SOME ASPECTS OF THE MORPHOLOGY OF LYMNAEA NATALENSIS KRAUSS (MOLLUSCA : BASOMMATOPHORA)

b y

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T H E S I S

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C O N T E N T S

1. INTRODUCTION.

In recent years, the morphology of gasteropods has received increased attention because a better knowledge of the morphology and systematics of this molluscan group is essential in the understanding and study of trematode life cycles, as it forms an important basis in the understanding of the developmental stages of flukes. Moreover, some of these snails also serve as intermediate hosts of the trematode parasites of man and his domestic animals. In order to use the morphological features critically in the description of freshwater molluscs, it is of fundamental importance to have a better understanding of the extent and the nature of the morphological variation (Hubendick, 1951a), because the amount of inter- and intraspecific variation presents one of the greatest difficulties encountered in the species demarcation in this suborder.

The range of variation in the various species of Lymnaea Lamarck is, as a general rule, characterized by the absence of clear geographical variation (Hubendick. 1951a), and, on the other hand, the range of variation within each separate population is very narrow (Hubendick, 1951a).

The problems arising from a study of the variation in this group of molluscs, are clearly illustrated by the investigations of Mozley (1935, quoted from Berrie, 1959), In his study of two species of Lymnaea, this author found that, in L. palustris (Müller) the range of variation in any one locality tends to approximate that which occurs over the whole territory occupied by this animal, and in L. emarginata Say the range of any one locality forms only a part of the geographical variation. In Berrie's (1959) view Mozley (1935) attributed the difference in the type of variation shown

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by these two species, to the fact that L. palustris, being of very common occurrence in the area of survey (Canada), had frequent opportunities for the interbreeding of stock to take place. L. emarginata, on the other hand, was of relatively rare occurrence which would make the transfer of individuals less likely and so allowed genetic differences to arise between the various colonies. Although Berrie (1959), in his study on the radula of L. peregra (Müller), which is fairly obiquitous in the area where he conducted his study (Northwestern Europe), expected the variation of L. peregra to resemble that of L. palustris, he actually found the opposite, viz., that it resembled that of L. emarginata. It is obvious, therefore, that while the range of variation occuring in a population may in some instances represent the total range of variation of the geographical species, it in other cases represents only a fraction of the total range of variation. On these data the assumption that the relative occurrence determines the type of variation range thus seems to be incorrect.

The nature of variation may largely be controlled in two ways, viz., ecophenotypically or genetically. Unfortunately, a study of the biological nature of the morphological characteristics has largely been neglected in the past (Hubendick, 1951a). It has often been suggested and, in some cases demonstrated, among others by Simroth et al.(1918), Baker (1928), Rotarides (1932) Wesenberg-Lund (1939), Boettger (1944), Hubendick (1951a), Schwetz (1954) and Stiglingh et al. (1962), that ecological factors influence the shell in a number of ways. The very features known to be influenced by ecological conditions unfortunately are those most commonly employed in species descriptions, viz., size and thickness of the

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shell, zebrine coloration and the position of growth lines (McCraw, 1957), colour, sculpturing (Stiglingh et al, 1962) acquiring of sexual maturity (Wright, 1957), and the degree of exertion of the spire in certain planorbid- and bulinid snails (Schwetz, 1954 and Stiglingh et al. 1962 respectively).

In the study of freshwater snail systematics it seems essential, firstly, to unravel the complex structure of a single snail population (Wright, 1957), in order to determine the amount and the nature of variation and, secondly, to compare several populations from different localities before one can properly establish the actual species characteristics (Boycott, 1914).

The state of confusion in the systematics of the family Lymnaeidae is, among other factors, primarily due to the great morphological uniformity in individual populations, coupled with a wide range of variation within the species (Hubendick, 1951a).

A cursory investigation of the literature dealing with the species of the genus Lymnaea, indigneous to Africa, reveals a general agreement that the large number of species described from this continent cannot all represent valid species. Between the years 1848 and 1939 no less than 11 species were described from or reported to occur in South Africa alone, of which Connolly (1939) recognises only two as actually occurring in this territory. These are L. natalensis and L. caillaudi Bourguignat. In 1954 Mandahl-Barth reduced L. caillaudi to a subspecies of L. natalensis but in a letter of later date to Professor J.A. van Eeden of this Institute he expresses the opinion that even the subspecies L. natalensis caullaudi can no longer be regarded as

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being distinct from L. natalensis natalensis.

An investigation aimed at a revaluation of the systematic units within the Lymnaeidae, induced Hubendick (1951a) to link L. natalensis with the species auricularia (L.), rubiginosa Michelin, rufescens Gray and swinhoei Adams, in the superspecies L. auricularia (L), although conceding that L. natalensis more probably represents a separate though closely related species of this unit.

As a possible contribution towards the ultimate solution of the problem the present investigation is aimed at determining some of those characteristics, of the subspecies L. n. natalensis, which show a narrow range of variation which can be used as taxonomic hallmarks.

To satisfy this aim, the material selected, was sampled from a single population of the same locality.

2. MATERIALS AND TECHNIQUE.

The type locality of L. n. natalensis given by Krauss (1848) was simply stated as: "Natal, commonly". The material used in this study, therefore, consisted of three collections, made at about six-monthly intervals at Henley Dam, on the Umsunduzi River, a tributary of the Umgeni River, in the Pietermaritzburg district, Natal (fig. 1).

All the snails were narcotised after the method suggested by Van Eeden (1958), fixed in ± 20% neutralized formalin and stored in 70% glycerine alcohol. The visceral mass was extracted with the aid of a pair of forceps. Dissections were made under water. Linear measurements of the shell were made from drawings, using a pair of sliding callipers. The outlines of the shell were drawn by means of projection through a photo-enlarger at a magnification of about 7X. For this

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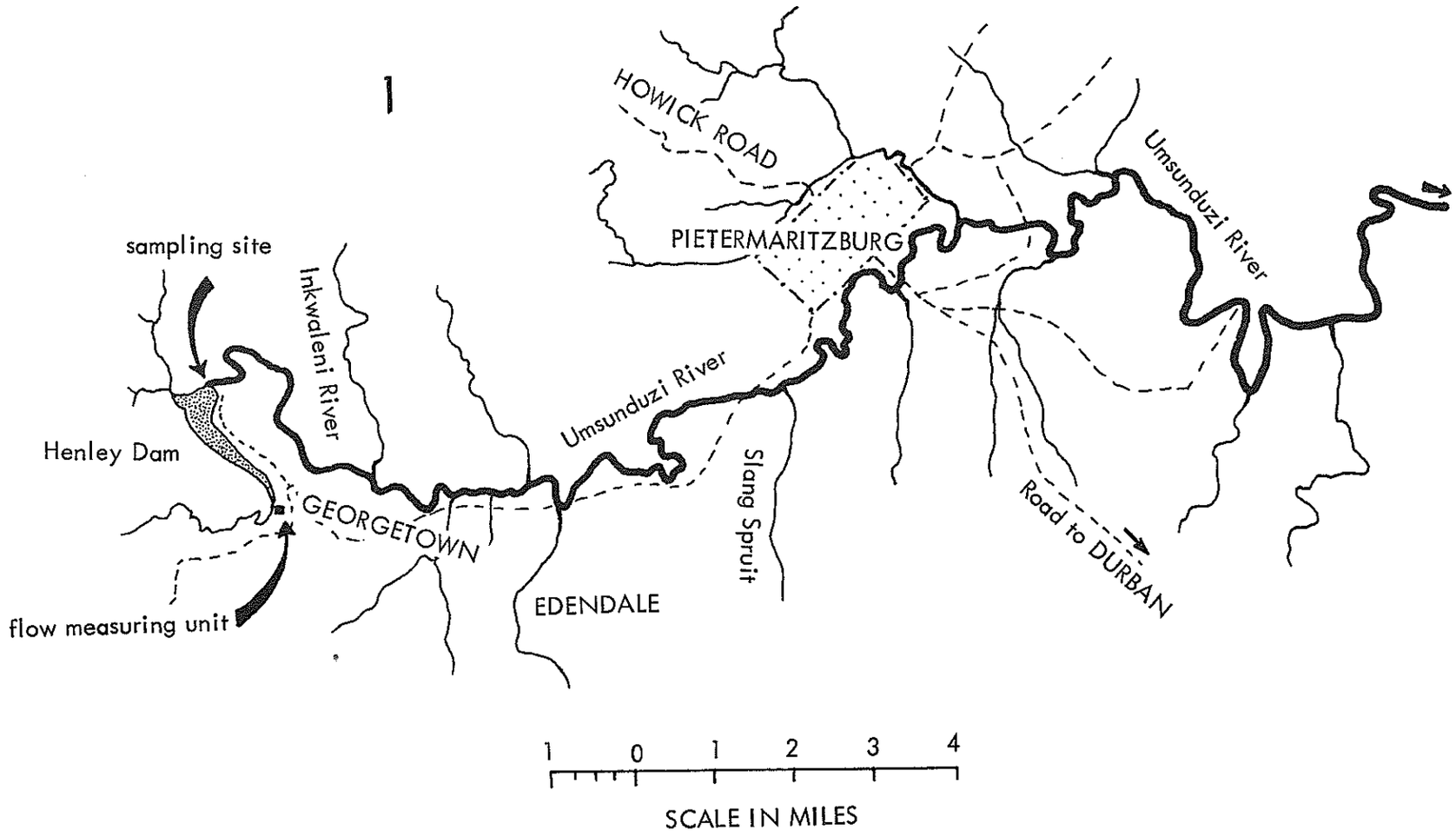


Fig. 1. Map showing location of the Henley Dam where the samples were collected.

purpose the shells were glued to a glass slide and inserted into the photo-enlarger. In the case of the angular increase of the spiral (p. 20), the measurements were made under a dissection microscope fitted with a screw micrometer eyepiece, at a magnification of 6X.

Whole mounts of the radulae were prepared according to the method described by van Eeden et al. (in press). The radula teeth were drawn at a magnification of about 2,200X, by means of projection through an inverted microscope, slightly modified as suggested by Goradkov (1961). The required measurements were made from these drawings by using a pair of sliding callipers.

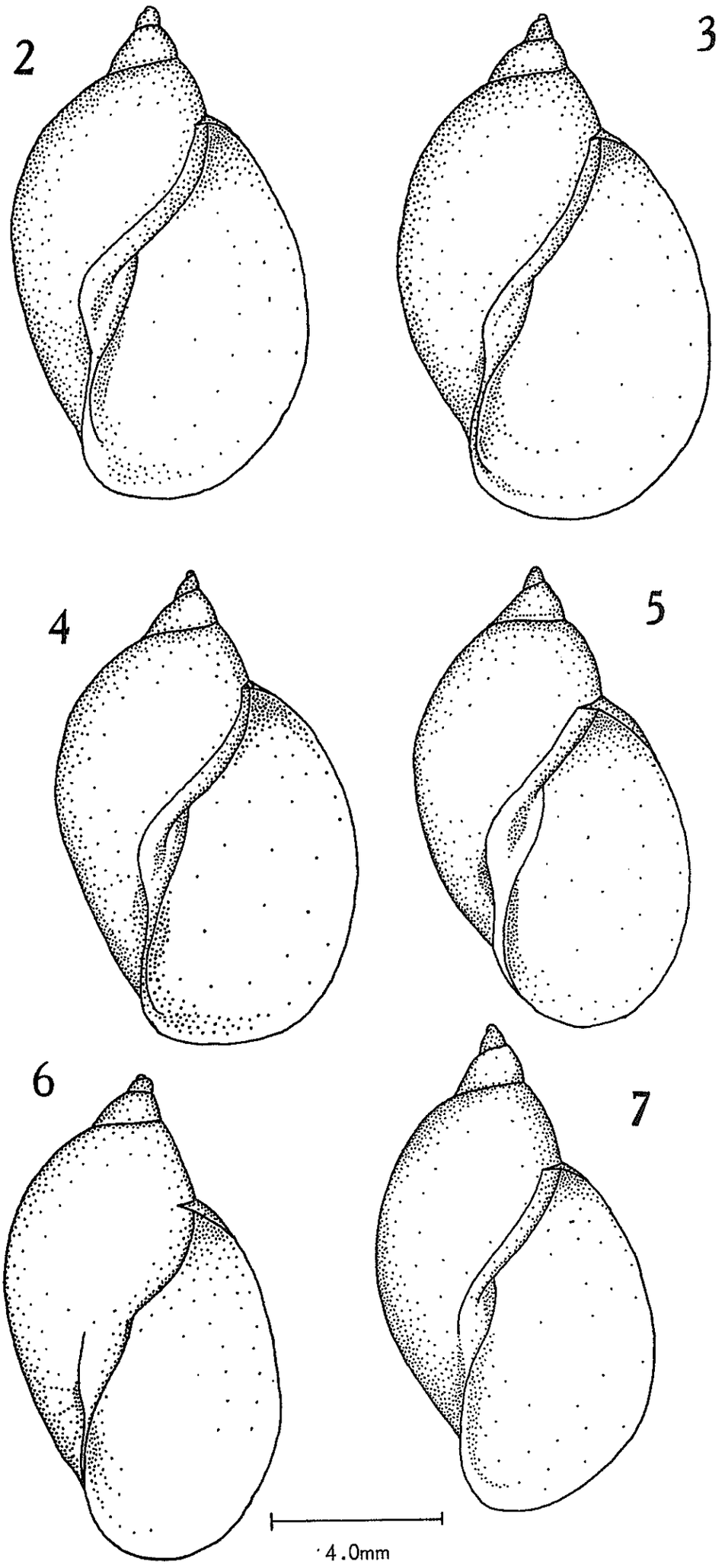
Whole mounts of 100 penes were made using the technique of Van Eeden (1958).

Specimens of each of the three collections were serially sectioned. The sections were cut from 5 to 10 μ thick and stained with Mallory's triple stain. To prevent the sand in the gizzard from damaging the microtome blade, it was necessary to remove the entire gizzard and part of the intestine, as suggested by Carriker et al. (1946). In addition to the above, the penis complex and proximal parts of the reproductive system were removed from some specimens and sectioned individually.

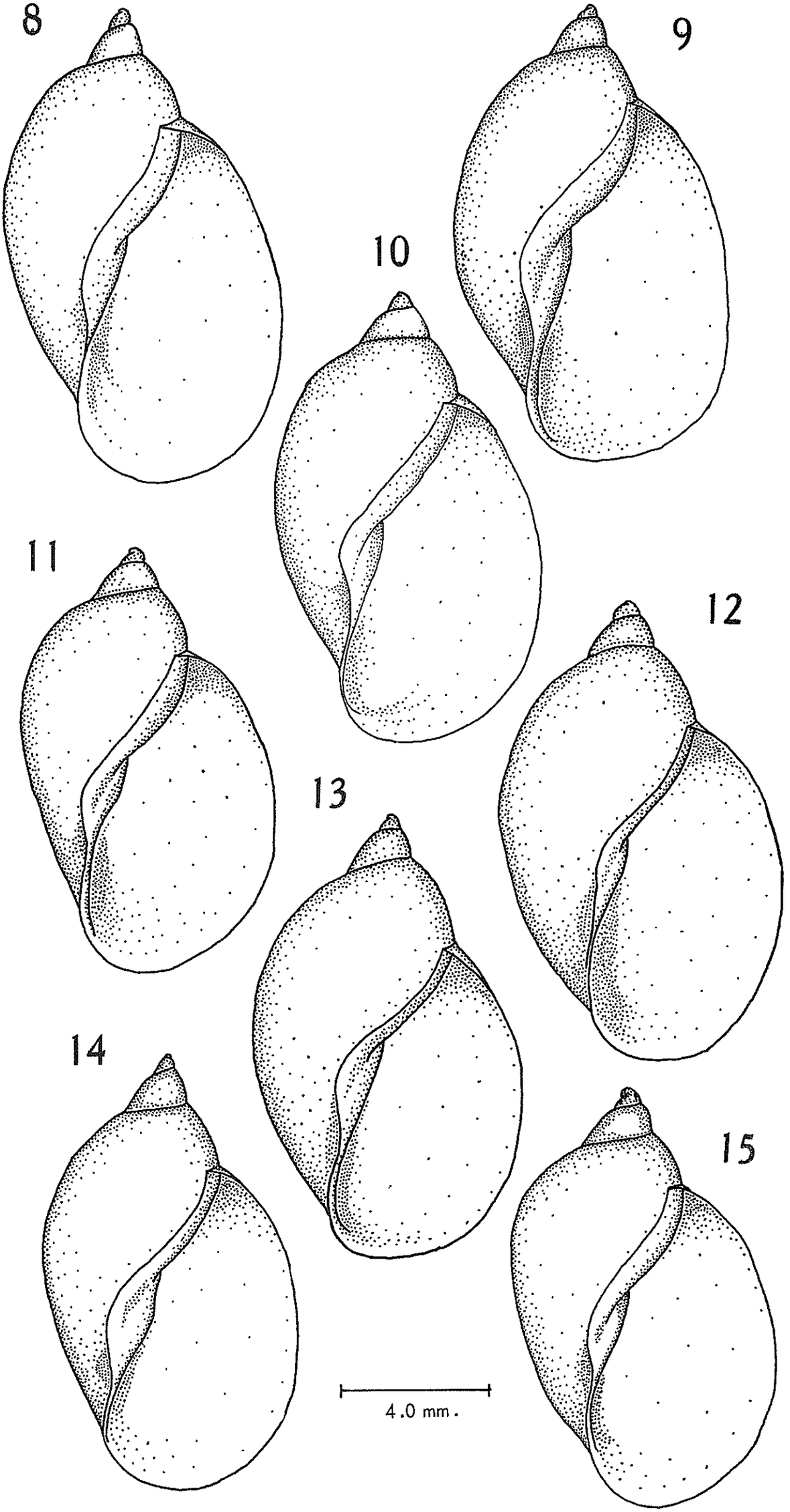
3. SHELL.

3.1. Morphological or Qualitative Analysis.

The criticism of Stiglingh et al. (1962) of the existing verbal descriptions of the shell of *Bulinus tropicus* (Krauss) likewise applies to *L.n. natalensis*. Figures 2 - 24, which depicts the variation in shape encountered in a series of 155 shells with a size range of 9.5 - 15.7 mm. from the same habitat, reveals that, whereas all these descriptions are valid for some shells,



Figs. 2 - 24. Some of the shell variations occurring in a sample of 155 specimens of L. n. natalensis.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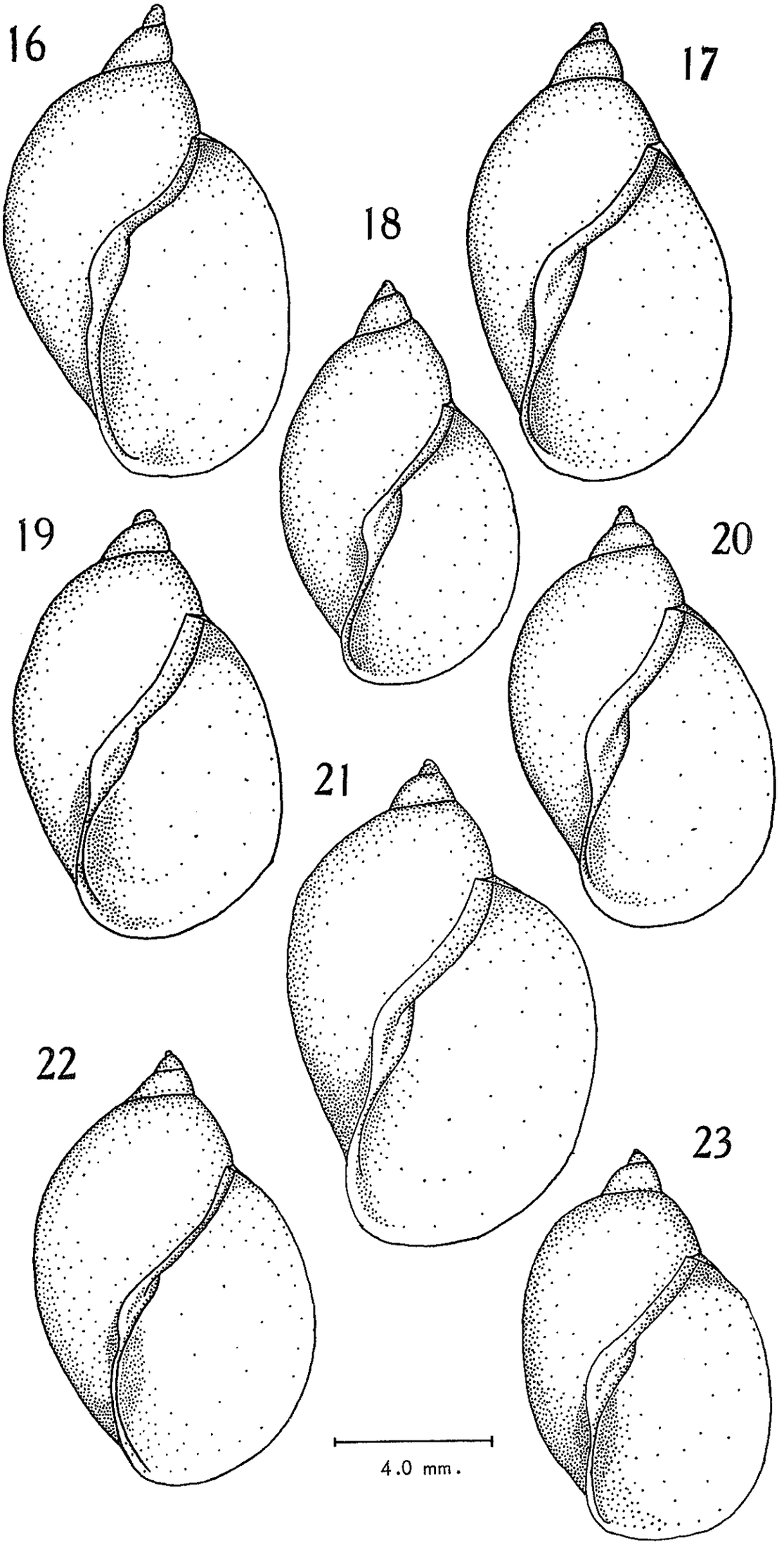
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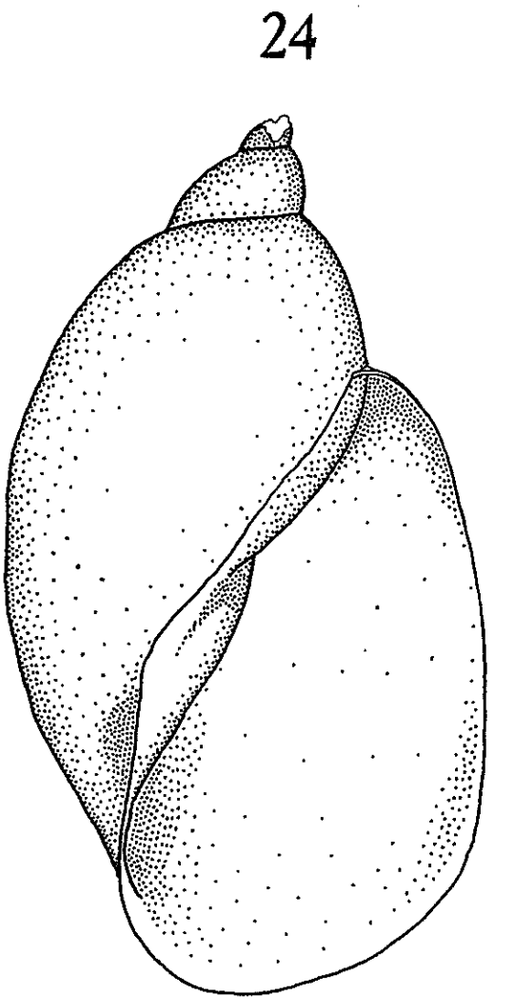

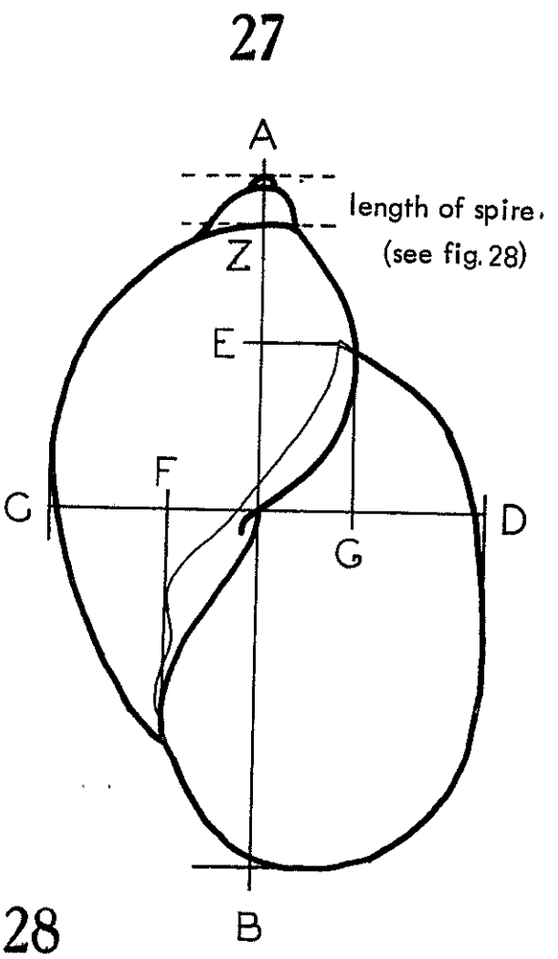

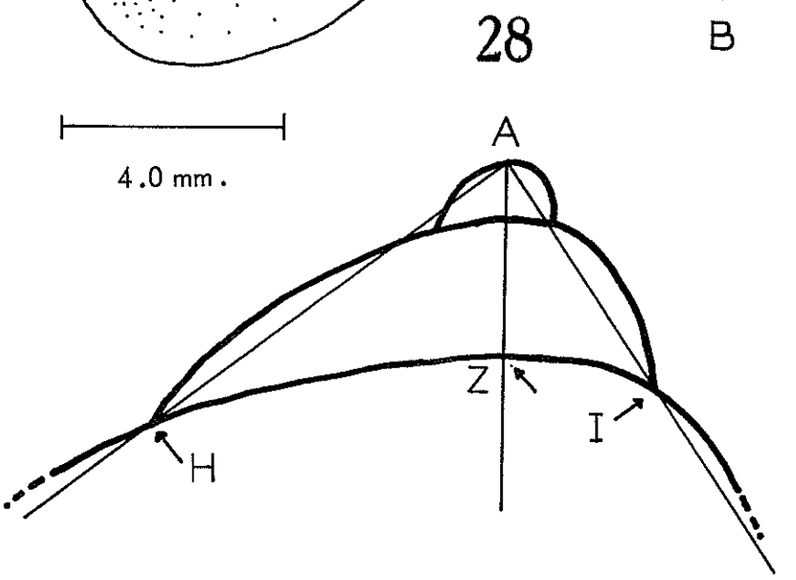

Fig. 27. Diagram illustrating the method of measuring the shell dimensions. A - B = Length (L); C - D = Breadth (B); E - B = Aperture Length (AL); F - D = Aperture breadth (AB); Z - B = Length of Ultimate whorl (UWL); C - G = Breadth of Ultimate whorl (UWB).

Fig. 28. Diagram illustrating the method of measuring the spire length (A - Z) and spire angle (HÂI).

none of them adequately characterizes the species.

With reference to general appearance, figs. 2 - 4 represent the shapes most commonly occurring in the samples, whilst figures 5 - 8 illustrate the most slender shells and figs. 21 - 23 the extreme "globose" shells. Due to the gradual change from one extreme shape to the other, I found it impracticable to determine the percentage occurrence of the specific shapes in the series.

The shape of the periphery of the left side of the ultimate whorl, viewed from the aperture, varies from bulbous in the apical region and straight or pointed towards the umbilicus (figs. 11, 15, 21), through evenly rounded throughout (figs. 5, 7, 12, 13, 18, 19, 20, 22), to shells displaying a slight bulbous or angular basal region (figs. 9, 15,23).

The outer lip of the aperture is evenly rounded in most cases but may also be slightly flattened (figs. 9 and 24) or faintly angular (figs. 7, 9, 16, 19, 23, 24).

The base of the aperture may join the columella in a broadly rounded curve (figs. 5, 6, 8, 14, 16), may be distinctly drawn out where it joins the columella (figs. 2, 7, 9, 10, 13, 18, 21) or may be intermediate between the two conditions.

The apical angle of the aperture varies from distinctly acute (figs. 13,17,18, 20) to almost or even 90° (figs. 2, 3, 4, 7, 8, 11, 16, 21).

3.2. Biometrical or Quantitive Analysis.

Biometrical analysis of shells, in spite of its limitations as a technique in the taxonomy of freshwater snails (Schutte and Van Eeden, 1959a), serves a most useful purpose in so far as it facilitates the exposure, and elimination from consideration, of those features

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of a population which might create a misleading picture of the actual species characteristics. Such features are, among others, immature specimens (Abbott, 1952), senescent survivors of older generations (Wright, 1957), successive generations in the adult range, and broken or malformed shells (Abbott, 1952).

Abbott (1952), Wright (1957), Hubendick (1951a) and Solem (1955) largely avoided this difficulty, and eliminated some of these above-mentioned features, by studying either adults only, or only a certain percentage of the adults in a sample. In the present study the main reasons for the different procedure adopted in the statistical treatment of certain alleged taxonomically important characteristics of the shell, are as follows:

1. The somewhat debatability of the method of determining snail maturity by means of the proposed "mirror image" method of Wright (1957) or the "percentage" method of Abbott (1952).
2. The absence of a tell-tale characteristic, such as the presence of a reflected lip in the adult snails of Mesodon ferrissi Pilsbry (Solem, 1955), in L. n. natalensis.
3. The presence, in the adult range of my series of specimens, of mainly two delimitable age ranges in each collection (fig. 25) which, if separated, would result in too few individuals to be statistically treated.

Fig. 25 is the size-frequency histograms of snail samples collected at roughly six-monthly intervals, from which shells of less than 9.5 mm. altitude are excluded. Observations made on the hermaphrodite organs established that snails of 9.5 mm. in shell length, and larger, are definitely sexually mature and by selecting only these

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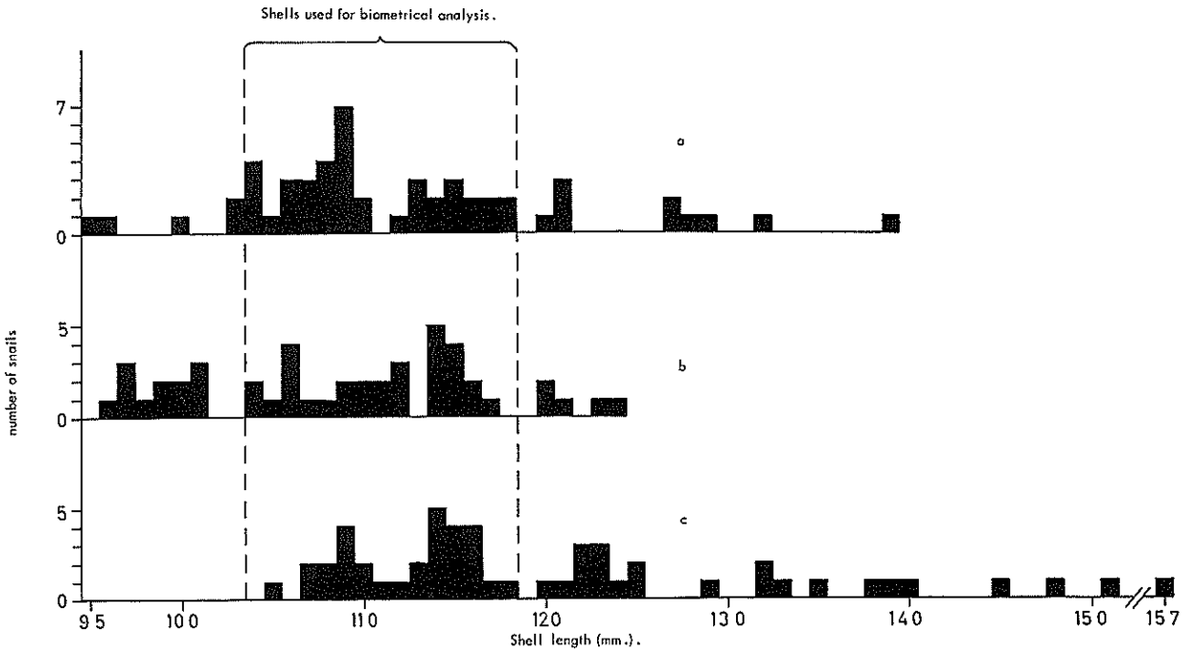

Fig. 25. Size-frequence histograms based on a total number of 155 specimens, of samples taken (a) June 1960, (b) February 1961 and (c) June 1961 at Hanley Dam.

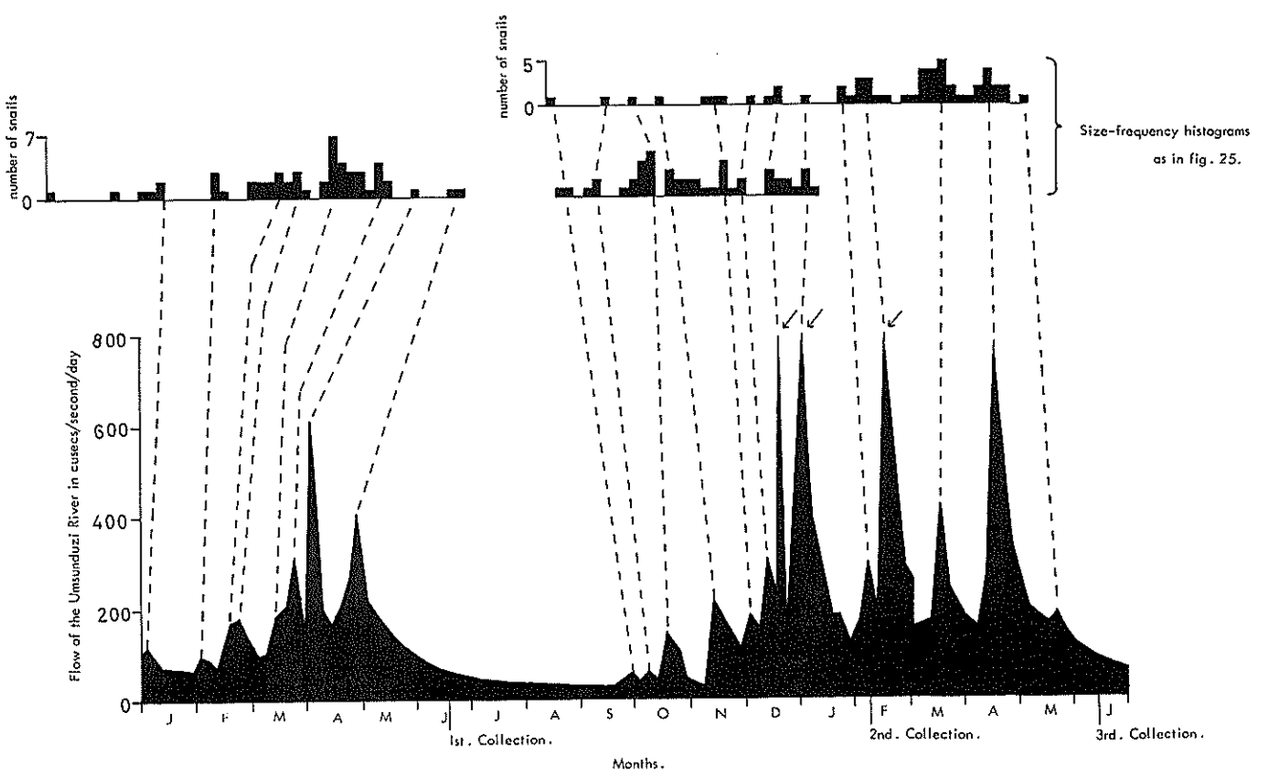

Fig. 26. Possible correlation between the flow of the Umsunduzi River (below) and the shell size distribution of the three samples (above). The size distribution histograms are the same as those in fig. 25. The arrows indicate peaks at which the true amount of flow exceeded the capacity of the flow meter - thus these peaks should be higher.

sizes, immature specimens were therefore eliminated. This, however, does not denote that a shell length of 9.5 mm. represents the transition between immature and mature stages, but is merely a convenient size for the elimination of all juveniles. However, even after elimination of the "juvenile element", which is considered to be responsible for the bimodality in the graphs drawn by Abbott (1952, p. 102 fig. 42), and Solem (1955, p. 86 fig. 2), a multimodal pattern (the peaks in the histograms, fig. 25) still prevails in each of the histograms drawn here. During regular visits to his collecting sites, McMullen (1947, quoted from Abbott, 1952), who noticed similar peaks in the measurements of colonies in his studies on the growth rates of the amphibious snail Oncomelania quadrasi Moellendorf, was able to establish that the waves of the young snails slowly move towards the main peak of the adults. Similar waves were also recorded by Solem (1955), McMullen et al. (1951) and Abbott (1952). Abbott (1952) referred to the first wave as "simply an aggregation of immature specimens", and considered it to be "a factor that will vary according to the reproductive cycle of that population" (p.100). In the analysis of the sizes in my samples, an aggregation of different ages can be seen in the adult wave. The reason for this will be indicated below. Abbott (1946) also showed that rain and flood periods brought about an increase in egg production which resulted in similar waves to occur in the measurements of the developmental stages of the eggs of Oncomelania. (quoted from Abbott, 1952).

If the flow of the Umsunduzi river, in which the collecting site is situated, be compared with the distribution of the sizes in the samples, my findings apparently confirm those of Abbott (1946). The comparison

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is done by reference to fig. 26, which illustrates the possible correlation between the size-frequency distributions of the three samples and the five-daily flow of the Umsunduzi river, expressed in cusecs/second/day, measured where the river enters the dam. The flow data were obtained from the Hydrographic Surveyor of the Department of Water Affairs. The peaks in the flow histogram indicate rains in the catchment area.

The sampling site of my collections is situated in cavities in solid rockbeds of the Ecca series (Schoonbee, in preparation) which were submerged in about 6 inches of very slow flowing water, directly below Henley Dam. The habitat was subject to occasional flooding as a result of the opening of the sluices of the dam after rains in the catchment area. Thus an increased flow recorded in the river also indicates flooding of the habitat. This resulted in a total replacement of the water in the habitat and also the washing away of a large portion of the population. This accounted for the relatively few specimens in the samples and also prevented over-population of an otherwise ideal habitat (i.e. nearly stagnant water, abundance of Algae for food and probably the absence of competitors, such as other snail species).

Two rain seasons were recorded from January 1960 to June 1961. The first season was shorter in duration and the rain was less in quantity than the second season. The first collection was made about one and a half months after the last rains of the first rain season (June 1960), the second about midway through the second rain season (February 1961) and the last about one and a half months after the last rains of the second rain season (June 1961).

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If the waves of the size frequency histogram be fitted with the peaks of the flow histogram, as is done by means of the dotted lines in fig. 26, a certain correlation is observed between the histograms, which may be interpreted as suggesting that a generation of snails originated after each flood, because two closely successive floods coincide with two closely successive waves or generations, and, likewise, lulls between floods are reflected by a greater spacing between the successive size waves (generations).

From this correlation between the flow, or more correctly, the flooding of the habitat, and the different shell sizes, it is deduced that:

1. The waves in the size frequency histograms represent survivors of different generations. This is in accordance with the interpretations of Abbott (1952), McMullen (1951) and Solem (1955).
2. Floods may be of considerable importance to the reproductive cycle in the population. This agrees with Abbott's (1952) statement and confirms the suggestion of Gaud (1956). In fact, Gaud maintains that the theory in which floods play a part is one which explains most satisfactorily the seasonal rhythms of Bulinus truncatus Audouin in Northern Africa, Egypt and Iraq.
3. Flood records can be used as an indirect indication of the number of generations and the relative ages of snails present in a population where this cannot otherwise be established. This knowledge can be used to eliminate the somewhat relative sorting of ages as was done by Schutte and Van Eeden (1959a).

A knowledge of the age and number of generations in a sample greatly facilitates the interpretation of the statistical results in so far as it reduces the possibility of mistaking variability due to age for variability due to other causes.

In order to simplify the complex features of the snail population chosen for the investigation, it was decided to take into consideration only those snails with a shell length of between 10.3 and 11.8 mm. i.e. the group falling between the two dotted lines in fig. 25. This particular size group was selected for more than one reason. In the first instance it was the size group most abundant in my samples. Secondly, a histological investigation of the hermaphrodite gland revealed snails with a shell length of 10.3 mm. to be definitely sexually mature. Moreover, the sample collected in June 1961 contained no specimens smaller than 10.3 mm. On the other hand, shells bigger than 11.8 mm. often showed erosion of the apex (fig. 24) which naturally affected the exactness of the measurements. An additional consideration was the fact that, by this selection, any senescent survivors of previous generations were automatically excluded.

Tables 1 - 4 represent the results of a statistical analysis of the following linear dimensions, measured as indicated in fig. 27. The symbols employed for the various dimensions, throughout this paper, are as follows:

L = entire shell length; B = maximum shell breadth; UWL = length of ultimate whorl; UWB = breadth of ultimate whorl; AL = aperture length; AB = aperture breadth.

In addition to the analysis in tables 1 - 4, normal distribution curves of the above-mentioned dimensions

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TABLE 1.

BIOMETRICAL ANALYSIS OF THE LINEAR DIMENSIONS OF 39 SHELLS FROM THE JUNE 1960 COLLECTION.

Dimensions	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L	10.95	0.4145	0.1718	10.32 - 11.70
B	6.75	0.3205	0.1026	6.00 - 7.50
UWL	9.95	0.4164	0.1734	9.2 - 10.7
UWB	4.33	0.2197	0.04829	3.9 - 4.8
AL	8.183	0.3941	0.1553	7.5 - 8.9
AB	4.95	0.2346	0.0550	4.5 - 5.4

TABLE 2.

BIOMETRICAL ANALYSIS OF THE LINEAR DIMENSIONS OF 29 SHELLS FROM THE FEBRUARY 1961 COLLECTION.

Dimensions	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L	11.05	0.4444	0.1975	10.37 - 11.71
B	7.01	0.2276	0.0518	6.6 - 7.4
UWL	10.10	0.4039	0.1636	9.4 - 10.7
UWB	4.64	0.1926	0.03706	4.1 - 5.0
AL	8.294	0.3448	0.1189	7.5 - 8.9
AB	4.97	0.1765	0.0311	4.5 - 5.3

T A B L E 3.

BIOMETRICAL ANALYSIS OF THE LINEAR DIMENSIONS OF 32 SHELLS FROM THE JUNE 1961 COLLECTION.

Dimensions	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L	11.26	0.3634	0.1321	10.54 - 11.77
B	7.18	0.3005	0.1963	6.4 - 7.8
UWL	10.20	0.3923	0.1252	9.4 - 10.7
UWB	4.67	0.2280	0.05250	4.1 - 5.0
AL	8.341	0.2729	0.0745	7.8 - 9.0
AB	5.07	0.1988	0.0395	4.6 - 5.5

T A B L E 4.

BIOMETRICAL ANALYSIS OF THE LINEAR DIMENSIONS OF 100 SHELLS FROM THE COMPOSITE SAMPLE

Dimensions	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L	11.099	0.4140	0.1714	10.30 - 11.80
B	6.96	0.4430	0.1963	6.00 - 7.80
UWL	10.07	0.3923	0.1531	9.2 - 10.7
UWB	4.53	0.2667	0.07118	3.9 - 5.0
AL	8.265	0.3480	0.1211	7.5 - 9.0
AB	4.99	0.2120	0.0450	4.5 - 5.5

were drawn (figs. 29 - 34). To facilitate comparison, the individual scales were either reduced or expanded to fit the same approximate horizontal scale, irrespectiv of the actual magnitude of the measurements.

Tables 1 - 4 show that the average values for all these dimensions were numerically smaller for the June 1960, sample than for the sample of the same month in 1961. This could be expected because younger snails were found to dominate the sample of the June 1960, collection (fig. 25a), whilst the equilibrium has shifted towards older age groups in the June 1961 sample (fig.25c) with a resultant increase of the average numerical values of the latter (fig. 35). The February 1961, collection (fig. 25b) on the other hand, is composed of more or less even numbers of younger and older generations, thereby providing a composite picture of both the June 1960 and June 1961 collections. It therefore occupies an intermediate position, with regard to the means, between the two respective June samples of the successive years 1960 - 1961.

A comparison between the coefficient of variability of the various dimensions of the June 1960 and June 1961 collections (table 5) indicates an overall greater variability in respect of the relevant characteristics of the latter. It can therefore be deduced, with some certainty, that the older age groups are less subject to variation than the younger ones.

In table 6 the sample means of the three respective collections are statistically compared with the aid of student's t-distribution tests on the 95% level of significance. From this table the following deductions can be made:

(a) Those/.....

T A B L E 5.

COMPARISON OF THE COEFFICIENT OF VARIABILITY OF THE LINEAR DIMENSIONS, EXPRESSED AS A %, OF THE RESPECTIVE COLLECTIONS AND THE COMPOSITE SAMPLE.

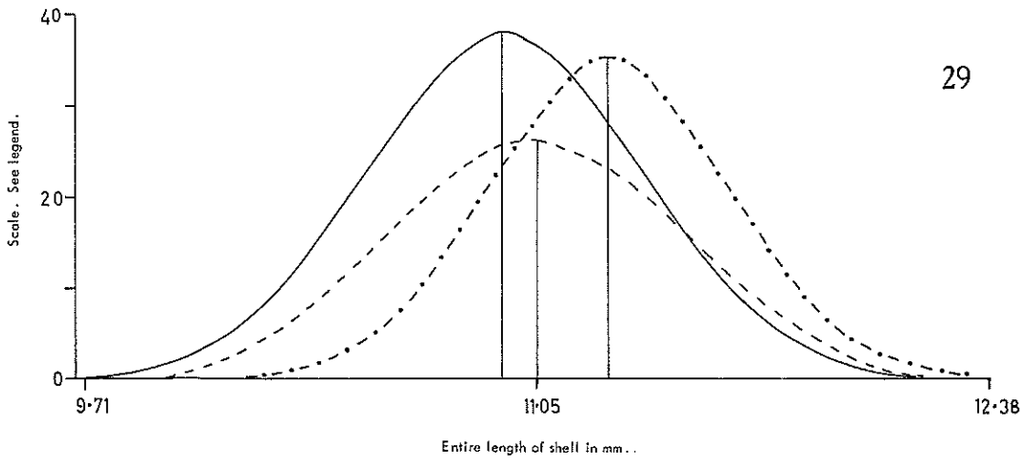
Dimensions	June 1960	February 1961	June 1961	Composite Sample
L	3.8	4.0	3.2	3.7
B	4.7	3.3	4.2	6.4
UWL	4.2	4.0	3.5	3.9
UWB	5.1	4.2	4.9	5.9
AL	4.8	4.2	3.3	4.2
AB	4.7	3.6	4.0	4.3

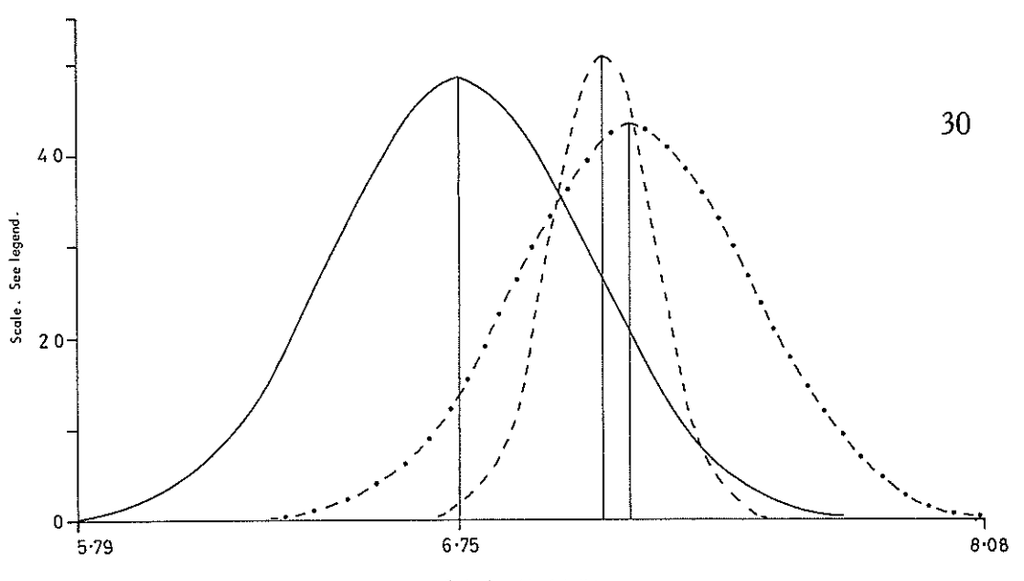
T A B L E 6.

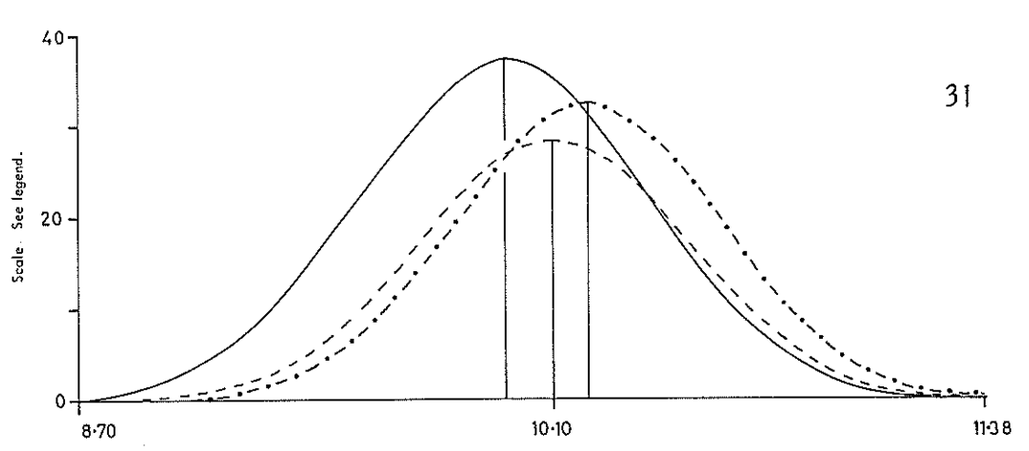
RESULTS OF A STATISTICAL ANALYSIS OF THE DIVERSITIES BETWEEN THE MEANS OF THE LINEAR DIMENSIONS OF THE THREE COLLECTIONS.

Collections compared	Degrees of freedom	Differences between the means of the dimensions					
		L.	B.	UWL.	UWB.	AL.	AB.
June 1960 and February 1961	67	—	+ +	—	+ +	—	—
June 1960 and June 1961	70	+ +	+ +	+	+ +	—	+
February 1961 and June 1961	60	+ +	+	—	—	—	+
Ratio of total number of insignificant, significant and highly significant differences.		1:0:2	0:1:2	2:1:0	1:0:2	3:0:0	1:2:0

— Denotes no significant difference between two samples; + denotes significant difference; ++ denotes highly significant difference.







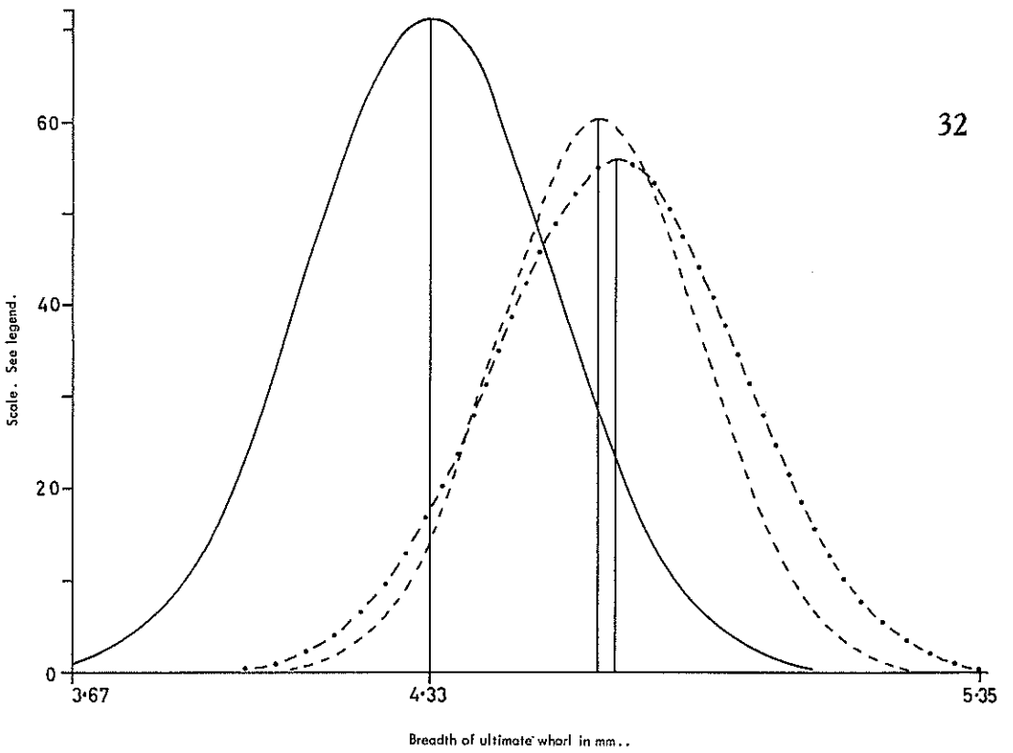
Legend. _____ June 1960 collection.

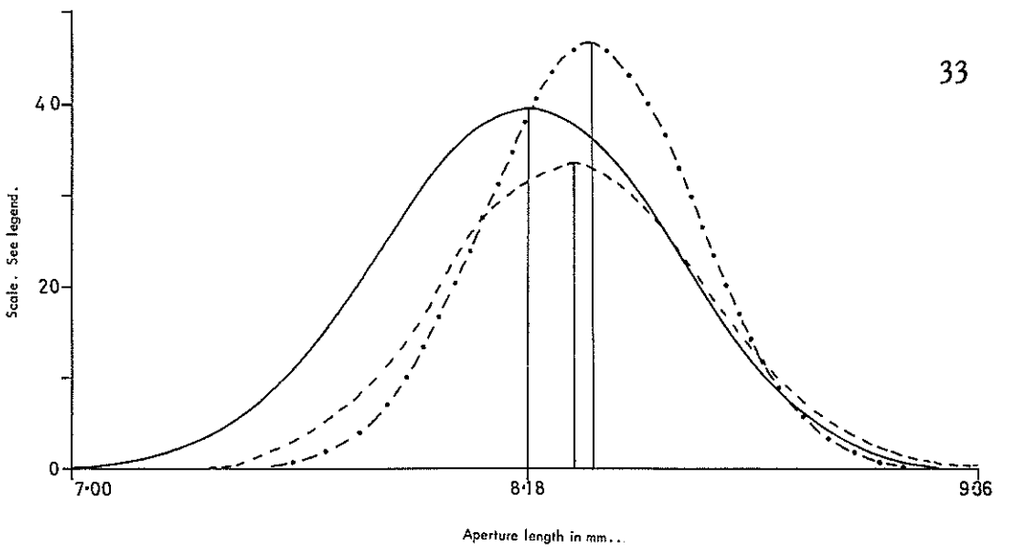
---------- February 1961 collection.

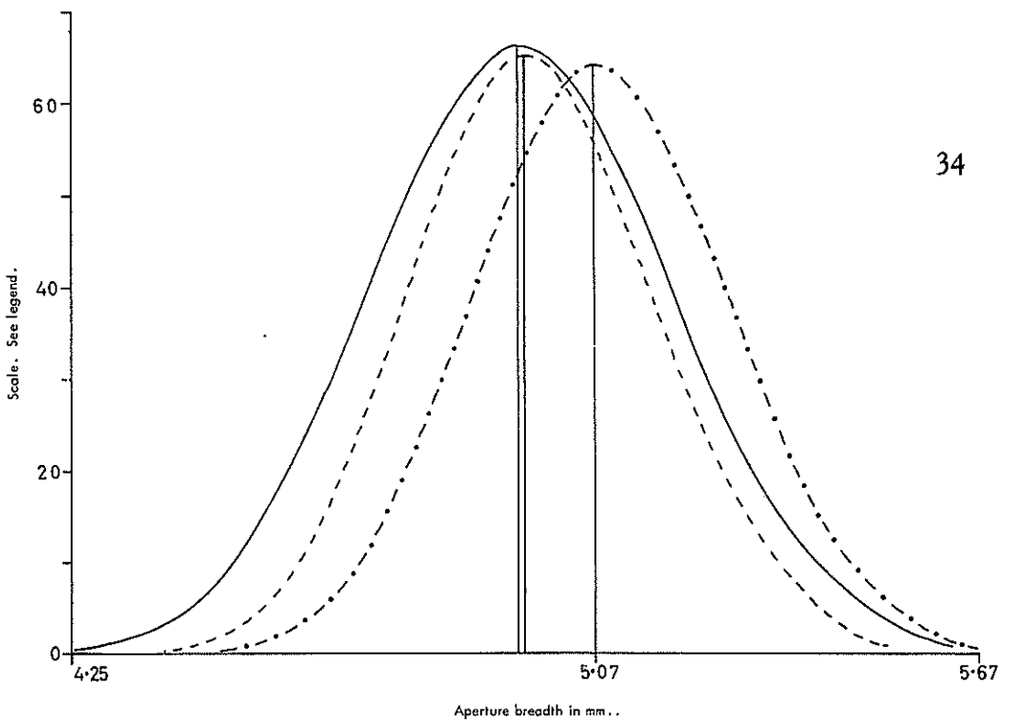
-.-.-.-.-.- June 1961 collection.

Ordinate scale = $\frac{\text{total number of individuals}}{\text{standard deviation}}$ times value given in tables of ordinate (Moroney, 1951, P. 118).

Figs. 29 - 34. Normal distribution curves of the linear dimensions under consideration.


32
60
40
20
0
Scale. See legend.
3·67
4·33
5·35
Breadth of ultimate whorl in mm..


33
40
20
0
Scale. See legend.
7·00
8·18
9·36
Aperture length in mm..


34
60
40
20
0
Scale. See legend.
4·25
5·07
5·67
Aperture breadth in mm..

(a) Those features where length dimensions of the shell are involved, viz., L, UWL and AL, show fewer differences of significance than the breadth measurements B, UWB and AB. This indicates that, in the three collections under discussion, length is less subject to extreme variations than the corresponding breadth measurements.

(b) The dimension AL (and possibly UWL, if the single significant difference be neglected), which does not show differences of significance between the sample means, although showing some variation (tables 1, 2, 3 and 4), might be a relatively reliable feature in the delimination of the species.

In order to establish whether the differences between the means of the samples were due to variation alone and not to subspecific differences, the Coefficient or Difference test (CD) (Mayr, et al, 1953) was applied. In none of these tests were the conventional level of subspecific difference exceeded. It can therefore be assumed that the differences in the means are due to normal variations to which a snail population is subject. As will be indicated below (p. 17), this variation could largely be attributed to the compositional distribution and overlapping of age groups in the different samples.

The ratios statistically analysed are:

1. Shell length : shell breadth (L/B). This ratio expresses, numerically, the situation of the whorls relative to each other or, more correctly, the phenomenon resulting from it (Hubendick 1951), as well as the relation between the increase in

diameter/.....

diameter of the body whorl and increasing shell length (Wright, 1957).

2. Shell length : length of aperture (L/AL). In this type of shell this ratio provides an indication of the degree of exertion of the spire, for if the spire is strongly depressed the ratio will approach unity and it will increase with the increasing exertion of the upper whorls, or more properly, the descent of the body whorl (Hubendick 1951a).
3. Length of aperture : breadth of aperture (AL/AB). This ratio gives an expression of the shape of the aperture for as it approaches unity so the shape approaches the circular condition etc.
4. Length of ultimate whorl : shell breadth (UWL/B).
5. Shell breadth : aperture breadth (B/AB). The two last mentioned ratios both reflect the degree of slenderness of the shell. As it increases so the shell becomes progressively more globose and visa versa.

These ratios were analyzed along similar lines as the linear dimensions. Among the information to be derived from the tables 7 - 10, the following may be noted. When compared in respect of similar ratios and size range, the mean values and scatter for the three samples differ from one another to a variable degree (See also the curves of figs. 36 - 40). The significance of these diversities between the means of the same ratios were tested with the students t-distribution tables at 95% level of significance, and the results are given in table 11.

These tests established that, in regard to the

embracing/....

T A B L E 7.

BIOMETRICAL ANALYSIS OF THE RATIOS OF THE MEASUREMENTS OF 39 SHELLS OF THE JUNE 1960 COLLECTION.

Ratio	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L/B	1.6297	0.06825	0.00466	1.54 - 1.78
L/AL	1.3446	0.03554	0.00126	1.28 - 1.46
UWL/B	1.4800	0.05938	0.00353	1.38 - 1.62
AL/AB	1.6621	0.07290	0.00532	1.52 - 1.84
B/AB	1.3677	0.04443	0.00197	1.28 - 1.50

T A B L E 8.

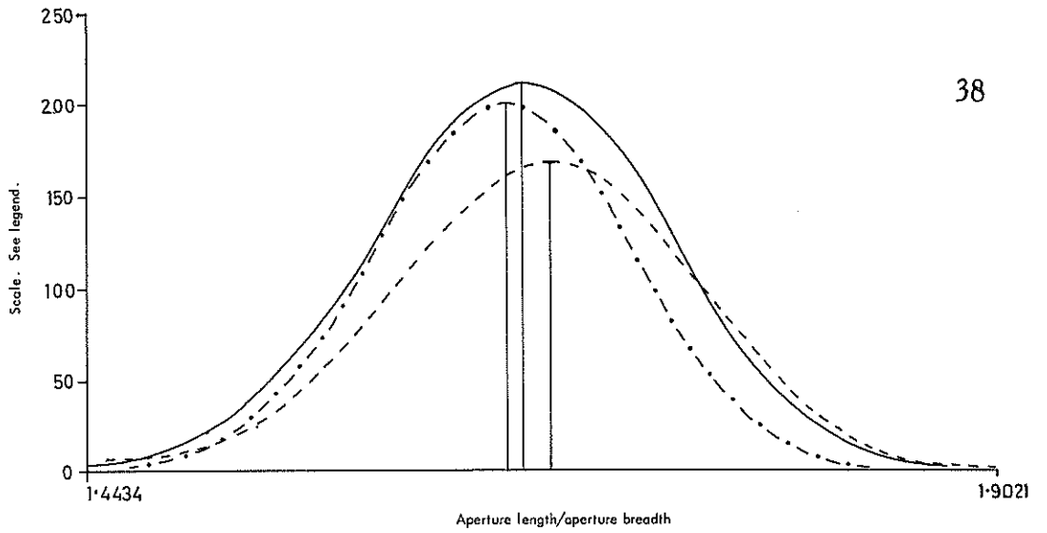
BIOMETRICAL ANALYSIS OF THE RATIOS OF THE MEASUREMENTS OF 29 SHELLS OF THE FEBRUARY 1961 COLLECTION.

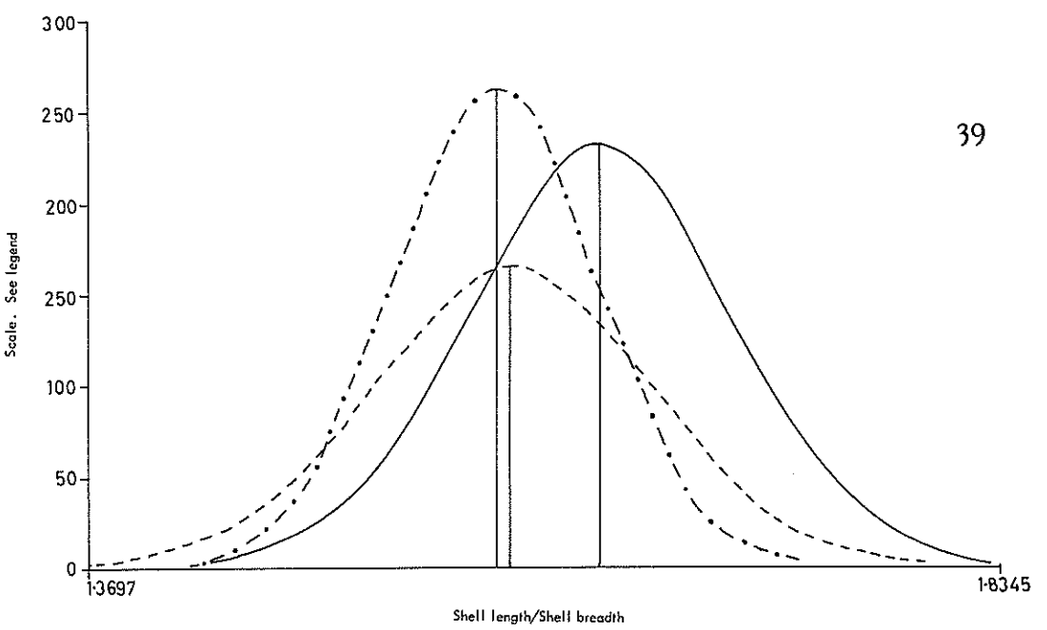
Ratio	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L/B	1.5841	0.0715	0.00511	1.48 - 1.70
L/AL	1.3435	0.0287	0.00082	1.30 - 1.44
UWL/B	1.4448	0.05071	0.00257	1.36 - 1.56
AL/AB	1.6759	0.0754	0.00568	1.48 - 1.82
B/AB	1.4172	0.0496	0.00246	1.30 - 1.52

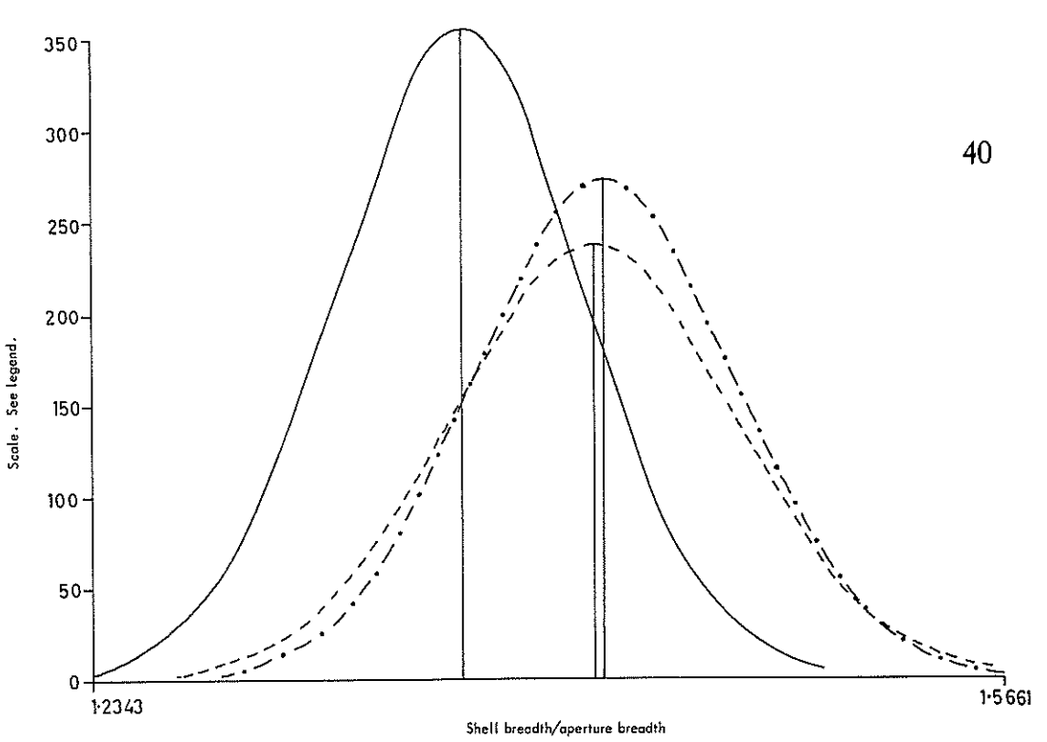
T A B L E 9.

BIOMETRICAL ANALYSIS OF THE RATIOS OF THE MEASUREMENTS OF 32 SHELLS OF THE JUNE 1961 COLLECTION.

Ratios	Mean (mm.)	Standard Deviation (mm.)	Variance (mm.)	Range (mm.)
L/B	1.5763	0.04952	0.00245	1.50 - 1.68
L/AL	1.3565	0.03456	0.00119	1.30 - 1.44
UWL/B	1.4275	0.03852	0.00148	1.36 - 1.50
AL/AB	1.6525	0.06330	0.00400	1.52 - 1.80
B/AB	1.4206	0.04751	0.00226	1.36 - 1.52


38
250
200
150
100
50
0
Scale. See legend.
1·4434
1·9021
Aperture length/aperture breadth


39
300
250
200
250
100
50
0
Scale. See legend
1·3697
1·8345
Shell length/Shell breadth


40
350
300
250
200
150
100
50
0
Scale. See legend.
1·2343
1·5661
Shell breadth/aperture breadth

embracing of the whorls and the relation between increasing length and increasing breadth of the body whorl (L/B), the relative size of the ratios shell length to aperture length (L/AL), and the shape of the aperture AL/AB, there exists no differences between the samples, and accordingly, no differences between younger and older snails. In regard to the slenderness of the shell (ratios UWL/B and B/AB) there exist variable significant differences between the collections, i.e. between younger and older snails.

The analyses of variability of the ratios (table 12) and the linear dimensions (table 5) suggest that the older snails are less subject to extreme variability than younger snails.

Scatter diagrams were plotted to determine the mutual relations of some of these linear dimensions and some of the ratios of these dimensions, in this limited size range (see page 11 and fig. 25). Some of those dimensions and ratios (UWB, UWL, B/AB), which vary considerably, were omitted in this analysis of correlation. Fig. 41 indicates that shell breadth (B) increases concordantly whith shell length (L). Similar relations are revealed between aperture length (AL) and shell length (L) (fig. 42), aperture length (AL) and length of ultimate whorl (UWL) (fig. 43), aperture length (AL) and aperture breadth (AB) (fig. 44). These relations indicate that the snails are still actively growing at the ages represented in my series.

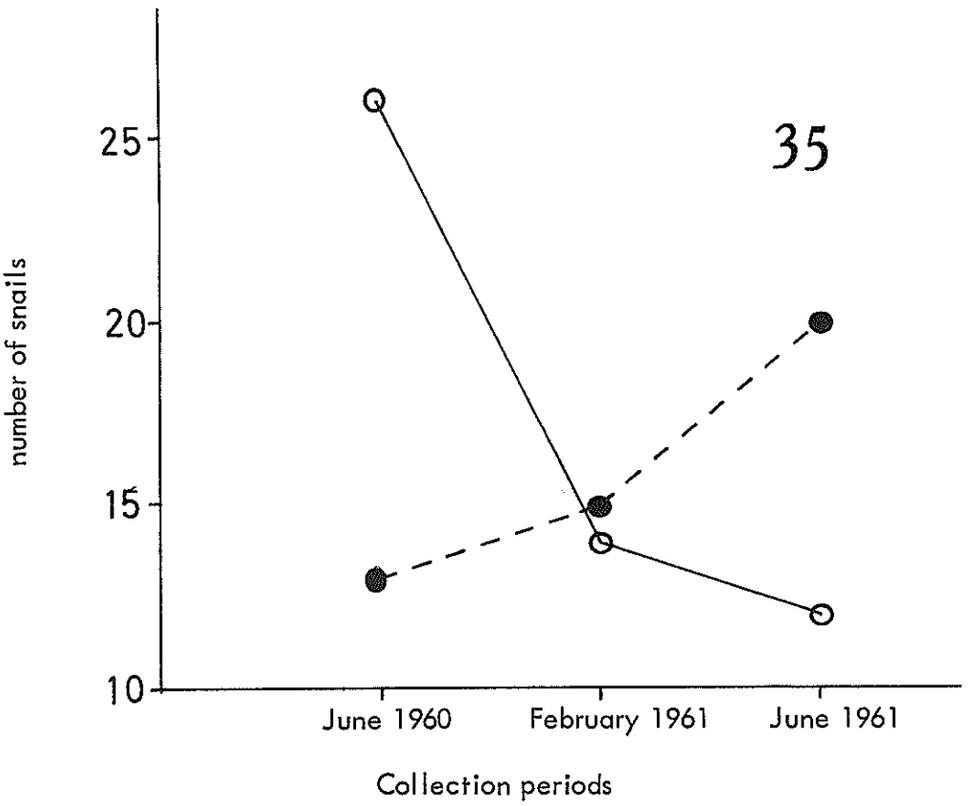
The ratio L/AL has been shown to increase with increasing length both in L. palustris (Peters, 1938) and in Bulinus (P.) jousseaumei (Dautzenberg) (Wright, 1957), and McCraw (1961) has demonstrated that in

L. humilis/....

T A B L E 12.

COMPARISON OF THE COEFFICIENT OF VARIABILITY, EXPRESSED AS A %, OF THE RATIOS OF THE RESPECTIVE COLLECTIONS AND THE COMPOSITE SAMPLE.

Ratio	June 1960	February 1961	June 1961	Composite sample
L/B	4.2	4.5	3.1	6.9
L/AL	2.6	2.1	2.6	4.1
UWL/B	4.0	3.5	2.7	3.8
AL/AB	4.4	4.5	3.8	6.1
B/AB	3.3	3.5	3.3	3.8



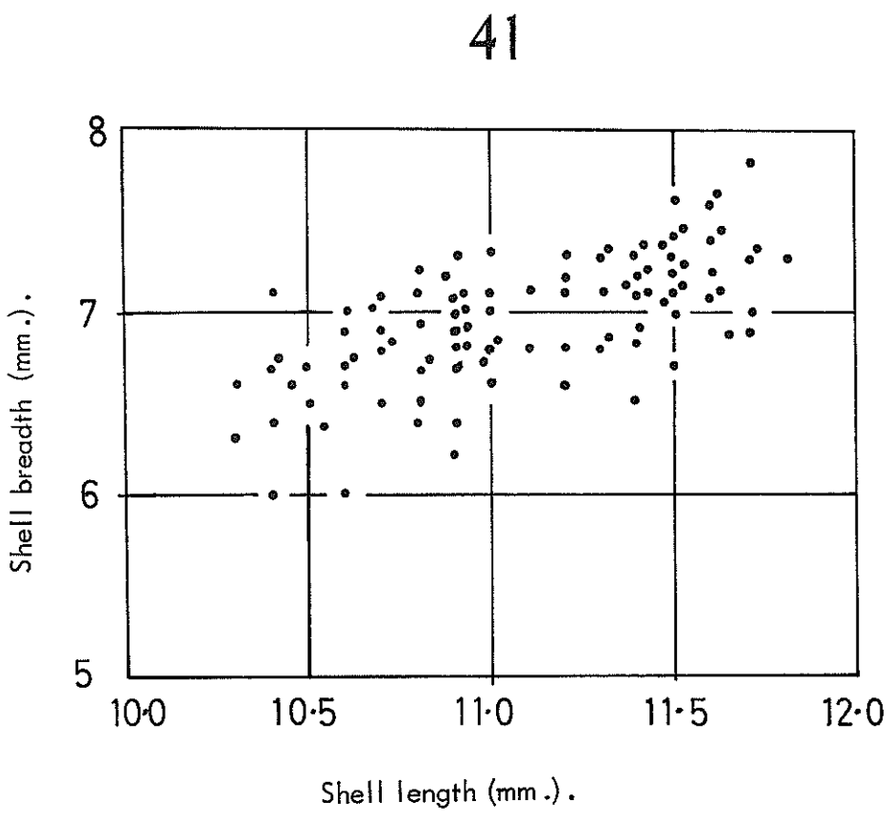
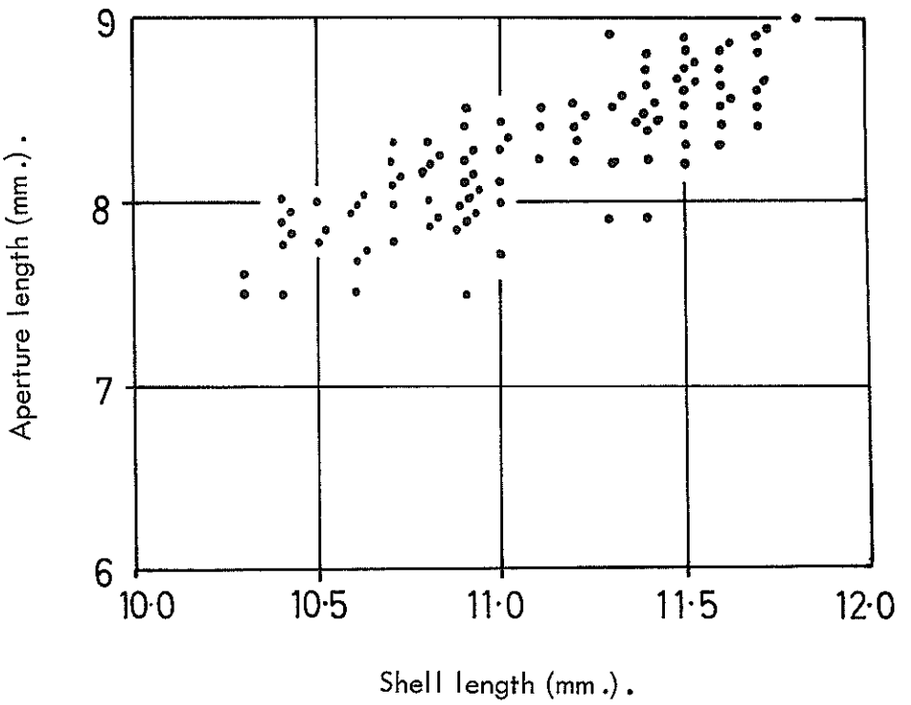


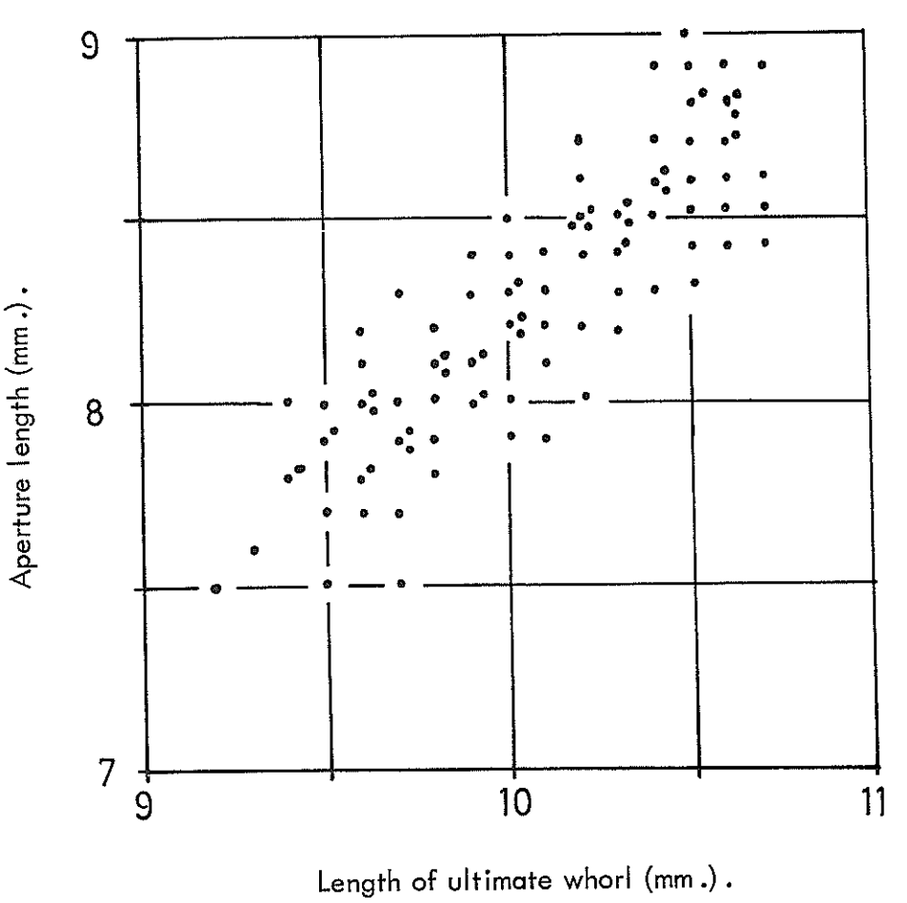
Fig. 35. The number of snails of each group plotted against the collection periods. The solid circles indicate snails with shell lengths of 11.1 mm. and larger. The white circles indicate snails with shell lengths less than 11.1 mm. The connecting lines denote the shifting of equilibrium from dominance of younger snails in the June 1960 sample, through nearly a balance between the age groups (sizes) in February 1961 to the dominance of the older age groups in the June 1961 sample.

Figs. 41 - 48. Diagrams illustrating the relations between linear shell dimensions and some of their ratios.

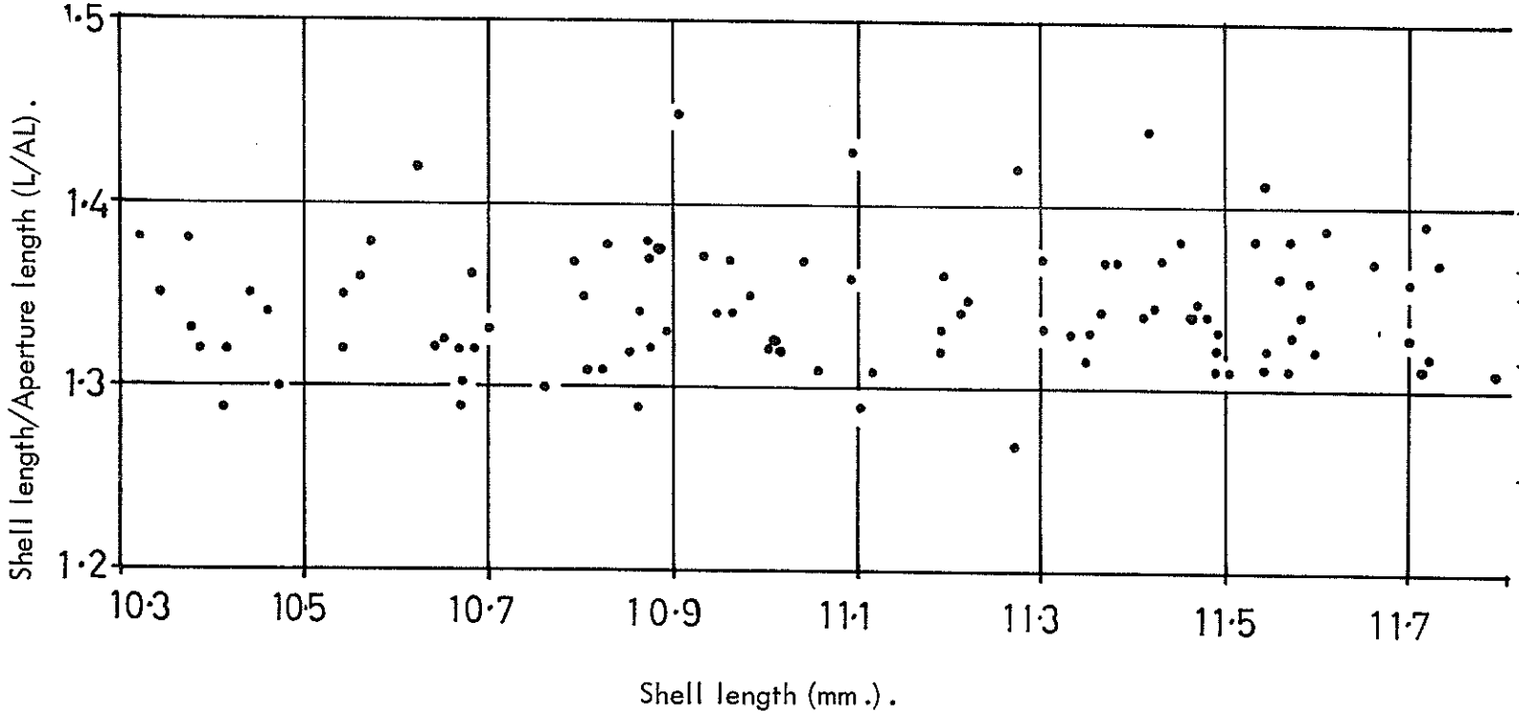
42


9
8
7
6
10·0
10·5
11·0
11·5
12·0
Aperture length (mm.).
Shell length (mm.).

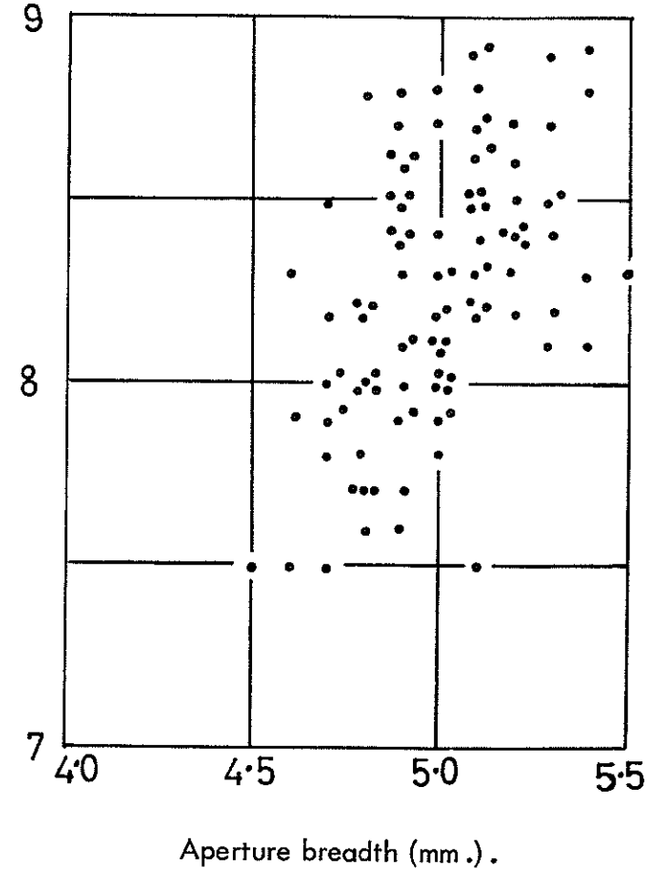
43


9
8
7
9
10
11
Aperture length (mm.).
Length of ultimate whorl (mm.).

45


1·5
1·4
1·3
1·2
Shell length/Aperture length (L/AL).
10·3
10·5
10·7
10·9
11·1
11·3
11·5
11·7
Shell length (mm.).

44

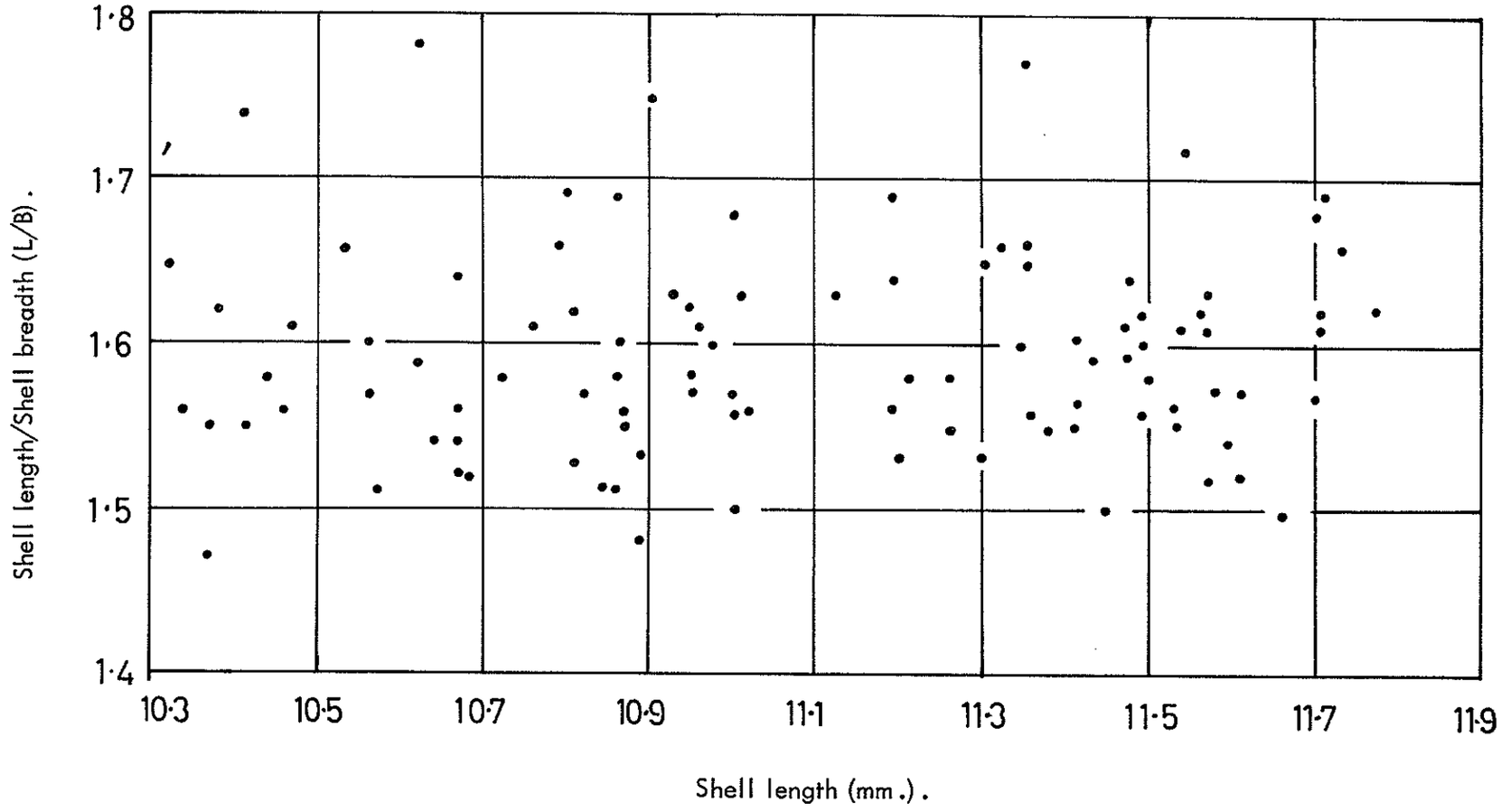

9
8
7
Aperture length (mm.).
4·0
4·5
5·0
5·5
Aperture breadth (mm.).

L. humilis Say the ratios shell breadth/length and aperture length/shell length change as the shell length changes.

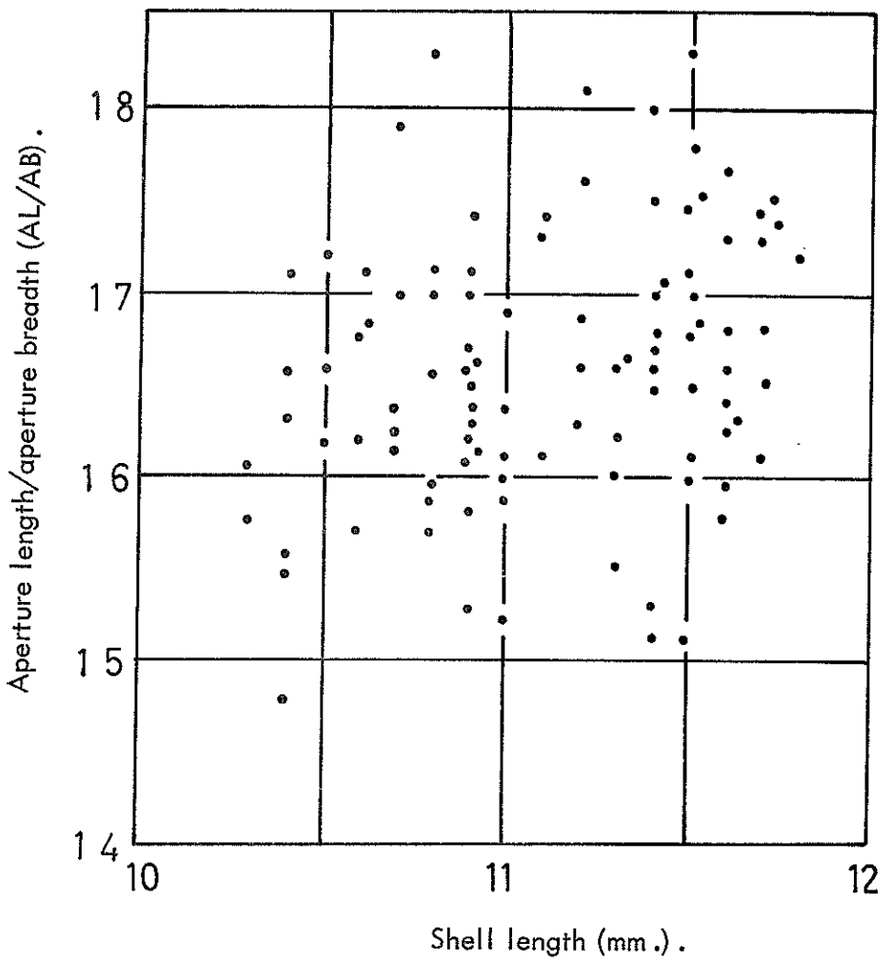
Fig. 45 shows that, in spite of increasing shell length, L/AL remains fairly constant in the size range 10.3 to 11.8 mm. This suggests that although this ratio changes during growth, as was demonstrated by Peters (1938), Wright (1957) and McCraw (1961), it remains constant in shells of similar sizes. This, furthermore, underlines the fact that where the ecological influences to which they were subjected were the same, snails of similar shell sizes are directly comparable with each other in respect of this ratio. The relations of the ratios L/B (fig. 46) and L/AL (fig. 45) to increasing shell length show the same tendencies, although the former (fig. 46) are subject to more extreme variations. The scatter diagram (fig. 47) reflects no correlation between the shape of the aperture AL/AB and increasing length (L), which indicates that the shape of the aperture is not affected by age. From fig. 48 it is evident that there likewise exists no relation between the shape of the aperture (AL/AB) and the relative positions of the whorls to each other as expressed by the ratio L/B. The shape of the aperture (AL/AB), as expressed by this ratio, might therefore prove to be a valuable criterion of the indentity of the species.

In order to test Wright's (1957) warning that the time of the year at which a particular sample was collected, is important, the composite sample, obtained by pooling the three different collections, was analysed statistically and compared with each of the three individual collections. The results of the

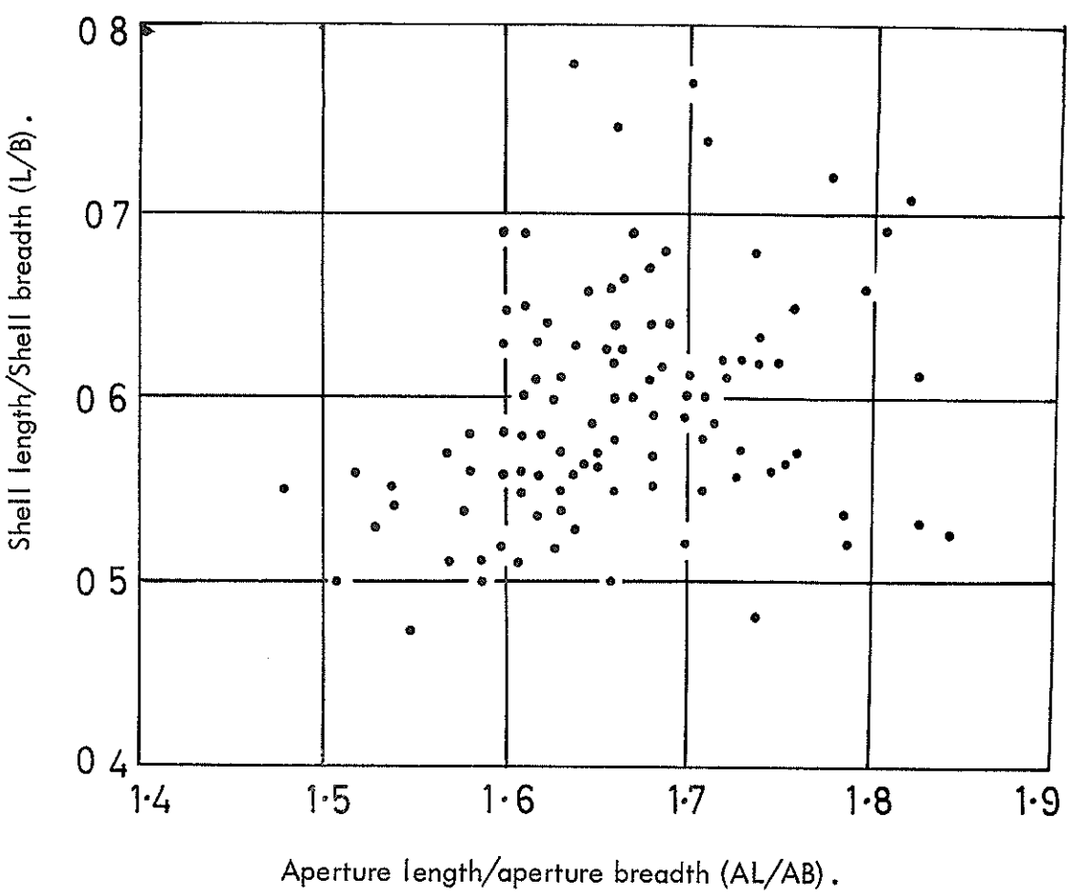
analysis/.....


1·8
1·7
1·6
1·5
1·4
Shell length/Shell breadth (L/B).
10·3
10·5
10·7
10·9
11·1
11·3
11·5
11·7
11·9
Shell length (mm.).

47


Aperture length/aperture breadth (AL/AB).
1 8
1 7
1 6
1 5
1 4
10
11
12
Shell length (mm.).

48


Shell length/Shell breadth (L/B).
0 8
0 7
0 6
0 5
0 4
1·4
1·5
1·6
1·7
1·8
1·9
Aperture length/aperture breadth (AL/AB).

analysis of the composite sample are tabulated in the same tables as those of the individual samples. The significance of the differences between the means of the samples and those of the composite sample were tested at the 95% level of the students t-distribution table and the results are recorded in tables 13 and 14.

Among the conclusions to be arrived at from a study of the relevant tables, the following may be mentioned:

With respect to both linear dimensions and ratios, the composite sample closely resembles only the February sample because they contain the same proportion of young and old snails and relatively few of the intermediate age groups. Likewise, the differences between the composite sample and the two June samples may be explained by the difference in the size groups which each contains and this, in turn, can be linked with the effect of rain periods on the two latter samples.

The composite samples, on the strength of its larger number of specimens, yields a more accurate estimate of the true characteristics of the population, but cannot provide reliable information on the variability due to specific influences to which a biological unit is subject. Finally it is inadvisable to attempt to deduce the characteristics of the species from a single sample since, as in the present investigation, only one out of three or even more, samples might sufficiently approach the actual species characteristics as revealed by a population.

It must, at this stage, be noted that the measurements of the largest samples examined in the foregoing analysis, are distinctly smaller than those given in the literature for adult specimens of L. n. natalensis. For instance, the length of a "typical shell" is given as 15 mm. (Krauss, 1848; Pilsbry, et al. 1927; Connolly, 1939;

TABLE 13.

RESULTS OF A STATISTICAL ANALYSIS OF THE DIVERSITIES BETWEEN THE MEANS OF THE ABSOLUTE DIMENSIONS OF THE RESPECTIVE SAMPLES COMPARED WITH THE COMPOSITE SAMPLE.

Collections compared with composite sample	Degrees of freedom	Differences between the means of the dimensions					
		L	B	UWL	UWB	AL	AB
June 1960	138	—	—	—	—	—	—
February 1961	128	—	—	—	—	—	—
June 1961	131	+	+	—	+	—	—
Ratio of total number of insignificant, significant and highly significant differences.		2:1:0	2:1:0	3:0:0	2:1:0	3:0:0	3:0:0

TABLE 14.

RESULTS OF A STATISTICAL ANALYSIS OF THE DIVERSITIES BETWEEN THE MEANS OF THE RATIOS OF THE RESPECTIVE SAMPLES COMPARED WITH THE COMPOSITE SAMPLE.

Collections compared with composite sample	Degrees of freedom	Differences between the means of the ratios				
		L/B	L/AL	UWL/B	AL/AB	B/AB
June 1960	138	—	—	+	—	+ +
February 1961	128	—	—	—	—	+
June 1961	131.	—	—	+	—	—
Ratio of total number of insignificant, significant and highly significant differences.		3:0:0	3:0:0	1:2:0	3:0:0	1:1:1

Mandahl-Barth, 1954) and as 15.82 mm. (De Azevedo, 1957). All the dimensions given by the latter author are based on five specimens. The largest specimen recorded is from Umbilo, Natal, and is 24.6 mm. long and 14.7 mm. broad (Connolly, 1939). The other dimensions given for the adult shell are as follows:

Shell breadth:

9.937	mm.	Krauss (1848)
9.2	mm.	Connolly (1939)
10.0	mm.	Mandahl-Barth (1954)
9.39	mm.	De Azevedo (1957).

Aperture length and breadth:

11.0	mm.,	6.1	mm.	Connolly (1939)
11.0	mm.,	7.0	mm.	Mandahl-Barth (1954)
12.98	mm.,	5.93	mm.	De Azevedo (1957).

Length of ultimate whorl:

13.5	mm.	Connolly (1939)
14.44	mm.	De Azevedo (1957).

Although it has already been decided (p. 16) that, where the conditioning ecological influences were the same, only shells of the same size are directly comparable with each other, the desirability has been felt to compare my own data, pertaining to dimensions and ratios, with those given for L. n. natalensis by other authors. In order to reduce the limitations of a comparison of this nature, Wright's (1957) method for determining the probable dimensions of the adult snails in his population was adopted. In the course of this procedure I compared the means of my samples firstly with the dimensions given in the literature and, secondly, with the exceptionally large specimens in my samples.

This/.....

This method involves the calculation of the percentage increase from the mean shell length, as determined in this study, to the shell length given in the literature, having done which, the means of the other dimensions employed in my analysis can be increased by the same percentage, thus rendering my data comparable with the dimensions given in the literature.

The practical application of this procedure is that the dimensions of specimens (or the means of a number of specimens from the same population) to be identified can be substituted either for the largest specimens in the sample (tables 27 - 32) or for the dimensions given in the literature (tables 15 - 26). The results of this procedure are given in tables 15 - 32, from which it is obvious that, apart from two of De Azevedo's (1957) dimensions, which could be due to different methods of measuring, the transformed data suggest that the technique could be reliable. However, confidence limits as to the magnitude of the differences between the transformed data and the real measurements, are yet to be calculated when more data are available of the magnitude of the differences which may be regarded as being significant.

3.3 Spire.

The spire of L. n. natalensis has been described as short (Krauss, 1848; Connolly, 1939; Hubendick, 1951a), acute (Krauss, 1848; Connolly, 1939; Hubendick, 1951a; De Azevedo, 1957), broad, narrow and occupying up to $^{1}/_{4}$ of the total height of the shell (Mandahl-Barth, 1954) and its contours merging gradually into those of the body whorl (Hubendick, 1951a).

Due to the high variability of the spire length (figs. 2 - 24)(in my series the coefficient of variability is 14%) it is not useful as a species characteristic

(Hubendick/.....

TABLE 15.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1960 COLLECTION AND THE DIMENSIONS GIVEN BY CONNOLLY (1939)

Dimensions	Means of June 1960 Collection	Increased Calculation	Dimensions given by Connolly (1939)	Difference
L	10.95	36.99%	15.0	-
B	6.75	9.25	9.2	0.05
UWL	9.95	13.65	13.5	0.13
AL	8.183	12.210	11.0	1.210
AB	4.95	6.78	6.1	0.68

T A B L E 16.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF FEBRUARY 1961 COLLECTIONS AND THE DIMENSIONS GIVEN BY CONNOLLY (1939).

Dimensions	Means of February 1961 collection	Increased Calculation	Dimensions given by Connolly (1939)	Difference
L	11.05	35.74%	15.0	-
B	7.01	9.52	9.2	0.32
UWL	10.10	13.71	13.5	0.21
AL	8.294	11.358	11.0	0.358
AB	4.97	6.75	6.1	0.65

T A B L E 17.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1961 COLIECTION AND THE DIMENSIONS GIVEN BY CONNOLLY (1939).

Dimensions	Means of June 1961 collection	Increased Calculation	Dimensions given by Connolly (1939)	Difference
L	11.26	33.21%	15.0	-
B	7.18	9.56	9.2	0.36
UWL	10.20	13.59	13.5	0.09
AL	8.341	11.111	11.0	0.111
AB	5.07	6.75	6.1	0.65

T A B L E 18.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF THE COMPOSITE SAMPLE AND THE DIMENSIONS GIVEN BY CONNOLLY (1939).

Dimensions	Means of Composite Sample	Increased Calculation	Dimensions given by Connolly(1939)	Difference
L	11.10	35.15%	15.0	-
B	6.96	9.41	9.2	0.21
UWL	10.07	13.61	13.5	0.11
AL	8.265	11.170	11.0	0.170
AB	4.99	6.74	6.1	0.64

T A B L E 19.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1960 COLLECTION AND THE DIMENSIONS GIVEN BY DE AZEVEDO (1957).

Dimensions	Means of June 1960 Collection	Increased Calculation	Dimensions given by De Azevedo (1957)	Difference
L	10.95	44.47%	15.82	-
B	6.75	9.75	9.39	0.36
UWL	9.95	15.37	14.4	0.97
AL	8.183	11.822	12.98	1.16
AB	4.95	7.15	5.93	1.22

T A B L E 20.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF FEBRUARY 1961 COLLECTION AND THE DIMENSIONS GIVEN BY DE AZEVEDO (1957).

Dimensions	Means of February 1961 Collection	Increased Calculation	Dimensions given by De Azevedo (1957)	Difference
L	11.05	43.17%	15.82	-
B	7.01	10.04	9.39	0.65
UWL	10.10	14.46	14.40	0.06
AL	8.294	11.88	12.98	1.10
AB	4.97	7.12	5.93	1.19

T A B L E 21.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1961 COLLECTION AND THE DIMENSIONS GIVEN BY DE AZEVEDO (1957)

Dimensions	Means of June 1961 Collection	Increased Calculation	Dimensions given by De Azevedo (1957)	Difference
L	11.26	40.50%	15.82	-
B	7.18	10.09	9.39	0.70
UWL	10.20	14.33	14.40	0.07
AL	8.341	11.119	12.98	1.26
AB	5.07	7.12	5.93	1.19

T A B L E 22.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF THE COMPOSITE SAMPLE AND THE DIMENSIONS GIVEN BY DE AZEVEDO (1957).

Dimensions	Means of Composite Sample	Increased Calculation	Dimensions given by De Azevedo (1957)	Difference
L	11.10	42.54%	15.82	-
B	6.96	9.92	9.39	0.53
UWL	10.07	14.35	14.4	0.05
AL	8.265	11.781	12.98	1.20
AB	4.99	7.21	5.93	1.28

TABLE 23.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1960 COLLECTION AND THE DIMENSIONS GIVEN BY MANDAHL-BARTH (1954)

Dimensions	Means of June 1960 collection	Increased Calculation	Dimensions given by Mandahl-Barth (1954)	Difference
L	10.95	36.99%	15.00	-
B	6.75	9.25	10.00	0.75
UWL	-	-	-	-
AL	8.183	12.210	11.00	1.210
AB	4.95	6.78	7.00	0.22

T A B L E 24.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF FEBRUARY 1961 COLLECTION, AND THE DIMENSIONS GIVEN BY MANDAHL-BARTH (1954).

Dimensions	Means of February 1961 Collection	Increased Calculation	Dimensions given by Mandahl-Barth (1954)	Difference
L	11.05	35.74%	15.00	-
B	7.01	9.52	10.00	0.48
UWL	-	-	-	-
AL	8.294	11.358	11.0	0.358
AB	4.97	6.75	7.0	0.25

T A B L E 25.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1961 COLLECTION AND THE DIMENSIONS GIVEN BY MANDAHL-BARTH (1954).

Dimensions	Means of June 1961 Collection	Increased Calculation	Dimensions given by Mandahl-Barth (1954)	Difference
L	11.26	33.21%	15.00	-
B	7.18	9.56	10.00	0.44
UWL	-	-	-	-
AL	8.341	11.111	11.00	0.111
AB	5.07	6.75	7.00	0.25

T A B L E 26.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF THE COMPOSITE SAMPLE AND THE DIMENSIONS GIVEN BY MANDAHL-BARTH (1954).

Dimensions	Means of Composite Sample	Increased Calculation	Dimensions given by Mandahl-Barth (1954)	Difference
L	11.10	35.15%	15.00	-
B	6.96	9.41	10.00	0.59
UWL	-	-	-	-
AL	8.265	11.170	11.000	0.170
AB	4.99	6.74	7.00	0.26

T A B L E 27.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1960 COLLECTION, AND THE LARGEST SPECIMEN OF THE JUNE 1960 COLLECTION.

Dimensions	Means of June 1960 Collection	Increased Calculation	Largest specimen of June 1960 Collection	Difference
L	10.95	27.1%	13.92	-
B	6.75	8.58	8.46	0.12
UWL	9.95	12.94	12.55	0.39
AL	8.18	10.40	9.87	0.53
AB	4.95	6.29	5.92	0.37

T A B L E 28.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF FEBRUARY 1961 COLLECTION AND THE LARGEST SPECIMEN OF THE FEBRUARY 1961 COLLECTION.

Dimensions	Means of February 1961 Collection	Increased Calculation	Largest specimen of February 1961 Collection	Difference
L	11.05	13.9%	12.48	-
B	7.01	7.99	7.23	0.76
UWL	10.10	11.51	11.57	0.06
AL	8.29	8.45	8.96	0.51
AB	4.97	5.66	5.38	0.28

T A B L E 29.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF JUNE 1961 COLLECTION, AND THE LARGEST SPECIMEN OF THE JUNE 1961 COLLECTION.

Dimensions	Means of June 1961 Collection	Increased Calculation	Largest specimen of June 1961 Collection	Difference
L	11.26	34.01%	15.09	-
B	7.18	9.62	9.17	0.45
UWL	10.20	13.67	13.95	0.28
AL	8.34	11.18	11.57	0.39
AB	5.07	6.79	6.98	0.19

T A B L E 30.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF THE COMPOSITE SAMPLE AND THE LARGEST SPECIMEN OF THE JUNE 1960 COLLECTION.

Dimensions	Means of Composite Sample	Increased Calculation	Largest specimen of June 1960 Collection	Difference
L	11.10	25.41%	13.92	-
B	6.96	8.73	8.46	0.27
UWL	10.07	12.63	12.55	0.08
AL	8.27	10.37	9.87	0.50
AB	4.99	6.26	5.92	0.34

TABLE 31.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF THE COMPOSITE SAMPLE AND THE LARGEST SPECIMEN OF THE FEBRUARY 1961 COLLECTION.

Dimensions	Means of Composite Sample	Increased Calculation	Largest specimen of February 1961 Collection	Difference
L	11.10	12.43%	12.48	-
B	6.96	7.83	7.23	0.60
UWL	10.07	11.32	11.57	0.25
AL	8.265	9.292	8.96	0.33
AB	4.99	5.61	5.38	0.23

T A B L E 32.

COMPARISON BETWEEN THE % INCREASE OF THE MEANS OF THE COMPOSITE SAMPLE, AND THE LARGEST SPECIMEN OF THE JUNE 1961 COLLECTION.

Dimensions	Means of Composite Sample	Increased Calculation	Largest specimen of June 1961 collection	Difference
L	11.10	35.96%	15.09	-
B	6.96	9.46	9.17	0.29
UWL	10.07	13.69	13.95	0.26
AL	8.265	12.237	11.566	0.67
AB	4.99	6.78	6.98	0.20

(Hubendick, 1951a; van Aardt, op.cit.). However, by measuring the increase in the distance between the apex and the peripheral contours of the whorls at 90°, 180°, 360° etc., Hubendick (1951a) established a useful formula whereby the phrase "the whorls increase rapidly" may be expressed numerically.

If the means of the measurements, taken after the manner described by Hubendick (1951a), of 100 shells of L. n. natalensis are plotted on the same scale (fig. 49) as similar curves drawn by Hubendick (1951a), the curve of this species is found to be about halfway between those obtained for the "lagotis" and "ovata" types. In this respect, therefore, L. n. natalensis represents a form intermediate between the two types mentioned. Support for this conclusion can be derived from a comparison of figs. 2 - 24 with Hubendick's (1951a) line drawings of the lagotis and ovata types in his figures 1b and c on p. 8. The spire of L. n. natalensis has the general outline of the lagotis type but is more depressed than that of the ovata type, or, expressed differently, its whorls embrace each other more than those of the lagotis type but less than those of the ovata type. An interesting feature of the L. n. natalensis curve (fig. 49) is the possession, at 540°, of a deviation similar to that exhibited by Hubendick's ovata type curve. This deviation represent an irregular increase of the whorl at this stage of growth, the cause of which is unknown to me.

The spire angle H $\hat{A}$ I (fig. 28) expresses the verbal description "acute" numerically. The mean value of this angle was found to be 70.0° ± 3.7° (standard deviation) with a variance of 1.4° and a coefficient of variability of 5.4% for the composite sample.

The/.....

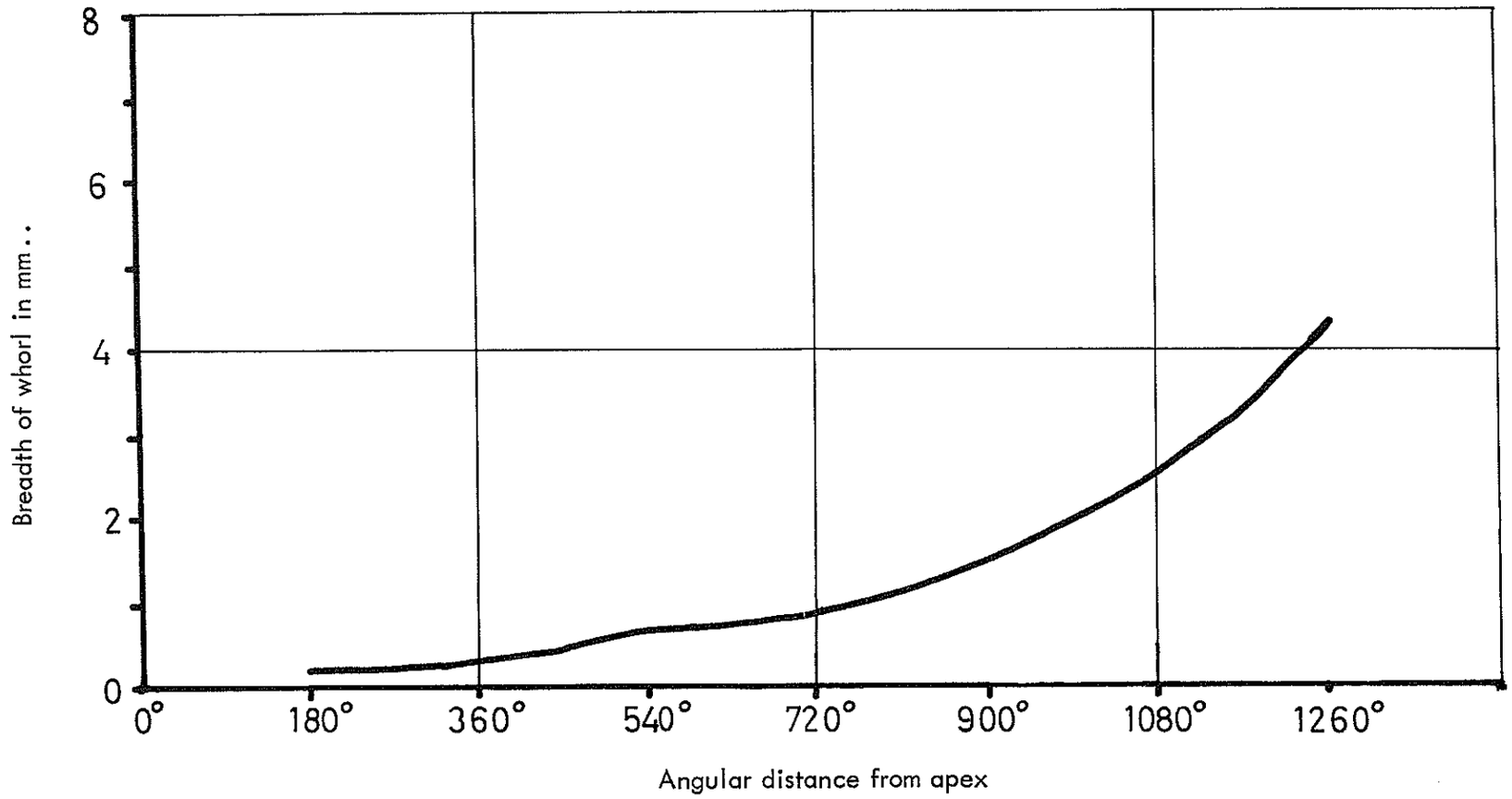


Fig. 49. Graph showing the relation between the increase in the breadth of the whorl and the widening of the angular distance from the apex based on the means of 100 shells.

The number of whorls in my composite sample, for the limited group studied, ranges from $3\frac{1}{2}$ - 4 (fig. 50) as compared with 5 (Krauss, 1848), 4 (De Azevedo, 1957) and 4 - 5 (Mandahl-Barth, 1954).

3.4. Description of Shell.

My series agrees with the following descriptions: The whorls increase rapidly (Connolly, 1939; Mandahl-Barth, 1954; De Azevedo, 1957), the ultimate whorl nearly comprising the entire shell (Connolly, 1939). The suture may be rather deep (Mandahl-Barth, 1954) and well defined (Connolly, 1939; De Azevedo, 1957) and the whorls are evenly rounded (Pilsbry et al. 1927; Mandahl-Barth, 1954; De Azevedo, 1957).

The colour ranges from greyish (Mandahl-Barth, 1954) to corneous yellowish (Krauss, 1848 and Connolly, 1939). The greyish shells usually seem to be more fragile and the colour is most probably dependant on ecological factors.

Some specimens display alternating dark and lighter bands, the socalled zebrine coloration. Hubendick (1951a) considers this phenomenon to be ecologically governed and of no taxonomic importance.

The callus which in most cases is white, may be absent in some specimens (figs. 2 - 24). Invariably a narrow umbilical chink is present. The shell is glossy (Krauss, 1848; De Azevedo, 1957). This is more evident in shells which had previously been cleaned with oxalic acid.

The shell is thin (Krauss, 1848; Connolly, 1939; Mandahl-Barth, 1954), fragile (De Azevedo, 1957), transparent (Krauss, 1848; Connolly, 1939) or semi-transparent (Mandahl-Barth, 1954).

The/.....

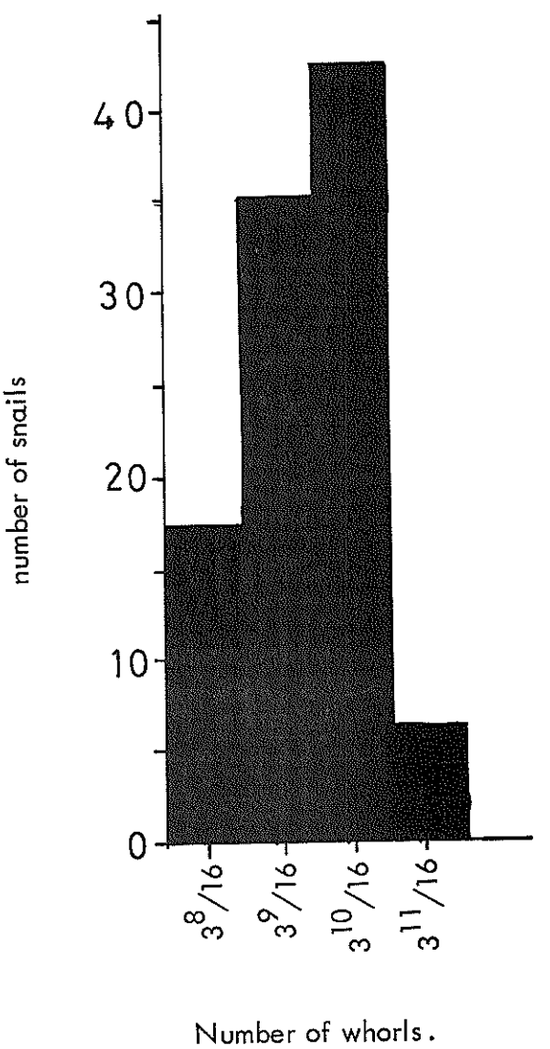


Fig. 50. Frequency histogram of the number of whorls.

The sculpture, in my series, consists of fine growth lines only and lacks any trace of the occasionally occurring longitudinal puckers referred to by Connolly (1939).

4. RADULA.

In spite of the limitations of the radula as a means to characterise species, particularly in the case of the Lymnaeidae (Annandale, 1925; Rosskowski, 1929; Wagner, 1930; Hubendick, 1951a), much may still be gained by supplementing the morphological data with a biometrical analysis, such as has been done by Berrie (1959) in his excellent paper on the radula of L. peregra. In order to be able to evaluate my own results in the light of Berrie's (1959) work, the biometrical methods adopted by this author has, to a large extent, been closely followed in the present investigation.

4.1 Morphology.

The radula formula of L. n. natalensis, as reflected by the mean teeth number of the tenth transverse row of 50 radulae, is as follows: 22 : 8 : 1 : 8 : 22 X 81.

The number of individual teeth varies as follows: (19 - 27) : (7 - 9) : 1 : (6 - 9) : (20 - 26) x (74 - 93).

As was found to be the case in various populations of the Australian lymnaeid, L. tomentos (Pfeiffer) (Boray, 1961), the number of teeth on one side of the central tooth may differ from that on the other side, suggesting that the two sides vary independently of each other. This conclusion is supported by my own biometrical analysis (p. 27).

For the sake of objectivity the first marginal tooth has been considered to be represented by that one, counting from the central, in which any one of the cones, usually the endocone, is subdivided into different denticles

(fig. 51/.....

(fig. 51, no. 10). In most cases this splitting of the cone into denticles occurs at the point where the transverse row is deflected anteriorly. Proceeding laterally from the central, the teeth become progressively more obliquely placed, larger, and the ectocone becomes much reduced and comes to lie further below the mesocone in each successive tooth. From the 9th to 11th teeth, the endocone is usually replaced by two or more denticles which, however, may be wanting altogether. In one radula out of 50, these denticles already occurred on the 7th tooth. The mesocone may sometimes be divided into two denticles of the same height as those of the endocone, though in most cases, it remains undivided and becomes reduced to about the same size as the denticles of the endocone.

Central.

The centrals are bicuspid (fig. 51) and very small compared to the other teeth on the radula. The small cusp on the right side of the main cusp seems to disappear after the 10th - 15th transverse row. The main cusp is larger in the first 10 transverse rows and diminishes in size further on, until only the base is left. This is due to detrition. It would appear that the cusps of the central teeth are more subject to detrition than the other teeth, because they are already worn where the other teeth are still unworn.

Lateral.

The laterals are tricuspid (plate 1 and fig. 51) and represent the largest teeth on the radula. The mesocones are the largest cusps on these teeth and, proceeding laterally, they become more pronounced (fig. 51). In most cases the endocone is undivided,

but/.....

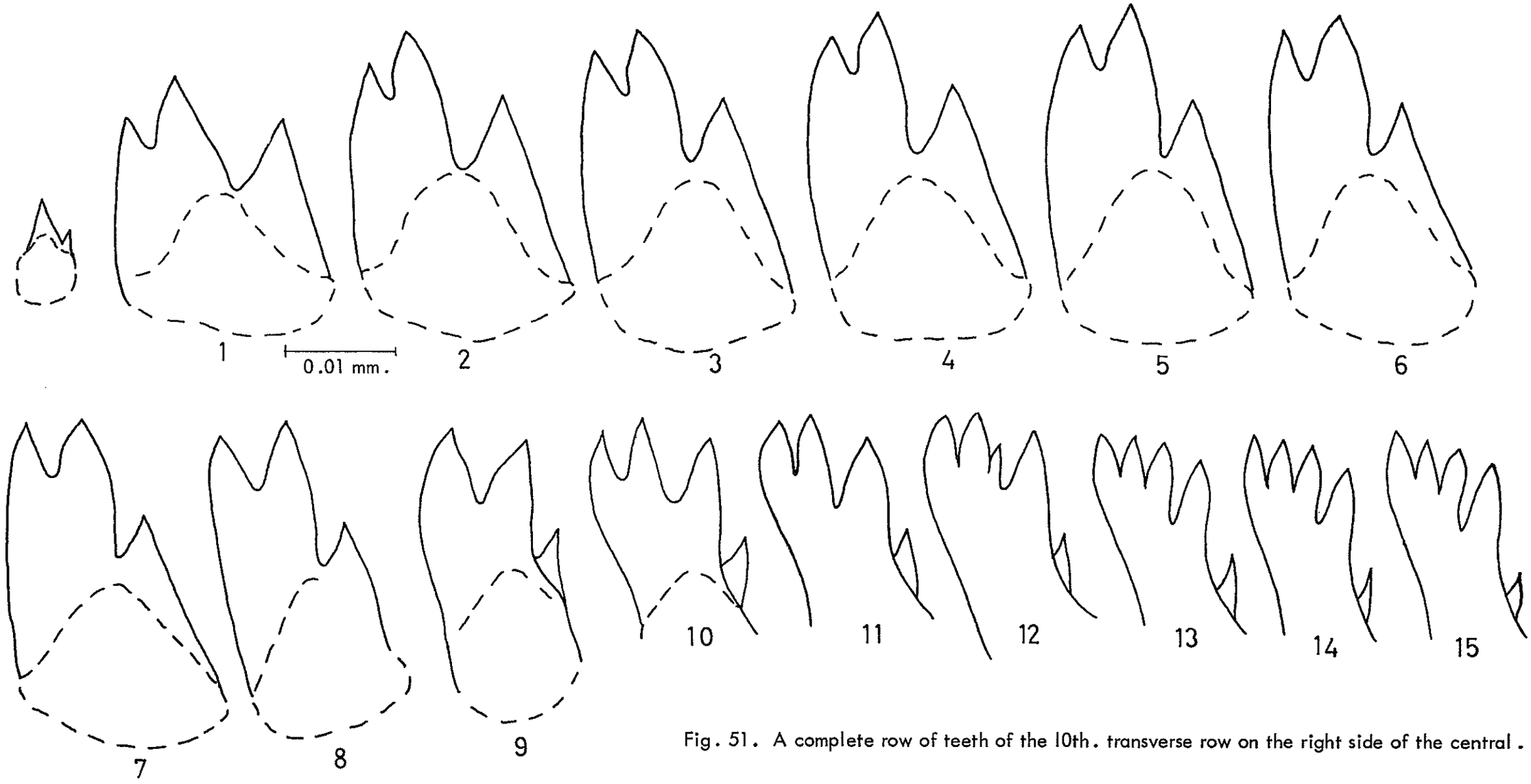
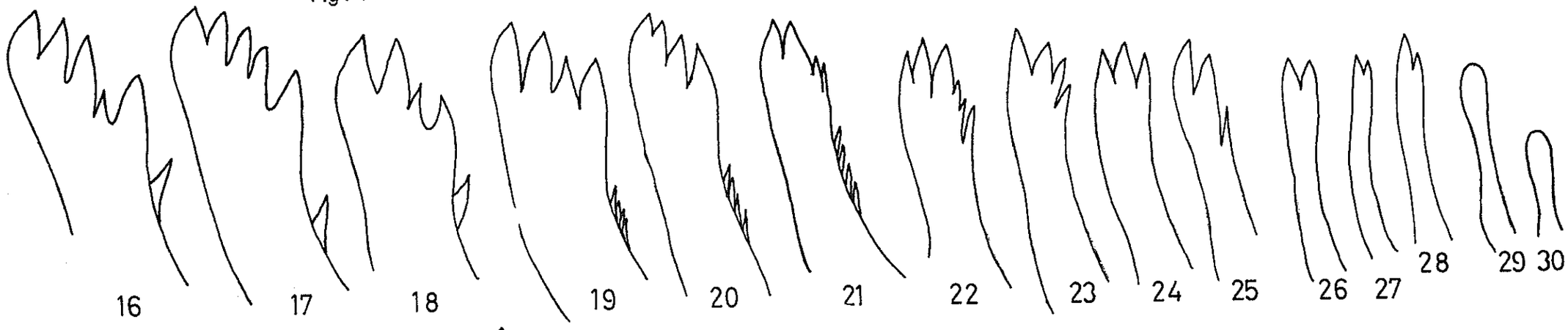


Fig. 51. A complete row of teeth of the 10th. transverse row on the right side of the central.

Fig. 51. Cont..



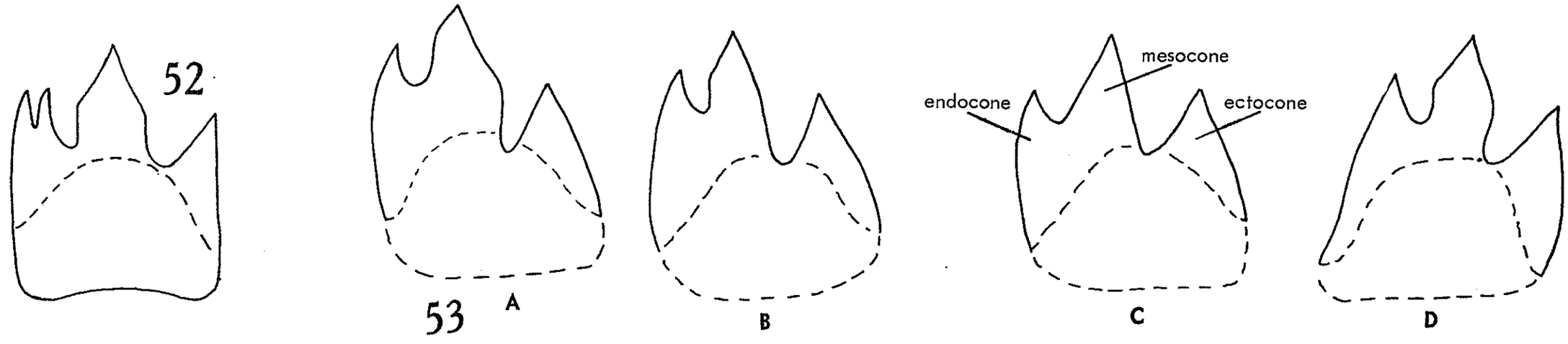


Fig. 52. A lateral tooth illustrating a divided endocone

Fig. 53. Shape of the cones of the 1st. lateral teeth. A = type 1 mesocone, B = type 2 mesocone, C = type 3 mesocone, D = type 2 endocone.

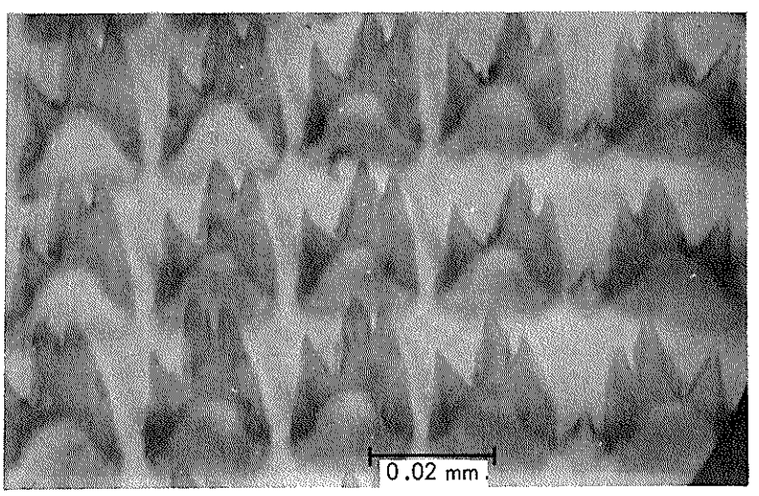


Plate 1. Some central and lateral teeth of the radula of L. n. natalensis.

but in a few specimens some of the endocones are divided into two small denticles (fig. 52). These cases are, however, regarded as anomalies.

The shape of the cones of some lateral teeth.

The first and sixth lateral tooth on both sides of the central of the 10th transverse row, were selected for the study. These teeth were examined in 50 radulae, twenty-five each from the February 1961 and June 1961 collections. Since the left and right sides of one transverse row were found to give independent records of the variability in teeth numbers, I combined the data obtained for the two sides, in order to get a larger sample, from which the conclusions can then be extracted. Thus the conclusions given below are based on 100 first lateral teeth and 100 sixth lateral teeth.

First lateral teeth.

Mesocones.

Three main types occur most commonly:-

The first type may be termed the angular type, because the edges converge from the base and then suddenly taper more sharply towards the apex (fig. 53A). This type was encountered in 66% of the February collection and 58% in the June collection.

The second type is asymmetrical in as much as only the median edge is angular, whereas the lateral edge may either be straight, convex or concave (fig. 53B). This type occurs in 30% of the February, and 32% of the June collections.

The third type is more or less triangular, both edges being either straight, convex or slightly concave to a variable degree (fig. 53C). This type occurs in 4% and 8% of the two successive collections.

Ectocones/.....

Ectocones.

The ectocones are simply triangular, about equilateral and variable in size (figs. 53A, B, C and D).

Endocones.

Two types occur:-

In the first type the median edge is convex while the lateral edge is concave (figs. 53A, B and C). This type was encountered in 88% of the February and in 82% of the June collections.

In the second type, the cone is simply triangular with both edges more or less straight (fig. 53D). This type occurs in 12% of the February and in 18% of the June collections.

An analysis of the foregoing data reveals that the most commonly occuring endocone-mesocone combinations, in order of frequency, are first type endocone with first type mesocone and first type endocone with second type mesocone. The remaining possible combinations are infrequent.

Sixth Lateral.

Mescocones.

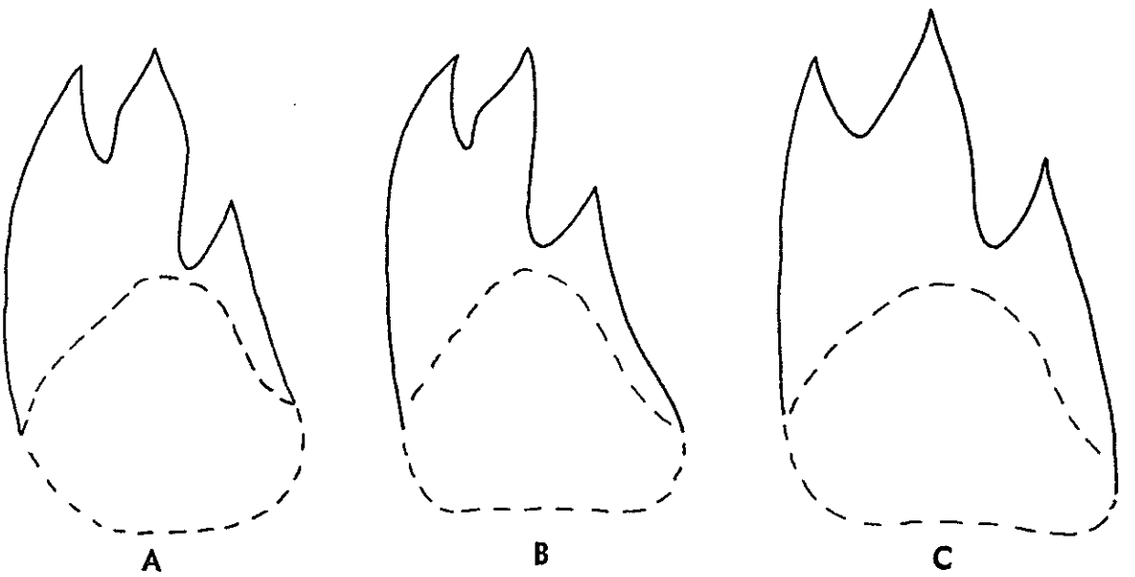
Four types occur:-

The first three types are the same as those described for the first lateral and are referred to in the same order (fig. 54A, B and C).

The fourth type (fig. 54D) is exactly the opposite of type two, the lateral edge being angular and the median edge straight, convex or concave.

Type 1 mesocone occurs in 58% and 54%, type 2 in 26% and 22%, type 3 in 14% and 18%, and type 4 in 2% and 6% of the February and June collections respectively.

Ectocone/.....



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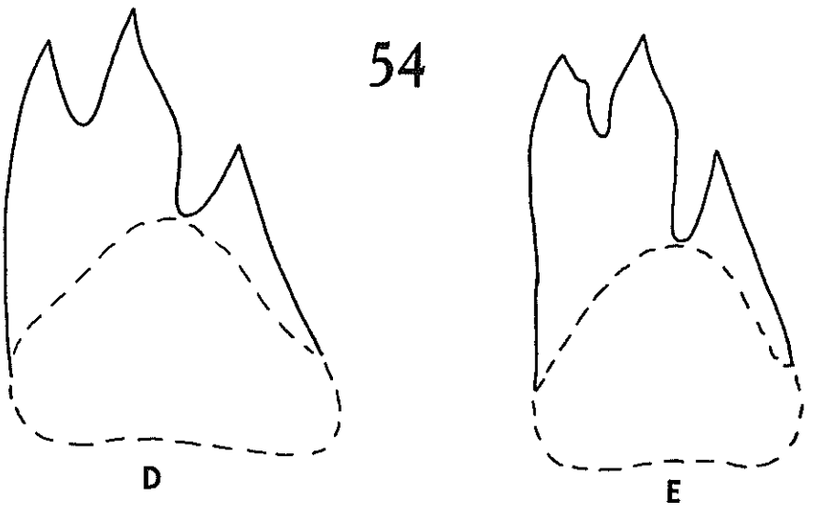

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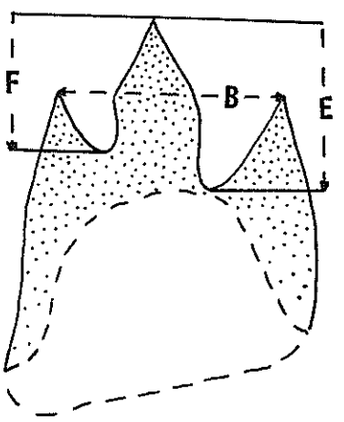


Fig. 54. Shape of the cones of the 6th lateral teeth. A = type 1 mesocone, B = type 2 mesocone, C = type 3 mesocone, D = type 4 mesocone, E = type 2 endocone.

Fig. 55. Diagram illustrating the method adopted for taking various measurements of the lateral teeth.

Ectocone.

This is identical to the ectocone of the first lateral tooth (fig. 54A, B, C, D and E).

Endocone.

Two types occur:-

The first type (fig. 54A, B, C and D) is similar to the first type described for the first lateral. This type of endocone occurs in 93% of the February, and 98% of the June collections.

The second type (fig. 54E) seems to bear a very small denticle on the median side. It occurs in 7% of the February, and in 2% of the June collections.

An analysis of the foregoing data reveals that the most commonly occuring endocone-mesocone combinations, in order of frequency, are first type endocone with first type mesocone and first type endocone with second type mesocone. The remaining possible combinations are infrequent.

Marginal.

The marginal teeth are multicuspid, elongated and obliquely placed. A "typical" marginal tooth (fig. 51) bears 4 - 5 denticles in a slightly oblique row and one or more denticles lower down on its lateral margin. These latter denticles represent the ectocone of the lateral teeth. Proceeding laterally, the teeth become longer and more slender and, at the same time, some of the denticles disappear progressively until only a few are left at the margin of the radula (fig. 51).

Where it is undivided, the denticle representing the mesocone is larger than the denticles of the endocone whereas, when divided into denticles, these are the same size or may be slightly larger as those of the endocones. The reduced cusp, representing the ectocone

of/.....

of the laterals, may occur on up to the 2nd or 3rd last marginal tooth, beyond which it disappears. This cusp may also be divided into 2 - 4 very sharp denticles on about the 18th tooth of the transverse row (fig. 51).

4.2 Biometrical Analysis.

The teeth were measured in the same manner as was done by Berrie (1959) (see fig. 55). The symbols (B/E, F/E) used to express the dimensions and ratios are the same as those employed by this author.

Comparison between the February 1961 and June 1961 collections.

A comparison is here made between certain teeth of specimens collected at the same locality during February and June 1961. Six specimens were chosen to represent each collection, in such a way that each specimen from one collection has a corresponding specimen of about the same shell length from the other collection.

Measurements were taken of six first laterals and six sixth laterals of each specimen. The teeth were studied on both sides of the central tooth of the tenth transverse row. This procedure was repeated on the 15th and 20th transverse rows.

An analysis of the data thus obtained is presented in tables 33 and 34. In table 33 the means, standard errors andthe standard deviations are given for the ratios calculated from the measurements taken. In a comparison of this kind the mean is of little value. The important figure is the standard deviation (Berrie, 1959), particularly when it is expressed as a percentage of the mean (coefficient of variability). In table 34 the coefficient of variability is plotted for the ratios under consideration.

The/.....

T A B L E 33.

COMPARISON OF CERTAIN RATIOS MEASURED AND CALCULATED FROM THE FEBRUARY AND JUNE 1961 COLLECTIONS.

The abbreviations used are explained on p.32 and in fig. 55.

	B/E		F/E		
Collection	1st lateral	6th lateral	1st lateral	6th lateral	
February 1961	1.236	1.055	0.708	0.551	Mean
	± 0.030	± 0.020	± 0.013	± 0.009	Standard error
	0.1821	0.1170	0.0764	0.0517	Standard deviation
June 1961	1.205	1.012	0.662	0.532	Mean
	± 0.023	± 0.012	± 0.013	± 0.007	Standard error
	0.1358	0.0737	0.0750	0.0439	Standard deviation

TABLE 34.

COEFFICIENTS OF VARIABILITY OF THE DATA IN TABLE 33.

	B/E		F/E	
Collection	1st lateral	6th lateral	1st lateral	6th lateral
February 1961	14.7%	11.1%	10.8%	9.4%
June 1961	11.3%	7.3%	11.3%	8.3%

The results can be seen to be very similar for both samples.

Mayr et al. (1953) suggest a method for deciding whether or not two samples were drawn from the same population. This involves calculating the Standard Error of the Difference (SED) between the means. This test has been applied to the samples here considered and, since in no case a significant difference was established, it was concluded that the two samples were drawn from the same population.

Variation between the teeth on the same radula.

To establish this, a radula was taken from a snail of which the shell length was nearest to the mean calculated for the sample in each case. Commencing at the sixth transverse row, the first and the sixth laterals on the same side of the central were measured in 25 consecutive rows. This procedure was followed for the February and June 1961 collections separately.

The results of this analysis are given in tables 35 and 36, from which it is evident that for each ratio, the first and sixth lateral on the same side of the central are subject to approximately the same degree of variability.

In the February collection the variability of these teeth, with respect to the B/E ratio, is twice that of the June collection, in spite of the fact that their means differ but slightly (table 36); with regard to the F/E ratio the two collections vary slightly.

Variation between the teeth of specimens from the same collection.

In order to gain a reliable picture of the degree of variation of the radula teeth of specimens from the same collection, it was decided, first of all, to

establish/.....

TABLE 35.

VARIABILITY OF THE TEETH FROM THE SAME RADULA.

Ratios	One specimen of the February 1961 collection.		One specimen of the June 1961 collection.		
	1st lateral	6th lateral	1st lateral	6th lateral	
B/E	1.296	1.069	1.223	1.069	Mean
	± 0.030	± 0.024	± 0.011	± 0.012	Standard error
	0.1476	0.1218	0.0536	0.0602	Standard deviation
F/E	0.645	0.532	0.571	0.552	Mean
	± 0.011	± 0.008	± 0.011	± 0.009	Standard error
	0.0570	0.0409	0.0530	0.0459	Standard deviation

T A B L E 36.

COEFFICIENTS OF VARIABILITY OF THE DATA IN TABLE 35.

Ratios	February 1961		June 1961	
	1st lateral	6th lateral	1st lateral	6th lateral
B/E	11.4%	11.4%	4.4%	5.6%
F/E	8.8%	7.7%	9.3%	8.3%

establish the variability with respect to the two ratios under discussion, in the first left lateral. This was likewise done for the 1st right, 6th left and 6th right laterals. Secondly the data of the left and right first lateral were combined and compared with the combined data of the 6th left and right laterals. Thirdly all the data thus obtained for the February collection were compared with that of the June collection.

To this end the first and sixth laterals on both sides of the central in the tenth transverse row were measured for 25 radulae. The calculations, based on these measurements, are recorded in tables 37 - 40.

The similarity between the 1st and 6th laterals with respect to the coefficient of variability of the B/E ratio, suggests that this ratio tends to vary similarly for these two teeth. This also holds true for the F/E ratio, and for both collections (tables 37 and 39).

The difference between the coefficients of variability of the two ratios, for the same tooth, suggests that B/E and F/E vary independently of each other, both in the first and the sixth laterals. This holds true for both collections (tables 38 and 40).

The above conclusions are further supported by the results obtained when testing the significance of the correlations between these ratios. These tests reveal that there exists a significant correlation not only between the B/E values of the first and sixth laterals, but also between their F/E values. The tests also established that any correlation which might exist between the B/E and F/E values of either the first or the sixth lateral is insignificant. These findings apply well to both collections.

All/.....

TABLE 37.

INTRACOLLECTION VARIABILITY OF THE FIRST AND SIXTH LATERALS OF 25 SPECIMENS FROM THE FEBRUARY 1961 COLLECTION.

Ratio	1st lateral		6th lateral		
B/E	left side	right side	left side	right side	
	1.224	1.246	0.995	1.034	Mean
	± 0.021	± 0.032	± 0.022	± 0.025	Standard error
	0.1034	0.1589	0.1074	0.1237	Standard deviation
	both sides		both sides		
	1.235		1.015		Mean
	± 0.019		± 0.017		Standard error
	0.1331		0.1185		Standard deviation
F/E	left side	right side	left side	right side	
	0.668	0.718	0.523	0.565	Mean
	± 0.015	± 0.017	± 0.007	± 0.004	Standard error
	0.0730	0.0868	0.0362	0.0180	Standard deviation
	both sides		both sides		
	0.693		0.544		Mean
	± 0.012		± 0.008		Standard error
	0.0834		0.0582		Standard deviation

TABLE 38.

COEFFICIENTS OF VARIABILITY OF THE DATA IN TABLE 37 (FEBRUARY 1961)

Ratio	1st lateral		6th lateral	
B/E	left side 8.4%	right side 12.7%	left side 10.8%	right side 12.0%
	both sides 10.8%		both sides 11.7%	
F/E	left side 10.9%	right side 12.1%	left side 6.9%	right side 3.2%
	both sides 12.0%		both sides 10.7%	

T A B L E 39.

INTRACOLLECTION VARIABILITY OF THE FIRST AND SIXTH LATERALS OF 25 SPECIMENS FROM THE JUNE 1961 COLLECTION.

Ratio	25 specimens				
	1st lateral		6th lateral		
B/E	left side	right side	left side	right side	
	1.217	1.197	0.976	0.966	Mean
	± 0.034	± 0.027	± 0.020	± 0.012	Standard error
	0.1689	0.1361	0.1004	0.0606	Standard deviation
	both sides		both sides		
	1.207		0.971		Mean
	± 0.021		± 0.012		Standard error
	0.1515		0.0823		Standard deviation
F/E	left side	right side	left side	right side	
	0.651	0.683	0.542	0.554	Mean
	± 0.014	± 0.016	± 0.019	± 0.008	Standard error
	0.0720	0.0795	0.0950	0.0408	Standard deviation
	both sides		both sides		
	0.667		0.548		Mean
	± 0.011		± 0.010		Standard error
	0.0767		0.0726		Standard deviation

T A B L E 40.

COEFFICIENTS OF VARIABILITY OF THE DATA IN TABLE 39 (JUNE 1961)

Ratios	25 specimens			
	1st lateral		6th lateral	
B/E	left side 13.9%	right side 11.4%	left side 10.3%	right side 6.3%
	both sides 12.6%		both sides 12.2%	
F/E	left side 11.1%	right side 11.6%	left side 17.5%	right side 7.4%
	both sides 11.5%		both sides 13.2%	

All the results summarised above may be interpreted as indicating that, while the same ratio (e.g. B/E or F/E) tends to vary similarly in the two teeth (1st and 6th lateral) studied, the two ratios vary independently of each other in each individual tooth. These two ratios, therefore, seem to give independent approximations as to the variability of the teeth studied in the collection involved. Thus, in the case of the laterals under consideration, an investigation of the B/E ratio approximates the variability of these teeth independently of the F/E ratio and the ratio B/E (or F/E) on the left side of the central reflects the variability independently of B/E (or F/E) on the right side. These conclusions are in accordance with the findings of Berrie (1959).

Among the conclusions to be derived from the above argumentation are:-

1. That the variability of any particular lateral on the radula, e.g. first lateral, can be more reliably determined by examining that tooth on both sides of the central.
2. That if the data of corresponding laterals from the left and right sides of the central (e.g. 1st or 6th laterals) be combined, than a study of only one of the ratios here considered provide an adequate measure of the variability of that lateral tooth.

It was finally established that, although there exists a certain amount of intracollection varability, it never approaches the level of statistical significance.

Comparison/.....

Comparison of the variability between teeth on one radula and teeth on different radulae, from the same collection.

An examination was made to determine whether variations between certain teeth on the same radula was as great as that between the same teeth on different radulae from the same collection.

For this comparison the data already obtained (tables 35 - 40) were used.

For L. peregra, Berrie (1959) obtained results from which he concluded that in all cases the standard deviation is much lower for the ratios of teeth from a single radula than for the ratios of teeth on different radulae from the same populations. This shows that there is less variation between the teeth on one radula than between the teeth on different radulae from the same population. For the June 1961 collection of my series of L. n. natalensis, I obtained results similar to those of Berrie, but the coefficients of varability for the ratios obtained for teeth from the same radula, differ less from those calculated for teeth from different radulae of the same population, than they do in the case of L. peregra (Berrie, 1959). On the whole this also applies to the February 1961 collection where, however, the relevant coefficients of variability of a few individual ratios were higher than those calculated for different radulae (tables 35 - 40).

Comparison of the variability of the shell and radula teeth.

When the data of the shell dimensions and ratios are compared with those of the teeth ratios, the coefficients of variability suggest that the former

is/.....

is less variable than the latter with regard to the indices under consideration (tables 34, 36, 38 and 40). A similar conclusion was reached for B. (Physopsis) africanus Krauss (Van Aardt, op.cit.).

Berrie (1959) maintains that it is important to determine whether any correlation exists between the ratios calculated for the teeth and the shell size of the same snail. Since, however, it was desirable to use specimens of a narrow size range in this study (see p. 11), it was not possible to determine the existing correlation if any.

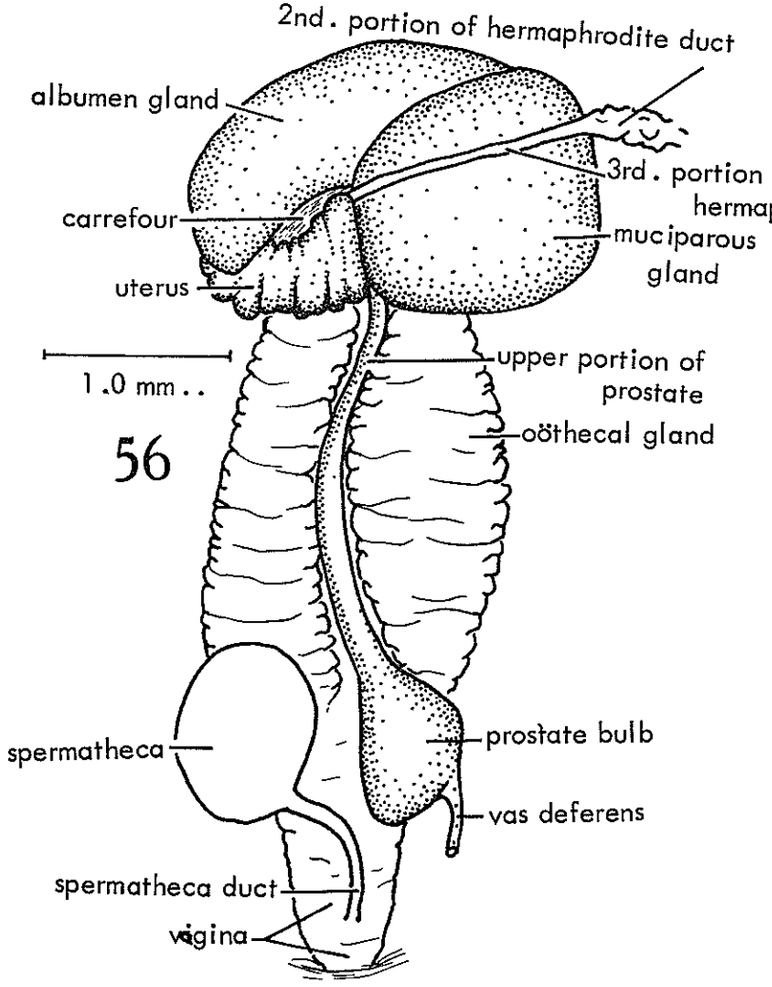
5. REPRODUCTIVE SYSTEM.

The reproductive system is treated under three headings, viz., the hermaphrodite gland and its duct, the female genital system and the male genital system (fig. 56).

5.1 The hermaphrodite gland and its duct.

Although the literature at my disposal contains no reference to the anatomy and histology of the hermaphrodite gland in L. n. natalensis, this structure has been investigated in various other snails such as the Pulmonata generally (Simroth, 1928), the Basommatophora (Boettger, 1944) the Planorbidae (Abdel-Malek, 1952) Bulinus (B.) contortus Michaud (= B. (B.) truncatus (Audouin)) (Larambergue, 1939), B. (P.) jousseaumei (Wright, 1957), Biomphalaria boissyi (Potiez & Michaud) (Abdel-Malek, 1954b), Heliosoma trivolvis (Say) (Abdel-Malek, 1954a), L. stagnalis appressa (Say) (Holm, 1946), B. tropicus (Krauss) (Stiglingh et al, 1962), B. (P.) africanus (Van Aardt, op. cit.) and L. humilis (McCraw, 1957).

Externally/.....



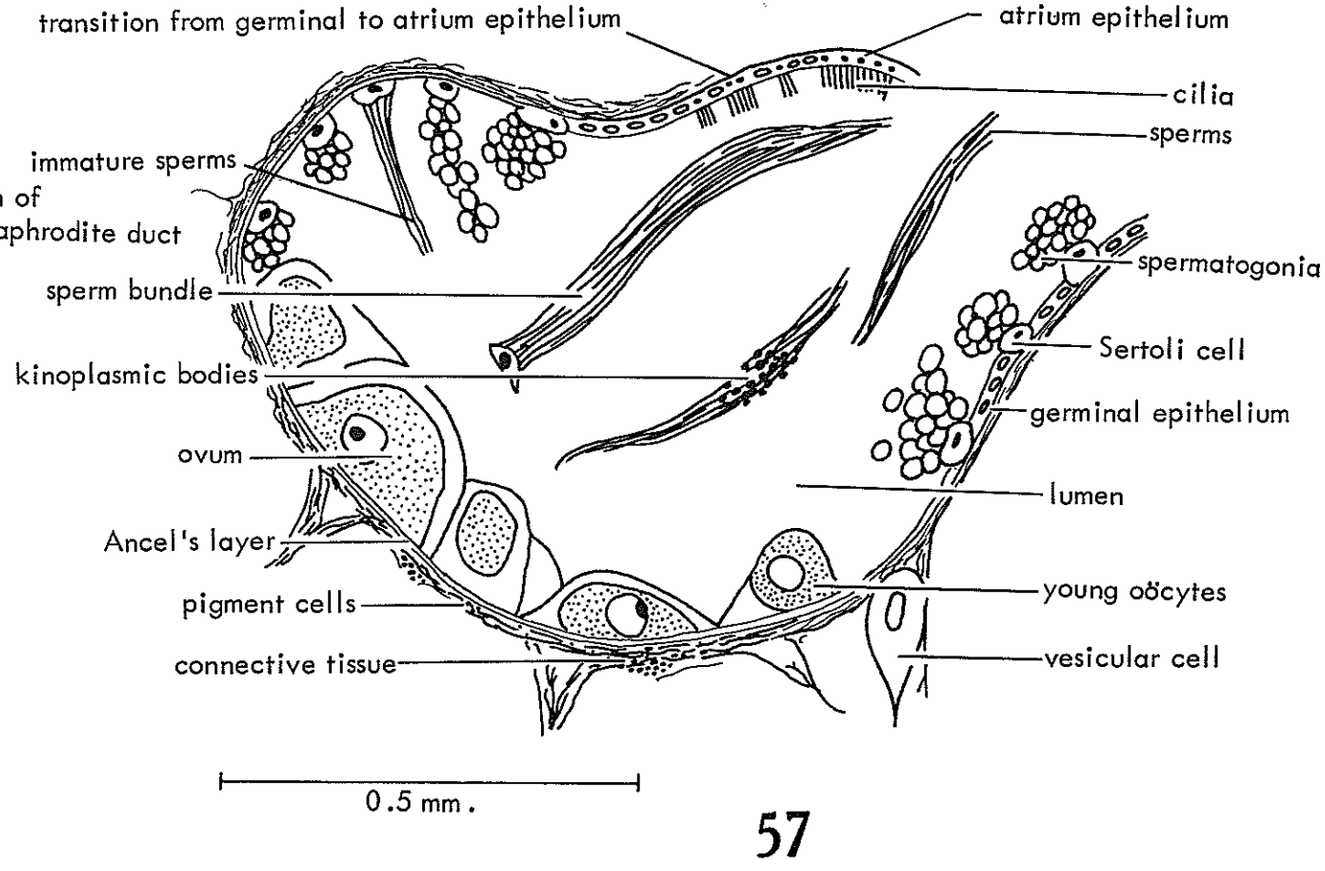


Fig. 56. Ventral aspect of reproductive system, in situ, excluding the hermaphrodite gland and penial complex.

Fig. 57. Semi-diagrammatic reproduction of a single acinus, illustrating the different histological elements associated with it.

Externally the hermaphrodite gland can be observed as an elongated, dichotomously lobulated sac composed of irregular lobules or acini which are separated from the liver lobules by connective tissue and blood spaces. In general it is similar to those described for L. humilis (McCraw, 1957) and L. stagnalis appressa (Holm, 1946).

As maintained by Stiglingh et al. (1962)the acini are arranged with their bases opening into the tubular atrium which is continuous with the hermaphrodite duct (fig. 47). The acini are covered externally by a connective tissue layer which is mostly continuous with the connective tissue covering the liver lobules. Ancel's layer which, according to Abdel-Malek (1954a), envelops each acinus, is present but the exact nature of its histology could not be determined.

In the basal region of the acinus, Ancel's layer is lined by germinal epithelium which is replaced by maturing ova and Sertoli cells on the sides and apex of the acinus. The germinal epithelium consists of a single layer of cells with elongate nuclei and simulates a syncytium as claimed by Schneider (1908), Simroth (1928), Boettger (1944) and, recently, by Van Aardt (op. cit.). Abdel-Malek (1954a), however, claims that, in H. trivolvis, the cell walls are distinct only in well fixed specimens.

The distribution of the germinal epithelium in the hermaphrodite gland of L. n. natalensis agrees with that of B. (B.) contortus (Laramberque, 1939), B. (P.) jousseaumei (Wright, 1957), H. trivolvis Abdel-Malek (1954a) and B. (P.) africanus (Van Aardt, op. cit.), in being restricted to the bases of each acinus. It therefore differs from Planorbis planorbis (!),

where/.....

where it is restricted to the common atrium (Boettger, 1944), and from the stylommatophoran snails Succinea ovalis Say (Hickman, 1931), Qxyloma retusa (Lea) (Lee, 1951, quoted from Abdel-Malek, 1954a) and L. stagnalis appressa (Archic, 1942) where the epithelium is claimed to be present in the apical portion of the acini as well.

The transition from germinal to atrium epithelium is rather gradual (fig. 57) and no such differentiated cells, as are described for B. (P.) africanus (Van Aardt, op.cit.) which mark the transition between the two epithelium types, could be detected in L. n. natalensis. At this transition, however, some ciliated cells with roundish, more intensely stained nuclei could be distinguished. At the opening of the acinus into the atrium the characteristic elongate nuclei of the germinal epithelium disappear altogether.

All stages of spermatogenesis and oögenesis can be observed in a single acinus (fig. 57). Like Larambergue (1939) and Stiglingh et al. (1962) I could not observe any differentiation of the acinus into the male and female zones, the two kinds of sexual elements occurring intermingled. Clusters of spermatogonia are attached to Sertoli cells or basal cells which are arranged along the wall of the acinus. Sperm clusters can also be seen, either floating freely in the lumen of the acinus or attached to Sertoli cells which may or may not be attached to Ancel's layer.

Simroth (1928) claims that, as soon as the undifferentiated cells of the germinal epithelium become differentiated into male and female elements, they leave the syncytium and complete their delelopment in the lumen of the acinus. This is apparently

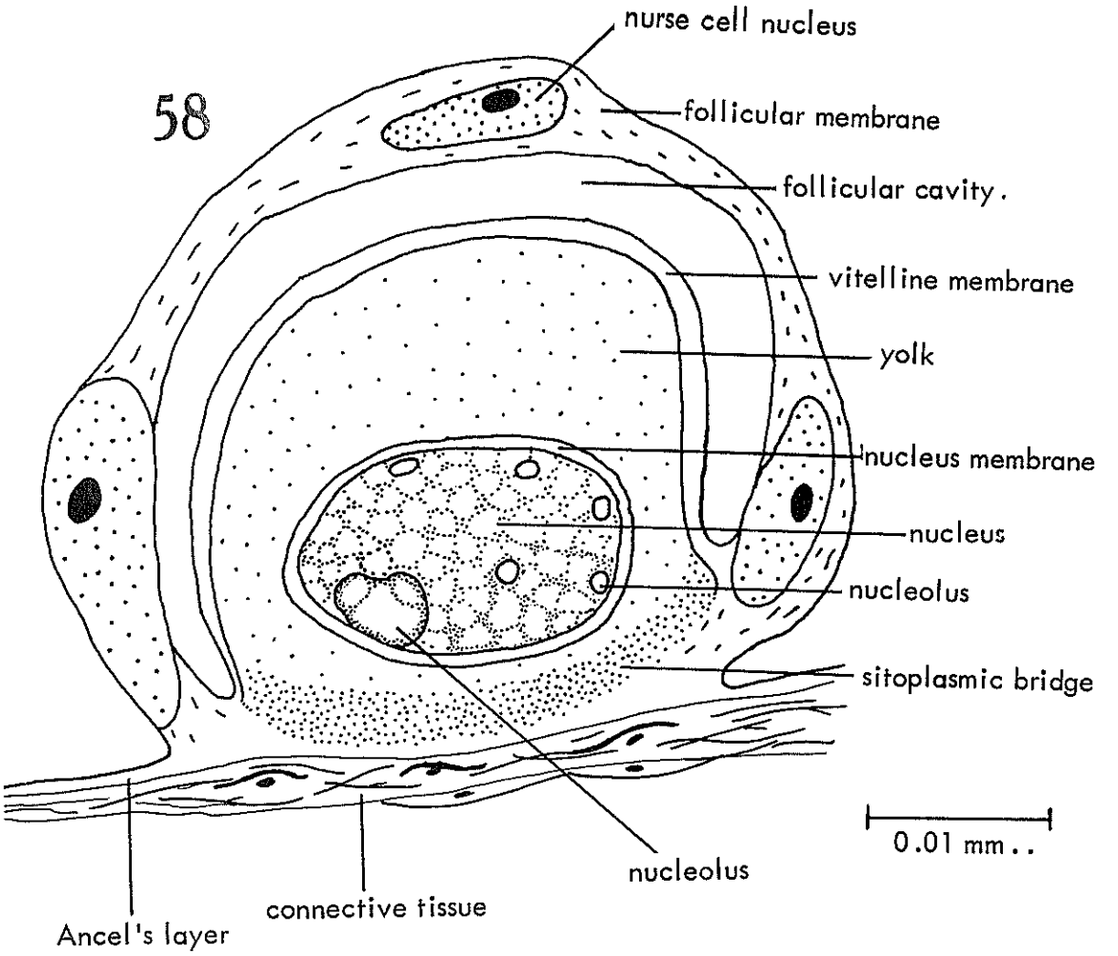
supported/.....

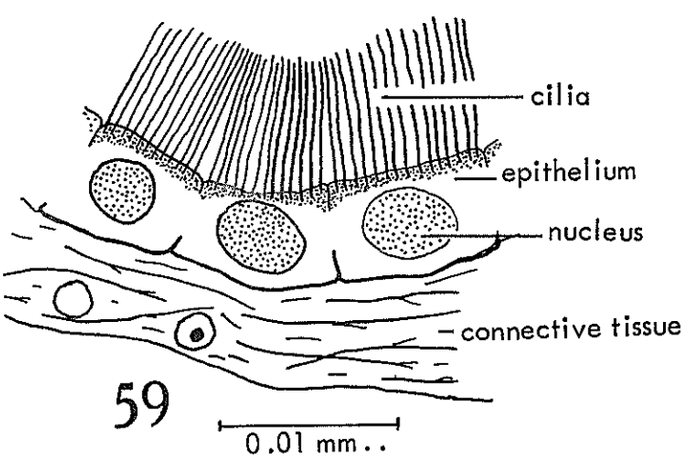
supported by Abdel-Malek (1954a), who mentions free sperm bundles as well as clusters of spermatozoa attached to Sertoli cells, occurring free in the lumen in H. trivolvis. My own observations, therefore, in part agree not only with those of Simroth and Abdel-Malek but also with Boettger (1944) and Stiglingh et al, (1962), who failed to find Sertoli cells floating free in the lumen.

The kinoplasmic bodies (fig. 47) on the axes of the spermatids, observed in Planorbis planorbis (Merton, 1930, quoted from Boettger, 1944), could also be recognised in L. n. natalensis. As in B. (P.) africanus (Van Aardt, op.cit.), more than one kinoplasmic body of different sizes can be seen on each spermatid. These bodies are best seen by examining unstained whole mounts of spermatids under phase contrast.

Immature oöcytes and spermatids (fig. 57) are largely confined to the basal parts of the acini, while as many as five to six maturing ova could be identified in the apical region of a single acinus. Wright (1957) reports six in B. (P.) jousseaumei, compared with two to three in H. trivolvis (Abdel-Malek 1954a).

A matured ovum is semi-diagrammatically presented in fig. 58. While only two nucleoli to a mature ovum has been described for Helix pomatia and Arion (Ancel, 1902 and Lamas 1910 respectively, quoted from Simroth, 1928), B. tropicus (Stiglingh et al., 1962) and B. (P.) africanus (Van Aardt, op.cit.), I found up to six in L. n. natalensis. One of these was bigger than the rest and seemed to be actively splitting into more smaller nucleoli which seem to migrate to the periphery of the nucleus.





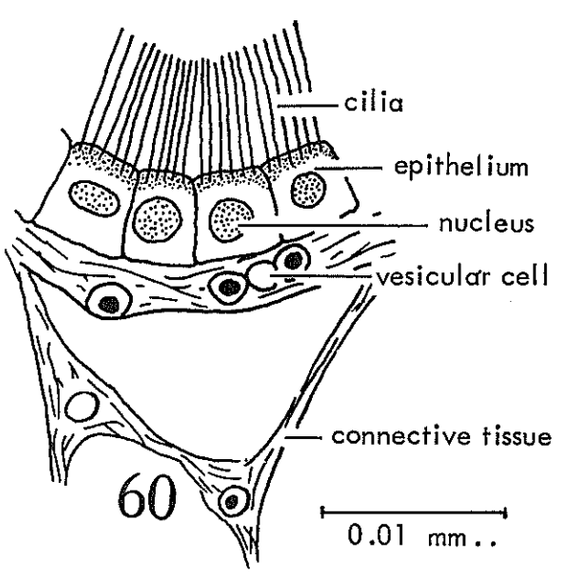


Fig. 58. Portion of wall of an acinus, showing a mature ovum.

Fig. 59. Epithelium of the atrium or 1st. portion of hermaphrodite duct.

Fig. 60. Epithelium of the seminal vesicle or 2nd. portion of hermaphrodite duct.

Abdel Malek (1954a) described the follicular cavity surrounding the ovum as being conspicuous on the side facing the lumen of the acinus and indistinct at the opposite side near the germinal epithelium. The condition in L. n. natalensis, where the yolk is not surrounded by a cavity on all sides, is depicted in fig. 58. Instead, the yolk is joined to the wall of the acinus by a substance which stains less deeply than does the yolk and which, for the sake of convenience, is here referred to as a cytoplasmic bridge. Furthermore, a definite membrane separates the yolk and the cytoplasmic bridge from the follicular cavity. This probably represents the vitelline membrane. A distinct nuclear membrane is also present.

The hermaphrodite duct can roughly be divided into three regions. The first, which is a very short tube, connects the atrium of the hermaphrodite gland with the second part of the duct. Its epithelial lining (fig.59) simulates a syncytium, with large, oval round, centrally placed nuclei. The cells are broader than high, and are distinctly ciliated. The length of the cilia is about 1.5 X the height of the cells.

The transition between the first and second parts of the duct is abrupt. The second region, usually termed the seminal vesicles (fig. 56), is characterized by several blind diverticulae. This portion is lined by a cuboidal ciliated epithelium (fig. 60) with round, centrally placed nuclei. The epithelial cells of this region are smaller than those of the first and do not resemble a syncytium. A few gland cells occur here and there between the epithelium cells. The third region forms the longest part of the hermaphrodite

duct/.....

duct and extends from the seminal vesicles up to the carrefour (fig. 56). It is circular in cross section and is lined by ciliated cuboidal epithelium (fig.61), the cilia of which create the impression of being more pliable than those occurring elsewhere in the duct. A longitudinal ridge traverses both the second and third regions of the hermaphrodite duct. It consists of ciliated, slender, columnar cells which tend to be basophilic in contrast with the rest of the epithelial lining which is acidophilic (fig. 62). The nuclei are centrally situated and the cilia are about as long as the cells are high.

The epithelium of all three regions of the duct is underlain by a layer of connective tissue, imbedded in which are numerous vesicular cells of various sizes. Outside the connective tissue of the third region there is a relatively thick layer of muscle fibres. All the regions of the duct are densely filled with sperms.

Where the hermaphrodite duct divides into the male and female duct systems, which are completely separated in this case, it receives the stout duct from the albumen gland, via a translucent fingerlike vesicle (carrefour of authors, or, fertilization pocket of Duncan, 1960). The mutual relations of these ducts are depicted in figs. 63 and 64. This arrangement is almost indntical to that of L. stagnalis appressa (Holm, 1946) but seems to differ from that obtaining in L. humilis (McCraw, 1957), where McCraw (1957) emphatically denies the presence of a carrefour. McCraw's (1957) figure 11, however, creates the impression that the duct of the albumen gland is slightly swollen where it joins the hermaphrodite duct. This swollen portion could very well represent

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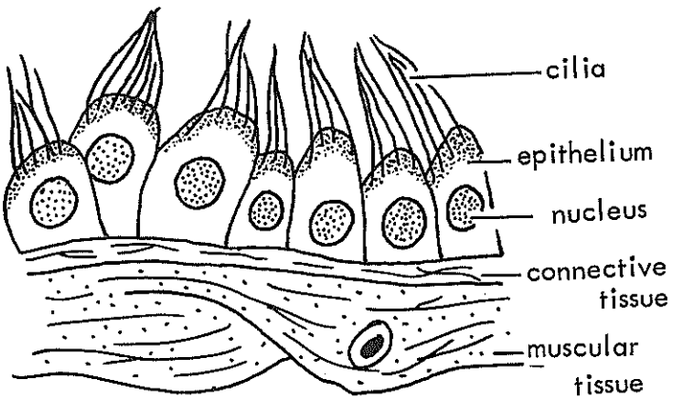

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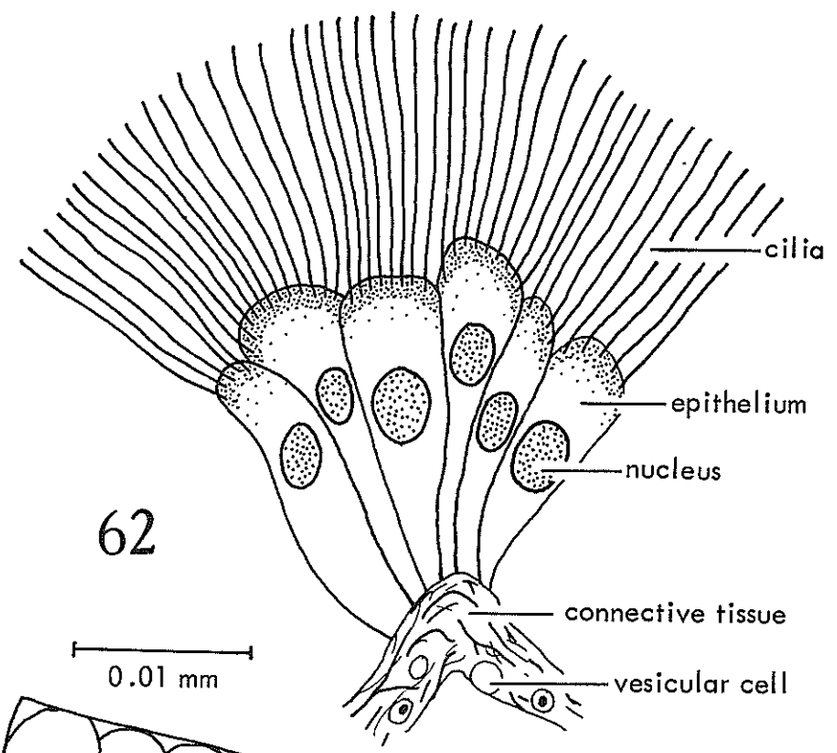

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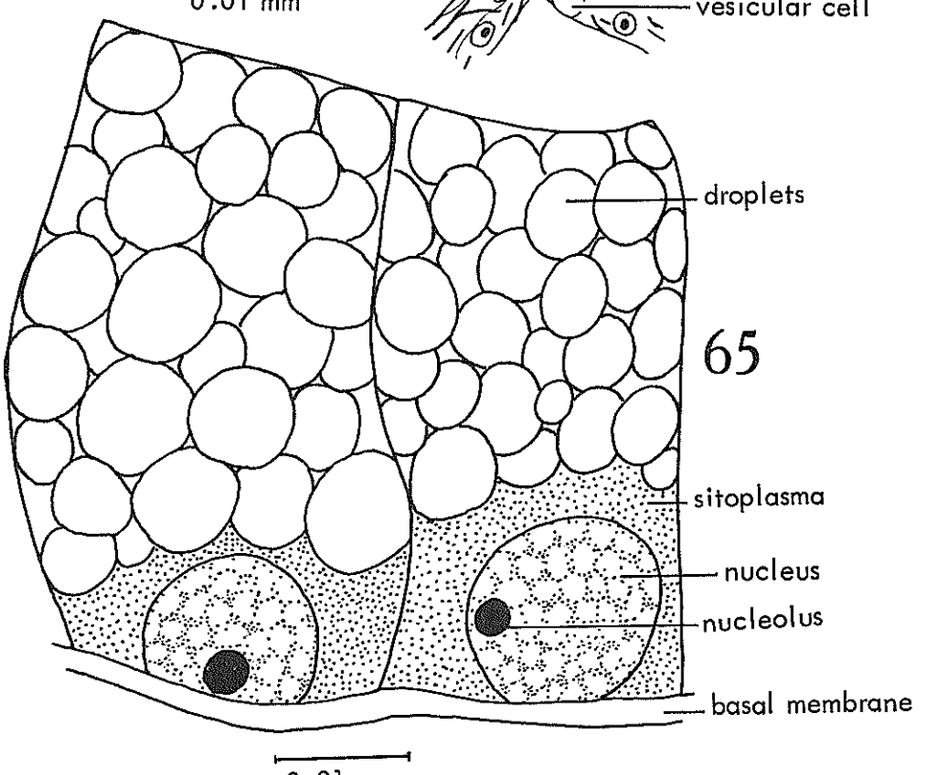

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Fig. 61. Epithelium of 3rd. portion of hermaphrodite duct.

Fig. 62. Epithelium of groove in hermaphrodite duct.

Fig. 65. Epithelium of albumen gland.

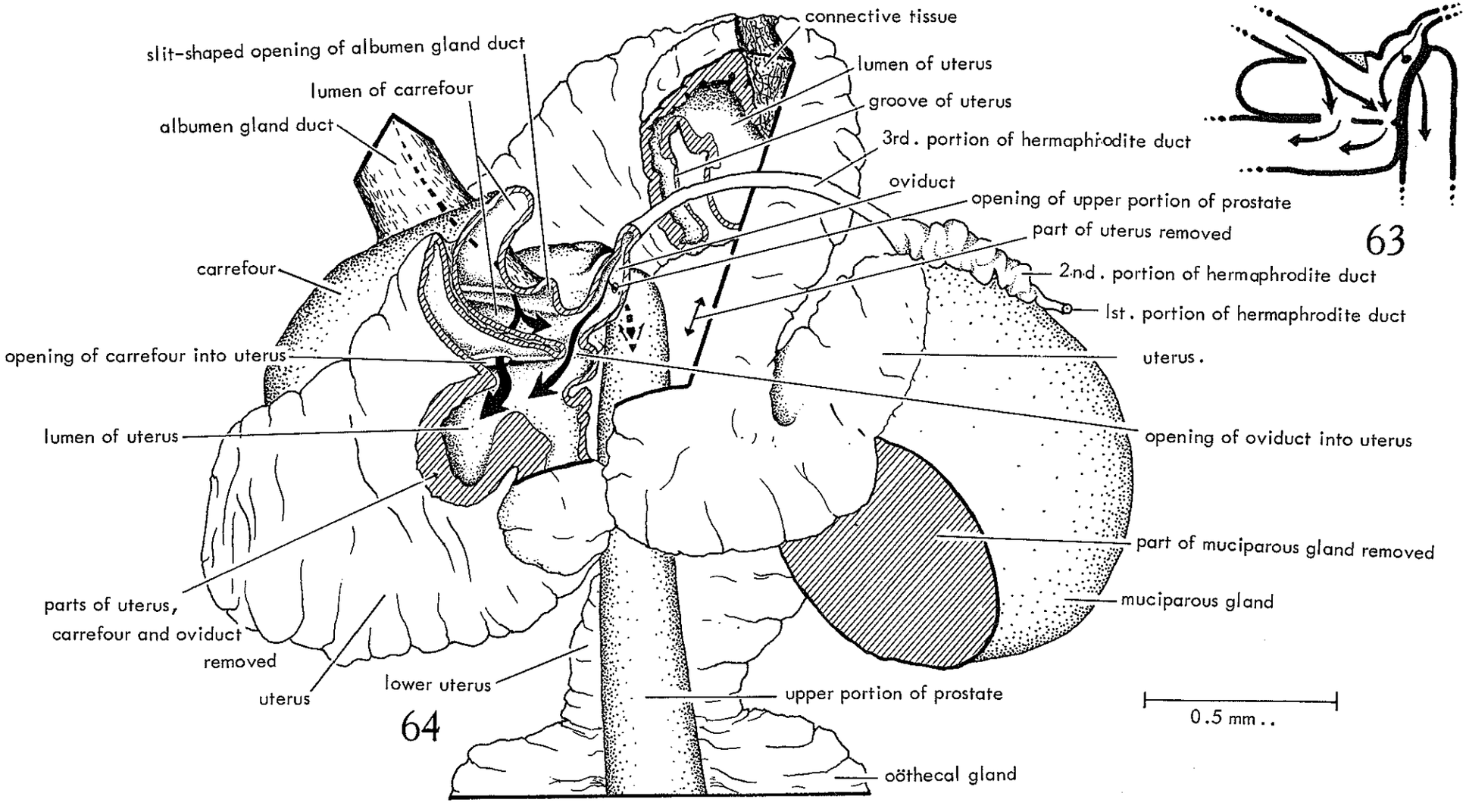


Fig. 63. Diagrammatical presentation of carrefour complex.

Fig. 64. A semi-diagrammatical presentation of the proximal parts of the reproductive system. A section is made through the carrefour complex to illustrate the relations, in situ, of the various ducts. Parts of the uterus and muciparous gland are also removed. The arrows indicate the openings only and do not suggest the paths followed by sexual products.

an underdeveloped carrefour, because the histology of this structure in L. n. natalensis is so similar to that of the albumen gland duct that it could, in this subspecies, be regarded as a greatly expanded termination to this duct. Should this interpretation be accepted, than L. n. natalensis and L. stagnalis appressa could be regarded as being merely less specialised in the degree of development of the carrefour than L. humilis.

5.2 The Female Genital System.

The albumen gland is more or less kidney-shaped and is slightly concave on the ventral and convex on the dorsal surface (fig. 56). On the whole the histology of the gland (fig. 65) is almost exactly similar to that of L. stagnalis appressa (Holm, 1946). However, the triangular cells described by this author as being wedged between the gland cells, could not be detected. Neither could the centro-acinar cells, reported to be present in Helix and Physa (Kraheska, 1912-1913, and Cavalie, 1902 respectively, quoted from Holm, 1946), be identified. According to Holm (1946) these cells are also absent in L. stagnalis appressa.

The duct of the gland passes alongside the semi-translucent carrefour into which it opens by a slit-shaped opening facing the apex of the coiled visceral mass (figs. 63 and 64). The epithelial lining of this duct (fig. 66) is similar to that of the carrefour where it consists of ciliated cells, with centrally placed nuclei and interspersed goblet cells, with spherical nuclei (fig. 67). The goblet cells are filled with a deeply staining secretory substance.

To the left, on the same side as the opening of the albumen gland duct, the hemaphrodite duct divides

into/.....

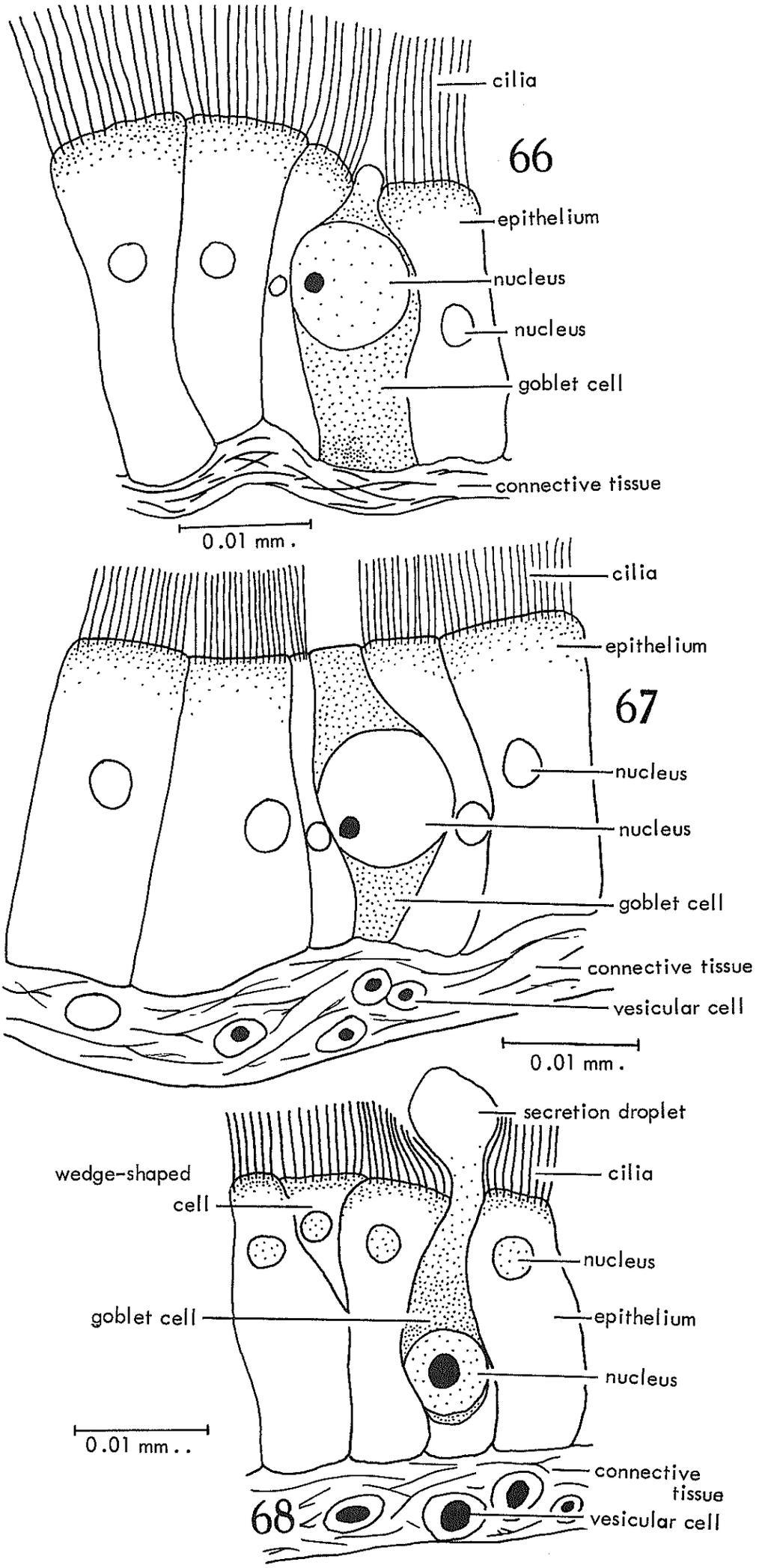


Fig. 66. Epithelium of albumen gland duct.

Fig. 67. Epithelium of carrefour.

Fig. 68. Epithelium of oviduct.

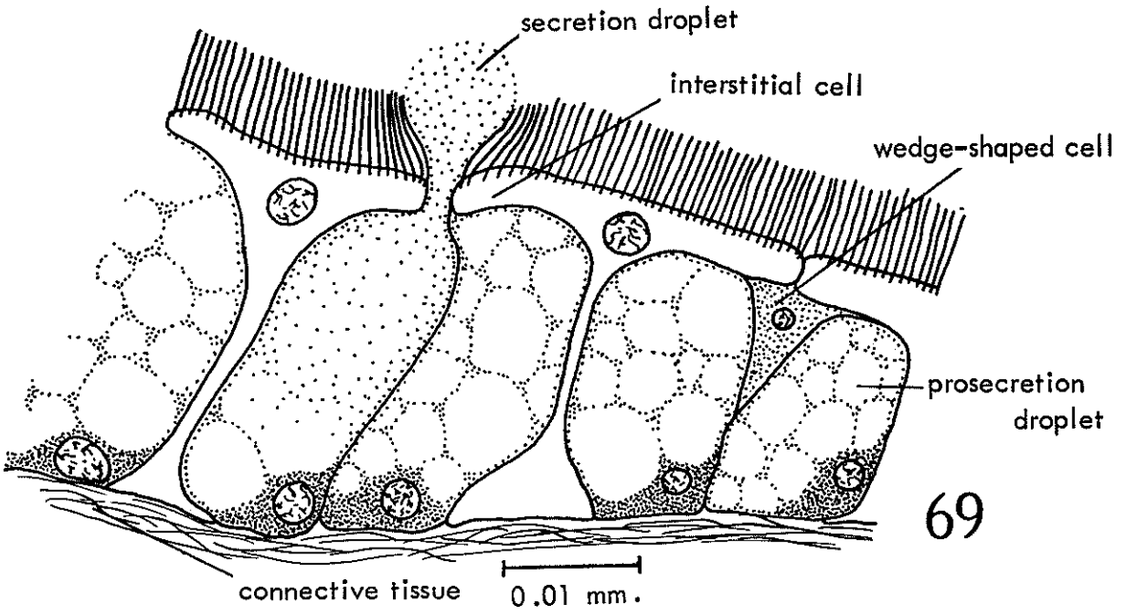
into the oviduct (oviduct I of Duncan, 1960) and the upper part of the prostate (vas deferens of Duncan, 1960). The former opens into the carrefour at one end and into the uterus (oviduct II of Duncan, 1960) at the other (figs. 63 and 64). The latter opening is the larger of the two, thus reversing the condition which seems to be conveyed by Holm's (1946) figure for L. stagnalis appressa.

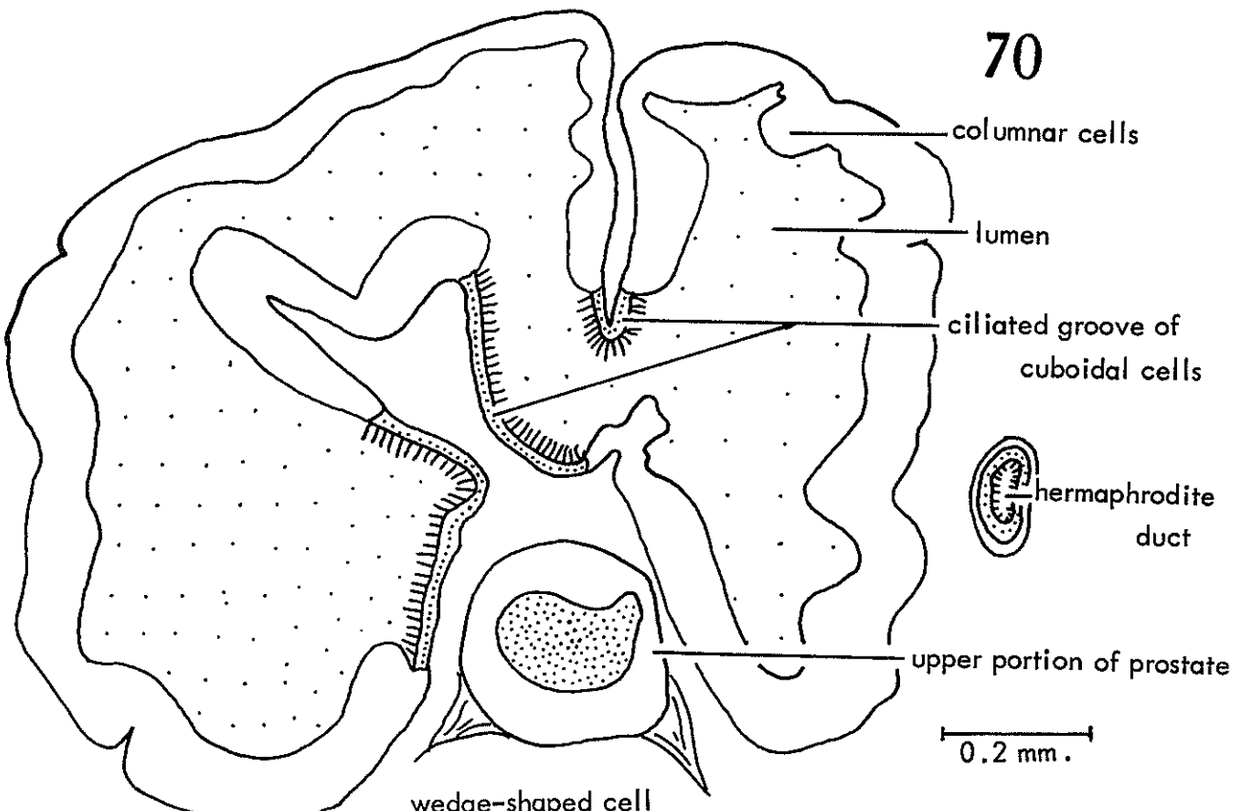
Apart from the subapically placed nuclei and the presence of wedge-shaped cells in the oviduct (fig. 68), the epithelial lining of the latter is similar to that of the carrefour.

The epithelial lining of the uterus (fig. 69) largely consists of large columnar cells with basal nuclei. The ciliated interstitial cells, recorded for L. stagnalis appressa by Duncan (1960), are wedged between the columnar cells and are more numerous in the distal parts of the uterus. Triangular cells are sometimes found wedged between the columnar cells. The cytoplasm immediately around the nucleus of the columnar cells, stains more deeply than the remainder of the cell. In the more distal part of the uterus, longitudinal grooves occur which are lined with ciliated cuboidal cells staining more intensely than the columnar elements. Figure 70 illustrates the relative position of cuboidal and columnar cells in this part of the uterus. These grooves converge into a single, similar, but much more reduced, groove in the oöthecal gland (uterus of Duncan, 1960).

The muciparous gland is similar to that of L. stagnalis appressa described by Holm (1946). Its epithelium (fig. 71) which is supported by a thin

layer/.....





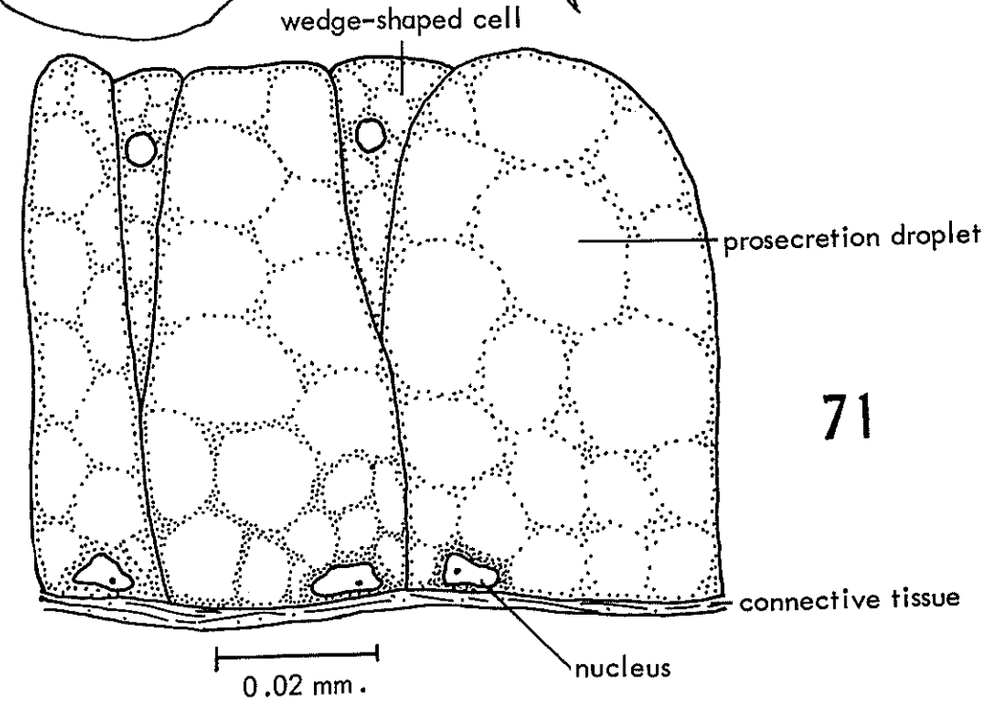


Fig. 69. Epithelium of uterus.

Fig. 70. Diagrammatic transverse section of the lower uterus showing the ciliated groove.

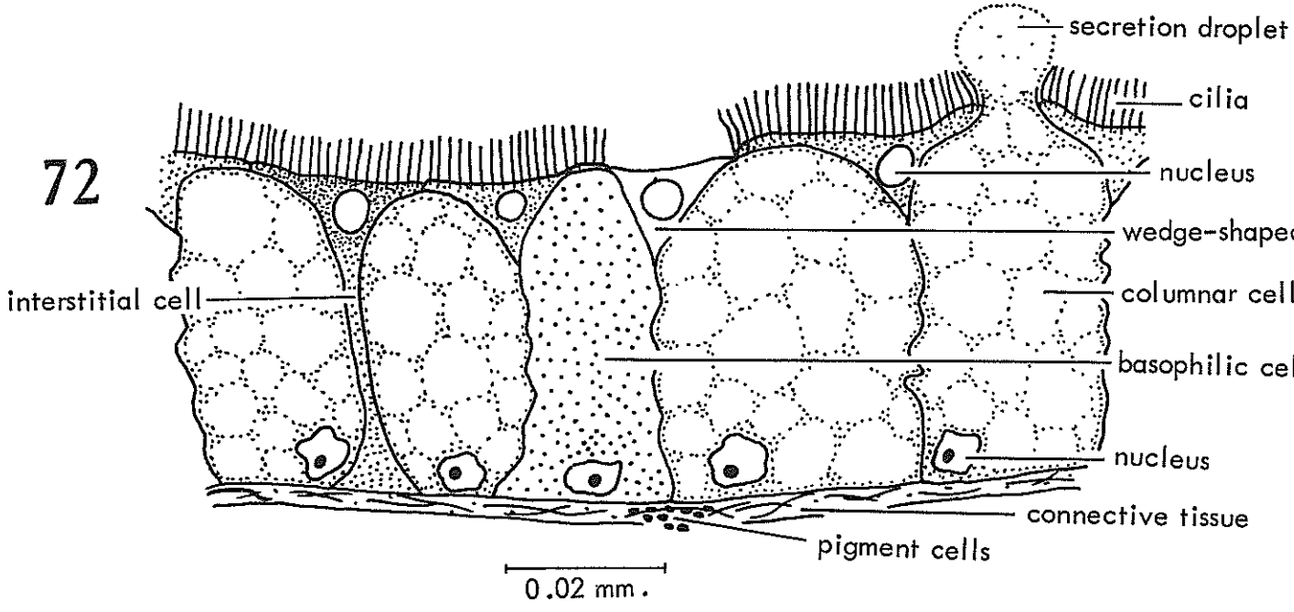
Fig. 71. Epithelium of muciparous gland.

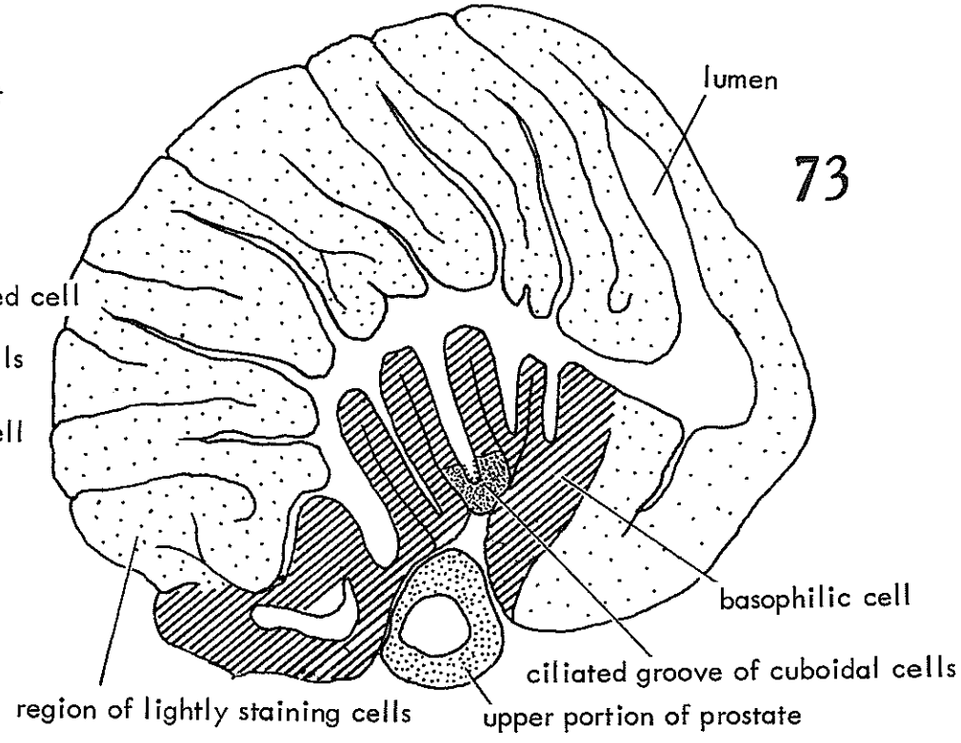
layer of connective tissue, consists of large, thin-walled columnar cells with irregularly shaped basal nuclei. The muciparous gland and uterus stand in open communication with each other with no true duct intervening between them. Nevertheless, the transition of epithelial cells from the one to the other is very abrupt.

Like the muciparous gland the lumen of the oöthecal gland is almost obliterated by the highly folded walls. The lining of columnar cells is underlain by a layer of connective tissue containing numerous pigment cells (fig. 72). In cross-section the walls of the columnar cells are wavy. The nuclei are basally placed and irregularly shaped. By reference to their affinity for the stains employed, two groups of columnar cells can be distinguished. The first group stains very lightly and contain prosecretion droplets whereas the second group stains dark blue (basophilic). Although the two cell types are dispersed between each other to a variable degree, they are mainly arranged in a definite way as illustrated in fig. 73. Apparently inactive columnar cells are so tightly wedged between the glandular elements that their nuclei are displaced to their apical regions. In the upper region of the gland, where the uterus merges into the oöthecal gland, ciliated interstitial cells occur between the columnar cells (fig. 72).

The ciliated groove mentioned in connection with those of the uterus, proceeds over the entire length of the oöthecal gland, on that side where it abutts against the upper portion of the prostate gland (fig. 73). The epithelium of the groove (fig. 74)

consists/.....





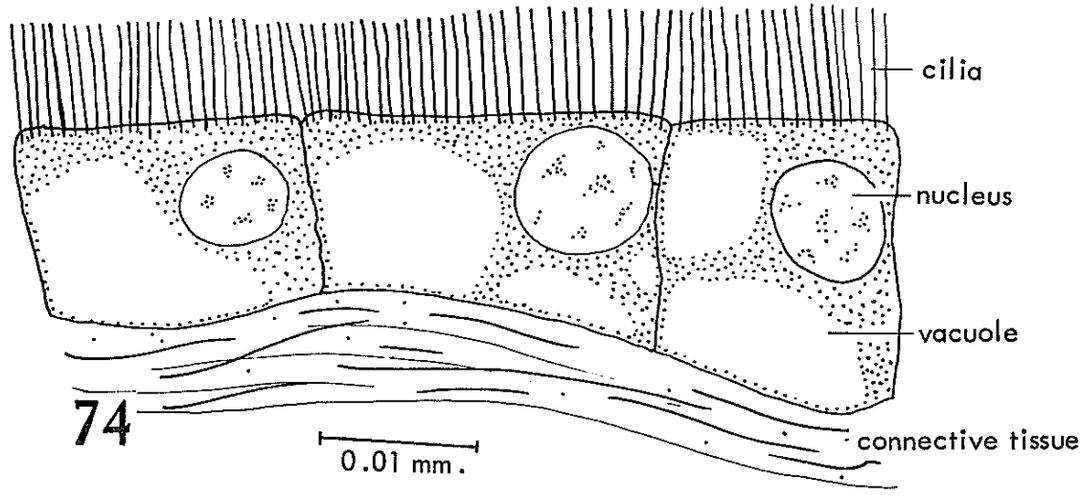


Fig. 72. Epithelium of oöthecal gland.

Fig. 73. Part of the wall of the oöthecal gland illustrating the distribution of the two cell types.

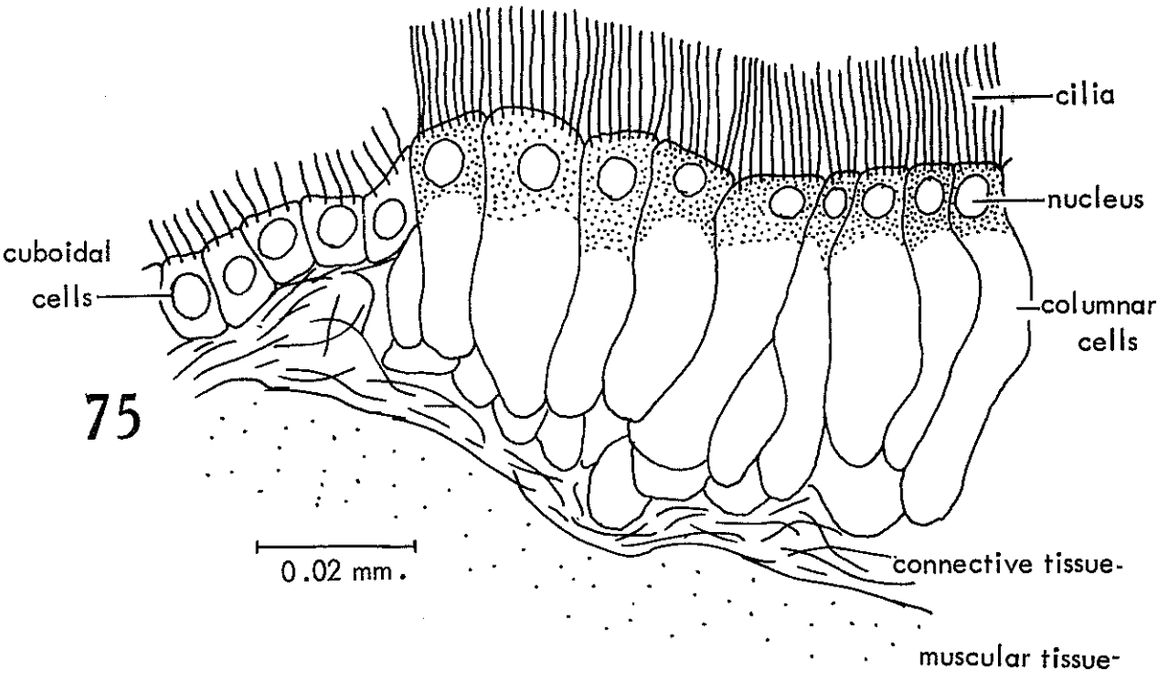
Fig. 74. Epithelium lining the groove of the oöthecal gland.

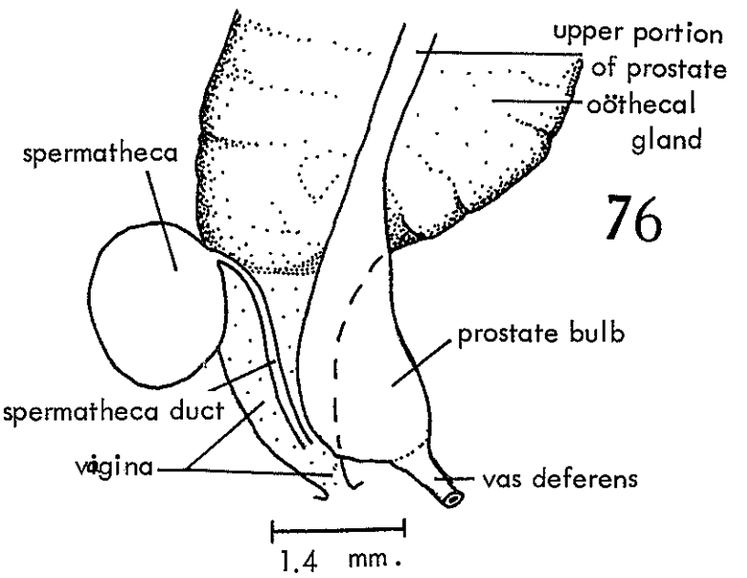
consists of vacuolated, ciliated, cuboidal cells with large nuclei. Distally the groove of the oöthecal gland becomes confluent with a similar though much shallower groove of the vagina.

The term vagina (fig. 76), as employed by different authors, does not always denote exactly the same structure. According to Baker (1928) it indicates that portion of the female duct which is situated distally to the entrance of the spermathecal duct. Larambergue (1928) and Hubendick (1951a) uses the term for the slender portion of the female duct distally to the broader oöthecal gland. In the light of the histological evidence, I give preference to the view held by Larambergue and Hubendick.

The walls of the vagina are irregularly folded. Its epithelial lining (fig. 77) is predominantly cuboidal and all the cells are ciliated. The groove, already referred to elsewhere, is characterized by being formed of larger, more strongly ciliated cells (fig. 75) than the rest of the vaginal wall. In my sections part of these cells remained unstained, whereas the apical portions tend to be acidophilic and contains finely dispersed granules. The nuclei are situated apically. Dispersed between the cuboidal cells are mucus secreting columnar cells identical to, but smaller than those of the oöthecal gland. The epithelial lining of the vagina is bounded externally by a layer of connective tissue and muscle fibres. The shape of the spermatheca (or receptaculum seminis of authors and bursa copulatrix of Duncan, 1960) and its duct, and their relations to other organs, depicted in fig. 76, remained fairly constant in all specimens examined. Due to unsatisfactory preservation, however, it could not be examined histologically.

The/.....





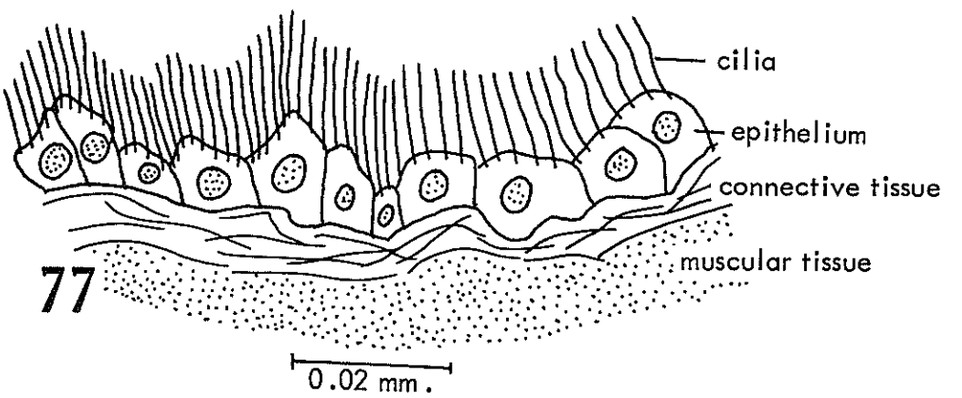


Fig. 75. Epithelium cells lining the groove of the vagina.

Fig. 76. Distal portion of the female reproductive system illustrating the mutual relations of the vagina, spermatheca and prostate.

Fig. 77. Epithelium of the vaginal wall.

5.3. The Male Organs.

The various elements in the penis complex are illustrated in figs. 78 and 79.

Praeputium.

The praeputium is a hollow cylindrical structure characterized by highly muscular walls. The pigment of the praeputium is evenly distributed over the whole organ and not concentrated in the proximal portion in clusters as reported by Hubendick (1951a). The muscular development is especially pronounced in two opposing longitudinal ridges or pilasters, that transverse the entire length of the organ and tapers off in the distal portion (fig. 89). The walls of the proximal portion of the praeputium are comparatively thin (figs. 84 and 89). The lumen is roughly H-shaped in cross-section and its epithelial lining consists of columnar cells some of which are slender and ciliated (fig. 80). Dispersed between the epithelium cells are numerous goblet cells, some of which contain mucus substance while others contain a neutral staining substance. The flask-shaped cells reported by Slugocka (1913) and Holm (1946) for Physidae and L. stagnalis appressa respectively, can also be observed in the connective tissue.

The epithelium described above is confined to the one leg of the "H". In the other leg the epithlium tends to become cuboidal with inconspicuous cell walls. They are densely ciliated and their cytoplasm stains a very dark blue-brown. A few goblet cells are distributed between these epithelium cells. The epithelium is bounded externally by a thick layer of connective and muscular tissue.

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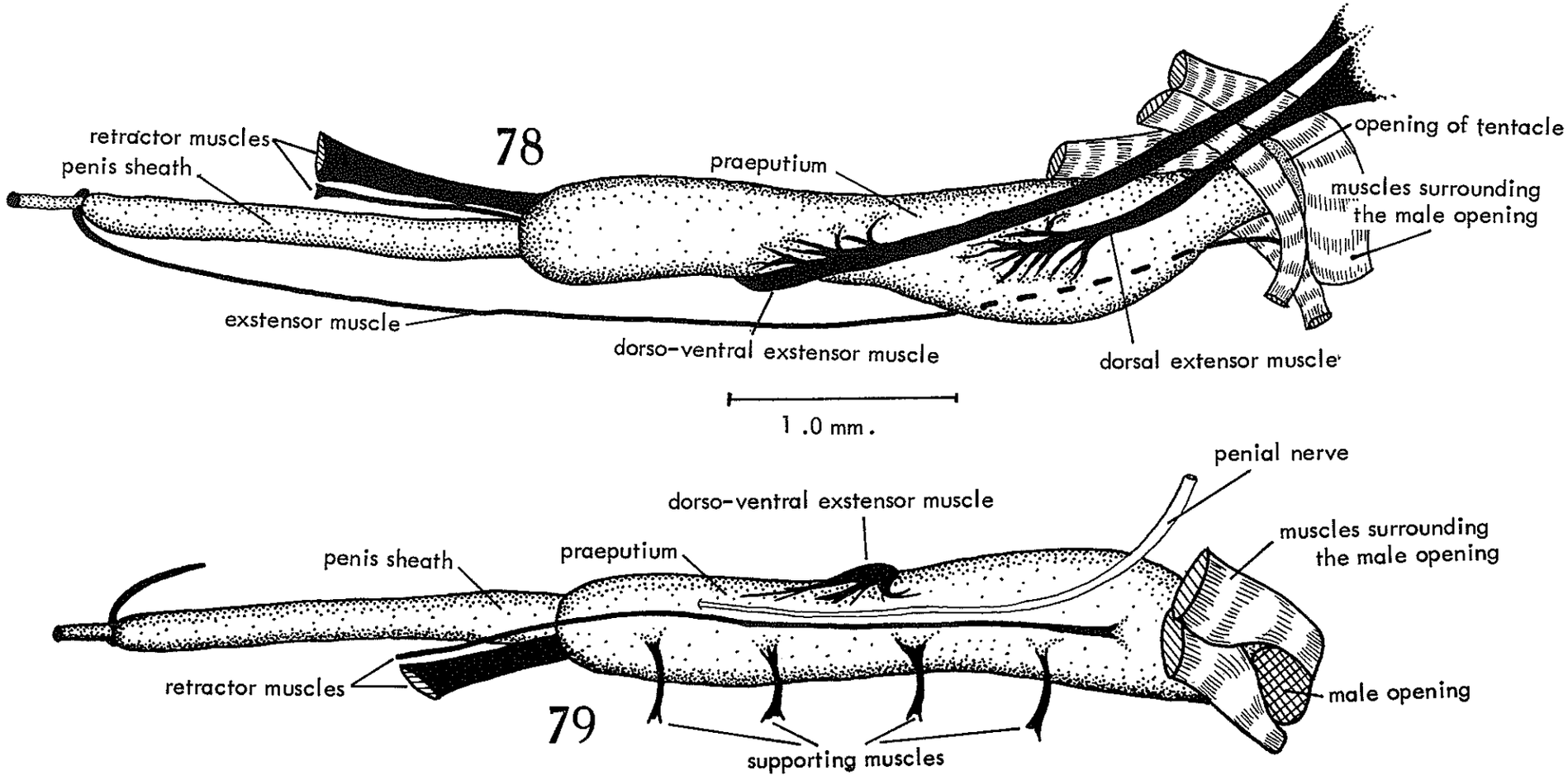
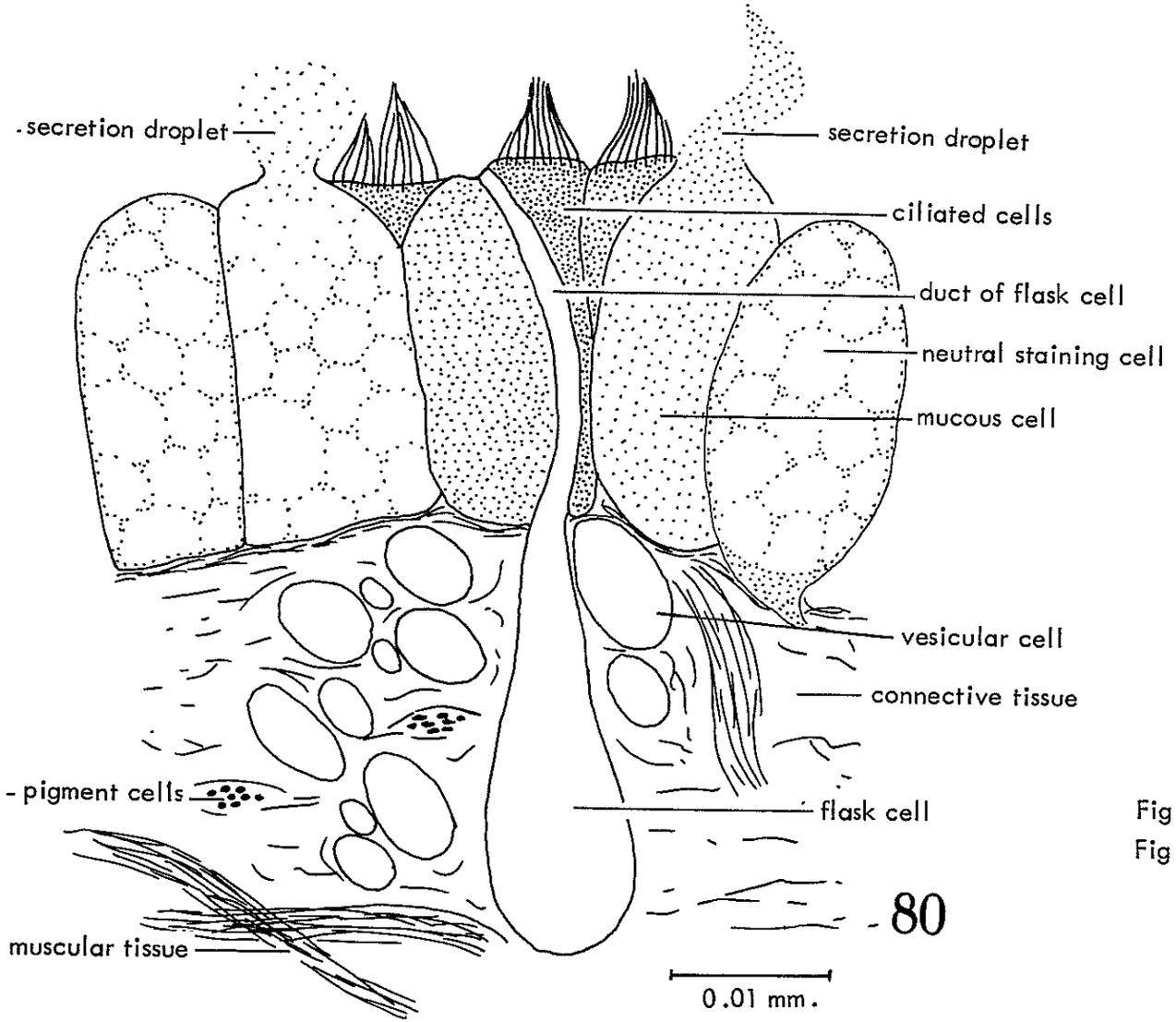


Fig. 78. Penial complex, dorsal aspect.
Fig. 79. Penial complex, ventral aspect.



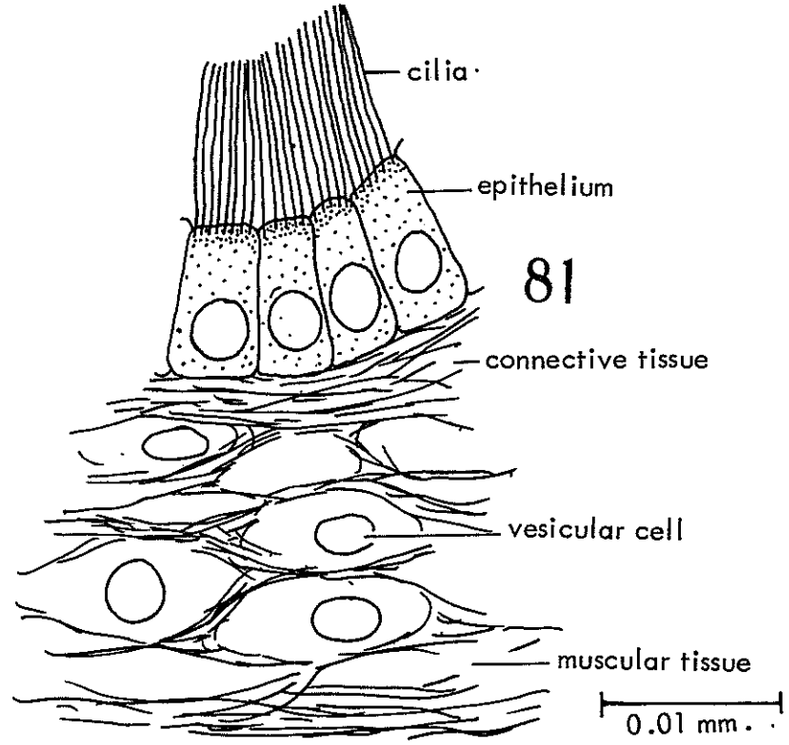
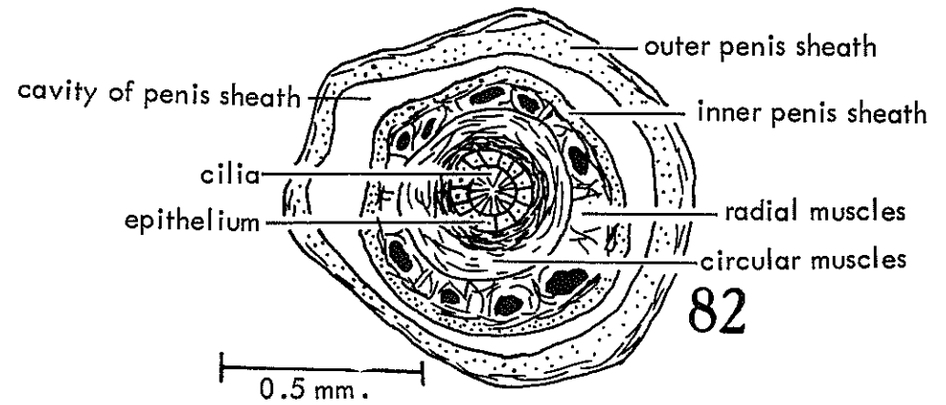
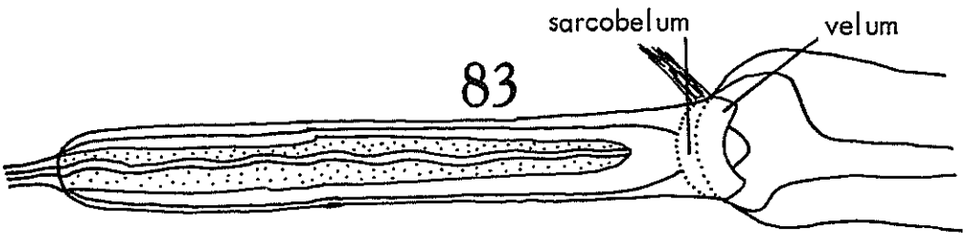
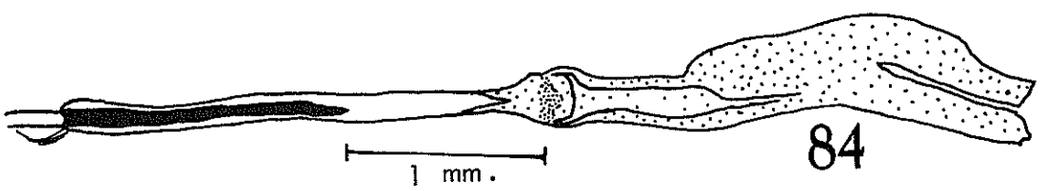
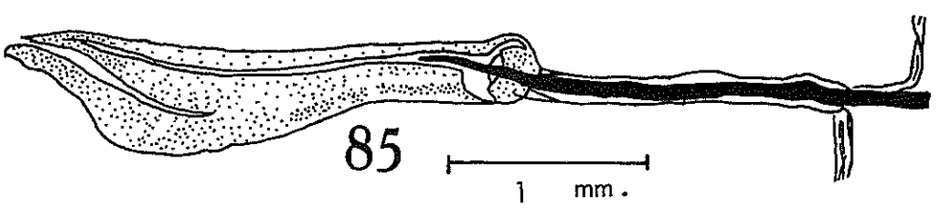


Fig. 80. Epithelium lining of proximal portion of praeputium.
Fig. 81. Epithelium of vas deferens.









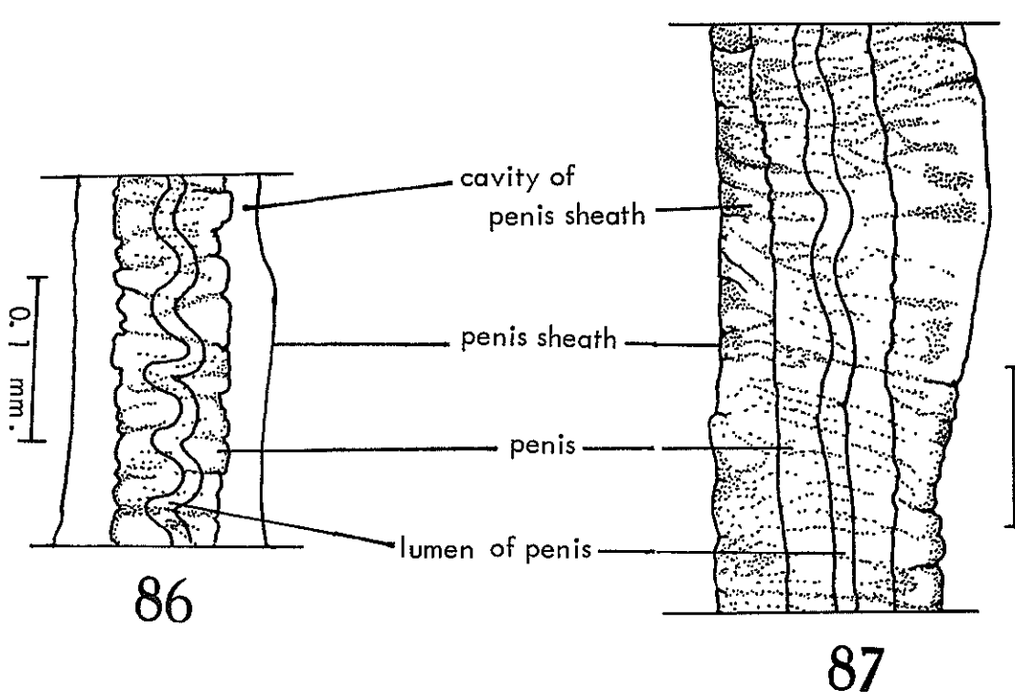
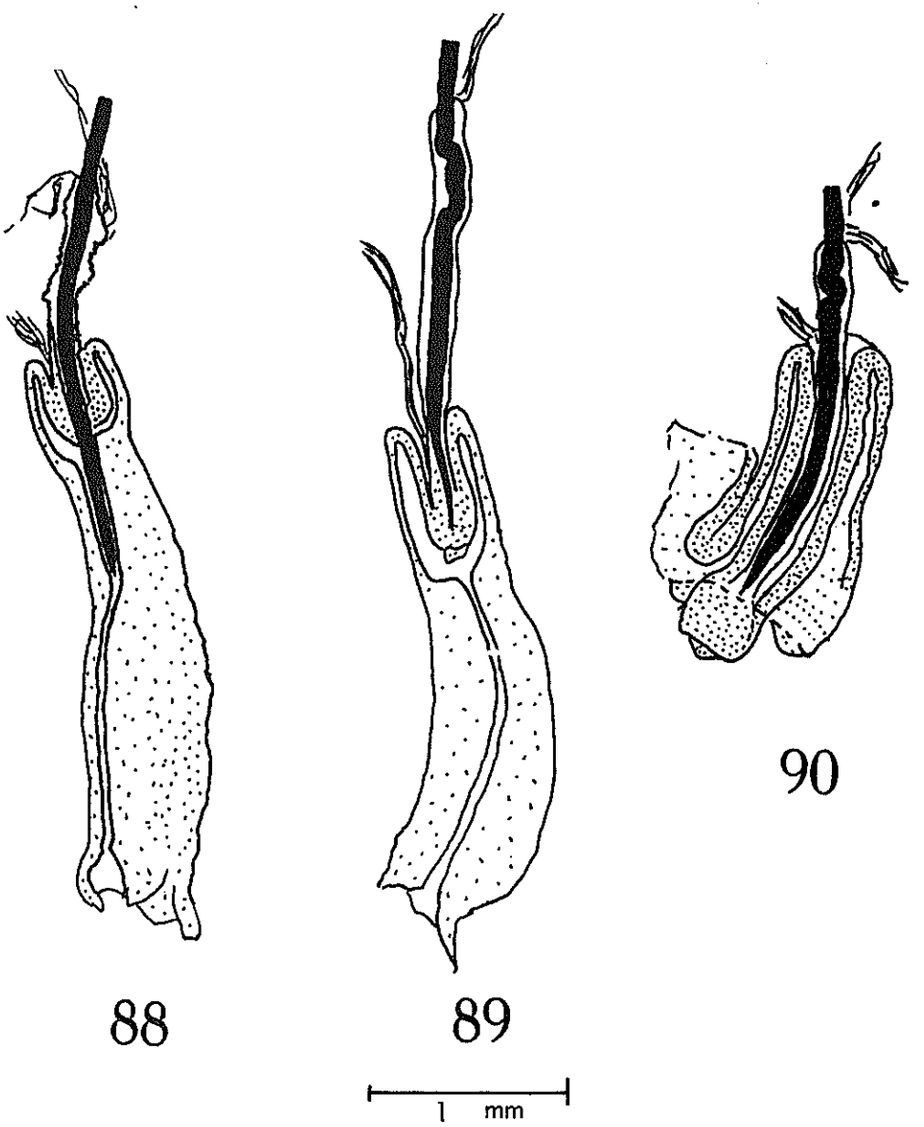


Fig. 82. Cross-section through penis and penis sheath.
Fig. 83. Diagrammatical presentation of portion of penial complex showing the velum and sarcobelum.
Fig. 84. Penial complex in which penis is shorter than penis sheath.
Fig. 85. Penial complex in which penis projects into the lumen of praeputium.
Fig. 86. Portion of penis showing wavy course of lumen while the penis sheath is smooth
Fig. 87. Portion of penis with more or less straight lumen and wrinkled penis sheath.



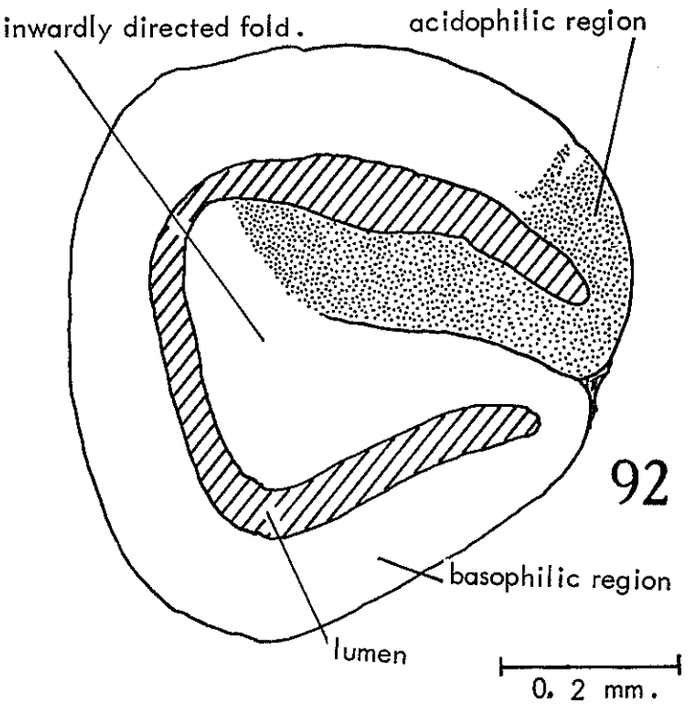


Fig. 88 - 90. Various degrees of contraction and relaxation of the praeputium.

Fig. 92. Cross-section through prostate bulb to illustrate the inwardly directed fold and the main distribution of the two cell types.

Apart from the above, Holm's (1946) description of this structure in L. stagnalis appressa is equally applicable to L. n. natalensis.

The penis sheath and penis.

The wall of the penis sheath consists of the same muscle layer as the praeputium although they are more poorly developed. The penis is highly muscular with a small lumen lined by ciliated cuboidal epithelium (fig. 82). The epithelium is successively bounded externally by a thick layer of circular muscle fibres and a layer of radial muscle fibres followed by layers similar to those of the penis sheath, but in reversed order. Holm (1946) designates these latter layers as the inner penis sheath. At the extreme tip of the penis, only the circular muscle layer persists, so that this end of the penis lies free in the cavity formed by the outer penis sheath.

The vas deferens.

The vas deferens is lined by ciliated cuboidal cells (fig. 81). The cilia are longer than the thickness of the cells and nearly obliterate the lumen. The wall of the vas deferens is further completed by a layer of dense connective tissue, below the epithelium and, outside this, a layer of circular muscle fibres in which are embedded numerous vesicular cells which may be as large as the epithelium cells.

The shape and position of the sarcobelum and velum, illustrated in fig. 83, seem to be identical to that figured by Hubendick (1951a, fig. 86).

Hubendick (1951a) draws attention to the fact that the different structures of the male reproductive system varies so much in shape and mutual relations within a single species of Lymnaea, that this system could not

be considered as being of taxonomic importance in the Lymnaeidae. My own observations lend support to this view. In some specimens of my series, for example, the penis is much shorter than its sheath (fig. 84), while in other specimens it extends beyond the velum well into the praeputium (fig. 85). These conditions, however, merely reflect different degrees of retraction and eversion respectively, at which the penis may be arrested at the time of fixation, for in the first case the lumen of the penis describes a wavy course and its sheath is completely smoothed out (fig. 86), whereas the second case presents exactly the opposite where the lumen of the penis is straight and the wall of the sheath is faintly wrinkled over its entire length (fig. 87). The praeputium is likewise subject to varying degrees of constraction and relaxation (figs. 88 - 90). In view of this no attempt was made to express, numerically, the ratios of penis/penis sheath and penis sheath/praeputium.

Prostate.

Externally two regions can be distinguished, viz., the upper flattened region and the lower bulbous region (fig. 46). In the latter region an inwardly directed fold partly occupies the lumen (fig. 92) which, in this region, is lined by two types of columnar cells (fig.91), viz., granular acidophils and granular basophils. Although these cell types are intermingled in places, they are largely concentrated in two definite regions as illustrated in fig. 92. The granules of the acidophilic cells are much larger than those of the basophilic cells and are more tightly packed. Large vacuoles occur between the granules in the basal part

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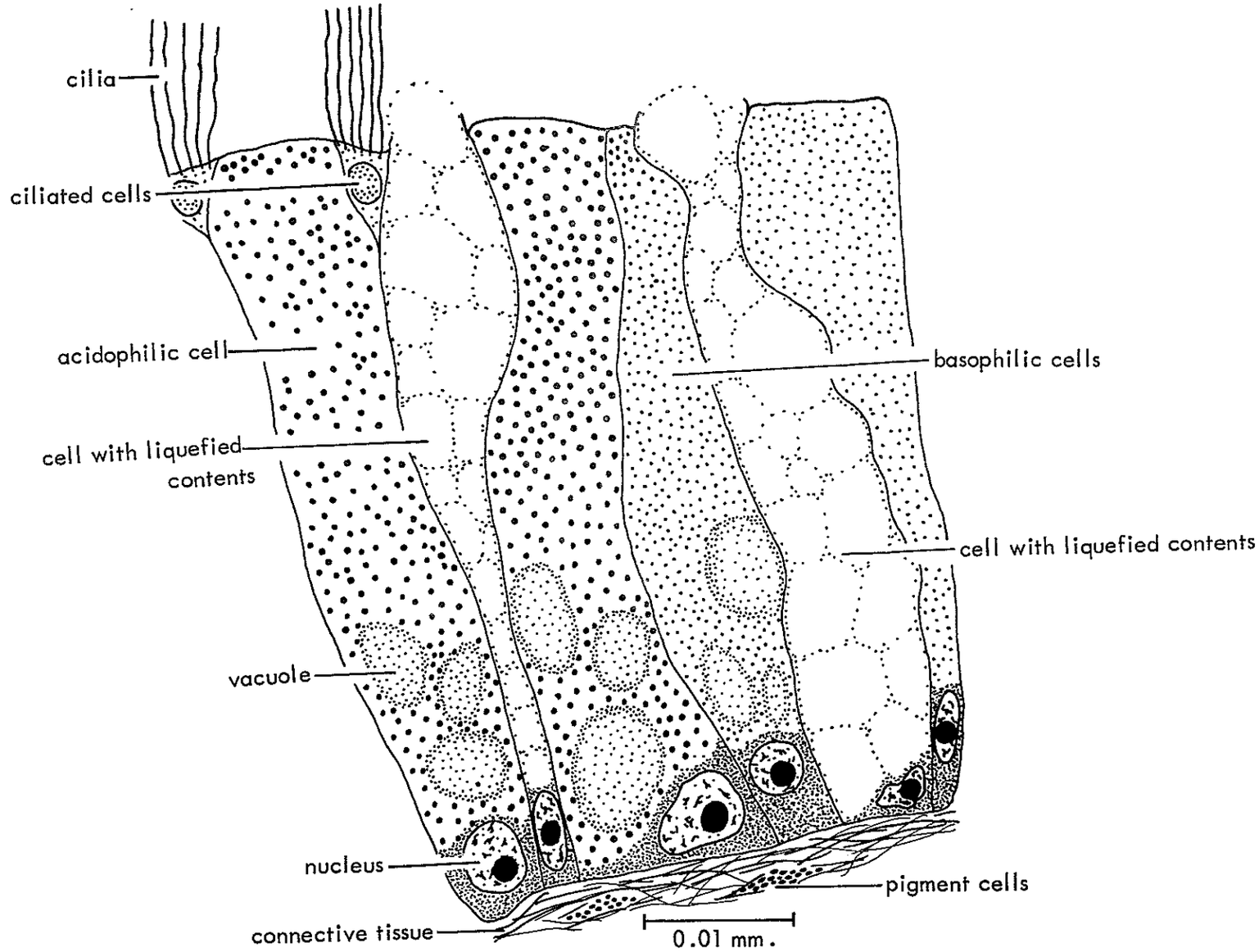

Fig. 91. Epithelium of prostate bulb.

of both cell types. Wedged between the distal ends of the columnar cells, are scattered wedge-shaped, ciliated cells with round nuclei which never reach the basement membrane so that the epithelium of this region of the prostate is of a pseudostratified type (fig. 91). This is in accordance with the findings of Holm (1946).

When actively secreting, the granules of the columnar cells coalesce and liquefy and the contents of the cells then appear to be neutral in staining affinity (fig. 91).

The wall of the upper flattened region of the prostate is not folded (fig. 73). Its epithelium seems to be similar to that of the bulbous region, though the acidophilic cells are greatly reduced in numbers. The mucous cells which Holm (1946) described for this part of the prostate in L. stagnalis appressa, could not be identified in L. n. natalensis. This region of the prostate communicates with the carrefour through a minute opening, which is most difficult to locate. Its position is illustrated in figs. 63 and 64.

6. SUMMARY.

1. In a study of freshwater snail systematics it seems essential to unravel the complex structure of a single snail population in order to determine the amount and nature of variation, before the actual species characteristics can be established. This study was undertaken to statisfy this aim for the subspecies L. n. natalensis.

2./.....

2. Special attention was paid to the shell, radula and reproductive system of three successive collections from the same habitat.
3. Existing verbal descriptions, although valid for some of the 155 shells examined, do not, adequately characterize the species.
4. By means of a biometrical analysis it was attempted to eliminate those features of a population which might create a misleading picture of the actual species characteristics.
5. A possible correlation is found between the size-frequency distributions of the three snail samples studied, and the value of flow of the river from which the samples were taken. From these correlations it is deduced that: survivors of different generations are present in each sample, floods are of considerable importance in the reproductive cycle of a population, and flood records can be used as an indication of the number of generations and the relative ages of snails in a population.
6. An analysis was made of linear, ratio and linear-ratio data pertaining to the shells of a selected group of snails of which the shell length varied between 10.3 - 11.8 mm.
7. In the successive samples a shifting of the equilibrium from the dominance of younger snails to the dominance of older snails is observed.

8/.....

8. It is concluded that older age groups are less subject to variation than younger ones, and that length dimensions are less subject to extreme variations than their corresponding breadth dimensions.

9. Among the linear dimensions; entire shell length, shell breadth, ultimate whorl length, ultimate whorl breadth, aperture length and aperture breadth, the two linear dimensions, aperture length and possibly ultimate whorl length, might be a relatively reliable feature in the delimitation of the subspecies.

10. Shells of different sizes differ significantly in their slenderness as expressed by the ratios ultimate whorl length/shell breadth and shell breadth/aperture breadth, but not frequently in respect of the ratios entire shell length/shell breadth, entire shell length/aperture length and aperture length/aperture breadth. The degree of slenderness is therefore unreliable as a species criterion.

11. The ratio entire length/aperture length was found to remain fairly constant in shells of approximately equal sizes and might constitute a convenient basis for the comparison of shells from different localities.

12. The shape of the aperture, as expressed by the ratio aperture length/aperture breadth, might be a valuable criterion of the identity of the species.

13/.....

13. It is inadvisable to attempt to deduce the characteristics of the subspecies from a single sample.
14. The radula teeth on opposite sides of the central vary independently of each other.
15. Several cone types are described for the lateral teeth.
16. The variability of any particular lateral on the radula can be more reliable determined by examining that tooth on both sides of the central.
17. Although, lateral radula teeth exhibit a certain amount of intracollection variability, it never approaches the level of statistical significance.
18. The shell constitutes a less variable morphological unit than the radula teeth in respect of the indices employed.
19. In the hermaphrodite gland the germinal epithelium is restricted to the bases of each acinus.
20. The transition between germinal and atrium epithelium is gradual.
21. The histology of the female- and male reproductive systems are described in detail.
22. As a result of the different degrees of contraction and relaxation of the penis, penis sheath and praeputium, no attempt was made to analyse the ratios of these organs statistically.

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