ducts which are completely separate in this case, it receives the duct from the albumen gland (AL.GL).

The mutual relations of these ducts are shown in fig.27. Basically they agree with the figures by Larambergue (1939) and Schutte and van Eeden (1959a) but differ from that given by Abdel-Malek (1952). In B. tropicus the short duct from the albumen gland opens into a pear-shaped sac, the carrefour, (CAR), embedded in the hilus of the albumen gland. This sac is lined by ciliated cuboidal cells with large nuclei. The proximal end of the oviduct (OVD) which is folded back on itself as illustrated in fig. 27 lies just to the left of this sac and is connected to the latter by means of a short wide duct into which both the hermaphrodite and sperm ducts (SP.D) open. Surprisingly enough this arrangement agrees well with that described for B. pfeifferi (Schutte and van Eeden, 1959b) and yet differs from the condition in Helisoma trivolvis as outlined by Abdel-Malek (1952). One would rather expect a closer resemblance between B. pfeifferi and H. trivolvis since they belong to the same subfamily, than between B. pfeifferi and B. tropicus which belong to different subfamilies. (Wright, 1957, also mentions a carrefour which, although not figured, seems to agree with that described by Abdel-Malek (1952) in being a dilatation of the oviduct a short distance from its point of origin.

Even though this structure does not seem to me to be homologous with that occurring in B. tropicus, I follow the example of Larambergue (1939) who applied the term to a structure similar to that of B. tropicus, occurring in B. contortus.

The albumen gland (AL.GL.) is more or less kidney shaped and is slightly concave on the ventral and convex on the dorsal surface. The posterior edge of the uterus fits into the hilus of the gland while the intestine is lodged in a groove (GR) along its posterior edge. The albumen gland consists of small lobules of large, closely packed cells filled with deeply staining secretory droplets (S.DR) similar to those found by Wright (1957). The duct of this gland is lined by ciliated cuboidal cells containing large nuclei.

(a) The female system.

The oviduct (OVD) is convoluted and proximally it is lined with a very glandular, columnar ciliated epithelium. It's walls are thickest towards the uterus. Fraga de Azevedo (1957) considers the dorsal glandular region of the uterus as representing a part of the oviduct and designates it as the dilatation of the oviduct, although most authors regard it as part of the uterus. This last-mentioned organ is broader proximally than distally and lies just below the floor of the mantle cavity and, like the albumen gland, is slightly concave ventrally and convex dorsally. The oviduct which enters it at the left posterior margin is surrounded at its base by an irregular sac (S) extending from the uterus. I have not encountered any reference to this structure in the literature but an apparently similar though less well developed sac appears to be figured by Larambergue (1939)

who, however, does not refer to it in the text. In B. tropicus the penis of the partner acting as the male is inserted into this sac into which the sperm is probably liberated. A similar interpretation is suggested by Larambergue's (1939) fig.44. In at least one instance the penis was found to have been inserted into the spermatheca. (fig.28). Dorsally and running obliquely across the posterior surface of the uterus, is the large well developed muciparous gland. (MU.GL). This consists of tall, large glandular cells arranged to form simple acini, the openings of which can be seen in regular longitudinal rows on the inside of the uterus. On the ventral side of the uterus the gland is restricted to the right hand posterior region. The cells secrete mucus and remain unstained except for their nuclei. The rest of the dorsal wall of the uterus is folded longitudinally, the region along the border of the muciparous gland being a darker yellow than the rest of the uterus. Fraga de Azevedo (1957) designates this darker portion as the nidamental gland (N.GL) while Abdel-Malek (1952) and Wright (1957) refer to it as the oöthecal gland. The longitudinal folds (F) are covered with tall, glandular cells with almost basally placed nuclei. There are large, round lighter staining areas present, probably representing secretory cells. This epithelium is not richly ciliated. The rest of the uterus is also folded but to a lesser degree and the ventral surface may be almost smooth. The cells in the latter region are very tall, bear numerous cilia and are interspersed with goblet cells.

The spermatheca (STH) is rounded and varies much in its size which is influenced both by the amount of sperm it contains, and the age of the snail. The spermathecal duct is short (fig. 25). The walls of the spermatheca are thin and covered with a few strands of connective tissue. On the inside they are lined by an epithelium of tall ciliated cells with centrally to basally placed nuclei. Both the duct and the vagina are lined by cells of this type but, although still ciliated, the cells of the latter become more cuboidal toward the female aperture.

(b) The male system.

The male reproductive system is of more use, taxonomically, as it is not subject to such great seasonal changes as those occurring in the female system. The sperm duct arises as a fairly narrow tube and is of the same diameter throughout. It is lined by a cuboidal ciliated epithelium with large nuclei, and is ensheathed by a thin layer of lightly pigmented connective tissue.

The prostate gland (PR.GL) is flat ventrally and convex dorsally where it abutts against the uterus. The gland consists of numerous fingershaped acini radiating from a more or less central point on its ventral surface. At this point the sperm duct enters and the vas deferens (V.D) leaves the gland, thus agreeing with the descriptions furnished by Larambergue (1939) and Wright (1957). Each acinus is deep and surrounded by a thin connective tissue sheath containing pigment cells as described by Wright. The simple epithelial lining consists of large secretory cells having large basal nuclei and conspicuous nucleoli. In gross dissection two zones may be distinguished in the gland, viz, a

peripheral opaque yellowish region, representing the apices of the acini, and a central whitish and more translucent one, representing the bases of the acini. The apical cells are full of secretory droplets which readily take up acid fuchsin. The translucent region stains very light blue and the cytoplasm appears to be less granular than in the apical cells. They contain large clear areas which probably represent masses of secretion. A narrow blue staining zone intervenes between the peripheral and central regions.

The vas deferens (V.D.) is lined by a cuboidal ciliated epithelium with large nuclei and is surrounded by a thick layer of circularly arranged muscle fibres interspersed with a few connective tissue fibres.

The penis sheath (P.S.) is club-shaped, the proximal end being broader. The surface is usually fairly smooth although it may be slightly constricted or even markedly bulging as figured by Hubendick (1947). It is thin proximally where the lumen is wide and conversely it is thick distally where the lumen is narrow. The walls of the proximal portion consist of a thin muscular layer containing scattered pigment cells and a few strands of connective tissue, and are not always of the same thickness throughout. At the distal end of the sheath where it joins the preputium (PP), the outer muscular layers are replaced by connective tissue and isolated muscular fibres. The preputium is of about the same diameter throughout and is straight whereas the penis sheath is always bent or convoluted. Numerous small muscles (EX.M) are attached along the anterior and posterior margins of the preputium. According to Fraga de Azevedo (1957) these are extensor muscles. A single large retractor muscle (RE.M) is inserted at the junction of

penis sheath and preputium. It has its origin in the columellar muscle as far back as the base of the uterus. Along the lines of attachment of the extensor muscles the preputial wall is swollen out into two longitudinal pilasters (PIL) similar to those occurring in other species of the Planorbidae described by Baker (1945), Hubendick (1946, 1955) Mandahl-Barth (1954, 1956) Fraga de Azevedo (1957) and Wright (1957), and Schutte and van Eeden (1959b). Contrary to Hubendick's (1947) statement that there are no muscular pillars proximally in B. tropicus Wright's (1957) statement that only one of the pilasters extends as far as the junction of penish sheath and preputium in B. jousseaumei, the pilasters do in the species examined, extend into that region. These pilasters actually determine the shape of the lumen of the preputium but since the degree of contraction of the preputium may influence it, care should be taken to select specimens with straight relaxed preputia when trying to elucidate the normal shape of the lumen. It appears that in B. tropicus the pilasters are situated opposite each other and are almost contiguous so that in transverse section the lumen is H-shaped. In certain cases, however, probably through unequal contraction of the muscles, the pilasters are not directly opposite each other and this results in an S-shaped lumen.

The epithelium lining the lumen of the preputium, which Hubendick (1947) describes as being cuboidal in B. tropicus, may be regarded as either cuboidal or columnar. This was also found to be the case in B. jousseaumei (Wright, 1957). Whereas this author found only a few ciliated cells in the lining of B. jousseaumei, and Hubendick (1947b) states that the preputium is non-

ciliated in the Planorbidae, the proximal region, in B. tropicus, is richly ciliated. The large goblet cells (G.C.) of B. jousseaumei are grouped together and penetrate into the muscular layer, but B. tropicus differs in both these respects. The differently staining cells mentioned by Wright (1957) are visible. The epithelium is underlain by a distinct basement membrane and the rest of the preputial wall consists of a loose meshwork of pigmented connective and muscular tissue interspersed with blood spaces.

Since the length of the penis sheath relative to that of the penis has been employed to characterise certain species of the genus Bulinus (Mandahl-Barth 1954, 1956), I have calculated this ratio for a number of specimens of B. tropicus (Table VI). From this table it is apparent that the ratio varies so much in each of the samples that it is impossible to use the ratio obtained from a single specimen either as a measure to characterise the species, or as a criterion to identify the particular specimen. The means for the various samples dealt with are relatively constant, fluctuating between 1.2 and 1.6. Moreover, from the analysis of the data it seems that the ratio does not change with age.

Inside the penis sheath two structures may be distinguished, viz., the epiphallus, which is a continuation of the vas deferens, and the penis. This organ opens into the preputium as indicated in fig. 29. The epiphallus is a narrow tube lined by cuboidal epithelial cells with large round nuclei and covered externally by a muscular layer. Histologically it therefore closely resembles the vas deferens except that the development of the muscular tissue is weaker than in the latter.

Distally the tube loses its circular appearance owing to the accumulation of muscular and connective tissue on either side, which produces a more or less oval shape. Scattered cells full of globules (GLO) occur in this connective tissue. From their appearance they seem to be glandular cells and as these globules do not stain at all, whereas the other secretions generally take up stains readily, they are probably mucous cells. The cells lining the lumen in this region are taller than elsewhere and the nuclei are basally placed. The epiphallus usually enters the penis subterminally. Neither this duct nor the penis proper contains any pigment cells.

The morphological and histological details of the walls of the penis (P) are depicted in fig. 30 . From this it is apparent that the wall of the penis consists of two layers, viz, an inner epithelial layer and an outer layer consisting of connective and muscular tissue. The latter forms a series of projections (PAP) directed toward the lumen and clothed with greatly elongated epithelial cells thus forming protuberances projecting into the lumen. Following Larambergue (1939), I refer to these protuberances as papillae. In surface view the arrangement of these papillae resembles that of the protuberances of a pineapple. Proximally the papillae are large while the muscular part of the walls of the penis are not thick. Distally the papillae decrease in size and the cells become more squat while the muscular layer increases in thickness. The large vacuolated cells described by Larambergue (1939) occur in this region. At its extreme tip the penis itself becomes thin walled and the epithelial cells cuboidal.

In most cases a short ridge occurs on the inside of the penis in line with the opening of the epiphallus. This ridge coincides with a groove on the external surface. In those cases in which the ridge is absent its position is generally betrayed by a slight concentration of longitudinal muscle fibres. To my knowledge no ridge of this kind has as yet been described for any of the buliids. In a few instances the penis and sheath could not be distinguished and the lumen of the sheath was filled with loose strongly pigmented connective tissue. As in the case of the ratio penis sheath/preputium, the ratio penis epiphallus is very variable. In the various samples this last mentioned ratio varies between 0.8 and 2.3, whereas the means of the different samples vary between 1.0 and 1.5. In spite of the apparently much greater variation than in the case of the ratio PS/PP, fig.31 reveals that most of the values of P/EP are concentrated around 1.3, 1.4 and there is a more normal distribution of the values than in the case of the ratio PS/PP.

VI. SUMMARY.

1. Special attention was paid to the three most important taxonomic characters, the shell, radula and penial complex but the other systems were also examined both morphologically and histologically.
2. The snail samples were selected both on the basis of their resemblance to typical specimens of B. tropicus and their geographical distribution. In spite of these precautions in the selection the present study of the shell once more emphasised the notorious polymorphism of this species.

3. The important role played by ecological variation in producing the widely diverging shell types, differing both in shape and texture, is discussed. Although two main adult types occur there is only one main type of juvenile, suggesting, as was observed by Schutte and van Eeden (1959a) that the form of the juvenile is less affected by the environment than is the case in the adults. This seems logical as the latter have been exposed to the modifying influences for a longer period than the younger snails.

4. A conchometrical analysis revealed that the shape of the spire varies immensely as does its apical angle and its length relative to the entire length of the shell. The spire was also found to be relatively shorter in the smaller forms than is the case in large specimens.

5. In respect of the shape of the aperture the adult shells usually fall into two main groups which not only change with age but probably also with varying ecological conditions. Although the columella region is fairly uniform in each sample it varies from one sample to the other.

6. An osphradium was found to be present and is described in detail.

7. The gill is normal but the anal region differs slightly from the descriptions given by previous authors.

8. The ratio kidney/ureter was found to vary between 2.0. and 4.4.

9. Only two of the taxonomically important ridges are present on the roof of the mantle cavity, the renal ridge and the median rectal ridge being absent. The intermediate mantle ridge differs from the figure given by Mandahl-Barth's (1956) in being longer, and in always

extending posteriorly to meet the lateral rectal ridge at the edge of the mantle cavity.

10. An account is given of the blood vessels draining the gill. The spherical bodies mentioned by certain authors as occurring in the pericardial ^{cavity} of certain planorbids were found to be present in a large number of specimens. They appear to be the eggs of an unidentified organism.

11. In the digestive system the jaw differs from the descriptions offered in the literature. A study of the general proportions of the radula revealed that the ratio length/breadth is fairly constant and this ratio may therefore prove to be useful in comparison with related species.

12. The sides of the teeth were found to be fluted and small denticles were detected between the cusps of the centrals and at the base of the mesocone of the laterals. The mesocone of the laterals is almost never simply triangular as is stated to be the condition in the tropicus group and in certain instances, it even approaches the arrowhead shape characteristic of the truncatus group.

13. In spite of the known limitations of radula formulae, a generalised formula for B. tropicus is offered:

1:6+2; 24 x 123. The salivary glands pass through the nerve ring.

14. The names applied to the various ganglia of the circumoesophageal ring are discussed and the nerves originating from them described.

15. In the hermaphrodite gland there is no division into the male and female zones, and the oocytes were found to have double nucleoli as is the case in certain other

pulmonates. The carrefour region differs from that of B. jousseaumei and H. trivolvis and agrees with the condition in B. pfeifferi.

16. Attention is focussed on an irregular sac extending from the uterus and partly surrounding the base of the oviduct.

17. In the prostate gland two main regions are distinguished. The occurrence of a short internal ridge in the proximal region of the penis is noted. The pilasters in the preputium extend as far as the junction of the latter with the penis sheath. The penis sheath/preputium ratio was found to vary considerably, but the means for the samples separately vary only between 1.2 - 1.6.

VII. LIST OF ABBREVIATIONS NO. 7.

A - auricle	ME - mesocone
AC - acinus	M.S - muscle strands
AL.GL - albumen gland	MU.GL - muciparous gland
A.L. - anal lobe	N - nucleus
AO - aorta	N.C. - nurse cell
B - base	N.GL - nidamental gland
B.C. - basal cells	NI - nucleolus
B.G. - buccal ganglion	O - osphradium
BL. - blood	OE - oesophagus
B.M. - basement membrane	OV - ovocytes
B.RET. - buccal retractor	OVO - oviduct
C - central cavity	p - penis
CA - common atrium	PA.G - parietal ganglion
CAE - caecum	PAP - papilla
CAP - capsule	P.C. - peripheral cavity
CAR - carrefour	P.COL - Posterior part of collar
C.G. - cerebral ganglion	PE.G - pedal ganglion
CIL.C. - ciliated cells	PER - pericardium
round osphradium	PI.C - pigment cell
CIR.R. - circumoesophageal	PIL - pilaster
aperture ring	PL.G - pleural ganglion
COL. - collar	PN - pneumostome
CR. - crown	P.P. - preputium
CRY - crystals	PR.GL. - prostate gland
C.T. - connective tissue	P.S. - penis sheath
D - denticles	P.V. - pulmonary vein
D.T.P. - dorsal tentacular	R - rectum
process	RE.M - retractor muscle
E - epithelium	R.SH - radula sheath
EC. - ectocone	R.V. - renal vein
EG. - eggs	S - sac
EM.C - large embryonic	SAL.GL - salivary gland
cells	S.B. - sperm bundle
EN. - endocone	S.DR - secretory droplets
EP. - epiphallus	SG - spermatagonia
EX.M - extensor muscles	S.K. - saccular part of kidney
F - fluted edge	SP - sperm
FO - fold	SP.D - sperm duct
FOO - foot	ST - statocyst
G - gill	STD. - spermatids
GAN - ganglion	STOM - stomach
G.C. - goblet cells	STH - spermatheca
G.E. - germinal epithelium	T.K. - tubular part of kidney
GI.C. - giant cells	T.N. - tentacular nerve
GLO - globules	U - ureter
GR - groove	U.C. - urine concretion
H.D. - hermaphrodite duct	V - ventricle
H.G - " gland	V.D. - vas deferens
I.M.R. - intermediate	V.G. - visceral ganglion
mantle ridge	V.S. - vesiculae seminales
INT. - intestine	V.T.P. - ventral tentacular process
J - jaw	
K - kidney	
L - lamella	
LAT.L - lateral lips	
L.L. - lateral lips	
L.N. - labial nerve	
L.R.R. - lateral rectal	
ridge	
M - muscular tissue	
MA - mantle	
M.C.F. - mantle cavity	
floor	

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IX. LITERATURE CITED.

- ABBOTT, R. 1952. A study of an intermediate snail host (Thiara granifera) of the oriental lung fluke (Paragonimus). Proc. U.S. Nat. Mus 102: 71-116.
- ABDEL-MALEK, E 1952. Morphology, bionimics and host-parasite relations of the Planorbidae. Diss. Univ. Michigan.
1954. Morphological studies on the family Planorbidae (Melusca: Pulmonata) 1. Genital organs of Helisoma trivolvis (Say) (Subfamily Helisomatinae F.C. Baker 1945). Trans. Amer. micros. Soc., 73, 2: 103 - 124.
- ALVES, W. 1956. The snail vectors in Southern Rhodesia. WHO/Bil. Conf./6.20 Aug.1956.
- BAINES, T. 1877. The gold regions of South East Africa. MacKay. Port Elizabeth.
- BAKER, F. 1928. Influence of a changed environment in the formation of new species and varieties. Ecology, 9:271.
- * BAKER, F. 1931. The classification of the large planorbid snails of Europe and America. Proc. zool. Soc. Lond., (2): 575-592.
- BAKER, F. 1945. The Molluscan family Planorbidae. University of Illinois Press Urbana.
- BAYER, F. 1955. B.tropicus and Chaetogaster. Proc. zool. Soc. Lond., 125: 407-409.
- BOETTGER, O. 1910. Die Binnenkonchylien von Deutsch-Südwestafrika. Abh.Senckenb. naturf.Ges. Frankfurt, XXXII:431-456.
- BOETTGER, C. 1944. Tierwelt Nord- und Ostsee, 35 Lieferung IX b₂ Basommatophora.
- BOYCOTT, A. 1928. Conchometry. Proc.Malac.Soc.Lond., 18: 8-31.
- * BUCHNER, O. 1890. Beiträge zur Kenntnis des Baues der Einheimischen Planorbiden. Diss. Stuttgart.
- CARRIKER, M & N Bilstad. 1946. Histology of the alimentary system of L. stagnalis apressa Say. Amer. micr. Soc. 65: 250-275.

- CAWSTON, F. 1922. Experimental infestation of freshwater snails with special reference to bilharziasis. S. Afr. J. Sci., 18:396.
- CAWSTON, F. 1923. Occasional hosts of some South African trematodes. Rep.S. Afr. Ass. Adv. Sci., 351-353.
- CAWSTON, F. 1925. A search for intermediate hosts and a study of their radulae. J. trop. Med.(Hyg.) XXVIII: 14-15.
- CAWSTON, F. 1925b. A contribution to the study of the radulae of freshwater Mollusca. J. trop. Med. (Hyg.) XXVIII: 365-366.
- CAWSTON, F. 1926. Gundlachia at Malvern, and an examination of the radulae of other intermediate hosts of trematode worms in Natal. Trans.roy.Soc. S.Afr., XIII: 39-42.
- CAWSTON, F. 1938. Some characteristics of Bulinus and Physopsis. J.Conch. 21: 71-72
- CONNOLLY, M. 1916. Notes on South African non-marine Mollusca. Ann.S.Afr.Mus., XIII: 179-190.
- CONNOLLY, M. 1931. The non-marine Mollusca of South West Africa. Ann.S.Afr.Mus., XXIX:277-335.
- CONNOLLY, M. 1939. A monographic survey of South African non-marine Mollusca. Ann.S.Afr.Mus., 33:
- DEGNER, E. 1922. Beiträge zur Kenntniss der Land und Süßwasserfauna Deutsch-Südwestafrikas. Ergebnisse der Hamburger deutsch-südwestafrikanischen Studienreise, 1911. Herausgegeben von W. Michaelson. Bd.11.
- DE MEILLON, B. 1948. Aspects of the natural history of Bilharzia in South Africa. S.Afr. med. J.,22: 253-260.
- * ELO, J. 1938. Das Nervensystem von Limnaea stagnalis (L) Lam. Ann. (bot.-zool) Soc. zool.-bot.fenn.Vanamo.
- FRAGA DE AZEVEDO, J. 1957. Estudos, ensaios e documentos XXXI. Bertrand (Irmaos) Lda.Lisboa.

- FULLER, C. 1932. Louis Trigardt's trek across the Drakensberg. van Riebeeck Soc. Cape Town.
- GABRIEL, C. 1939. The freshwater Mollusca of Victoria. Mem.national Mus., Melbourne., 11.
- GERMAIN, L & M. NEVEU-LEMAIRE. 1926. Essay on medical malacology. Ann.Parasit.hum.comp. IV: 286-305; 352-384.
- HAAS, F. 1922. Untersuchungen über den Einfluss der Umgebung auf die Molluskenschale. Paläont.Z. 4:120-127.
- HUBENDICK, B. 1945. Studien über das Wachstum der Radula bei L. limosa. Arkiv för Zoologi, Band 36A (21).
- HUBENDICK, B. 1946. The anatomy of Bulinus with a discussion of the term prostate and its sense in the Basommatophora. Proc. malac.Soc.Lond., 27, 5: 186-196.
- HUBENDICK, B. 1947a. Studies on Bulinus. Arkiv för Zoologi. Bd. 40 A, 16.
- HUBENDICK, B. 1947b. Phylogenetic relations between the higher limnic Basommatophora. Zool. Bidr. Uppsala. Bd. 25: 141-164.
- HUBENDICK, B. 1955. Phylogeny in the Planorbidae. Trans. zool.Soc.,Lond., 28,6: 453-542.
- HUBENDICK, B. 1951. Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature and distribution. Kungl.Svenska Vetenskapsakademiens Handlingar. Fjärde Serien. Band 3,1.
- KRAUSS, F. 1848. Die Südafrikanischen Mollusken. Ebner & Seubert, Stuttgart.
- *LACAZE-DUTHIERS, H.de. 1872. Du Système Nerveux des mollusques Gastéropodes Pulmonés Aquatiques. Arch.Zool.Exp.gen., 1: 437.
- LARAMBERGUE, M.de. 1939. Etude de l'autofécondation chez les Gastéropodes Pulmonés. Recherches sur l'aphallie et la fécondation chez Bulinus (Isidora) contortus Michaud. Bull.biol.France et Belgique. Tome LXXIII: 19 - 213.

- MANDAHL-BARTH, G. 1954. Freshwater molluscs of Uganda and adjacent territories. Ann.Mus.Congo belge. Série in 8^o, 32.
- MANDAHL-BARTH G. 1956. African vector snails of bilharziasis. 11 Bulinus. WHO/MH/AS/81a.56.
- MELVILLE, J & J. PONSONBY. 1903. Physa zuluensis n.sp. Ann.nat.Hist.XII: 606.
- MOZLEY, A. 1939. The freshwater Mollusca of Tanganyika territory and Zanzibar Protectorate and their relation to human schistosomiasis. Trans.roy.Soc.Edin. 59: 687-744.
- MOZLEY, A. 1951. The snail hosts of Bilharzia in Africa. H.K. Lewis, London.
- NEUHAUS, W. 1952. Wachstum und Variation den Schnecken-gehäuse. Biol.Zbl. 71(9/10):470-486.
- PELSENEER, P. 1895. "Prosobranches" aeriens et Pulmonés branchifères. Arch.Biol., 14:351.
- PILSBRY, H & J. BEQUAERT. 1927. The aquatic molluscs of the Belgian Congo. With a geographical and ecological account of Congo malacology. Bull.amer. Mus.nat. Hist., LIII: 69-602.
- PORTER, A. 1922. Some modern developments in animal parasitology. Rep. S.Afr.Ass.Adv.Sci., XIX: 64-94.
- PORTER, A. 1938. Larval Trematoda found in certain South Africa Mollusca with special reference to schistosomiasis. Publ.S.Afr.Inst. med.Res. 8,42.
- QUICK, H. 1933. Isidorella pyramidata (Sow.). J. Conch. 19: 322.
- *QUICK, H. 1933. Isidorella pyramidata (Sow.). A correction J.Conch., 20:50.
- ROTARIDES, M. 1932. Das ökologische Formproblem der Weichtiere. Allattani Közlemények, XXIX, 3-4: 151-164.
- *SARASIN, P & F. SARASIN. 1898. Die Süßwasser-Mollusken von Celebes. Materialien zur Naturg. der Insel Celebes. 1. Wiesbaden.
- SCHUTTE C.H.J. & J.A. VAN EEDEN, 1959a. Contributions to the morphology of Biomphalaria pfeifferi (Krauss). 1. The shell and radula. Ann. Mag.Nat.Hist.Ser.13, 11:1-20.

- SCHUTTE C.H.J. & J.A. VAN EEDEN, 1959b. Contributions to the morphology of Biomphalaria pfeifferi (Krauss). 11 Internal Anatomy. Ann.Mag. Nat.Hist. (in press).
- SCHWETZ, J. 1952a. Sur la confusion actuelle dans la classification des Planorbes centro-africanis et les moyens pour y remédier. Mém.Inst.colon.belge Sci.nat., 8:5-29.
- SCHWETZ, J. 1952b. Nomenclature simplifiée des mollusques africains vecteurs de bilharzioses. Suggestion pour une discussion raisonnée sur une future classification. Bull. Soc.Pat.exot., 45: 381-388.
- SCHWETZ, J. 1954. L'influence du milieu sur la taille et la forme du meme Planorbe ou du meme Bulinus. Ann.Soc.zool.Belg. 85(1): 23-34.
- SIMROTH, H & G.GRIMPE 1918. Weichtiere (Mollusca) in Brehms Tierleben, Erster Band. Bibliographisches Institut, Leipzig und Wien.
- SIMROTH, H. 1928. Pulmonata in Bronns Klassen und Ordnungen des Tier-Reichs., 3 Band, Mollusca, 2 Abteilung 2 Buch.Leipzig.
- STILES. 1931. Opinions rendered by the international commission of zoological nomenclature. Opinions 115-123, Smithson.misc.Coll.73
- VAN EEDEN, J.A. 1958. Two useful techniques in freshwater malacology. Proc.malac.Soc.Lond., 33, 2: 64-66.
- VERDCOURT, B. 1948. The staining of radulae. Stain Technology, 23, 3.
- WATSON, H. 1925 (In Connolly) The non-marine Mollusca of Portuguese East Africa. Trans.roy.Soc. S.Afr. 12: 105-220.
- WESENBERG-LUND C.1939. Biologie der Süßwassertiere. Julius Springer. Wien.
- WRIGHT, C.A. 1957. Studies on the structure and taxonomy of Bulinus jousseaumei Dautzenberg. Bull.Mus.(Nat.Hist.) Zool. 5, 1.
- Publications indicated by * were not seen in the original.

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- FIG.15. Histology of a kidney lamella.
- FIG.16. Frequency distribution of the ratio kidney/ureter.
- FIG.17. Two diagrams illustrating the blood vessels leaving the heart.
- A 1) vessel to the intestine
 2 and 3 vessels supplying the stomach
 4) vessel supplying caecum
 5) vessel supplying liver
- B 1) vessel supplying caecum
 2) " " oesophagus
 3) " " cardiac stomach
 4) cephalic artery to buccal mass
 5) vessel to albumen gland
- C Vessel passing over the stomach to the intestine
- FIG.17b. Figure of the heart showing eggs in the pericardial cavity.
- FIG.18. Transverse section through one of the above-mentioned eggs.
- FIG.19. The jaw and lateral lips.
- FIG.20a) Lateral tooth illustrating the various parts.
- FIG.20b) A central tooth and half of a transverse row of teeth of a specimen from sample B.
- FIG.20c) Variations in the central teeth of the radula.
- FIG.20d) First lateral teeth of specimens from sample G.
- FIG.21a) The salivary glands.
- FIG.21b. Transverse section through a salivary gland.
- FIG.23. Diagram of the buccal ganglia and their nerves.
- FIG.24. Illustration of a statocyst on a pedal ganglion.
- FIG.25. Diagram of the reproductive system (excluding the penial complex).

- FIG.26. The ovotestis.
- FIG.27. Diagram of the carrefour region.
- FIG.28. Figure of a penis in the spermatheca.
- FIG.28b. Diagram of the dorsal view of the uterus.
- FIG.28c. Semidiagrammatic figure through uterus to show the structure of the muciparous gland.
- FIG.28d. A Portion of the ventral wall of the uterus.
- FIG.28e. Muciparous gland cells.
- FIG.28f. Histology of the spermatheca.
- FIG.29. The penial complex.
- FIG.29b. Transverse sections of the sperm duct and vas deferens.
- FIG.30. Transverse section of penis.
- FIG.30b. Epiphallus sections through proximal and distal regions.
- FIG.30c. Histological detail of the preputium.
- FIG.31. Frequency distribution of the ratio's PS/PP, and P/EP.
- TABLE I Comparison of the means and means of modal classes of certain ratios for the samples separately and combined (T). Mo.mean - mean of modal class.
- TABLE II Table showing means of the ratios shell length/aperture height (L/AH) and shell length/breadth (L/B). n - number of specimens in sample.
- TABLE III Table of mean values of the ratio shell length/spire (L/S), the mean spire angle, and the labrum depression angle.
- TABLE IIIb Table of mean values of the ratios shell breadth/aperture breadth (B/AB) and aperture height/breadth (AH/B).

TABLE IV The mean values of the ratio length/breadth (L/B) of the radula for the samples separately, combined, and for snails with shells of 7.7 mm. and less, and snails larger than 10 mm.

TABLE V Table showing the size of the central and lateral teeth, given by various authors, calculated from figures by them, or from my own specimens. The height of the crown of the first lateral was measured.

TABLE VI Table of the mean ratios of penis sheath/preputium (PS/FP) and penis/epiphallus (P/EP) in the samples separately and for snails of different sizes.

TABLE I

Sample	$\frac{AH}{AB}$			$\frac{B}{AB}$			$\frac{L}{AH}$			$\frac{L}{B}$			$\frac{AH}{B}$			$\frac{AH}{L}$			$\frac{S}{AH}$		
	Mean	Mo	Mean	Mean	Mo	Mean	Mean	Mo	Mean	Mean	Mo	Mean	Mean	Mo	Mean	Mean	Mo	Mean	Mean	Mo	Mean
W	1.5	1.5	1.5	1.5	1.5	1.4	1.4	1.5	1.5	1.4	1.4	1.5	1.0	1.0	1.0	0.7	0.7	0.2	0.2	0.2	0.2
D	1.5	1.4	1.5	1.4	1.4	1.4	1.4	1.4	1.4	1.3	1.3	1.4	1.0	1.0	1.0	0.7	0.7	0.1	0.1	0.1	0.1
B	1.4	1.4	1.6	1.6	1.4	1.4	1.4	1.4	1.4	1.4	1.3	1.3	0.9	0.9	0.9	0.7	0.7	0.2	0.2	0.2	0.2
S	1.4	1.4	1.6	1.6	1.6	1.6	1.4	1.6	1.6	1.4	1.4	1.4	0.9	0.9	0.9	0.6	0.6	0.2	0.2	0.2	0.2
K	1.5	-	1.4	-	1.3	1.3	1.4	-	1.4	1.4	-	1.0	-	-	-	0.8	-	-	-	-	-
A	1.3	1.4	1.5	1.5	1.6	1.6	1.4	1.6	1.6	1.4	1.4	1.5	0.9	0.9	0.9	0.6	0.6	0.2	0.2	0.2	0.2
H	1.5	1.5	1.6	1.5	1.5	1.5	1.4	1.5	1.5	1.4	1.4	1.5	1.0	1.0	1.0	0.7	0.7	0.2	0.2	0.2	0.2
M	1.4	1.4	1.6	1.5	1.5	1.5	1.3	1.5	1.5	1.3	1.3	1.3	0.9	0.9	0.9	0.7	0.7	0.2	0.2	0.2	0.2
G	1.5	1.5	1.5	1.6	1.5	1.5	1.4	1.5	1.5	1.4	1.4	1.4	1.0	1.0	1.0	0.7	0.7	0.2	0.2	0.2	0.2
T	1.4	1.4	1.5	1.5	1.5	1.5	1.4	1.5	1.5	1.4	1.4	1.4	0.9	0.9	0.9	0.7	0.7	0.2	0.2	0.2	0.2

TABLE II

Sample	$\frac{L}{AH}$		$\frac{L}{B}$			
	n	mean	n	Range	mean	Interval
W	47	1.4	47	1.2 - 1.6	1.4	0.4
D	12	1.4	12	1.3 - 1.5	1.4	0.2
B	40	1.4	40	1.1 - 1.5	1.3	0.4
S	16	1.6	11	1.2 - 1.5	1.4	0.3
K	11	1.3	11	1.3 - 1.5	1.4	0.2
A	15	1.6	15	1.2 - 1.6	1.4	0.4
H	10	1.5	10	1.3 - 1.5	1.4	0.2
M	10	1.5	10	1.2 - 1.4	1.3	0.2
G	10	1.5	10	1.3 - 1.6	1.4	0.3
T	171	1.5				

TABLE III

Sample	$\frac{L}{S}$		Spire angle			
	n	mean	n	Range	mean	Interval
W	23	9.7	20	81 - 113	97.6	32
D	12	15.2	10	90 - 130	112.8	40
B	40	9.2	40	80 - 134	93.5	54
S	16	7.3	10	74 - 102	86.4	28
K	11	12.5	9	90 - 119	104.4	29
A	15	6.7	10	58 - 88	78.1	30
H	10	8.0	10	75 - 104	87.9	29
M	10	9.0	9	86 - 127	96.0	41
G	10	9.3	10	87 - 102	93.6	15

TABLE III

Labrum depression angle

Sample	n	Range	mean	Interval
W	12	54 - 64	58.6	10
D	10	53 - 60	58.3	7
B	40	53 - 61	57.1	8
S	10	53 - 62	58.6	9
K	9	56 - 64	58.4	8
A	10	52 - 65	58.8	13
H	10	57 - 66	61.7	9
M	8	55 - 62	57.3	7
G	10	52 - 61	57.4	9

TABLE IIIb.

 $\frac{B}{AB}$

Sample	n	Range	mean	Interval
W	47	1.4 - 1.7	1.5	0.3
D	12	1.4 - 1.6	1.5	0.2
B	40	1.4 - 1.9	1.6	0.5
S	15	1.4 - 1.7	1.6	0.3
K	11	1.4 - 1.5	1.4	0.1
A	12	1.4 - 1.6	1.5	0.2
H	10	1.5 - 1.8	1.6	0.3
M	10	1.5 - 1.6	1.6	0.1
G	10	1.4 - 1.7	1.5	0.3

 $\frac{AH}{B}$

Sample	n	Range	mean	Interval
W	47	0.9 - 1.0	1.0	0.2
D	12	0.9 - 1.0	1.0	0.1
B	40	0.8 - 1.0	0.9	0.2
S	16	0.8 - 0.9	0.9	0.1
K	10	1.0 - 1.0	1.0	-
A	12	0.8 - 1.0	0.9	0.2
H	10	0.9 - 1.0	0.9	0.1
M	10	0.8 - 0.9	0.9	0.1
G	10	0.9 - 1.0	1.0	0.1

TABLE IV

Ratio L/B of radula

Sample	n	Range	mean	Interval
W	46	2.1 - 3.0	2.5	0.9
D	11	2.2 - 3.1	2.5	0.9
B	31	2.1 - 2.7	2.4	0.6
S	6	2.3 - 2.6	2.4	0.3
K	7	2.3 - 2.9	2.6	0.6
A	9	2.3 - 2.7	2.4	0.4
H	8	2.2 - 2.9	2.6	0.7
M	10	2.2 - 2.7	2.4	0.5
G	9	2.2 - 2.8	2.4	0.6
7.7 mm	30	2.3 - 2.9	2.5	0.6
10 mm	24	2.2 - 3.1	2.5	0.9
T	134	2.1 - 3.1	2.5	1.0

TABLE V

Height of Teeth					
Author	Central	Lateral	Author	Central	Lateral
Connolly			Mandahl-		
1939	0.009	0.01	Barth	0.007	0.01
			1956		
Hubendick			Fraga de		
1947	0.01	0.01	Azevedo	0.006	0.009
			1957		
Cawston			Myself		
1925	0.033		B ₁₃	0.01	0.02
			10.0 mm		
Cawston			Myself		
1926	0.02	0.03	B ₄₁	0.010	0.012
			5.84 mm		

TABLE VI

PS/PP				
Sample	n	Range	mean	Interval
W	39	0.8 - 2.1	1.5	1.3
D	11	1.0 - 2.0	1.5	1.0
B	29	0.9 - 2.3	1.3	1.4
S	12	1.0 - 1.8	1.3	0.8
K	10	1.0 - 1.6	1.3	0.6
A	10	1.0 - 1.7	1.4	0.7
H	8	1.1 - 2.3	1.2	1.2
M	8	1.3 - 2.0	1.6	0.7
G	10	1.0 - 1.4	1.3	0.4
7.7 mm	34	0.8 - 1.9	1.4	1.1
10 mm	24	1.0 - 2.3	1.4	1.3

TABLE VI

P/EP				
Sample	n	Range	mean	Interval
W	37	1.0 - 2.8	1.4	1.8
D	10	1.2 - 2.2	1.5	1.0
B	25	0.9 - 2.1	1.3	1.2
S	12	0.9 - 1.5	1.2	0.6
K	10	0.9 - 1.3	1.1	0.4
A	10	0.8 - 1.6	1.0	0.8
H	8	0.9 - 2.3	1.2	1.4
M	8	0.9 - 1.4	1.4	0.5
G	10	1.0 - 2.1	1.4	1.1
7.7 mm	28	0.9 - 2.8	1.3	1.9
10 mm	21	0.9 - 2.2	1.4	1.3

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