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Dedicated to Mrs. W.S.S. van Benthem Jutting

The distribution of introduced mollusc species in Southern Africa

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"Your worth is very dear in my regard.
I take it, your own business calls on you,
And you embrace the occasion to depart."
Shakespeare — The Merchant
of Venice, Act I, Sc. I

Artificial distribution patterns of animals and plants may be defined as those caused or fostered deliberately or accidentally by man. Consequently we can distinguish two types of artificial distribution, viz., that of animals accidentally distributed by man (rats, mice, insects, slugs, etc.) and that of animals deliberately transported by man (domestic and pet animals; species involved in transmission of game animals and biological control of insects and plants, etc.). A considerable proportion of accidentally transported animals is made up of non-marine molluscs and it appears that there are few countries on the seaboard that have not yet experienced the immigration of some foreign pulmonate. Accidental transport, invasion and establishment can only be successful in species which have a wide ecological tolerance; not only must they be able to survive the voyage, but in their new country they usually have to adapt themselves to a different climate, soil and vegetation, while at the same time having to compete with the indigenous fauna for available ecological niches. All immigrant animal species are subject to these factors, which have been proven to be of prime importance in South Africa by the (abundant) survival and proliferation of adaptable bird species such as *Passer domesticus, Sturnus vulgaris* and *Acridotheres tristis*, as opposed to the disappearance of less adaptable species such as *Turdus ericetorum* and *T. merula.*

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Among all countries in Southern Africa (the subcontinent south of the Zambezi and Cunene Rivers), South Africa proper has had more than its share of these migrations. Various authors have dealt with immigrant molluscs (e.g., BARNARD, 1948; BIGALKE, 1937; CONNOLLY, 1916, 1939; DÜRR, 1946; FORCART, 1963; JOUBERT & WALTERS, 1951; WALDÉN, 1961) but more information has been obtained recently. At the present the list stands at 24 species belonging to eleven families of the subclass Gastropoda Pulmonata (dates of introduction or first discovery added between brackets):

1. *Lymnaea columella* Say, 1817 (1944),
2. *Physastra dispar* (Sowerby, 1873) (so far in aquarium tanks only, 1944),
3. *Vallonia pulchella* (Müller, 1774) (1846),
4. *Arion hortensis* Férussac, 1819 (before 1939),
5. *Arion intermedius* Normand, 1852 (1898),
6. *Vitrea cristallina* (Müller, 1774) (1890),
7. *Oxychilus alliarius* (Miller, 1822) (± 1894),
8. *Oxychilus cellarius* (Müller, 1774) (1846),
9. *Oxychilus draparnaudi* (Beck, 1837) (± 1908),
10. *Zonitoides arboreus* (Say, 1816) (before 1912),
11. *Milax gagates* (Draparnaud, 1801)[1]) (1873, or even before 1848),
12. *Limax flavus* Linnaeus, 1758 (before 1900),
13. *Limax maximus* Linnaeus, 1758 (1900),
14. *Limax nyctelius* Bourguignat, 1861 (before 1939),
15. *Limax valentianus* Férussac, 1823 (1961),
16. *Deroceras caruanae* (Pollonera, 1891) (1963),
17. *Deroceras laevis* (Müller, 1774) (before 1898),
18. *Deroceras reticulatus* (Müller, 1774) (before 1898),
19. *Subulina octona* (Bruguière, 1792) (1905),
20. *Testacella maugei* (Férussac, 1819) (before 1893),
21. *Bradybaena similaris* (Férussac, 1821) (± 1860),
22. *Cochlicella ventricosa* (Draparnaud, 1801) (1909),
23. *Theba pisana* (Müller, 1774) (1881),
24. *Helix aspersa* Müller, 1774 (± 1854).

Deroceras caruanae is new to the South African list (George, Cape Province, det. Dr. C. O. van Regteren Altena; Natal Museum). As can be seen from the list, ten species of slugs (naked pulmonates not including *Testacella*) make up almost 42% of the total; only two species are freshwater dwellers, viz., *Lymnaea columella* and *Physastra dispar*. Few published data are available on imported freshwater pulmonates, but it seems most likely that at least *Lymnaea columella* is more widely distributed than our records show. There is in the Natal Museum a sample of an as yet unidentified species of *Physa* from Pretoria (probably originally a species from North America),

[1]) QUICK (1960: 155) records that the identity of South African specimens has not been established beyond doubt.

which clearly indicates that the list of 24 imported species is as yet far from complete.

The following species have for various reasons not been included in the list: *Pupisoma japonicum* Pilsbry (status and affinities not yet sufficiently clear, at least in the author's opinion), *Cecilioides acicula* (Müller) (do.) and *Achatina fulica* Bowdich. The latter has failed to establish itself (see CONNOLLY, 1916 : 188, and 1939 : 325—326; the unique specimen is in the Natal Museum, Moll. No. 1612). BRAGA (1952: 121, pl. 1 4) records *Achatina fulica* from Lourenço Marques, Mozambique. However, both figure and measurements show clearly that his specimens belong to *A. immaculata* (Lam.); in empty shells out in the open the columellar region looses its pink colour quite soon, which accounts for it being confused with *A. fulica.* The latter is always much more slender than *A. immaculata,* so that usually it is not difficult to separate both these species.

QUICK (1952 : 183) incorrectly mentions *Vertigo antivertigo* (Drap.) as living in Bechuanaland; it is only known in subfossil condition from "a surface deposit of uncertain age" (CONNOLLY, 1939 : 403).

It appears from the list that the imported species originate from the following areas: Europe and Mediterranean region (19 species, viz., nos. 3—9, 11—18, 20, 22—24), North America (2 species, nos. 1 and 10), Australia (no. 2 only) and two species from uncertain tropical sources (nos. 19, from America?, and 21, from Asia?). The 19 species from Europe are partly from western and central Europe and partly from the Mediterranean region. It seems that species from the latter region are particularly well adapted to South African conditions; *Theba pisana* has thrived beyond expectation and has become the commonest local snail in many places (e.g., Port Elizabeth). The following list of localities of immigrant snails has been compiled from the literature (BARNARD, 1948; CONNOLLY, 1939; DÜRR, 1946; FORCART, 1963; JOUBERT & WALTERS, 1951; WALDÉN, 1961), from data kindly supplied by Dr. K. H. Barnard, from material in the Natal Museum and from notes of the present author. The species involved are cited by their numbers between brackets, while the geographic names are preceded by the figures for the total number of recorded foreign species. All localities in and around Cape Town and the Cape Peninsula have been taken as one; the same has been done for some localities under Cape Flats.

All localities on table I have been set out on the first map (fig. 1); the length of the symbols used indicates the number of introduced species in the various localities. A thorough examination of this map reveals a number of interesting facts, which are discussed below.

First of all, the general pattern strikes one as a typical example of artificial distribution which can be traced back to transport by sea. Few localities are further from the sea coast than a hundred miles in a straight line, viz., Bulawayo, Victoria Falls, Windhoek District, Pretoria, Johannesburg, Bloemfontein, Smithfield, Royal Natal National Park, Cathedral Peak area, Sani Pass, Dundee, Weenen, Kimberley, Cradock, or only 14 = 20% out of a total of 69 recorded localities.

TABLE I

Southern Rhodesia

1 Bulawayo (8)
1 Victoria Falls (19)

South West Africa

1 Windhoek District (17)

Transvaal

1 Skukuza, Kruger Nat. Pk. (17)
5 Pretoria (3, 10, 12, 24, unid. spec.)
1 Johannesburg (24)

Mozambique
(Portuguese East Africa)

1 Lourenço Marques (23)

Orange Free State

1 Bloemfontein (14)
1 Smithfield (12)

Natal

1 Royal Natal Nat. Pk. (17)
1 Cathedral Peak area (17)
1 Sani Pass (hotel) (10)
1 Underberg (17)
1 Dundee (10)
1 Weenen (10)
1 Estcourt (21)
2 Balgowan (1, 24)
1 Boston (17)
1 Howick (17)
1 Hilton (10)
11 Pietermaritzburg (3, 5, 10, 12, 13, 14, 15, 17, 18, 21, 24)
1 Thornville (17)
1 Albert Falls (17)
1 Gillitts (24)
1 Shongweni Dam (1)
4 Durban (17, 21, 23, 24)
1 Verulam (10)
1 Umhlali (12)
1 Scottburgh (17)
1 Natal South coast (22)

Cape Province

4 Kimberley (8, 9, 10, 24)
1 Kokstad (17)
1 Butterworth (24)
1 Komga (24)
2 Queenstown (10, 17)
1 Cathcart (10)
5 East London (10, 18, 23, 24, unid. *Limax*)
2 Kingwilliamstown (3, 10)
1 Bedford (23)
2 Port Alfred (10, 23)
4 Grahamstown (3, 7, 10, 24)
1 Alexandria (22)
9 Port Elizabeth (1, 3, 10, 11, 12, 15, 22, 23, 24)
1 Uitenhage (23)
3 Somerset East (3, 8, 10)
1 Cradock (23)
4 George (11, 16, 23, 24)
3 Wilderness (22, 23, 24)
2 Mossel Bay (23, 24)
1 Cango Caves (19)
1 Still Bay (22)
1 Swellendam (10)
1 Storms Vlei (11)
1 Ashton (11)
1 Bredasdorp (22)
1 Cape Agulhas (23)
1 Caledon (18)
2 Gordon's Bay (22, 23)
3 Somerset West (8, 22, 23)
5 Stellenbosch (1, 8, 18, 23, 24)
1 Faure (23)
5 Cape flats (1, 5, 11, 18, 22)
17 Cape Town and Cape Peninsula (3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 18, 20, 22, 23, 24)
2 Robben Island (23, 24)
1 Melkbosstrand (3)
1 Darling (23)
1 Langebaan-Saldanha Bay (23)
1 Vredenburg (23)
2 Ceres (14, 18)

Indeed, this becomes even more striking if we limit ourselves to places within 50 miles from the seashore; to the 100-mile list we have only to add Skukuza (Kruger Nat. Pk.), Underberg, Estcourt, Balgowan, Boston, Howick, Kokstad, Queenstown, Somerset East, Bedford and Ceres, making for 14 + 11 = 25 = 36% of the grand total. This typical pattern shows clearly both the comparatively recent date of white settlement (with its means of marine transport over long distances) and the slow rate of dispersal of successful immigrant milluscs. It is significant that there is

apparently a correlation between the number of foreign species, the age and importance of the harbour cities, and their distance from Europe via the Cape of Good Hope (the usual route for mail ships and freight):

City	First settlement	Harbour	Number of species
Cape Town	1652	class I[2])	17
Port Elizabeth	1799	class II	9
East London	1836	class III	5
Durban	1824	class I	4

At the various ports cargo is off-loaded and conveyed inland by train. It is shown clearly by the high number of immigrant species that Cape Town is the oldest harbour, which at the same time is closest to Europe by sea. A number of freighters unloads the bulk of their goods here and only much smaller quantities in the ports on the east coast. This is clearly shown by the decreasing number of immigrant species when one travels northward along the coast. Incidentally, Cape Town has also a rather suitable climate for European species. Durban occupies a special position in this table, because much of its shipping traffic comes from Europe via Africa's east coast and from the East, which has probably accounted for the importation of e.g., *Bradybaena similaris.*

In this respect it strikes one as odd that Beira, the second most important harbour city in Mozambique (Portuguese East Africa) is not on the list; very probably this is due to our still rather sketchy knowledge of the malacofauna of this country. It might also be due to the fact that the white population is numerically not very strong, which, of course, is reflected by the ocean-going traffic. Incidentally, it might be of interest to mention that we have only one record from Lourenço Marques (*Theba pisana*, fide JOUBERT & WALTERS, 1951) and that the European sparrow (*Passer domesticus*) is unknown to Mozambique.

In considering the general map (fig. 1) attention has to be drawn to some other contributary factors. The high figures for Cape Town and Pietermaritzburg might be due to the activities of the South African and Natal Museums, respectively, because the major part of taxonomic research concerning the molluscs of Southern Africa has been (and is being) done at these institutions. The absence of interest in non-marine moluscs in cities such as Johannesburg, Pretoria and Bloemfontein might on the other hand account for the low number of immigrant snails known from these centres. It seems incredible that *Helix aspersa* appears to be the only foreign pulmonate known to occur in Johannesburg, Southern Africa's commercial capital and most populous city with rail and road links throughout the country and also a major international airport. In this respect, the novelty of air transport and more strictly enforced quarantine measures may be enumerated as contributory causes.

Another point worthwhile to consider is a number of inland and/or rather remote localities such as the Victoria Falls, Bulawayo, Windhoek District, Skukuza (Kruger National Park), Smithfield, Royal Natal National Park, Ca-

[2]) Calculation based on number of vessels calling and cargo landed.

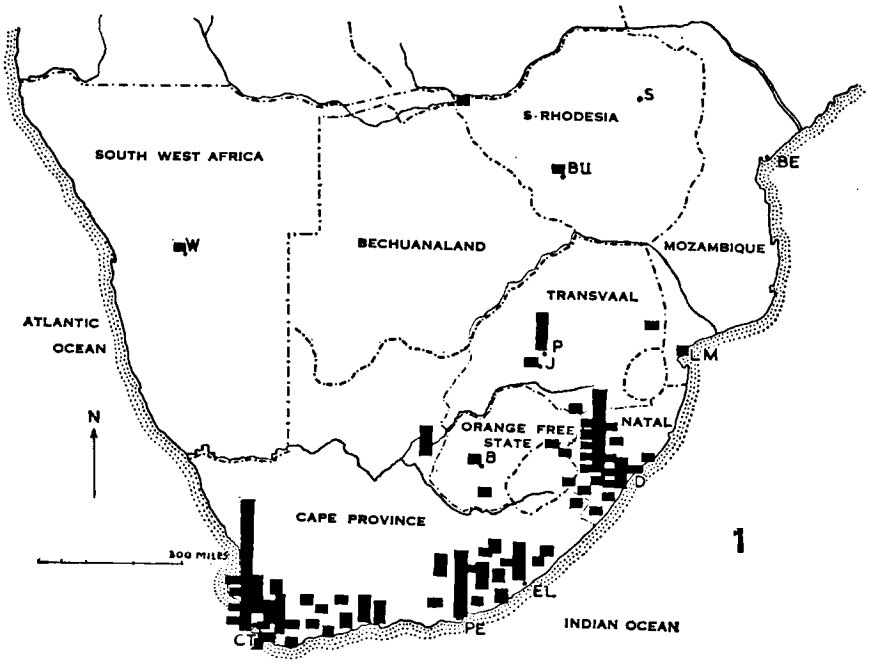


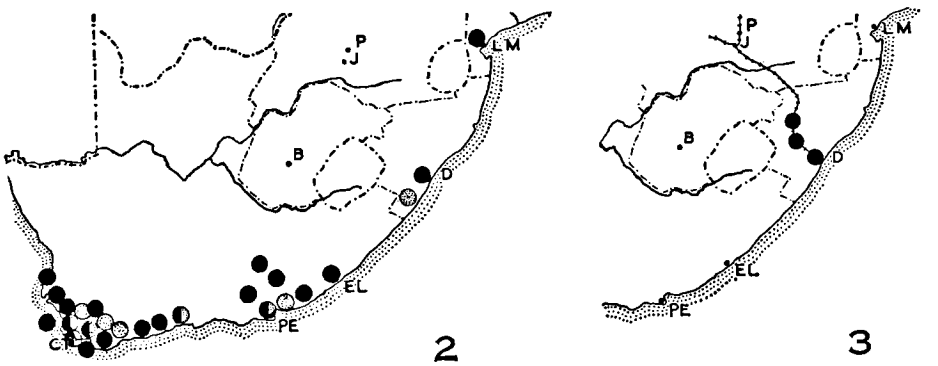
FIG. 1. Map of Southern Africa, showing all localities from which foreign pulmonates have been recorded. The length of the symbols indicates the number of species in every locality. Abbreviations: B = Bloemfontein, BE = Beira, BU = Bulawayo, CT = Cape Town, D = Durban, EL = East London, J = Johannesburg, LM = Lourenço Marques, P = Pretoria, PE = Port Elizabeth, S = Salisbury, W = Windhoek.

thedral Peak area, Sani Pass, Underberg and Kimberley. Some of these are important centres of population and consequently of rail, road, and to a lesser degree air traffic, e.g., Bulawayo (S. Rhodesia's second city, founded 1893), Windhoek (South West Africa's capital, founded 1870), and Kimberley (railway and diamond mining centre, founded 1871). Considering these one wonders about the absence of records from Salisbury (dating from 1890); on the whole, however, one may say that inland settlements are usually not as old as coastal ones and the development of Southern Rhodesia is indeed of comparatively recent date.

Some of the more remote localities are either on main railway lines and/or of considerable appeal to tourists: Victoria Falls (famous tourist attraction on only railway line to N. Rhodesia and the Congo), Skukuza (headquarters of Kruger National Park with large rest camp and staff village on branch railway line), Smithfield (on main road Bloemfontein-East London), Royal Natal National Park, Cathedral Peak area, Sani Pass, Underberg (Drakensberg Mts. resorts and approaches). This again, makes one wonder, why other tourist attractions, such as the game reserves in Zululand, are still free from imported pulmonates.

Few of the 24 listed species have achieved a wide distribution. Of only ten species more than five recorded localities are known and of only five species more than ten, viz., *Zonitoides arboreus, Deroceras laevis, Cochlicella ventricosa, Theba pisana* and *Helix aspersa.*

The distribution of few immigrant species shows a coherent pattern. *Cochlicella ventricosa* and *Theba pisana* have typical coastal patterns (fig. 2), which seem to agree with the type of distribution they show in Europe (see e.g., GERMAIN, 1930 : 182, who reports sub *Theba pisana*: "Espèce très xérophile fréquentant les stations sèches, arides et chaudes, plus spécialement celles où l'influence maritime se fait sentir; .....") and elsewhere outside their natural range (see e.g., COTTON, 1954). QUICK (1952 : 188, table 2), also records for this species "...., Transvaal, Orange Free State, Demaraland, Kaokovelt, Griqualand West, Ovamboland, ..." There is, however, no evidence for this in CONNOLLY (1939), nor in the South African, Transvaal and Natal Museums.



FIGS. 2—3. Distribution patterns of immigrant snails in South Africa. 2, distribution of *Cochlicella ventricosa* (dotted circles) and *Theba pisana* (black dots), where both occur half circles have been used; 3, distribution of *Bradybaena similaris.* For abbreviations see fig. 1.

Bradybaena similaris seems to follow the main railway line from Durban to Johannesburg (fig. 3). Examples of very widely distributed immigrant species are *Vallonia pulchella* (Pretoria, Pietermaritzburg, Kingwilliamstown, Grahamstown, Port Elizabeth, Somerset East, Melkbosstrand, Cape Town and Cape Peninsula) and *Oxychilus cellarius,* which is known from Bulawayo, Kimberley, Somerset East, Somerset West, Stellenbosch, Cape Town and Cape Peninsula. Incidentally, both the latter species were discovered in 1846 and consequently were the first immigrant species to become known in South Africa.

However, while many immigrant species have hardly survived and only seem to be able to hold their own in a very limited area (e.g., *Vitrea cristallina* and *Testacella maugei*, both since the 1890s in Cape Town only), others have proliferated to such a degree as to become agricultural (*Cochlicella ventricosa, Theba pisana*, see JOUBERT & WALTERS, 1951) or horticultural pests

(*Helix aspersa*). It is significant that some species which have become pests are among the earliest introduced: *Helix aspersa* (± 1854, third foreign species to be introduced or discovered), *Theba pisana* (1881, sixth do.), while the discovery of *Cochlicella ventricosa* only dates from 1909 (sixteenth do.), which shows how phenomenal its dispersal has been (fig. 2).

The rate of dispersal of immigrant snails is difficult to calculate because natural dispersal is closely interwoven with artificial dispersal by rail, road or ship. For example, it is quite likely that *Theba pisana* has travelled coastwise from port to port, filling up the gaps in between by natural means (fig. 2).

The above data show clearly that the distribution of immigrant species is strongly influenced by man and his means of transport; a first selection takes place on the arrival of the foreign species, after which establishment and both natural and artificial dispersal may occur.

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