DISTRIBUTIONAL TRENDS OF FOUR SPECIES OF FRESHWATER SNAILS IN SOUTH AFRICA WITH SPECIAL REFERENCE TO THE INTERMEDIATE HOSTS OF BILHARZIA*

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INTRODUCTION

Urinary bilharziasis has been known to occur in South Africa since 1864 when it was first discovered by Harley in the vicinity of Humansdorp. Its first local snail intermediate host, now known as *Bulinus* (*Physopsis*) *africanus* (Krauss) was only discovered in 1916 by Becker. In 1957 Mandahl-Barth also recorded *Bulinus* (*Physopsis*) *globosus* (Morelet) from this country whereas Krauss had already described what is now called *Biomphalaria pfeifferi* from Natal in 1848. Up till now these three species are the only established intermediate hosts of *Bilharzia* known to be endemic in the Republic of South Africa.

In the course of surveys conducted since 1956 by the Zoology Department of the Potchefstroom University, the Department of State Health Services, the Medical Ecology Centre of the S.A.I.M.R., Johannesburg, and numerous other collaborators and supplemented in 1963–64 by Dr. D. S. Brown of the British Medical Research Council, a large amount of preserved freshwater snail material has been collected and lodged in the Zoology Department of the Potchefstroom University. Most prominent in these samples, because they are easily recognised as snails by untrained field staff, are the three species already mentioned together with *Lymnaea natalensis* Krauss and *Bulinus* (*Bulinus*) *tropicus* (Krauss). All these species, incidentally, are either of medical or veterinary importance. The present paper is an attempt to analyse some aspects of the distribution of these species which, in the subsequent discussion, will be referred to by their generic or subgeneric names. In the analysis no distinction is made between *B.* (*P.*) *africanus* and *B.* (*P.*) *globosus*.

The geographic distribution in south east Africa of the individual species listed here are dealt with by van Eeden, Brown and Oberholzer (1965). The locality records of that paper are also employed in the present paper, the approach of which is similar to that adopted by van Eeden (1965) which deals with the Transvaal only.

TOPOGRAPHY AND OTHER ASPECTS OF THE REGION

These features can here only be touched on by reference to Map 1.

The region discussed is bounded in the north by the Limpopo, Molopo and Orange rivers. Topographically it is divided into an interior plateau and a diversified tract of country

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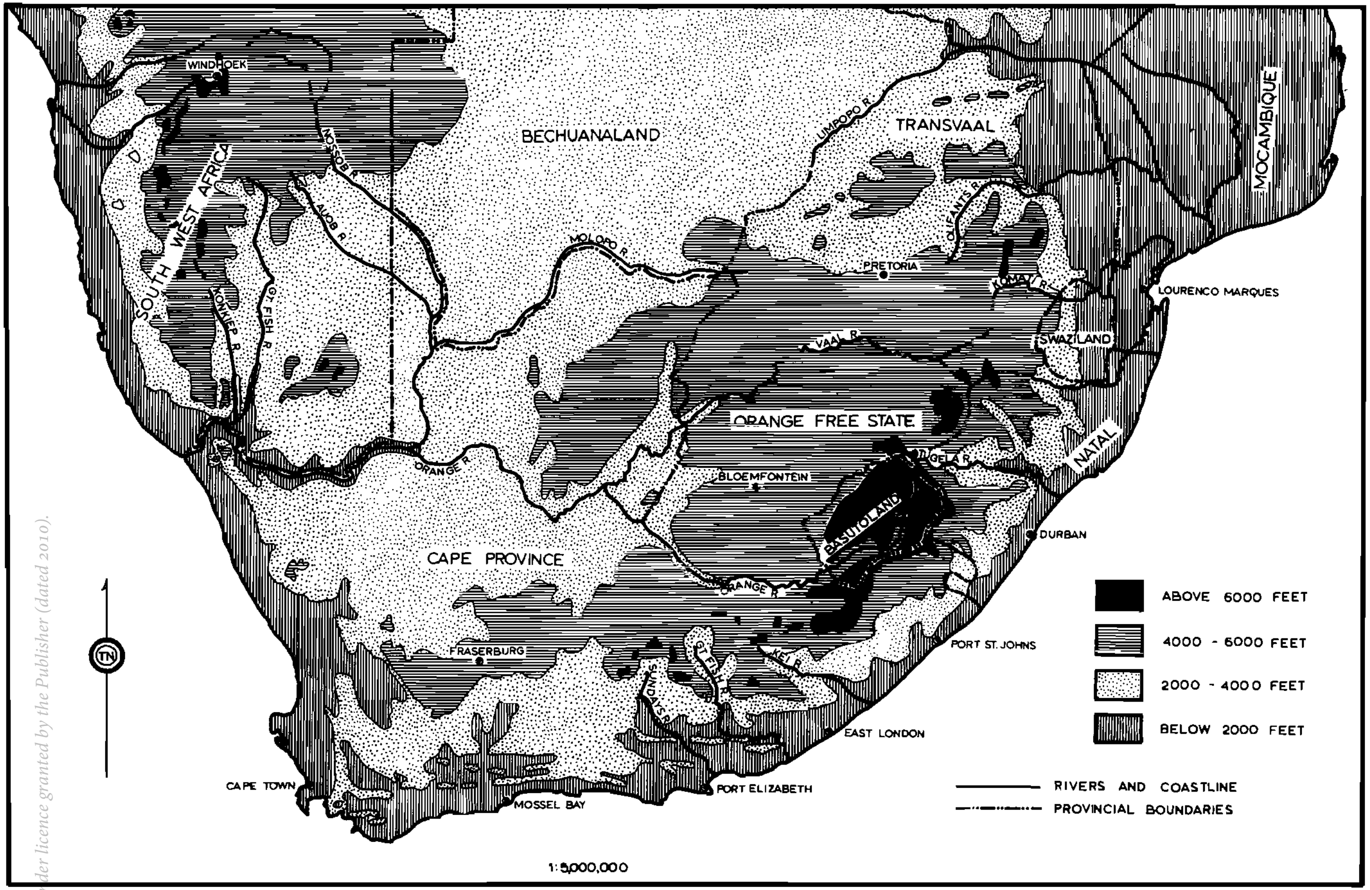


Map 1. Map of South Africa and neighbouring territories showing the most important altitudinal contours.

surrounding the plateau on the east, south and west. The two regions are separated by an escarpment known as the Drakensberg in the Transvaal and Natal and the Sneeuberg, Stormberg, Nieuweveld, Roggeveld, Bokkeveld and Kamies mountains in the Cape Province. About 40 per cent of the region lies within the 4,000 ft. contour and mainly on the interior plateau while the area below 1,500 ft. is merely a narrow fringe around the coast.

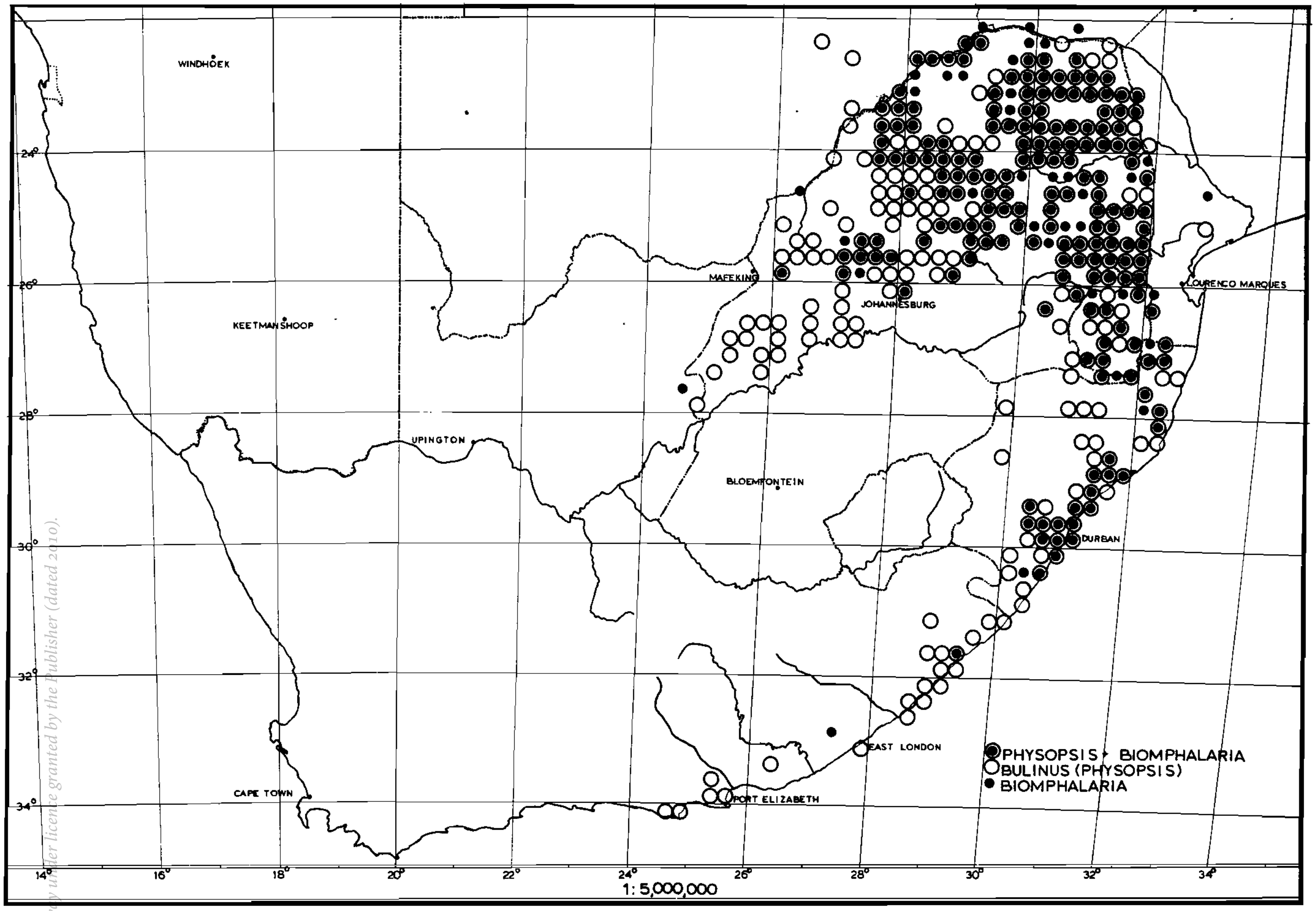
The climate is characterised by well marked summer and winter seasons. Maximum air temperatures of 30 to 35C are common in the summer whereas minimum temperatures below freezing point, coupled with widespread frost, are frequent at inland stations in winter. On the Highveld daily fluctuations in the air temperatures of approximately 19C in winter and 14C in summer are not uncommon.

The annual precipitation, confined to the summer over 83 per cent of the country, decreases from east to west. It is spasmodic and interspersed with long dry periods so that suitable naturally occurring snail habitats, which are greatly influenced by the considerable evaporation figure, are often rare and seasonal in large areas. The sub-tropical eastern coastal area enjoys the highest annual rainfall.

GENERAL DISTRIBUTION OF THE INTERMEDIATE HOST SNAILS

The overall picture outlined by Porter (1938) still holds good (Map 2). It is, however, obvious that *Biomphalaria* is more restricted in its distribution than *Physopsis* and, generally speaking, seems to occur largely at altitudes below 4,000 ft. although populations have also been found up to 5,000 ft. above sea-level (Fig. 3).

Although, in the Transvaal, both genera tend to thin out towards the west, this tendency is more marked for *Biomphalaria* for, whereas, in terms of the number of samples collected, the ratio *Physopsis/Biomphalaria* in the eastern Transvaal roughly is 1:1, this gradually changes in favour of *Physopsis* which, for practical purposes, is the only one represented west of the 27° E.Long. (Map 2). The more restricted distribution of *Biomphalaria*, which seldom occurs in the absence of *Physopsis*, must however be accounted for by factors other than altitude *per se* or the temperatures associated with it for the north-western Transvaal certainly cannot be regarded as Highveld (Map 1). Disregarding four apparently isolated populations the present western limit of *Biomphalaria* appears to coincide with the 27° E.Long. and that of *Physopsis* with the 25° E.Long. whereas the southern limit of the former is in line with the 31° S.Lat. and that of the latter with the 34° S.Lat. *Physopsis*, moreover, also occurs at higher altitudes than *Biomphalaria* (Fig. 3) and is the only one of the two genera which has thus far invaded the Vaal river catchment area where it has been collected from restricted areas (Map 2). The greater part of the Vaal river drains typical South African Highveld which lies mainly above 5,000 ft. above sea-level. This river, as also the Orange river, is of particular importance in South Africa in view of the existing and planned irrigation and water conservation schemes in their catchment areas.



Map 2. Geographic distribution of *Physopsis* and *Biomphalaria* relative to each other.

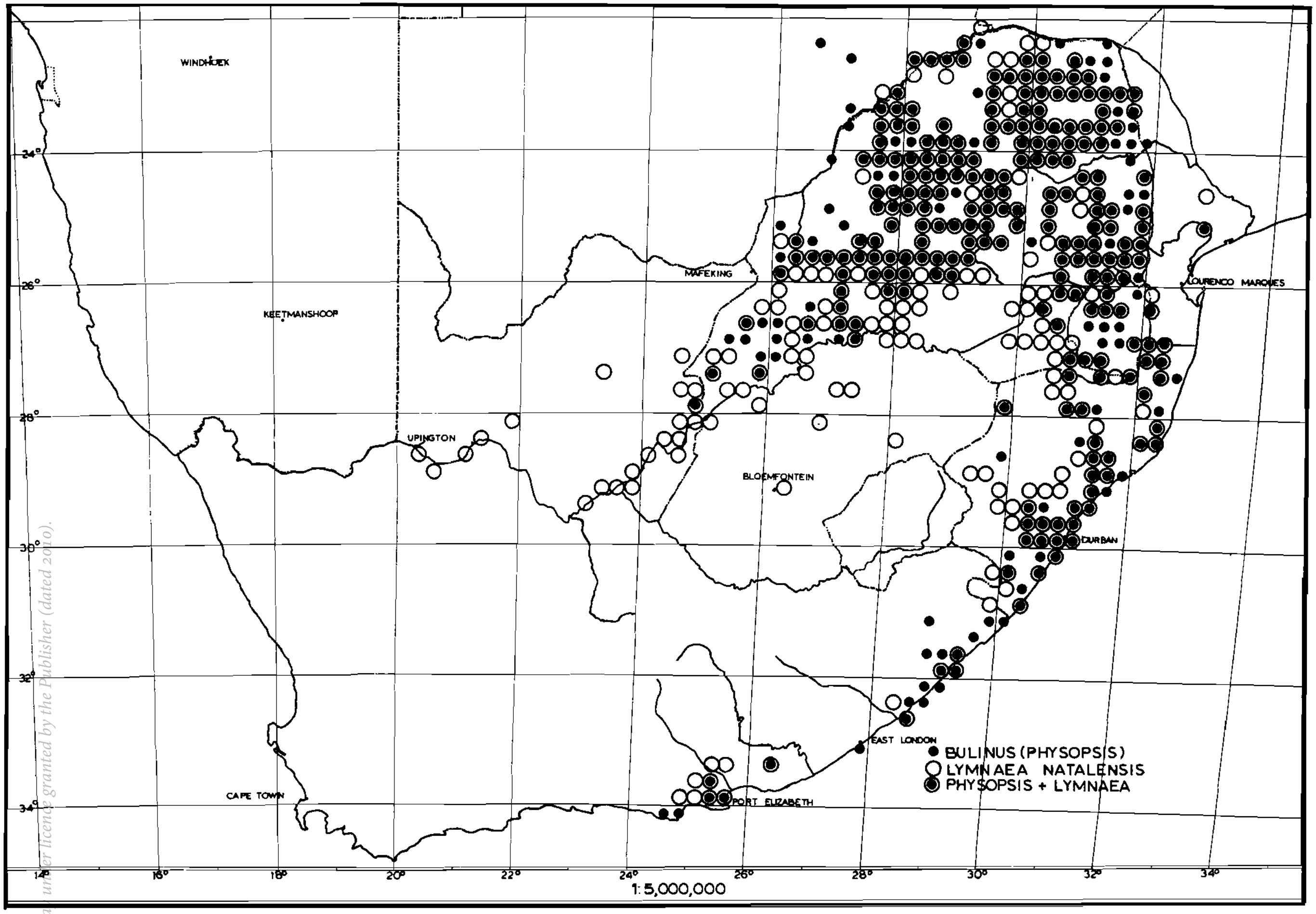
DISTRIBUTION OF THE VECTOR SPECIES RELATIVE TO THAT OF OTHER FRESHWATER SNAILS

In view of the high incidence of bilharziasis in different parts of the world, Africa and South Africa and the rôle of man in continually creating new and highly suitable snail habitats through his agricultural and other practices, the question as to whether the disease is in the process or capable of spreading to new areas of this country becomes increasingly important. We know that freshwater snails can and do spread to new areas and indeed a remarkable example of this is reported by van Eeden & Brown (in press) who have established that *Lymnaea columella* Say, unknown in South Africa until 1944, has already colonised vast areas of this country. The answer to the question posed above hinges on two issues viz. the ability of the area(s) in question to support the intermediate host snails and the ability of the parasite to complete its life cycle in the snail host under the climatic conditions prevailing in the potential new area(s).

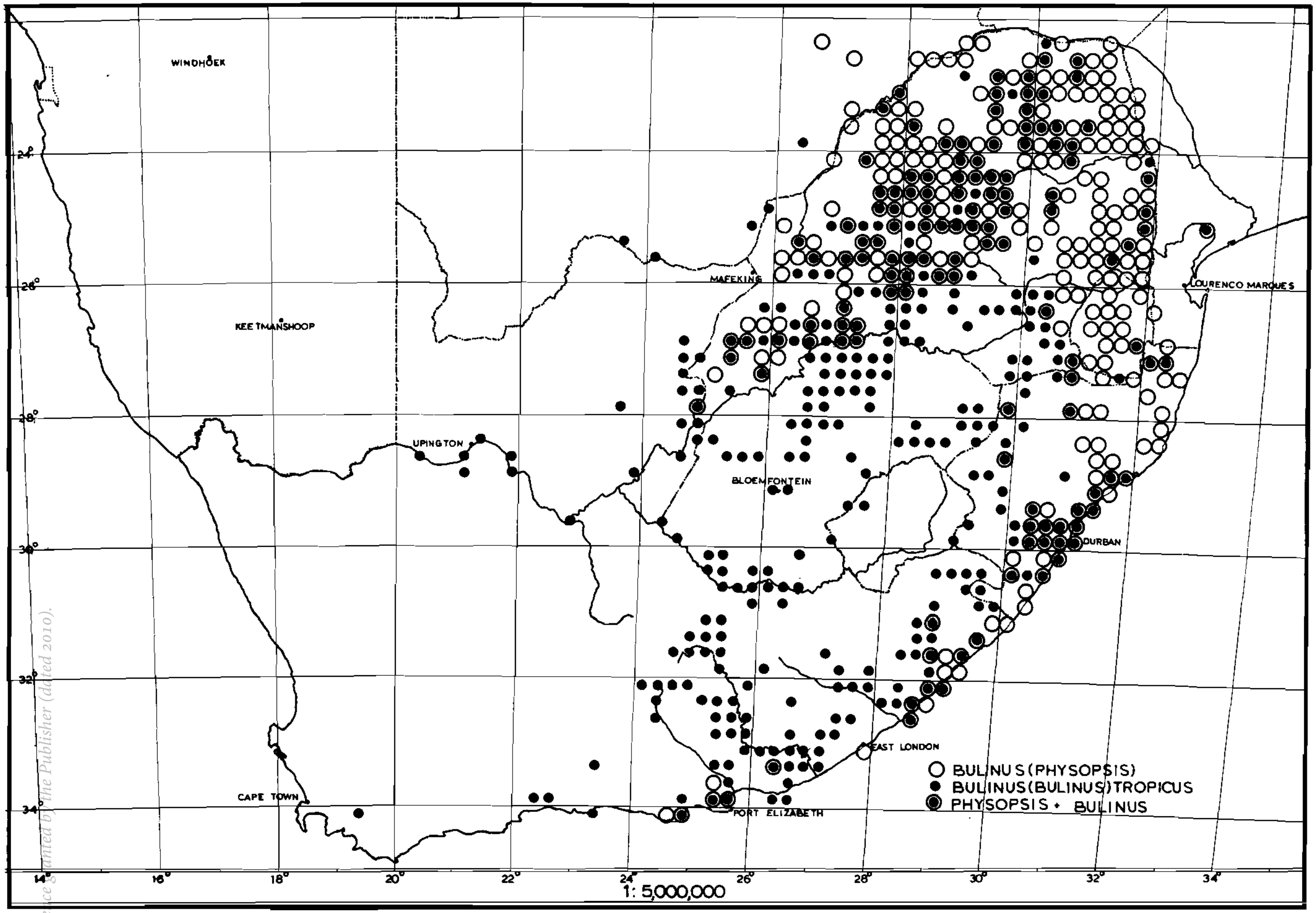
Up till now investigations of the habitat in South Africa, at the level at which this has thus far been attempted (Frank, 1965 and Schutte & Frank, 1964) have not produced any conclusive criterion whereby the suitability of any potential new area can be assessed. We therefore propose to deal only with the second aspect by approaching it from the point of view of the distributional patterns of other freshwater snails.

As mentioned earlier on the snails most constantly occurring in our samples, apart from the intermediate host species, are *L. natalensis* and bulinids belonging to the *tropicus* group. For the present purpose the latter are all considered as representing *B. tropicus*. The almost regular occurrence of *Physopsis* wherever *Biomphalaria* is found has already been referred to and is also reflected in Map 2 but a cursory examination of our samples also reveals that *Lymnaea* is very often found in the same areas as *Physopsis*. This contrasts strongly with *Bulinus* which is less commonly collected from these areas. These observations lead to a more systematic analysis of the association between *Physopsis*, *Lymnaea* and *Bulinus* in the Transvaal (van Eeden, 1965). This analysis has subsequently been extended to include the whole of the Republic of South Africa and Swaziland in so far as this area has been surveyed and it is obvious from Maps 3, 4 and 5 that this distributional trend also applies to the larger area. In fact, in many of the best known Bilharzia areas such as Nelspruit–White River, Tzaneen, Nylstroom–Warmbad, Zululand (Northern Natal) and Swaziland *Lymnaea* is very common whereas *Bulinus* is either only sparsely represented or almost absent. To these may be added the Kruger National Park which, but for the absence of man, would have been Bilharzia country. By contrast the Orange Free State and the interior of the Cape Province where bilharziasis is either not yet known to occur or where positive reports regarding its occurrence are subject to doubt, *Lymnaea* is either absent or very patchily distributed and *Bulinus* predominates.

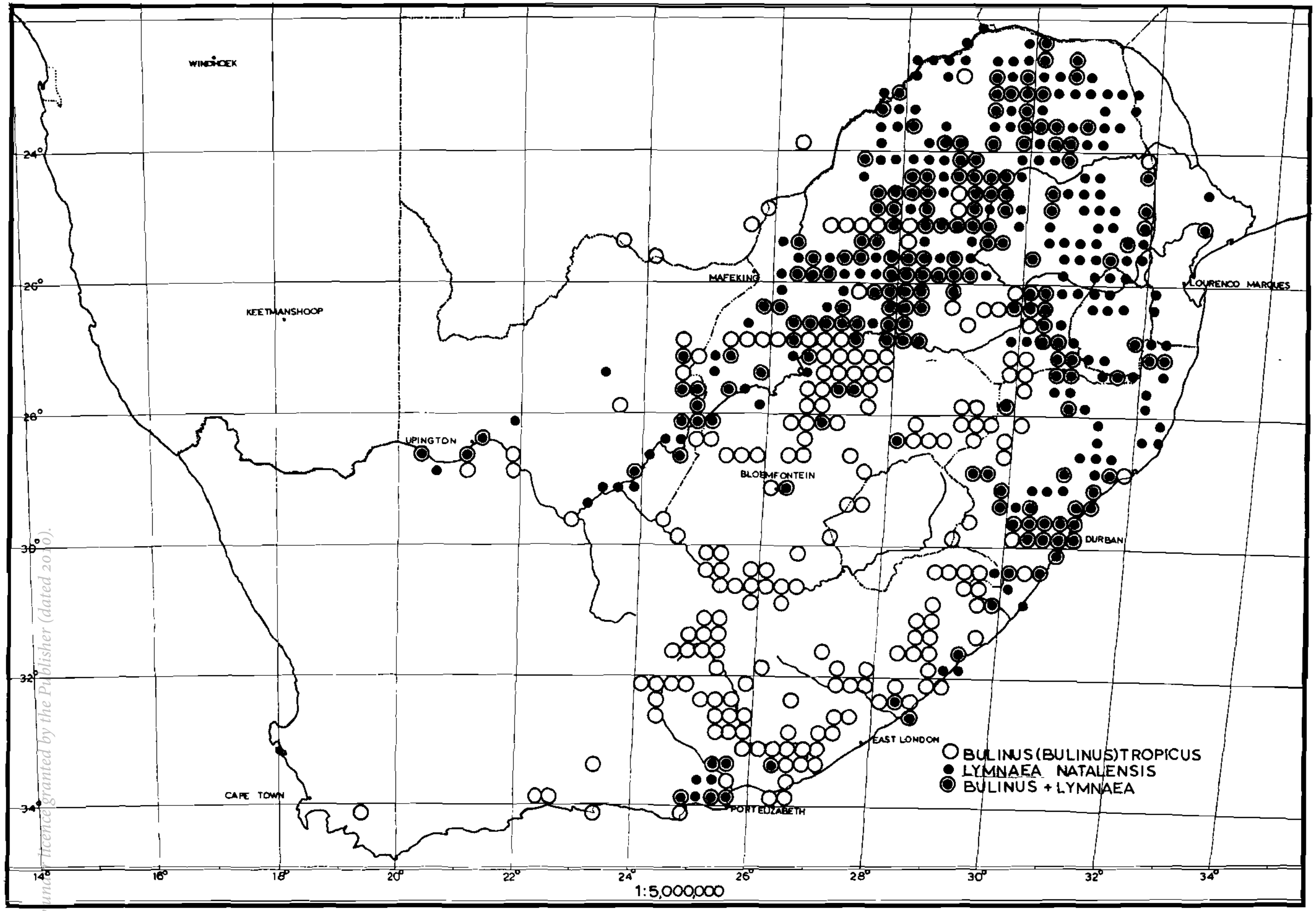
To facilitate mapping the snail distribution, a $\frac{1}{4}°$ square map is used in which every square degree is subdivided into $\frac{1}{16}$ square degrees. In our collection catalogues every snail sample is assigned to the particular $\frac{1}{16}$ square degree from which it was collected by making use of a code number referred to as a locus. In order to be able to analyse the degree and nature of the



Map 3. Geographic distribution of *Physopsis* and *Lymnaea* relative to each other.



Map 4. Geographic distribution of *Physopsis* and *Bulinus* relative to each other.



Map 5. Geographic distribution of *Lymnaea* and *Bulinus* relative to each other.

association between the three genera in question statistically, only the number of samples containing one or more of these genera were counted in all those loci where at least one sample of one genus was collected. This amounted to 3,671 samples collected from 506 loci. These data were then subjected to the following series of analyses in which *Lymnaea* is represented by *L*, *Physopsis* by *P* and *Bulinus* by *B*.

1. The percentage of the total number of loci ($P2$, $L2$ and $B2$) and sampling places (P1, L1 and B1) within each locus from which at least one specimen of any one of the three genera was collected. The values obtained from the 3,671 localities were $P1 = 35\cdot 7$ per cent, $L1 = 39\cdot 4$ per cent and $B1 = 24\cdot 9$ per cent. Of the 506 loci $P2$ was present in $54\cdot 2$ per cent, $L2$ in $60\cdot 1$ per cent and $B2$ in $60\cdot 3$ per cent. Thus *Bulinus* was collected from the smallest number of localities (24·9 per cent) spread over the largest area (60·3 per cent). In terms of the number of samples *Bulinus* therefore revealed the lowest average density ($B = 1\cdot 81$ samples) per locus. If the two values obtained above for each genus be expressed as a ratio, e.g. $P2$ over $P1$, then $P = 1\cdot 5$, $L = 1\cdot 5$ and $B = 2\cdot 4$. The greater similarity between *Physopsis* and *Lymnaea* as regards this ratio is matched by the closeness of their respective average densities expressed as samples per locus viz. $P = 2\cdot 59$ and $L = 2\cdot 86$. If the average density per locus be calculated only for those loci from which each particular genus was recovered then $P = 4\cdot 78$, $L = 4\cdot 76$ and $B = 3\cdot 00$.

2. Figure 1 represents an analysis of the total number of loci in which each of the three genera were either found alone or shared the locus with one or both the other genera. In this diagram 100 per cent is considered as being equivalent to 360° and the percentages are represented as so many degrees out of 360°. Thus P/B/L is the total of P, B and L and covers approximately 170° out of 360°. The rest of the diagram must be interpreted similarly. Again P and L gave similar results as each occurred alone at almost the same number of loci while B was found alone at far more. The number of loci containing either two or all three genera is 54·9 per cent of the total, and in this group $P + L$ is $\pm$ 2x $B + L$ and $B + L$ is $\pm$ 2x $P + B$. Only 19·7 per cent of the total number of loci produced all three genera.

3. If the number of loci containing any two of the genera, whether the third is present or not, be expressed as a percentage of the total number of loci in which these combinations occur then $P + L = 42\cdot 2$ per cent, $B + L = 32\cdot 2$ per cent and $P + B = 25\cdot 6$ per cent. Thus the series $P + L > B + L > P + B$ obtained in the previous analysis still applies.

4. If all those loci in which *Physopsis* was present is analysed for the percentage occurrence of *Physopsis* alone or in combination with either or both the two other genera then $P + L = 37\cdot 2$ per cent; $P + B + L = 36\cdot 1$ per cent; $P = 18\cdot 3$ per cent and $P + B = 8\cdot 4$ per cent. Thus

$$P + L > P + B + L > P > P + B \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (a)$$

The corresponding values for those loci containing *Lymnaea* and those containing *Bulinus* are as follows:

Lymnaea: $L + P = 33\cdot 5$ per cent; $L + P + B = 32\cdot 6$ per cent; $L + B = 17\cdot 8$ per cent and $L = 16\cdot 1$ per cent

or $L + P > L + B + P > L + B > L \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (b)$

Bulinus: $B = 42\cdot 3$ per cent; $B + L + P = 32\cdot 5$ per cent; $B + L = 17\cdot 7$ per cent and

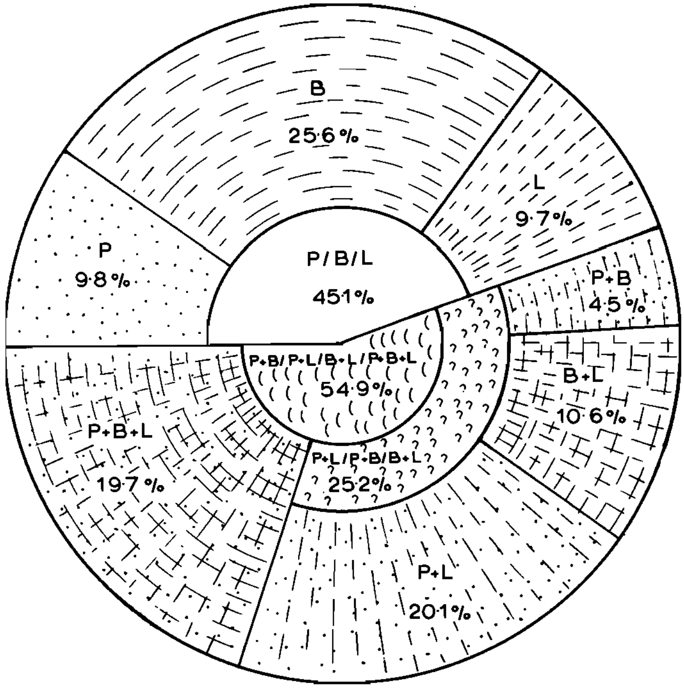


Fig. 1. Diagrammatic representation of the percentages of the total number of loci in South Africa from which *Physopsis*, *Lymnaea* and *Bulinus* were either collected alone or shared the locus with either or both of the other two.

$B + P = 7 \cdot 5$ per cent

or $B > B + P + L > B + L > B + P$ .... (*c*)

We thus obtain three series of information (*a*), (*b*) and (*c*) from which, in the present context, the following merits special emphasis: Wherever *Physopsis* and *Lymnaea* were found they more often occurred in the same locus than either of them occurred alone or in any other combination. This strongly contrasts with *Bulinus* which more often occurred alone than in combination with either or both of the other two genera.

5. Correlation coefficients, interpreted as association coefficients, for the three possible combinations in one locus between any two of the three genera yield the following values in which r is the association coefficient and p, b and l refers to the genera under discussion. Thus the association coefficient between *Physopsis* and *Lymnaea* is given by rpl.

rpl $= +0 \cdot 9$; rbl $= +0 \cdot 5$; rpb $= +0 \cdot 2$.

These values indicate that, apart from occurring in the same locus in 9 out of 10 cases the number of positive localities for *Physopsis* and *Lymnaea* per locus varies similarly in 9 out of 10 cases. It may also be interpreted that conditions are such that if *Lymnaea* was present alone then *Physopsis* would be able to exist in the same locus in 9 out of 10 cases should it be introduced. By contrast *Physopsis* and *Bulinus*, in 8 out of 10 cases, do not vary in a like manner. It may be significant that the association coefficients calculated for square degrees are of the same order as those calculated for the $\frac{1}{16}$ square degrees. This might be interpreted as

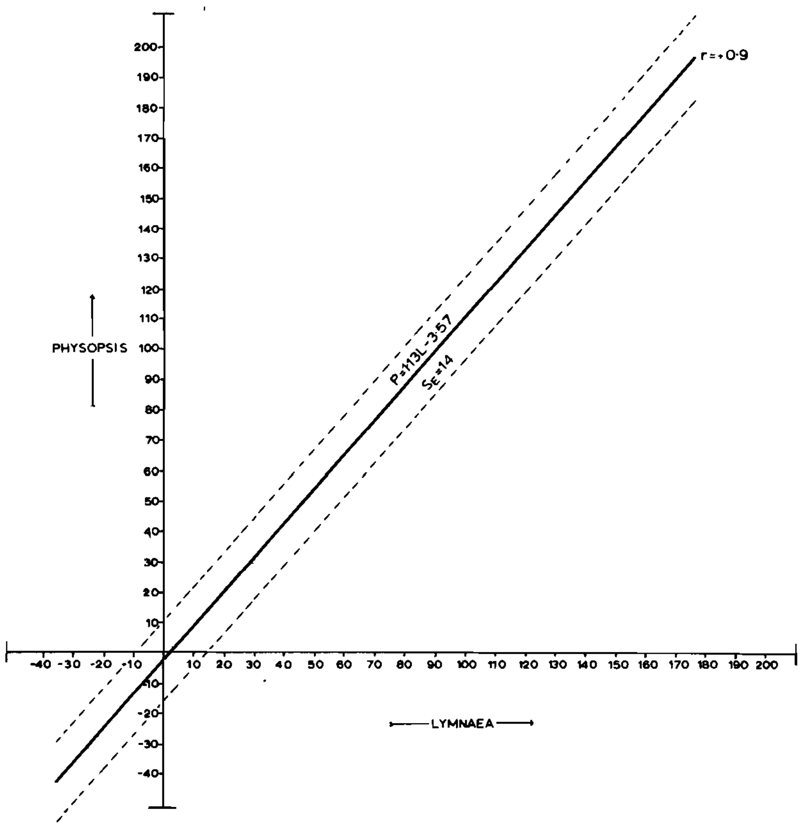


Fig. 2. Regression line calculated for the degree of association between *Physopsis* and *Lymnaea* in the same locus or square degree.

indicating that the factors conditioning the association in a locus operate in a similar manner in the square degree or larger area.

The foregoing data may be taken to suggest that in 9 out of 10 loci where both *Physopsis* and *Lymnaea* are found, that locus may show optimal ecological conditions for both. This is hardly ever true for *Physopsis* and *Bulinus*. In fact, where association coefficients were calculated for certain restricted areas such as, for instance, the Kruger National Park, negative values were actually obtained for *Physopsis* and *Bulinus* (van Eeden, 1965).

6. In order to be able to estimate the probability of the occurrence of one genus in a particular area, given the presence of the other, regression formulae were calculated and graphs drawn for the three possible combinations of the three genera. From these and from the association coefficients calculated, it was obvious, however, that whereas *Lymnaea* may be regarded as a useful indicator snail for predicting the probable presence or absence of *Physopsis* in a given area, or the suitability of that area for colonisation by *Physopsis*, those

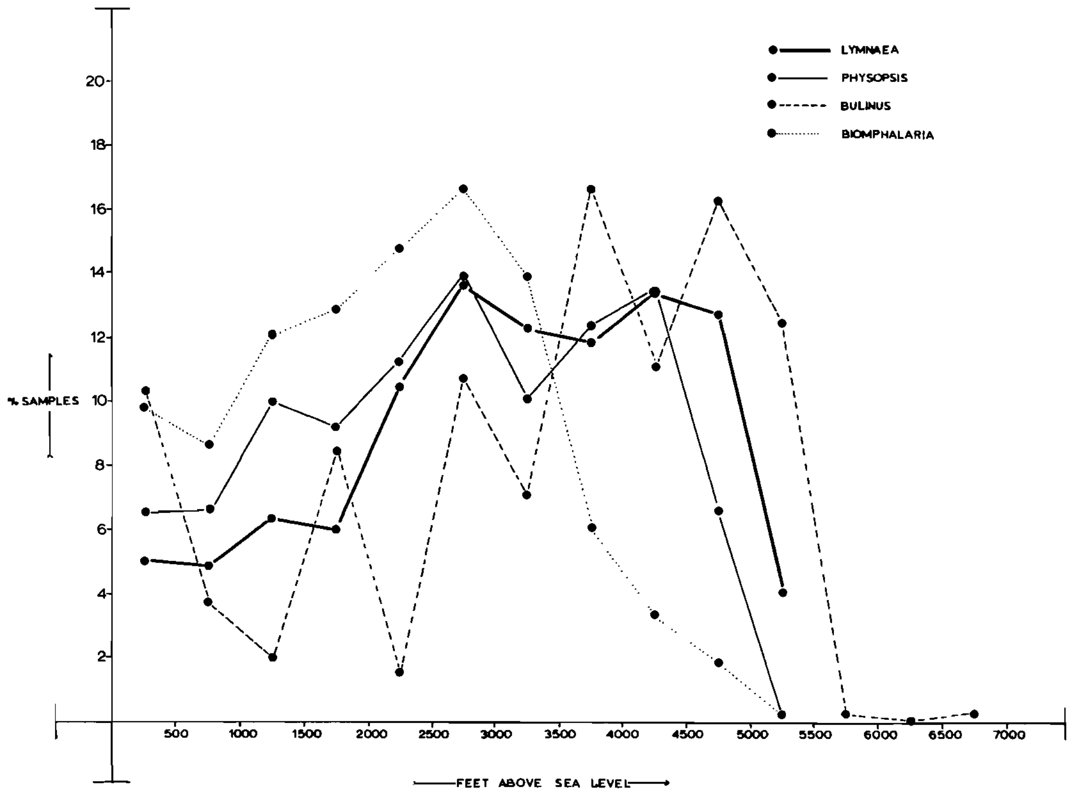


Fig. 3. Graphic representation of the altitudinal distribution of *Biomphalaria, Physopsis, Lymnaea* and *Bulinus* in South Africa.

associations involving *Bulinus* as a partner are too unreliable for this purpose. Consequently only the regression line for the *Lymnaea–Physopsis* association is given here (Fig. 2). From this figure we may estimate that where *Lymnaea* had been found in 100 localities from one locus or square degree the chances are 9 to 1 that *Physopsis* will be recovered from or will be able to exist in between 95 and 123 localities in the same locus or square degree should it be introduced into that area. Where, however, the value for *Lymnaea* drops to below 16, the possibility exists that *Physopsis* may either be absent or unable to live there.

DISCUSSION

The above analysis is, unfortunately, subject to certain limitations. The snail samples employed were collected over a period of 8 to 9 years, and therefore during different seasons

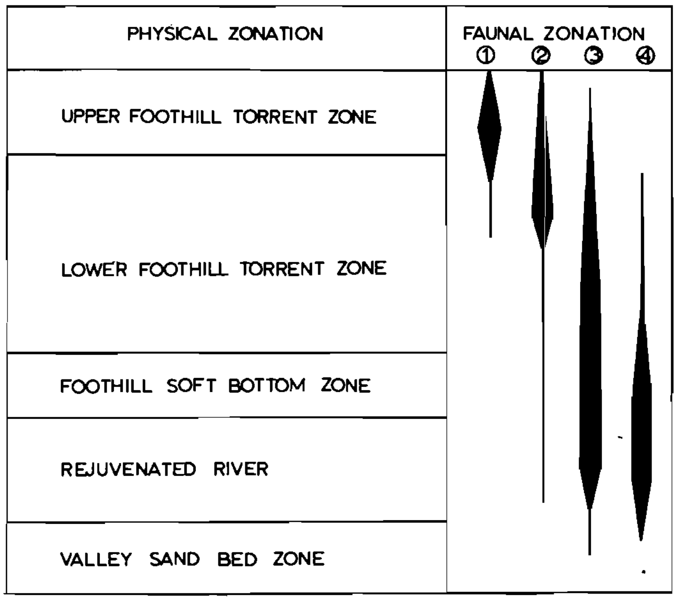


Fig. 4. Distribution of *Physopsis*, *Lymnaea* and *Bulinus* in the biological zones of the Umgeni river, Natal (After Schoonbee).

and under different climatic conditions. We have no information as to which loci were unsuccessfully tested for the presence of snails. The surveys were not done equally intensively in all the areas and it is not known whether those areas which yielded no samples contained few or no suitable snail habitats or whether they were merely surveyed less intensively. Finally the snail density per habitat and the relative numbers of the different species in the habitat could not be taken into consideration. The analysis, therefore, only reflects tendencies in geographic distribution and association and does not pretend to be valid for the habitat as well. However, as pointed out by van Eeden (1965) an analysis of 235 *Physopsis* habitats in the Transvaal proved this genus to have been associated with *Lymnaea* in the same habitat in 66·8 per cent of the habitats analysed and with *Bulinus* in only 10·2 per cent of the habitats. In 19·2 per cent of the habitats it occurred in the absence of *Lymnaea*. In another systematically surveyed area (van Eeden *et al*, 1964) *Physopsis* shared the habitat with *Lymnaea* in 49 out of 53 cases but in no single instance with *Bulinus* alone. In only 3 habitats did it occur alone.

The closer similarity between *Physopsis* and *Lymnaea* than between either of these and *Bulinus*, both in respect of their actual distribution (Maps 3, 4 and 5) and the distributional trends revealed by the statistical analyses is supported by the altitudinal distribution of the samples in our collection as depicted in Fig. 3. Although there is much in this figure that cannot yet be explained it is obvious that the graphs for *Physopsis* and *Lymnaea* show the same fluctuation pattern and, on the whole, diverge widely from that for *Bulinus*. It is only at 3,000 ft. that the three graphs form simultaneous peaks. Whereas the percentage occurrence of *Physopsis* and *Lymnaea* already starts dropping at 3,000 ft. as, incidentally, also happens with *Biomphalaria*, *Bulinus* reaches its peak at 4,000–5,000 ft. It is, furthermore, interesting to note that the four species included in this figure seem to show a definite series as regards their tolerance of conditions associated with altitude, *Biomphalaria* being the first to become less abundant with increasing altitude, followed successively by *Physopsis*, *Lymnaea* and *Bulinus*. Exactly the same sequence is observed in their geographic distribution, *Biomphalaria* having the most restricted and *Bulinus* the most wide-spread distribution.

In the course of a hydrobiological investigation of the Umgeni river, Natal, Schoonbee (in preparation) came to the conclusion that the river can be divided into biological zones characterised by the greater abundance and poor representation or absence of certain faunal elements in each case. It may be more than a mere coincidence that *Physopsis*, *Lymnaea* and *Bulinus* are associated with zones 2, 3 and 4 respectively (Fig. 4), *Lymnaea* thus occupying the zone intermediate between the other two.

During a series of river pollution studies in the same river catchment area the same author (1963) found that *Physopsis*, *Lymnaea* and *Bulinus*, bear a certain relation to each other in respect of their tolerance of organic pollution. Thus where this type of pollution sets in *Physopsis* is the first to disappear from that portion of the river followed by *Lymnaea* and then by *Bulinus*. As the river recovers from pollution the three genera repopulate it in the reverse sequence. Schoonbee's results therefore appear to indicate that *Lymnaea* is intermediate between *Physopsis* and *Bulinus* in regard to certain ecological requirements. This would be in line with our own findings concerning their geographic and altitudinal distribution.

The results of the analysis of the snail distributional trends in the Transvaal lead van Eeden (1965) to conclude that they might reflect a similarity between *L. natalensis* and the intermediate host snails, more particularly *B.* (*P.*) *africanus*, as regards the conditions required for their successful existence in which they appear to differ significantly from *B.* (*B.*) *tropicus*. The present analysis which is based on a larger amount of material from a more extensive and more diversified area supports this conclusion. On this and the other evidence cited we feel justified in upholding the view (van Eeden, 1965) that, in South Africa, *L. natalensis* may be regarded as an indicator species of the suitability or otherwise of a particular area for colonisation by the South African *Physopsis* species. Thus, where *L. natalensis* is relatively abundant and *B.* (*B.*) *tropicus* is rare or absent that area may, at the time of the survey, be regarded as potentially suitable for *Physopsis*. In fact, according to Fig. 2 the chances that the latter subgenus will also be found there are extremely good. Where *L. natalensis*, however, is absent or rare the probability of finding *Physopsis* approaches zero (cf. the Orange Free State). In such areas *B.* (*B.*) *tropicus* usually predominates. It may of course be that the *Lymnaea* populations made use of in this reasoning actually represent more than one species or different geographic races. Although this might affect the different numerical values calculated, it seems unlikely that it will completely nullify the synthesis.

ACKNOWLEDGEMENTS

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