STUDIES ON THE LAND MOLLUSCS OF ZULULAND
with notes on the distribution of land molluscs in Southern Africa

BY

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with 34 text-figures and four plates

CONTENTS

1. INTRODUCTION

The fauna and flora of Zululand, situated in South Africa to the south-east of Swaziland, are of particular interest to the biogeographer. To the north the area is connected with the East African lowlands through the Mozambique plains, to the west it is bounded by the Drakensberg range, to the east by the Indian Ocean, and while no definite barrier can be found towards the south, one does generally find that certain fauna elements of East African affinities do not occur across the Tugela River or further south. The majority of these species, however, are not known to occur further south than St. Lucia Bay. Topographically the Tugela River is usually considered to be the southern border of Zululand, which administratively is part of the Province of Natal.

The land molluscs of Zululand and particularly Tongaland (NE. Zululand) are not very well known. A few records are given by Connolly (1939), mainly from material gathered in the first decade of the twentieth century by the Natal Museum's collector F. Toppin. Toppin returned with a wealth of material, which was taken under extremely difficult conditions and which was also unfortunately very incomplete, because it was collected during general expeditions. His instructions stipulated that he had to collect all natural history specimens he could lay his hands on. Since Toppin's days terrestrial molluscs from Zululand have been only occasionally obtained for the Natal Museum, e.g., by the well-known naturalist H. W. Bell-Marley. Little, if anyhing, has reached other institutions. Connolly (1939) has recorded most of Toppin's and of the later material, although there is still quite a number of as yet unidentified samples in the Natal Museum. Haas (1936) also gives a few Zululand data; his records from "Mkuzi" are obviously from Mkuzi village on the railway line and not from the Mkuzi Game Reserve.

In 1964 the present author conducted a land mollusc survey of the Mkuzi and Ndumu Game Reserves in Tongaland. The results of this expedition are of great interest, but it was decided to round these off by working out a number of ancillary projects in order to be able to present a more comprehensive picture of the terrestrial mollusc fauna of Zululand. Consequently this paper incorporates the results of three studies, viz., a revision of the genus *Metachatina* (fam. Achatinidae), which has its head-quarters in Zululand, a survey of the land molluscs of the Mkuzi and Ndumu Game Reserves, and new records for Zululand. For the latter two chapters many data on the genus *Gulella* have been taken from a forthcoming revision of the genus in Southern Africa. Although seemingly unrelated the three subjects are to a certain extent integrated in the chapter on the distribution of the terrestrial molluscs of Zululand. In order to see the fauna of this area in its proper relation to that of the adjoining countries a final chapter on the distribution of land molluscs in Southern Africa concludes the zoogeographical part.

The odd mixture of miles, feet, inches and metric units requires explanation. In Southern Africa feet and inches are still widely used to indicate altitudes and rainfall, while at the same time statute miles are used for distances on land. In many cases data have been given according to both systems. Frequently both labels and literature are solely in miles, feet and inches, but conversion is not always advisable because of odd results such as for example the 305 m contour instead of the 1000 ft. contour, etc. Conversions are in round figures being based on one inch = 25 mm, one foot = 30 cm and one mile = 1600 m. Where distribution maps show patterns instead of localities, these patterns are not exact and solely serve to indicate rough distributions, maps being too bold or too conservative as the case may be.

The following abbreviations have been used: alc. — alcohol; BM — British Museum (Natural History), London; DM — Museum and Art Gallery, Durban; KLT — collection K. L. Tinley, Gorongosa, Mozambique; KNP — Kruger National Park collections at Skukuza, the headquarters of the Biologist; l/d — ratio length to maximum diameter of shells; MGR — Mkuzi Game Reserve; MT — Musée Royal de l'Afrique Centrale, Tervuren; MW — Naturhistorisches Museum, Vienna; NGR — Ndumu Game Reserve; NM — Natal Museum, Pietermaritzburg; RMNH — Rijksmuseum van Natuurlijke Historie, Leiden; SAM — South African Museum (Natural History), Cape Town; TP — collection T. Pain, London (eventually to be deposited in the National Museum of Wales, Cardiff); ZMA — Zoölogisch Museum, Amsterdam.

2. ACKNOWLEDGEMENTS

Many persons have assisted with data, specimens, access to collections under their care and sundry information; acknowledgements are due to Dr. C. O. van Regteren Altena (Leiden), Prof. Dr. P. L. G. Benoit (Tervuren), Dr. P. H. Boshoff (Johannesburg), Dr. D. S. Brown (London), Mr. H. E. Coomans (Amsterdam), Dr. L. Forcart (Basle), Dr. J. R. Grindley (Port Elizabeth), Dr. H. Janus (Stuttgart), Dr. R. Kilias (Berlin), Mr. B. H. Lamoral (Pietermaritzburg), Mr. W. J. Lawson (Durban), Dr. O. E. Paget (Vienna), Mr. T. Pain (London), Mr. J. F. Peake (London), Dr. A. Riedel (Warsaw), and Mr. N. Tebble (London). Thanks are also due to Senior Rangers Erasmus and Hancock of the Mkuzi and Ndumu Game Reserves respectively, for assistance in the field. Moreover, the author owes a debt of gratitude to his friend Ken L. Tinley (Parque Nacional da Gorongosa, Mozambique) for data from his unpublished reports, critically reading parts of the manuscript and help during the Tongaland survey of 1964; Tinley's unparalleled knowledge of the natural history of this part of South Africa has indeed materially assisted in the preparation of this paper. Dr. J. C. Poynton (Johannesburg) has also kindly scrutinized parts of the manuscript and given us the benefit of his knowledge. Dr. B. Verdcourt (Maidenhead) has throughout many years freely given of his malacological knowledge, for which the author is profoundly grateful. Prof. Dr. J. van der

Vecht (Leiden) has read and commented upon much of the initial stages of his paper. The trouble taken by these gentlemen is greatly appreciated. Mrs. W. H. van Bruggen (née Gorter) has served as field and laboratory assistant under frequently trying conditions; her very substantial help is gratefully acknowledged here.

A grant of the South African Council for Scientific and Industrial Research (C.S.I.R.) has covered the major part of the expenses of the expedition to Zululand and Swaziland in 1964; additional funds were supplied by the Natal Museum by courtesy of the director, Dr. J. A. Pringle. A subsidy of the Bolk-Fonds of the Koninklijke Nederlandse Akademie van Wetenschappen (Bolk Fund of the Royal Netherlands Academy of Sciences) has enabled the author to spend a month in 1967 at the British Museum (Natural History) in order to study critical specimens.

Mr. H. Heijn, staff artist of the Department of Systematic Zoology, has drawn figs. 1, 4, 6, 10, 12, 14-34; Mr. B. R. Stuckenberg of the Natal Museum has kindly made the photograph on plate 4. The photographs on pl. 1 are published by courtesy of the British Museum (Natural History).

3. REVISION OF THE GENUS METACHATINA

Although *Metachatina kraussi* (Pfr.) (family Achatinidae, Gastropoda Pulmonata), South Africa's largest land snail, commonly occurs in the coastal bush around Port Natal (founded in 1824, now officially called Durban), it was only described as late as 1846. It was probably the absence of columellar truncation which led the early conchologists to classify it with *Bulimus* or even *Limicolaria* rather than with *Achatina*. Only about sixty years later it came to be realized that the species merited a genus of its own close to *Achatina*: Pilsbry (1904) in his famous Manual of Conchology established *Metachatina* as a genus for the reception of *Bulimus kraussi* Pfeiffer, 1846.

The present author has collected many new data so that a re-appraisal of the genus and its species has now become possible. Seventy odd specimens have been examined by the writer and data on another dozen shells have been supplied by courtesy of various colleagues.

In the following pages nomenclature, shell, anatomy, biology, distribution, variation and evolution of the single species recognized will be discussed.

Metachatina Pilsbry, 1904

Bulimus auct., sensu lato, p.p.
Achatina Lamarck, 1799, p.p.
Livinhacia Crosse, 1889, p.p.
Metachatina Pilsbry, 1904, Man. Conch., (2) 16: 307; Thiele, 1931, Handb. Syst.

Weichtierk., 1: 559: Connolly, 1939, Ann. S. Afr. Mus., 33: 294; Zilch, 1959, Handb. Paläozool., 6 (2): 369.

Type by monotypy: *Bulimus kraussi* Pfeiffer, 1846.

Shell large, solid, achatinoid, ovate-acuminate; apex obtuse, large and rounded; aperture ovate, outer lip simple, no columellar truncation; shell subrimate or with closed umbilicus. Anatomy as in family; radula with ectocones on lateral teeth. Restricted to southeast Africa.

The most salient character is the absence of columellar truncation, which sets the genus apart from its allies *Achatina* Lamarck, 1799, and *Archachatina* Albers, 1850. However, among the Achatinidae the absence of columellar truncation is by no means limited to *Metachatina*, although in Southern Africa only *Burtoa* Bourguignat, 1889, appears to share this peculiarity of the shell.

Metachatina kraussi (Pfeiffer, 1846)

Bulimus kraussi Pfeiffer, 1846, Symb. Hist. Helic., 3: 85; Krauss, 1848, Südafr. Moll.: 78, pl. 5 fig. 4; Pfeiffer, 1848, Monogr. Helic. Viv., 2: 184; Reeve, 1849, Conch. Icon., 5: pl. 63 fig. 436 (col.).

Limicolaria kraussi; Adams, 1858, Gen. Rec. Moll., 2: 133; Pfeiffer, 1881, Nomenclat. Helic. Viv.: 262.

Achatina kraussi; Nevill, 1878, Hand List Moll. Ind. Mus., 1: 146; Rochebrune & Germain, 1904, Mém. Soc. Zool. France, 17: 12.[1])

Livinhacia kraussi; Crosse, 1889, J. Conchyl., 37: 111; Kobelt, 1893, Conch. Cab., 1 (10): 7, pl. 2 fig. 1 (col.); Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 178; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 595 (59); Junod, 1899, Bull. Soc. Vaud., 35: 279.

Burtoa kraussi; Bourguignat, 1889, Moll. Afr. Equat.: 95.

Metachatina kraussi; Pilsbry, 1904, Man. Conch., (2) 16: 308, pl. 23 figs. 46, 48 (col.); Connolly, 1912, Ann. S. Afr. Mus., 11: 188; Pilsbry, 1919, Bull. Am. Mus. Nat. Hist., 40: 83, fig. 35 (map); Thiele, 1931, Handb. Syst. Weichtierk., 1: 559; Haas, 1936, Abh. Senckenb. Naturf. Ges., 431: 12, 102; Connolly, 1939, Ann. S. Afr. Mus., 33: 294, fig. 25 (radula); Barnard, n.d. (1951), Beginner's Guide S. Afr. Shells: 149, pl. 22 fig. 10; Zilch, 1959, Handb. Paläozool., 6 (2): 369, fig. 1347; Van Bruggen, 1965, Rev. Zool. Bot. Afr., 71: 80; Verdcourt, 1966, Rev. Zool. Bot. Afr., 74: 111; Van Bruggen, S. Afr. Animal Life, in the press.

Achatina fuscolabris von Martens, 1860, Die Helic.: 202, 204; Von Martens, 1889, Sitz.-Ber. Ges. Naturf. Fr. Berlin: 163.

Achatina planti Pfeiffer, 1861, Proc. Zool. Soc. London: 25, pl. 3 fig. 6 (col.); Pfeiffer, 1861, Novit. Conch., 2: 160, pl. 43 figs. 1, 2 (col.); Pfeiffer, 1868, Monogr. Helic. Viv., 6: 218; Paetel, 1889, Cat. Conch.-Samml., (ed. 4) 2: 240.

Metachatina planti; Pilsbry, 1904, Man. Conch., (2) 16: 309, pl. 37 figs. 10, 11 (col.).

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1) Not to be confused with *Achatina kransi* Reeve, 1842 (changed by Pfeiffer in the same year to *A. Kraussi*, which is not an emendation in the sense of the International Code of Zoological Nomenclature, and validly emended to *A. kraussi* by Pfeiffer in 1848), now considered to be a variety of *Achatina (Achatina) zebra* (Bruguière, 1792). Possible confusion may be increased by the type locality, viz., "Cape Natal" = Durban; this is incorrect since the species in question does not occur further north than East London.

Livinhacia kraussi var. *planti*; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 178.

Metachatina kraussi var. *planti*; Connolly, 1912, Ann. S. Afr. Mus., 11: 189; Connolly, 1939, Ann. S. Afr. Mus., 33: 296.

Livinhacia kraussi var. *elongata* Junod, 1899, Bull. Soc. Vaud., 35: 279.[2]

Metachatina kraussi var. *elongata*; Connolly, 1925, Trans. R. Soc. S. Afr., 12: 165, Connolly, 1939, Ann. S. Afr. Mus., 33: 295; Braga, 1952, An. Junta Invest. Ultram. Est. Zool., 7: 120, pl. 12.

Metachatina kraussi var. *elongatula* Germain, 1935, Mem. Estud. Mus. Zool. Univ. Coimbra (1) 80: 8, error pro *elongata*.

Original description: "376. Bulimus Kraussi Pfr. — T. perforata, ovato-acuta, solidiuscula, irregulariter rugosa, striis longitudinalibus et transversis confertis granulata, sub epidermide castanea, decidua albida, spadiceo-nebulosa et maculata; spira pyramidata, apice obtusa; anfr. 7-8 planiusculi, ad suturam crenulato-rugosi, ultimus spiram subaequans; columella arcuata, subtorta, compressa, castanea; apertura ovalis, intus lactea; perist. simplex, acutum, castaneo-limbatum, marginibus callo castaneo, introrsum diffuso junctis, columellari angulatim reflexo, perforationem suboccultante. Long. 100, diam. 50 mill. — Natal. (Krauss.)".

Adult shell large, fairly slender, ovate-acuminate, solid, subrimate or with closed umbilicus. Spire produced, whorls 7-9, fairly convex to almost flat, with fine criss-cross sculpture, fading away below the periphery of the body whorl, strong growth lines; suture simple to subcrenellate. Aperture acuminate-ovate, peristome slightly incrassate, labrum straight and almost vertical in profile, columella straight to slightly oblique, margin strongly but narrowly reflected for its entire length over the umbilicus. Nepionic whorls granulate, but usually worn. Shell covered with a thin, dull brown, deciduous periostracum; underneath dirty white with a faint purplish tinge and chestnut flame pattern on early whorls, which pattern is well-developed above the periphery in juvenile shells. Outer lip, columellar and parietal areas chestnut brown, which colour is continued into a narrow band inside the labrum; interior whitish. In juvenile shells only the columellar area is brown. In worn shells the brown colour may disappear altogether.

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2) Although the var. *elongata* is usually attributed to H. A. Junod, a few authors have quoted the name of P. Godet. The paper, an appendix to another article, has no formal author, its title reading "Mollusques receuillis par M. H.-A. Junod, au Delagoa." The introduction, evidently written by Junod himself, states that identifications are due to Godet, but concludes with: "Je laisse maintenant la parole à M. Paul Godet, me contentant d'intercaler quelques détails dans sa nomenclature." Thus it is not clear whether Junod or Godet is the author of new names, so that in the present paper the tradition to attribute the var. *elongata* to Junod has been respected.

The juvenile shells have a truncate columella; adult shells have a columella which more or less smoothly merges into the labrum. There is a lot of variation in this area and hardly any two specimens are identical in this respect.

The measurements (see table 1) are subject to a good deal of variation (fig. 1), which in the past has led to the separation of the varieties *planti* Pfeiffer, 1861 (based on a shell with repaired damage, pl. 1) and *elongata* Junod, 1899 (the usual type of shell in northern Zululand and southern Mozambique). Connolly (1925: 166) was the first to remark upon the great size of shells from Mozambique as compared to those from Natal. However, a full range of intermediate shells is now available so that these so-called varieties have been relegated to the synonymy. The size of adult shells appears to range from 96.2 to 159.0 mm without any obvious gaps. Space restrictions prevented measurements of the aperture and last whorl being shown in the table. Those measurements of six randomly selected specimens are shown below (numbers refer to table 1):

No.	Locality	Aperture	Last whorl
4	Durban	50.0 × 35.5	75.5 mm
18	Durban	56.0 × 39.5	83.5 mm
32	Durban	50.0 × 41.5	84.0 mm
49	Ingwavuma	72.0 × 48.0	104.0 mm
57	Kosi Bay	69.5 × 43.0	106.5 mm
67	Bhanga Nek	73.0 × 49.0	115.0 mm

Occasionally slight aberrations have been found, such as a brown tubercle on the centre of the paries in specimen no. 33. This may have been caused by irritation of the mantle or by a foreign body.

Unfortunately the holotype of *Bulimus kraussi* Pfr. in the Staatliches Museum für Naturkunde, Stuttgart, West Germany, was destroyed in the Second World War (Janus, in litt.). The holotype of *Achatina planti* Pfr. is preserved in the British Museum (Natural History), London (Reg. no. 1966276) (pl. 1); that of *Livinhacia kraussi* var. *elongata* Junod in the Musée d'Histoire Naturelle, Neuchâtel, Switzerland, and of *Achatina fuscolabris* von Martens in the Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt Universität, Berlin, East Germany.

TABLE 1

Measurements of adult shells of *Metachatina kraussi* (Pfr.)

No.	*Locality*	*Collection*	*Length × max. diam.*	l/d
1	Durban	ZMA	96.2 × 47.7 mm	2.0
2	Durban	ZMA	96.9 × 49.5 mm	2.0
3	Durban	ZMA	97+ × 50.1 mm	1.9+

No.	*Locality*	*Collection*	*Length* × *max. diam.*	l/d
4	Durban	NM	99.0 × 50.0 mm	2.0
5	Durban	ZMA	100.7 × 49.7 mm	2.0
6	"Natal"	SAM	100.9 × 51.4 mm	2.0
7	Durban	BM	102.0 × 56.9 mm	1.8
8	Durban	BM	102.5 × 56.6 mm	1.8
9	"Natal"	ZMA	102.7 × 52.2 mm	2.0
10	Dukuduku	NM	103.5 × 54.5 mm	1.9
11	Dukuduku	NM	104.0 × 55.5 mm	1.9
12	"Natal"	ZMA	104.0 × 56.2 mm	1.8
13	Durban	BM	104.0 × 63.8 mm	1.6
14	Umfolosi River	SAM	105.2 × 46.5 mm	2.3
15	Kelso	NM	107.0 × 50.5 mm	2.1
16	Durban	NM	108.0 × 53.5 mm	2.0
17	Umfolosi River	SAM	110.5 × 47.7 mm	2.3
18	Durban	NM	112.5 × 56.5 mm	2.0
19	Durban	BM	112.6 × 60.0 mm	1.9
20	"Natal"	NM	113.5 × 51.0 mm	2.2
21	Glencoe	DM	113.5 × 60.5 mm	1.9
22	Durban	NM	115.0 × 53.0 mm	2.2
23	Glencoe	DM	115.0 × 58.5 mm	2.0
24	Durban	BM	115.9 × 59.3 mm	1.9
25	Scheepersnek	NM	116.0 × 56.0 mm	2.1
26	Durban	SAM	116.3 × 54.0 mm	2.1
27	Durban	RMNH	117.3 × 60.6 mm	1.9
28	Durban	BM	117.9 × 63.3 mm	1.9
29	Kelso	NM	118.0 × 56.5 mm	2.1
30	Ginginhlovu	NM	118.5 × 61.0 mm	1.9
31	Durban	SAM	118.8 × 57.8 mm	2.0
32	Durban	NM	119.5 × 57.0 mm	2.1
33	Tongaat	NM	119.5 × 60.5 mm	2.0
34	Tongaat	BM	121.8 × 64.9 mm	1.9
35	"Natal"	SAM	122.8 × 62.4 mm	2.0
36	Durban	DM	124.0 × 60.0 mm	2.1
37	Tongaat	SAM	124.2 × 57.5 mm	2.2
38	"Mozambique"	BM	124.6 × 59.8 mm	2.1
39	Tongaat	NM	125.0 × 61.5 mm	2.0
40	Tongaat	NM	126.0 × 54.5 mm	2.3
41	Tongaat	NM	128.0 × 64.0 mm	2.0
42	Tongaat	SAM	128.7 × 59.6 mm	2.1
43	"Natal"	BM	130.5 × 60.9 mm	2.1
44	"Zululand"	BM	131.2 × 71.3 mm	1.8
45	Kosi Bay	NM	132.0 × 63.5 mm	2.1
46	"Zululand"	BM	132.5 × 68.3 mm	1.9
47	"Mozambique"	BM	133.1 × 63.0 mm	2.1
48	Durban	RMNH	133.1 × 66.9 mm	2.0
49	Ingwavuma	NM	137.5 × 69.0 mm	2.0
50	Makowe	NM	137.5 × 70.5 mm	1.9
51	Kosi Bay	NM	138.0 × 66.0 mm	2.1
52	Makowe	NM	139.0 × 71.0 mm	1.9
53	Vila Luiza	RMNH	139.9 × 64.7 mm	2.2
54	Rikatla	NM	141.0 × 66.0 mm	2.1

55	Nyalazi River	NM	141.0 × 67.5 mm	2.1
56	Kosi Bay	NM	143.5 × 65.0 mm	2.2
57	Kosi Bay	NM	146.0 × 60.5 mm	2.4
58	Kosi Bay	NM	146.5 × 60.5 mm	2.4
59	Bhanga Nek	NM	148.0 × 65.0 mm	2.3
60	Vila Luiza	RMNH	149.5 × 66.6 mm	2.2
61	Nkovugeni Estuary	NM	151.5 × 66.0 mm	2.3
62	Ingwavuma Road	NM	154+ × 70.5 mm	2.2+
63	Bhanga Nek	NM	155.0 × 66.0 mm	2.3
64	Kosi Bay	NM	155.5 × 66.5 mm	2.3
65	Vila Luiza	RMNH	156.0 × 69.6 mm	2.2
66	Bhanga Nek	NM	158.0 × 61.5 mm	2.6
67	Bhanga Nek	NM	159.0 × 68.5 mm	2.3

Notes. No. 4 is not yet completely adult, but almost so; the labrum is still somewhat sharp. No. 64 is almost full-grown, although the lip is still thin.

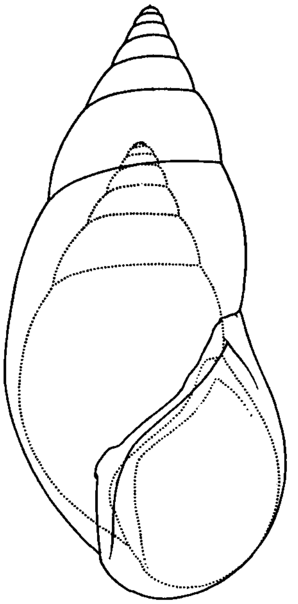
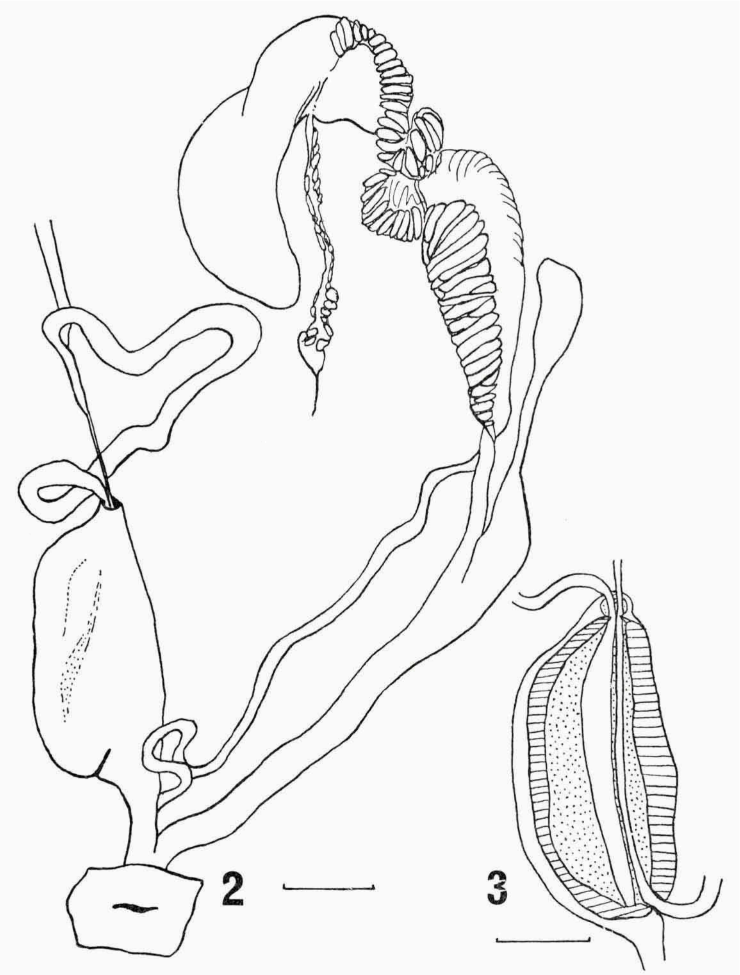


Fig. 1. Outlines of the two forms of shell in *Metachatina kraussi* (Pfeiffer); large shell from Vila Luiza, Mozambique, leg. P. H. Boshoff, length 156.0 mm, no. 65 of table (RMNH), smaller shell from Salisbury Island, Durban, Natal, leg. H. J. Lam & A. D. J. Meeuse, length 117.3 mm, no. 27 of table (RMNH).

Because I failed to make notes about the one specimen seen alive by me (no. 55), I have to quote Connolly (1939: 295) for a description of the animal: "Two animals from Zululand are yellowish grey on the body, head and neck dark grey, with a broad pale streak on each side, extending from base of upper tentacles, lower part of body and tail yellowish grey".

While the general anatomy agrees closely with that of other Achatinidae (cf. e.g., Van Benthem Jutting, 1951), the genitalia (fig. 2) show a number of significant characters. The penis is partly ensheathed in a very large and muscular sac and exhibits a very long apical loop, such as is known in *Achatina immaculata* (cf. Mead, 1950, s.n. *A. panthera*; Van Bruggen, 1966a), but very much longer than in the latter. The vas deferens enters the penial sheath at its base. The sheath is very thick indeed; inside penis and vas deferens run closely parallel (fig. 3). This also shows that less than half the penis is enclosed in the sheath. The spermatheca has a short and thick



Figs. 2-3. *Metachatina kraussi* (Pfeiffer), 2, genitalia; 3, opened penis sheath, penis on the left, vas deferens on the right. Scale in both figures 10 mm.

duct, which is appreciably swollen at the junction of this duct and the vagina. The penial retractor muscle is attached to the complex columellar muscle close by the insertion of the right tentacular retractor muscle.

A total of five adults (three from Durban and two from Zululand) was dissected and no differences can be detected in the genitalia of Natal and Zululand specimens, except, of course, in size.

Connolly (1939) has given details of the radula and jaw of a Durban specimen. The former measures 16 × 8 mm and has "130 rows of teeth fully developed", while the formula is 65-1-65 (Connolly's text-fig. 25 on p. 295). For the present study radulae of two specimens were extracted; these show the following particulars:

Natal, Durban	15.5 × 8.5 mm, ± 150 rows, formula 69-1-69
Zululand, Nyalazi R.	16.0 × 9.0 mm, ± 143 rows, formula 77-1-77

These generally agree with Connolly's description; the central tooth is very insignificant indeed. The jaw is of the usual achatinoid type, the one from the Zululand specimen being less horse-shoe shaped than the one from the Natal specimen. The former has a span of 8.5 mm, the latter of 8.0 mm. Obviously the differences in radula and jaw are of an individual rather than of a subspecific nature.

Specimen no. 20 ("Natal, 1905") was found to contain 31 eggs. These are ovoid-spheroid, the biggest measuring 11.8 × 9.7 mm, the smallest 9.4 × 8.3 mm, and an average egg 9.7 × 8.5 mm. Specimen no. 32, collected by O. Bourquin in Burman Bush, Durban North, on 22 December 1963, was found to contain 26 eggs, having the following measurements: 10.6 × 9.0 mm (biggest), 8.7 × 8.4 mm (smallest), 10.2 × 8.9 mm (average). All these eggs were fully mature with hard yellowish-white shells. Among the sample collected at Vila Luiza by Dr. Boshoff (see sub "Distribution"), there was found one egg, which presumably also belongs to *M. kraussi*; this measures 7.3 × 6.0 mm. Occasionally empty specimens of Achatinidae contain empty, but otherwise undamaged, egg shells, which presumably were stored in the uterus of the animal in question.

Few published data on the biology of *M. kraussi* are available. As already correctly noted by its original describer the species inhabits sheltering types of vegetation: "in sylvis" (Pfeiffer, 1846). A variety of labels mentions coastal scrub, bush or forest, dune scrub or forest and "among bushes and cycads" (Vila Luiza specimens). Haas (1936: 12) writes about having collected it "in einer Bananen-Pflanzung". A specimen from Durban (no. 5) was taken on a refuse dump on Salisbury Island. Unfortunately authors or labels usually do not mention whether the specimens in question were collected alive or not. The species is restricted to various types of fairly humid vegetation; it is only active in damp weather conditions, such as after rain (no. 55 was taken on the road after heavy showers), early in the morning or on overcast days. Direct sunshine kills it quickly; no. 49 was collected on a road where it had died in the sun after having been activated by some light rainfall. It is not known whether *M. kraussi* is able to secrete a protective epiphragm in order to temporarily close the aperture of the shell; many other achatinids are able to do so, although some sylvicolous species may have lost this faculty which in many drier parts of Africa is of great survival value. Specimen no. 32 was killed by a large *Natalina,* very probably *N. cafra* (Fér.). All South African Rhytididae, to which family *Natalina* belongs, are carnivorous, mainly preying on soft invertebrates such as worms and molluscs. Various large species of this family occur in the same area and habitat as *M. kraussi,* so that it seems reasonable to consider species of *Natalina* normal predators of this large achatinid.

Distribution (fig. 4). — The localities, enumerated from south to north, have been extracted from data of museum specimens and from the literature. Full particulars of material from new localities are given here at the same time.

Natal. The type locality for *Metachatina kraussi* is "Natal" (Pfeiffer, 1846), which has been emended by Krauss (1848) as "In sylvis prope Natalbai". Natal Bay is now called Durban Bay and thus Durban must be considered the type locality. The species is known to occur in the following localities in Natal (see map): (1) Kelso (NM; Connolly, 1912, 1939 — formerly called Alexandra Junction); (2) Umlaas River mouth (Pfeiffer, 1848; Connolly, 1912, 1939; Pilsbry, 1904); (3) Durban and environs (also Bellair, Burman Bush, Cape Natal, Durban Bay, Natal Bay, Port Natal, Salisbury Island; BM, DM, NM, RMNH, SAM, ZMA; Connolly, 1912, 1939; Nevill, 1878; Pilsbry, 1904); (4) Tongaat (BM, NM, SAM; Connolly, 1912, 1939); (5) Tugela Mouth (south bank, coastal bush, leg. A. C. and W. H. van Bruggen, 3. I. 1964, NM); (6) Glencoe (don. J. P. Venter, DM); (7) Scheepersnek, Vryheid District (leg. Mrs. Beater; locality also spelt Scheepsnek, NM).

Zululand. *Metachatina kraussi* was first reported to occur in Zululand by Connolly (1912: 189): "Eastern Zululand (Toppin)". The following localities have since become known: (8) Mfongosi (Connolly, 1939); (9) Ginginhlovu (NM; Connolly, 1939); (10) Richards Bay (Tinley, in litt.); (11) Umfolosi River (don. H. J. Prigsy, SAM); (12) Dukuduku Forest (leg. F. Toppin, VIII. 1905, NM); (13) St. Lucia (Haas, 1936); (14) Nyalazi River (on road, leg. J. A. Pringle, XI. 1965, NM); (15) Hluhluwe

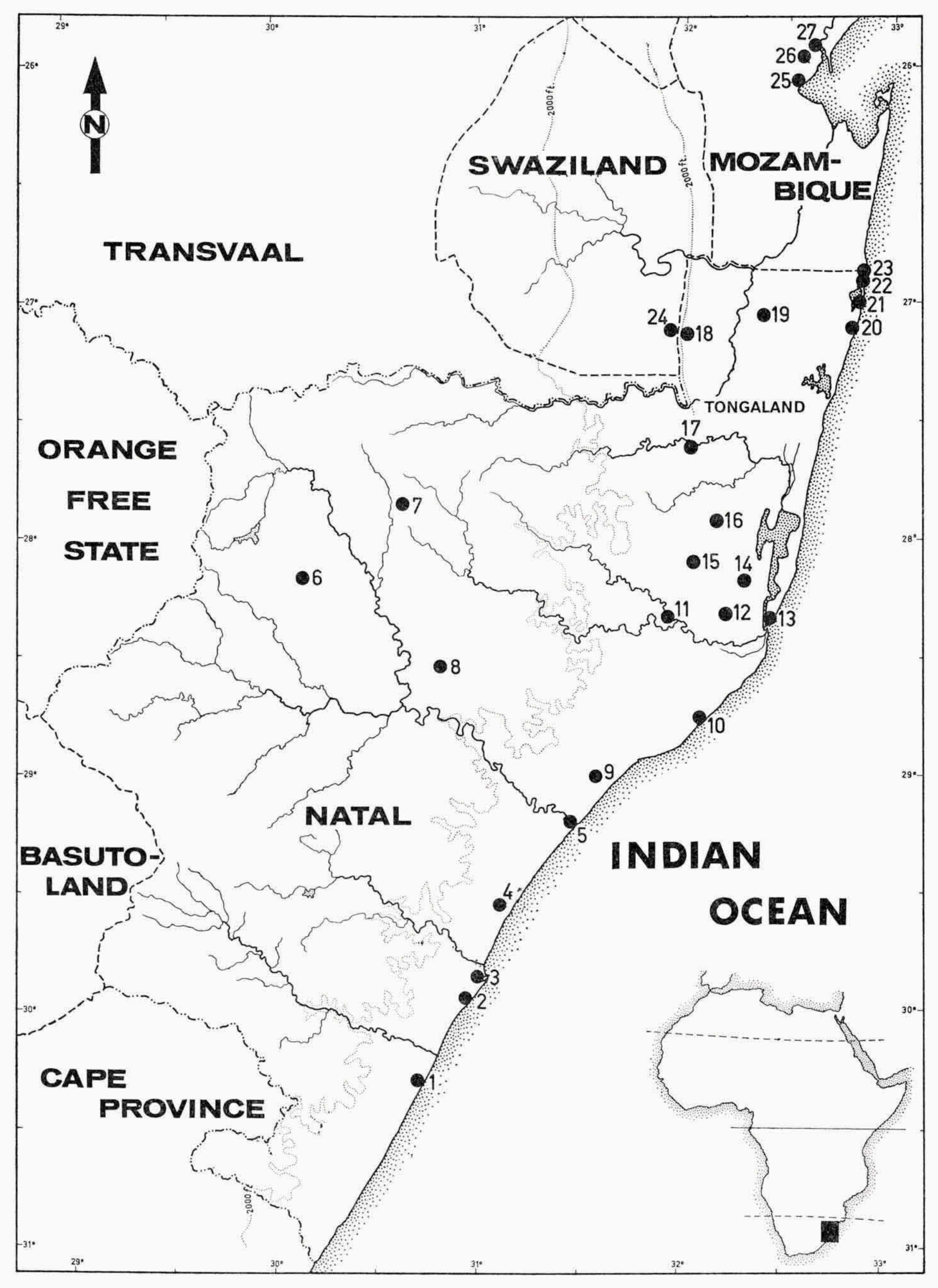


Fig. 4. Distribution of *Metachatina kraussi* (Pfeiffer). See text for key to locality numbers.

Game Reserve (NM, Lund University Museum; Van Bruggen, in the press); (16) Makowe (leg. H. C. Burnup, NM); (17) Mkuzi (Haas, 1936); (18) Ingwavuma (in the village, 2000 ft., leg. A. C. and W. H. van Bruggen, 9. I. 1964, NM); (19) Sihangwane Bush (Connolly, 1939); (20) Dog Point (± 15 miles S. of Kosi Bay, NM); (21) Bhanga Nek (15 miles S. of Mozambique border, dune forest, leg. O. Bourquin, XII. 1964-I. 1965, NM); (22) Kosi Bay (NM; Connolly, 1912, 1939); (23) Nkovugeni Estuary (dune scrub, leg. A. C. and W. H. van Bruggen, 15. I. 1964, NM).

Swaziland. In 1964 the species was found in Swaziland near the Ingwavuma Road by A. C. and W. H. van Bruggen (NM) (24).

Mozambique. The species was first discovered in Portuguese East Africa by Junod (1899), who described the var. *elongata* from Rikatla near Lourenço Marques. Mozambique records are far fewer than those from Natal and Zululand. Only three localities are on record: (25) Lourenço Marques (also Delagoa Bay; Braga, 1952; Connolly, 1925, 1939; Pilsbry, 1904); (26) Rikatla (NM; Junod, 1899; Connolly, 1912, 1925, 1939); (27) Vila Luiza (8 miles NW. of village, among bushes and cycads, leg. P. H. Boshoff, 1966, RMNH).

Furthermore there are some specimens from "Mozambique" (e.g., BM), which may either be interpreted as referring to the whole country or the ancient and important port city in the northern parts of this area. The latter can hardly be the case as the city of Mozambique is situated far north of the Zambezi River, while *Metachatina kraussi* very probably does not even cross the Limpopo River. The few records for Portuguese East Africa may be due to a dearth of collectors, but may also be caused by the species reaching its northern limits somewhere beyond Lourenço Marques.

Occasionally wrongly localized specimens are found in collections (e.g., Wynberg, Cape Peninsula, ZMA), some of which have appeared in print (e.g., Kahama Dist., Tanganyika; Ambati, Ethiopia; see de Rochebrune & Germain, 1904; Pilsbry, 1919; Verdcourt, 1966a). As has already been stressed by Verdcourt (1966a), it is most unlikely that the species really occurs in these localities. Usually the species is easily recognized, which minimizes the chance of wrong identifications.

Thus it appears that *M. kraussi* has only a restricted distribution in a narrow stretch of country from the Natal South Coast to just north of Lourenço Marques. All localities except two are within 80 km (= approximately 50 miles) from the coast; only Scheepersnek and Glencoe are approximately 175 km (= slightly more than 100 miles) from the shores of the Indian Ocean. Most coastal localities are from sea level up to about 180 m (= 600 ft.). However, two groups of localities, viz., those on the

Lebombo escarpment from Ingwavuma southward, and those on the foothills of the Drakensberg range (Scheepersnek, Glencoe, Mfongosi) are considerably higher. Those in the former group are not higher than about 600 m (= 2000 ft.), while those in the latter are somewhat more elevated: Scheepersnek 1217 m (= 4055 ft.), Glencoe 1300 m (= 4302 ft.), Mfongosi 600-750 m (= 2000-2500 ft.). It should be noted that *M. kraussi* does not occur in the Tongaland plain in between the coastal dunes and the Lebombo escarpment except at Sihangwane Bush, loc. no. 19.

An attempt to explain this seemingly puzzling distribution pattern will be found in chapter 6 on p. 76.

It seems worth while to try to correlate size and shape with distribution. A study of table 1 and fig. 4 reveals the following. Nos. 6, 9, 12, 20, 35, 38, 43, 44, 46 and 47 are insufficiently localized and will not be included in the discussion. The length of the shells is seen to increase from south to north, which is demonstrated by the following figures of size classes:

I length 95-110 mm ... Kelso to Umfolosi and Dukuduku
II length 110-125 mm ... Kelso to Scheepersnek and Umfolosi
III length 125-140 mm ... Durban to Vila Luiza
IV length 140-159 mm ... Nyalazi River to Vila Luiza

The areas of size classes I and II considerably overlap on the coast, while some of the others have smaller overlaps; however, the existence of a cline is quite evident. It is also obvious that towards the north the shells become more slender, as illustrated by the following table with the localities arranged from south to north:

l/d:	Kelso-Durban	Glencoe-Scheepersnek	Tongaat-Ginginhlovu	Umfolosi-Makowe	Ingwavuma-Tongaland	Mozambique
1.6	1	—	—	—	—	—
1.7	—	—	—	—		
1.8	2	—	—	—	—	—
1.9	5	1	2	4	—	—
2.0	8	1	3	—	1	—
2.1	5	1	1	1	2	1
2.2	1	—	1	—	2	3
2.3	—	—	1	2	5	—
2.4	—	—	—	—	2	—
2.5	—	—	—	—	—	—
2.6	—	—	—	—	1	—
total no. of shells	22	3	8	7	13	4

Unfortunately the material is too limited to allow conclusions to be drawn but it seems likely that the average l/d tends to increase towards Mozambique

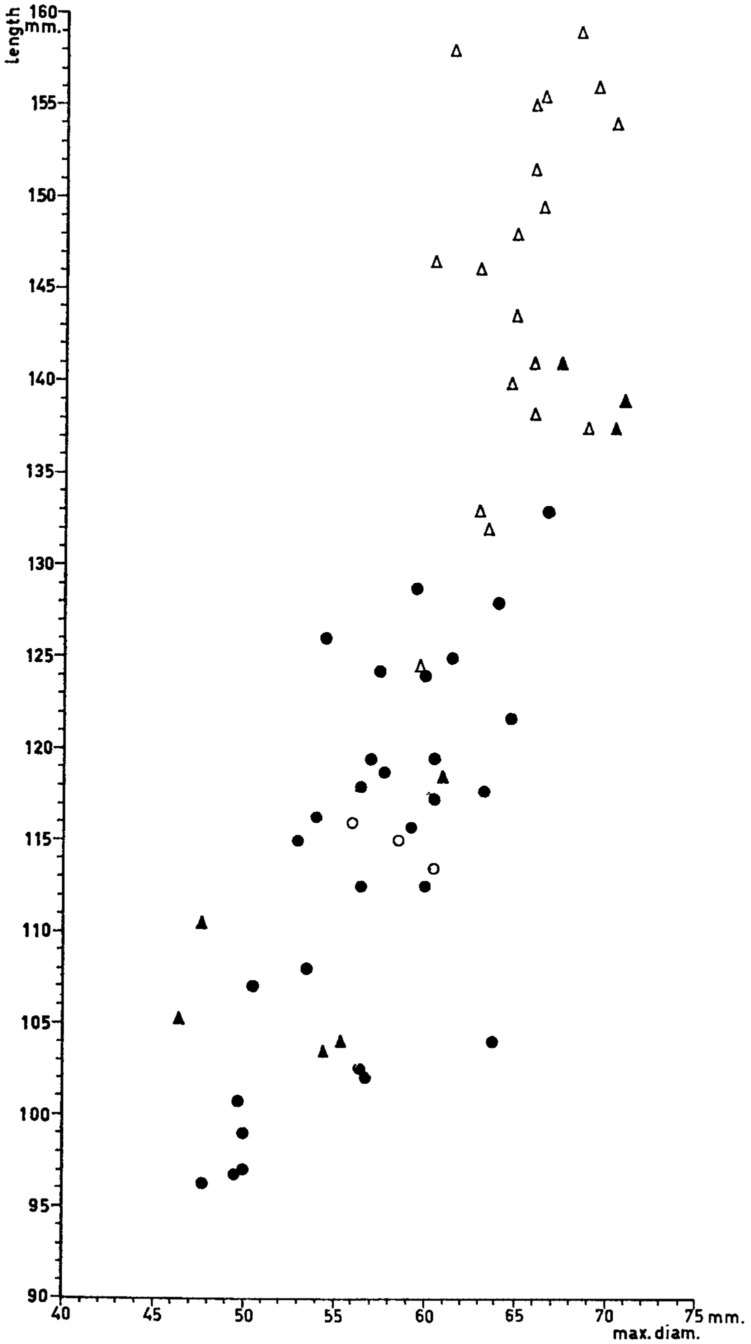


Fig. 5. Measurements of specimens from table. Key to symbols: dots (shells from Kelso to Tugela Mouth), circles (shells from Glencoe, Scheepersnek and Mfongosi), triangles (shells from Tugela Mouth to Mkuzi) and open triangles (shells from Mkuzi to Vila Luiza). Graph by Mrs. W. H. van Bruggen and H. Heijn.

Fig. 5 graphically depicts the increase in size and l/d towards the north. The localities have been roughly divided into four groups from south to north, for which groups different symbols have been used. Attention is particularly drawn to the overlap in size in the various groups.

It is a well-known fact that greatest size in invertebrates is usually reached under optimal conditions. For gastropods this has been worked out by Rensch (1932) and concisely formulated by Mayr (1942: 92): "Land snails reach their greatest size in the area of optimum climate within the range of the species". In this case it is the area with the highest temperatures combined with suitable humidity conditions because of the largely tropical nature of the Achatinidae. In this context it is interesting to mention that the mean July 18° C. isotherm cuts right across the country inhabited by *M. kraussi* somewhere in the St. Lucia area in Zululand (see map 3 in Poynton, 1964: 260). This isotherm encompasses the tropical region as defined by Köppen (1931) as a climate in which the coldest month has a mean temperature of over 18° C. Although this is an artificial line because of the very slow temperature gradient, Poynton has shown its importance for the distribution of the Amphibia of Zululand and Natal "as marking the limit of the Palaeotropical Region." (Poynton, 1964: 225). The air temperature decreases with increasing latitude as shown by the mean daily temperature in Lourenço Marques (25°58′ S.) at the northern limits of distribution of *M. kraussi* at 22.0° C. as compared to Durban (29°50′ S.) not far from the southern limits of the species with 20.5° C. The air temperature also decreases with altitude, which may account for the comparatively small shells of specimens from Glencoe and Scheepersnek. No noticeable differences in colour pattern and intensity of pigmentation of the shell have been found in the material available for this study.

In conclusion some speculation on the evolution of the monotypic genus under consideration seems quite in order. It is difficult to evaluate the position of *M. kraussi* within the family Achatinidae. Undoubtedly as a genus *Metachatina* is well separated from the other genera; the combination of characters such as large size, absence of columellar truncation, the colour pattern around the aperture, and the peculiar distribution, make it stand well apart from allied genera. Large size, combined with the absence of columellar truncation and limited distribution seem to indicate that it is a fairly recent offshoot of the family. Among the Prosobranchia columellar truncation, concurrent with the development of a sipho, is considered a comparatively new development (Siphonostomata); consequently it occurs mainly in more advanced groups, such as the Rhachiglossa and Toxoglossa. Among the pulmonates, however, columellar truncation is usually rare and, because of the absence of a sipho, may have arisen quite independently from that among the Prosobranchia. Although sometimes columellar truncation occurs as a juvenile feature of the shell, few pulmonate families exhibit this in the adult stage, such as e.g., Amastridae, the Achatinacea (consisting of the families Ferussaciidae, Subulinidae, Achatinidae and Megaspiridae) and the Oleacinidae. The Amastridae are fairly primitive, the Achatinacea are usually placed somewhere midway between the primitive and more advanced pulmonates, while the Oleacinidae are only slightly more advanced than the Achatinacea; this shows that absence of columellar truncation, at least among the pulmonates, may be considered a comparatively advanced character. The evidence of the above features, however, is far from conclusive.

Mead (1950: 280 sqq.) has contributed an interesting chapter on the phylogenetic relationships of the anatomically known Achatinidae. This author has shown that there is a tendency towards penial enlargement, resulting in a penial loop apical to the sheath. In *Metachatina* this loop is comparatively well developed, probably even more so than in any other genus of the family. This again does seem to indicate that *Metachatina* represents a recent and more advanced type of Achatinidae.

The isolation in southeastern Africa, far from the area in equatorial Africa where the family originally must have evolved, may point towards the fact that *M. kraussi* is either an ancient species surviving only in a marginal area or that it represents a new development near the tropical limits of the family. In Southern Africa the Achatinidae reach their southern limits around the George District (Cape Province) in a progressively narrower coastal strip, while south of Natal the number of species shows a rapid decline. This in fact is the typical distribution of tropical animal and plant species in Southern Africa (cf. Poynton, 1964). The more advanced nature of various characters as indicated above rather points towards the fact that the genus *Metachatina* is a comparatively new development in a submarginal area of the family.

4. Land molluscs of the Mkuzi and Ndumu Game Reserves

Because of the outstanding interest of the plains of northeast Zululand it was decided to investigate the terrestrial molluscs of the Mkuzi and Ndumu Game Reserves in order to assess the presence of tropical East African species in this particular area. Much of Zululand has already been opened up, but there are still places where flora and fauna have suffered less than elsewhere. The above-mentioned game reserves have been kept reasonably intact, although in the past both have not escaped neglect and even mismanagement. At the moment they are under excellent care, but certain trends in the development of this part of South Africa have given rise to great anxiety about the future. In January, 1964, an expedition was undertaken on which eleven days were spent in these game reserves in addition to shorter visits to other localities in Zululand and Swaziland.

4a. Topography, climate and vegetation

General data on Tongaland (N.E. Zululand, fig. 6) are few and far between (e.g., Roberts, 1936), so that a concise description of the area is not altogether out of place.

The Ndumu Game Reserve (pl. 3) occupies about 100 square kilometers (25.000 acres) in northeastern Zululand on the border of Mozambique. The northern boundary is formed by the Usutu River, which at the same time acts as international boundary; the eastern boundary lies somewhat east of the Pongola River, while the western and southern boundaries are largely straight and artificial. The numerous streams, rivers and pans are characteristic for this game reserve, which is mainly maintained as a sanctuary for hippopotamus. The climate is hot with a low rainfall, and midsummer droughts from 7 to 30 days duration are a common feature; morning mist occurs regularly in the winter season. The recorded rainfall varies from 500 to 675 mm (20 to 27 inches) per annum, the average for six years being 575 mm (23 inches). The monthly mean temperature in January is 26° C., and in July 19° C.; the whole plain lies within the 18° C. mean midwinter (July) surface temperature isotherm, which is usually taken to denote a tropical climate (see p. 19).

Thanks to Tinley (1964, and in litt.) extensive data on the vegetation are available. Six main types of vegetation may be distinguished:

I. Riverine and flood plain vegetation, of which the riverine forest and woodland is most important; this is characterized by high trees such as *Ficus sycomorus* (up to 28 m high), *Trichilia dregeana* and *Rauvolfia caffra.* This type of forest occurs mainly along the Usutu and Pongola Rivers in patches of various sizes.

II. Drainage line communities, mainly *Acacia detinens* thicket (along the southern border).

III. Rhyolite outcrop community.

IV. Deciduous tall *Acacia nigrescens* tree savanna and savanna woodland on stony soils; this type of vegetation is found in the southwestern corner of the reserve and on the south bank of the Nyamiti Pan.

V. Dry thicket, shrub and woodland on red and grey sandy soils, divided into *Acacia tortilis* woodland with thicket (extensively distributed in the northern area, e.g., around Shoku Pan) and *Acacia grandicornuta* — *Albizzia*

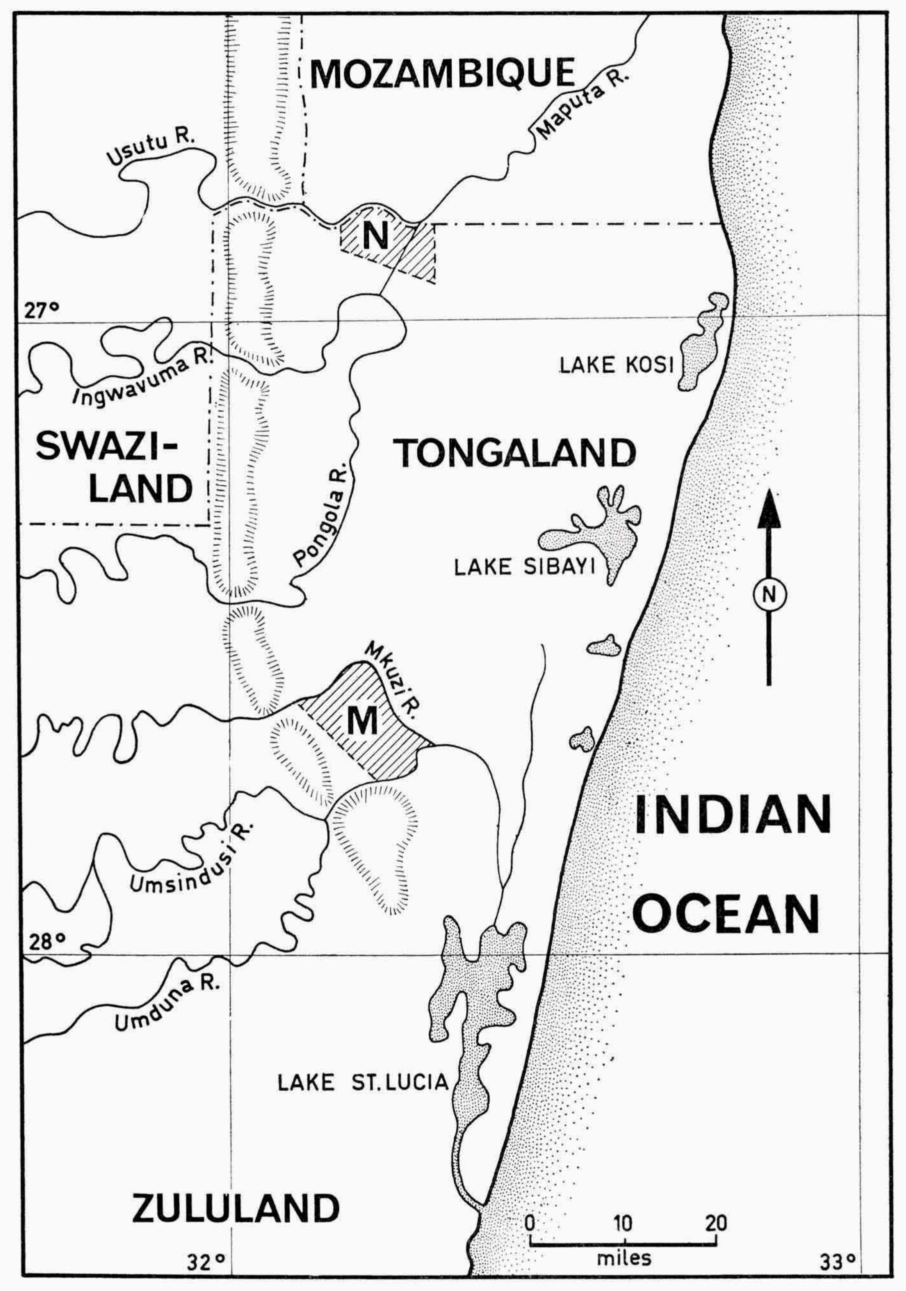


Fig. 6. Map indicating the position of the Mkuzi and Ndumu Game Reserves (M and N respectively).

evansii — *Albizzia anthelmintica* thicket mosaic (central area, Mahemane thicket, e.g., south of Banzi Pan).

VI. Xeric semi-deciduous forest and deciduous broadleaf savanna woodland on Plio-Pleistocene sands, divided into *Sclerocarya caffra* — *Terminalia sericea* — *Acacia burkei* savanna woodland (Ndumu Hill, area southwest of rest camp) and *Newtonia* — *Cleistanthus* — *Pteleopsis* xeric semi-deciduous forest (Khondo Forest, Engabatini Forest).

The Mkuzi Game Reserve (pls. 2, 3) occupies approximately 250 square kilometers (62.000 acres) east of the crest of the Lebombo range and south of the Mkuzi River; in fact the northern and eastern boundaries are formed by the Mkuzi River. The climate is hot with a low rainfall and sometimes periods of prolonged drought; during such periods the Mkuzi River may be reduced to a few pools of stagnant water in an otherwise sandy waste, underneath which there is still a fair flow of water. In the wet season this river sometimes flows very strongly, which incidentally shows that in many cases rivers are no barriers at all for the dispersal of certain animals. The Usutu and Pongola Rivers are permanent rivers. Few climatic data are available, such as the average annual rainfall for 13 years being 600 mm (24 inches); on the whole the climate closely resembles that of the Ndumu Game Reserve.

The area is similar to that of the Ndumu Game Reserve, although there is only a very limited amount of surface water. Data on the vegetation are not as yet available, but generally the same types of vegetation occur as have been described from the Ndumu Game Reserve. According to Tinley (personal communication) four main types of vegetation are represented by the following localities: Nhlonhlela Pan area and Mbanyana Bush (type II, viz., *Spirostachys africanus* woodland, and *Acacia detinens* thicket respectively); two miles from rest camp on road to gate (type IV, *Acacia nigrescens* tree savanna with *Acacia nilotica* and *Euclea daphnoides* thicket); Mhlala Bush, Gwambane, Malalaleni and Udisa area [type V, viz., *Acacia grandicornuta* — *Commiphora neglecta* thicket (Mhlala Bush) and *Acacia tortilis* savanna woodland and thicket (other localities)]; rest camp area, Bube Pan area (type VI, viz., *Sclerocarya caffra* — *Terminalia sericea* — *Acacia burkei* — *Combretum* savanna woodland, and *Newtonia* — *Cleistanthus* — *Pteleopsis* xeric semi-deciduous forest respectively). On the east-facing slopes of the Lebombo range in the Mkuzi Game Reserve the cover is chiefly *Combretum apiculatum* tree savanna and savanna woodland with evergreen ravine forest in gorges and along mountain streams.

4b. Systematic list

Only the latest literature references have been given. In the main the nomenclature and system of Zilch (1959-1960) have been followed.

GASTROPODA PROSOBRANCHIA

Pomatiasidae

Tropidophora (Ligatella) ligata (Müller, 1774)

Van Bruggen, 1966: 100; Van Bruggen, 1966a: 320.

MGR: Nhlonhlela Pan area (very common, variable in size, shape and bands); Udisa area (four, no bands); rest camp area (no or one band, one well-marked specimen); on road from rest camp to gate (one, no bands): sand forest, under logs, 30-31 May 1962, leg. D. G. Broadly (variable sample) (all NM); Mantumu Hill, KLT.

NGR: around Nyamiti Pan (one, no bands); halfway gate and rest camp (three unbanded and one with well-marked bands) (all NM).

Tropidophora (Ligatella) insularis (Pfeiffer, 1852)

Van Bruggen, 1966: 100.

MGR: Nhlonhlela Pan area (1 specimen, NM).

NGR: not observed.

Notwithstanding its fairly wide umbilicus the specimen is somewhat dubiously referred to *T. insularis*.

Tropidophora (Ligatella) plurilirata Fulton, 1903

Connolly, 1939: 549.

MGR: on road from rest camp to gate (NM).

NGR: not observed.

Recorded by Haas (1936: 33, 102) from "Mkuzi".

GASTROPODA PULMONATA

Veronicellidae

Laevicaulis natalensis natalensis (Krauss, 1848)

Forcart, 1967: 512; Van Bruggen, 1968: 48.

MGR: on road from rest camp to gate; sand forest, V-VI. 1962, leg. D. E. van Dijk (all NM); part of stomach contents of *Ichneumia albicauda* (Cuv.), 8. VIII. 1962, leg. J. E. Dixon (NM).

NGR: Pongola River forest near pump house (common): fig tree forest, confluence of Pongola and Usutu Rivers; around Nyamiti Pan (all NM).

The specimens from the stomach of a giant mongoose (*Ichneumia albicauda*), mentioned by Dixon (1964, Sample No. 5, p. 47), also belong to the present species (NM). All material was identified by Dr. L. Forcart.

Representatives of the Veronicellidae in Southern Africa appear to be drought-resistant slugs. Although they are also found in tropical rain forest, the thick and comparatively large mantle covering the whole animal may be considered an adaptation to dry conditions. This has also contributed to make the veronicellids successful emigrant snails in the tropics. Veronicellidae are definitely tropical (i.e., adapted to high surface temperatures) in their ecological requirements and distribution (see also chapter 7 and and Van Bruggen, 1968).

Pupillidae

Pupoides calaharicus (Boettger, 1886)

Van Bruggen, 1966: 104; Van Bruggen, 1966a: 327.

MGR: Nhlonhlela Pan area; Mhlala Bush (all NM).

NGR: not observed.

The specimens from Mhlala Bush were found in cracks of the bark of a tambootie tree (*Spirostachys africanus*), at a height of about 1½ m; very probably these were caught by dry weather after a heavy shower, which caused these normally ground-dwelling snails to climb the tree. An average specimen from Nhlonhlela Pan area is 5.2 mm long.

By virtue of its faculty to produce a thick epiphragm the species of *Pupoides* are also adapted to an arid climate. *Pupoides* avoids high rainfall areas, but is able to endure low temperatures. The genus enjoys a very wide distribution throughout the drier parts of all continents except Europe. Pilsbry (1921: 108) characterizes *Pupoides* as a "tropical genus of arid regions or relatively dry stations in humid areas", which certainly holds good for *Pupoides calaharicus* in Southern Africa. The status of the species has been discussed by Van Bruggen (1966a).

Enidae

Rachis jejuna (Melvill & Ponsonby, 1893), fig. 10

Van Bruggen, 1966: 100; Van Bruggen, 1966a: 329; Van Bruggen, 1967b: 8.

MGR: Nhlonhlela Pan area (very common); Mhlala Bush; Udisa area; Gwambane; Malalaleni (all NM); rest camp area = Mantumu Hill (very common, NM, also KLT).

NGR: Engabatini Forest; rest camp; halfway gate and rest camp (all NM); south of Nyamiti Pan, KLT.

Fairly variable in shape and convexity of the whorls; frequently with peripheral band, reaches good sizes:

Mhlala Bush (MGR)	17.3 × 7.9 mm
rest camp area (MGR)	17.5 × 7.6 mm
	17.9 × 7.8 mm
	18.0 × 8.3 mm
Nhlonhlela Pan area (MGR)	19.0 × 8.6 mm
	19.2 × 8.5 mm
	19.2 × 8.6 mm
	19.2 × 9.3 mm
	19.5 × 8.7 mm
	19.6 × 8.9 mm

The latter specimens to date are the biggest known, none of these has more than 7½ whorls. The body of *R. jejuna* is yellowish grey, the tentacles are grey and the black faeces in the rectum are visible through the transparent body wall.

The measurements of these Tongaland specimens may be summarized as follows: 17.3-19.6 × 7.6-9.3 mm, l/d 2.06-2.30. According to Van Bruggen (1966a) Kruger National Park specimens have the following measurements: 16.4-18.6 × 6.6-7.6 mm, l/d 2.20-2.42. From these data it is obvious that Tongaland populations are characterized by comparatively long and obese shells, while those of the Kruger National Park are much smaller and at the same time noticeably more slender. The climate of the Kruger National Park differs little from that of Tongaland, except for a somewhat lower rainfall and a slightly lower mean annual temperature. Also, the Kruger National Park is situated at a much higher altitude. In this respect it is interesting to note that a close examination of the distribution in the Kruger National Park (Van Bruggen, 1966a: fig. 11) shows that the smallest specimens were obtained in the driest area.

R. jejuna has so far in Zululand only been recorded from the banks of the Pongola River (Connolly, 1939); the localities in the Mkuzi Game Reserve are now the southernmost known for the species.

Recently the indefatigable collector Ken L. Tinley has obtained the species in South West Africa, thereby considerably expanding the known distribution. One specimen in diapause was collected in the northeast sandveld of the Etosha National Park "on shrub stems" on red sandy soil beneath *Terminalia prunioides* woodland and thicket in October 1967 (RMNH). Formerly *R. jejuna* was not known to occur west of Gwelo, Rhodesia, approximately 1375 km east of the Etosha National Park. The species, which consequently is new to South West Africa, is now known to be widely distributed in suitable arid and subarid habitats from Tongaland to Mozambique, Rhodesia and South West Africa (fig. 10, p. 32). Very probably it is restricted to certain types of vegetation, such as have been described in chapter 4a on pp. 21-23 (types II, IV, V and VI, woodland, savanna and thicket in various combinations with usually trees such as *Terminalia). Rhachistia sticta* frequently accompanies *Rachis jejuna*; comments on the distribution of the two species will be found on p. 31-32.

The specimen of *Rachis jejuna* from the Etosha National Park measures 15.0 × 7.0 mm, l/d 2.14, and has 6¾ whorls. Compared to the above data on size and shape it is a somewhat stunted shell; this may be due to the low rainfall of its South West African habitat, which is situated within the 20 inches isohyet and possibly enjoying the poorest rainfall within its range. Throughout its range *R. jejuna* has so far only been observed to favour the low rainfall areas. A preliminary conclusion that the largest shells are somehow correlated to a comparatively high rainfall does not seem to disagree with the findings of Rensch (1932).

R. punctata (Anton, 1839) occurs over an enormous area from Mozambique to India, including the islands of Madagascar, Zanzibar and Ceylon. West African records are probably secondary. 3) This species reaches its southernmost limits in Mozambique, in fact it is known from only one locality south of the Zambezi (Tete on the south bank). In addition the author has not found the species during his explorations in Rhodesia and Mozambique. South of the Zambezi *R. punctata* is replaced by *R. jejuna*; a close similarity in shell combined with anatomical data as supplied by Seshaiya (1932), Connolly (1939) and Van Bruggen (1966a) testifies to the close relationship of the two species. Undoubtedly *R. jejuna* has a common ancestry with *R. punctata*, having adapted itself to the dry savannas of Southern Africa. It is perhaps a matter of taste whether to consider *R. jejuna* a subspecies of *R. punctata* or to consider it a full species. In the author's opinion the latter may be preferred, because throughout its wide range *R. punctata*, although quite variable, has as far as known not given rise to any subspecies and also because *R. jejuna* and *R. punctata* are usually easily separated.

Edouardia cf. **caffra** (Pfeiffer, 1848)

Connolly, 1939: 424.

MGR: not observed.

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3) Both Pilsbry (1919: 304) and Germain (1935: 26) think it likely that *Rachis punctata* was accidentally imported by the Portuguese in traffic between such places as Goa in India and Loanda in Angola; this is easily accomplished by specimens in diapause adhering to lumber or plants. This hypothesis is seemingly confirmed by the presence of the species near port cities. However, to the present author a somewhat simpler solution has offered itself, viz., accidental transport from Mozambique to Angola around the Cape of Good Hope. A regular and frequent traffic between Portuguese East and West Africa is conducted throughout the year and it is perhaps more plausible to accept the shorter route as being most likely.

NGR: fig tree forest, confluence of Pongola and Usutu Rivers (NM).

A single juvenile shell of 12.7 × 9.4 mm, l/d 1.35, dark brown and with a bluntly angulate periphery on the body whorl, cannot be matched to any of the known South African species of the genus, but very probably belongs to *E. caffra*; this species has no peripheral angulation in adult shells, but "younger shells are distinctly, though bluntly, angulate" (Connolly, 1939: 424). So far *E. caffra* is only known from its type locality in the Transvaal, Mt. Mohapaani, Witfontein Mountains, W. Transvaal (not in Botswana, see Gyldenstolpe, 1934: 266, a reference obviously unknown to Connolly); new for Zululand.

The use of *Edouardia* in preference to *Conulinus* requires some explanation. Zilch (1959: 194) has synonymized *Edouardia* Gude, 1914, with *Conulinus* Von Martens, 1895; in the past this has been followed and various species quoted by Connolly (1939) sub *Edouardia* have in the past been enumerated by the present author sub *Conulinus*. This, however, is not acceptable, because the species assembled under the name *Edouardia* have microspiral engraving on the apex of the shell as distinct from *Conulinus* sensu Connolly (1939) and Verdcourt (1966). The latter two authors have also dwelt upon the nomenclatorial difficulties with regard to the above names.

Edouardia arenicola (Benson, 1856)

Connolly, 1939: 427.

MGR: Nhlonhlela Pan area (NM).

NGR: not observed.

Edouardia meridionalis (Pfeiffer, 1848)

Van Bruggen, 1967b: 9, s.n. *Conulinus meridionalis*.

MGR: on road from rest camp to gate (NM).

NGR: not observed.

New for Zululand. According to Sherborn (1928) the correct date for this species is 1848 and not 1847 as quoted by Connolly (1939) and others.

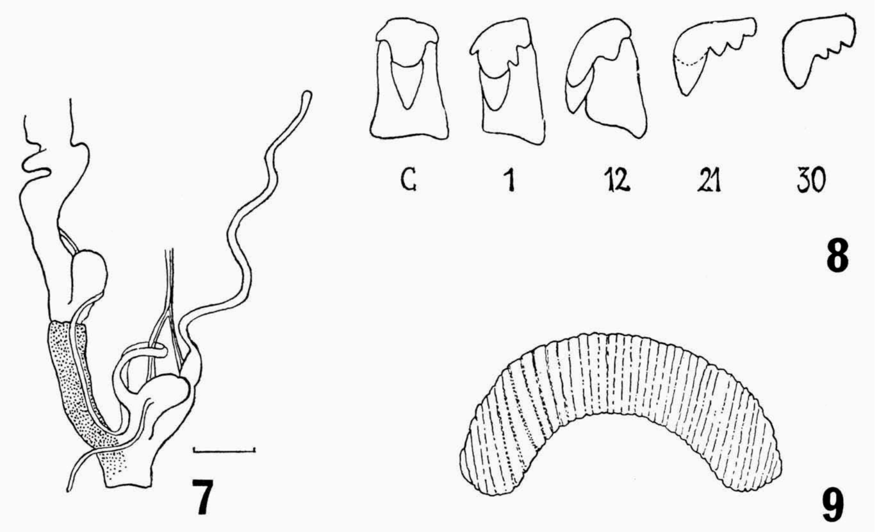
Edouardia cockerelli (Pilsbry, 1933), figs. 7-9

Connolly, 1939: 429.

MGR: not observed.

NGR: near Shoku Pan, on trunk of *Commiphora* (NM).

Only one live specimen was obtained. The shell measures 16.0 × 12.5 mm, l/d 1.28, and is straw-yellow in colour. It is not yet fully adult and the body whorl is slightly angulate. The animal was dissected in order to obtain genitalia, jaw and radula. Unfortunately the fragile shell had to be sacrificed. The genitalia are depicted in fig. 7. The penis has a very long appendix of about 20 mm. The epiphallus is thick and bulbous; from the epiphallus springs a fairly long and thin caecum. The thick vas deferens is looped between its origin and the penio-vaginal angle; at the latter point it suddenly becomes much thinner. The forked retractor muscle is attached to the base of the penial appendix and at the junction of the epiphallus and vas deferens. The vas deferens makes its loop around this branch of the retractor muscle. The large basal vagina is heavily pigmented resulting in a dark grey colour. The spermatheca is short, bulbous and almost ductless.



Figs. 7-9. *Edouardia cockerelli* (Pilsbry), near Shoku Pan, Ndumu Game Reserve (NM). 7, genitalia, scale 4 mm; 8, selected radula elements, highly enlarged; 9, jaw, span approximately 1 mm.

Unfortunately few data are available on the genital anatomy of species of the genus *Edouardia*; only *E. junodi* Conn. has been dissected and described by Hugh Watson in Connolly (1925: 155-158, text-fig. 17, pl. 8 figs. 5-7). Although one learns here that "Its general anatomy is of the same type as that of the other South African species of *Conulinus* which have been dissected", no other published data are available. Fig. 5 on pl. 8 in Connolly (1925) depicts the anterior part of the immature male genital organs of *E. junodi* Conn., which figure shows a striking resemblance to fig. 7 in the present paper.

Verdcourt (1966) has figured the genitalia of various East African species of *Conulinus* sensu Connolly, 1939, which is a different genus altogether. However, Verdcourt's figures 7-10 indicate that East African Enidae species of an allied genus have much the same type of genitalia.

The jaw (fig. 9) has a span of about 1 mm and is regularly arched with numerous coarse vertical folds; these folds are coarser and fewer than those of the jaw of *E. natalensis* (Krss.).

The radula measures 3.0 × 1.2 mm, and has about 130 transverse rows; the formula is 39-1-39 or 25-14-1-14-25. Radula elements (fig. 8) closely resemble those of *E. natalensis*, although the latter usually has fewer laterals and marginals (radula from Durban specimen: 19-12-1-12-19 × 114; do. from Pietermaritzburg specimen: 20-12-1-12-20 × 135).

E. cockerelli is evidently a rare species, until now only known from The Bluff, Durban; new for Zululand.

Edouardia conulus (Reeve, 1849)

Connolly, 1939: 431.

MGR: Mhlala Bush (NM).

NGR: around Nyamiti Pan (4, NM); Mabenane Bush, KLT.

The Ndumu specimens are sometimes slightly angulate at the periphery, but never show any bands and are always easily separated from *E. meridionalis* (Pfr.).

Edouardia sordidula (von Martens, 1897)

Van Bruggen, 1966a: 334, s.n. *Conulinus sordidulus*.

MGR: Nhlonhlela Pan area (common); Mhlala Bush; rest camp area (common) (all NM).

NGR: edge of Khondo Forest; Engabatini Forest; rest camp area (all NM).

The largest specimens from the Mkuzi Game Reserve measure 14.2 × 6.4 mm, 7½ whorls (leg./don. D. E. van Dijk), 13.3 × 6.1 mm (Nhlonhlela Pan area) and 12.6 × 6.3 mm (do.) respectively. The species is not known to grow to such a size in the Kruger National Park (Van Bruggen, 1966a).

Edouardia spec. indet.

MGR: rest camp area, one juvenile, not to be identified with any of the above species.

Rhachistia sticta (von Martens, 1859), fig. 10

Van Bruggen, 1966: 100; Van Bruggen, 1966a: 336; Van Bruggen, 1967b: 9.

MGR: Nhlonhlela Pan area; Mhlala Bush; Udisa area; Bube Pan area;

Mbanyana Bush; rest camp area; on road from rest camp to gate (all NM); Masinga Forest, in cracked bark of a tree, "4 ft high", KLT.

NGR: edge of Khondo Forest; around Nyamiti Pan (NM, also KLT).

The largest shells measure 23.6 × 12.5 mm (Mbanyana Bush, MGR) and 23.0 × 11.5 mm (around Nyamiti Pan, NGR) respectively.

Van Bruggen (1967b) has dwelt upon the distribution of *Rhachistia sticta,* which was up to the present thought to be restricted to a fairly narrow strip along the coast of the Indian Ocean from the Tugela River northwards into Central and East Africa and as far west as the Lundi area in Rhodesia. However, just like *Rachis jejuna* (vide supra), the present species appears to have a much wider distribution westward (see fig. 10 on p. 32). Once again the ecologist Ken L. Tinley has obtained additional material proving the occurrence in South West Africa. Five specimens are labelled as follows: "Mashi Flood Plain, Western Caprivi Strip", where they were collected "from amongst leaf litter" in "marginal flood plain woodland and thicket" in May, 1966 (RMNH). The shells are small, the largest specimen measuring only 18.0 × 9.7 mm.

As far as its ecological requirements are concerned, this species is somewhat enigmatic. Tinley (in litt.) comments as follows: "... they (i.e. *Rachis jejuna* and *Rhachistia sticta*) have always been associated in my experience with thicket or forest or woodland on *sandy* soil. In fact all the specimens of these two collected were in typical 'Tonga-like' conditions." "It is possible that with further collecting these two may be found to show a sandveld distribution in east and southern Africa mostly above the 500 mm isohyet (at this rain limit thicket can be supported on sandy soil). I made a careful search for these two molluscs in adjacent areas of clayey soils where thicket was common on termite hills — but found nothing. This just may be a lead in understanding their pattern of distribution." This agrees with the findings of the present author in Tongaland and the Kruger National Park. However, *Rhachistia sticta* also occurs in various types of forest, which come close to tropical rain forest, such as the Amatongas Forest near Gondola, Mozambique, at 1700 ft.

Succineidae

Succinea striata Krauss, 1848

Van Bruggen, 1966a: 343.

MGR: not observed.

NGR: around Nyamiti Pan, under log in short grass under fever trees (NM).

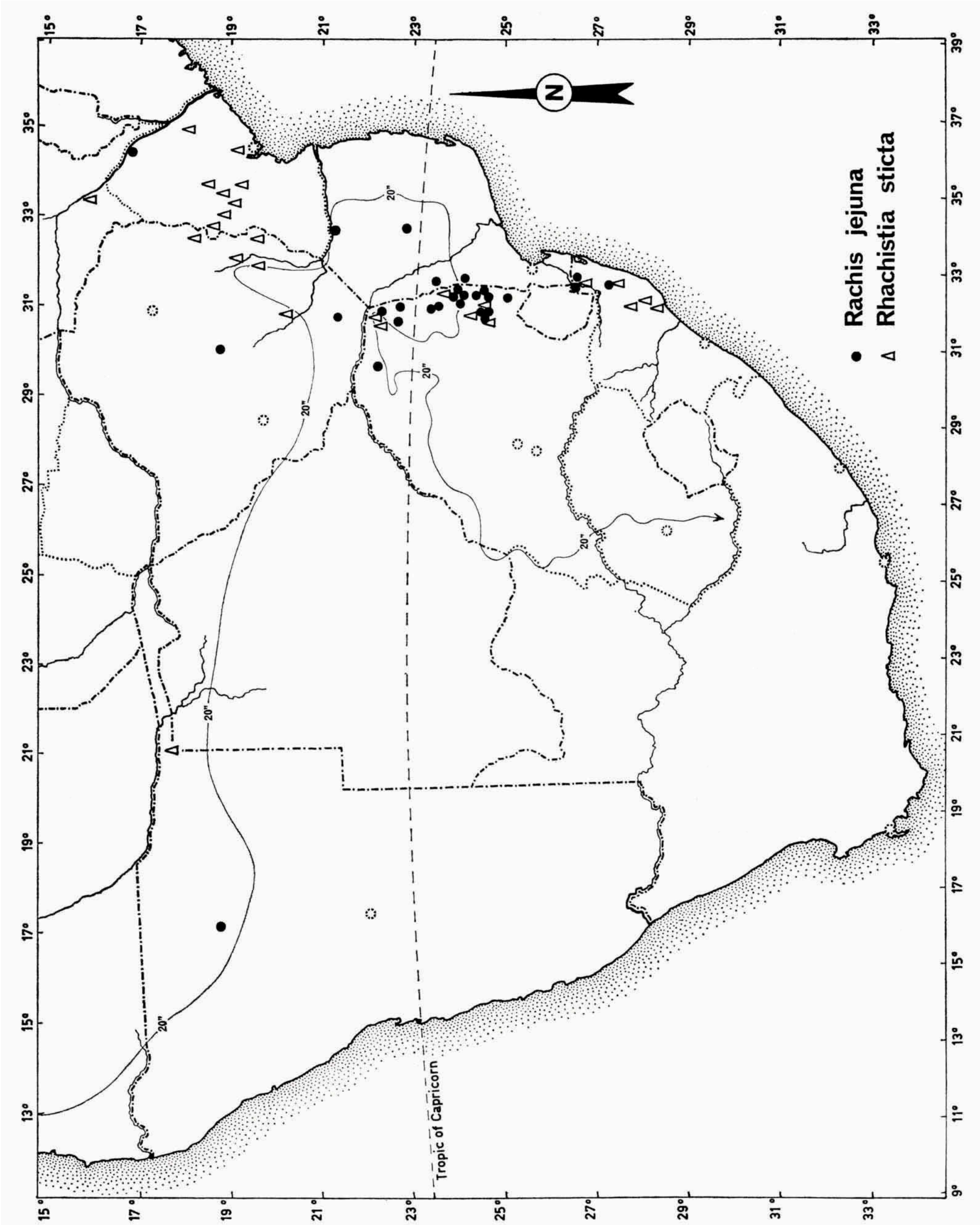


Fig. 10. Distribution of *Rachis jejuna* (Melvill & Ponsonby) and Southern African distribution of *Rhachistia sticta* (Von Martens). Attention is drawn to the new records for South West Africa. The 20 inches = 500 mm isohyet has been shown as a thin line marked with 20".

Endodontidae

Trachycystis bathycoele (Melvill & Ponsonby, 1892)

Connolly, 1939: 210.

MGR: not observed.

NGR: riverine forest on Pongola River bank east of Khondo Forest (on bark of living and dead trees); fig tree forest, confluence of Pongola and Usutu Rivers (all NM).

The spire is a little less depressed than in specimens from Pietermaritzburg, Winkelspruit and Ntimbankulu (NM). New for Zululand.

Trachycystis (Chalcocystes) burnupi (Melvill & Ponsonby, 1892)

Connolly, 1939: 194.

MGR: Nhlonhlela Pan area; rest camp area (all NM).

MGR: Banzi Pan bush (NM)".

The closely allied species *T. aenea* (Krss.) also occurs in Zululand, see sub "Other new records for Zululand".

Euconulidae

Guppya rumrutiensis (Preston, 1911)

Van Bruggen, 1967b: 10.

MGR: not observed.

NGR: Pongola River forest near pump house (one specimen on a piece of bark on ground in thick riverine forest, maj. diam. 2.1 mm); near Shoku Pan (in little patch of gallery forest with large trees, maj. diam. 2.2 mm) (all NM).

This species, which has only recently been reported from the Kruger National Park (Van Bruggen, 1966a, discovery of the species in Zululand already announced here), reaches its southern limits in Tongaland; it is a tropical element, which occurs as far north as Kenya. A short while ago Mr. Lamoral of the Natal Museum obtained two additional shells (NM), which are labelled as follows: "From forest humus in various areas on the eastern side of lake Sibaya, 24 to 30 June 1967". This so far appears to be the southernmost locality for the species. New for Zululand.

Urocyclidae

Sheldonia (Kerkophorus) poeppigii (Pfeiffer, 1846)

Van Bruggen, 1966a: 350.

MGR: not observed.

NGR: fig tree forest, confluence of Pongola und Usutu Rivers (NM).

Urocyclus (Elisolimax) flavescens (Keferstein, 1866)

Forcart, 1967: 542; Van Bruggen, 1968: 51.

MGR: near warden's house (NM); "Nagana Reserve" = Mkuzi Game Reserve (Connolly, 1939: 167, s.n. *Urocyclus pallescens* Ckll.).

NGR: rest camp area; Pongola River forest near pump house; on road to Nyamiti Pan; around Nyamiti Pan; fig tree forest, confluence Pongola and Usutu Rivers (all NM).

All specimens were identified by Dr. L. Forcart. The live colour varies from yellowish-grey to various shades of yellow; some individuals are almost white.

Subulinidae

Pseudoglessula (Kempioconcha) boivini (Morelet, 1860)

Van Bruggen, 1966: 101; Van Bruggen, 1966a: 358; Verdcourt, 1967: 53-54, 56 sqq.

MGR: Nhlonhlela Pan area (very common); Mhlala Bush (do.); Udisa area; loop road past Udisa; Mbanyana Bush; Bube pan area; rest camp area = Mantumu Hill (very common, also KLT); on road from rest camp to gate (all NM).

NGR: edge of Khondo Forest; Engabatini Forest; around Nyamiti Pan (common, also KLT); on road from rest camp to gate (all NM); Mabenane Bush, KLT.

The shells from the Mkuzi Game Reserve do not quite reach the size of those from the Ndumu Game Reserve, the largest shells measuring 21.3 (Nhlonhlela Pan area), 21.0 (Mhlala Bush), 21.4, 21.2 and 20.6 mm (rest camp area) respectively; the largest shells from the Ndumu Game Reserve are 22.4 (Engabatini Forest), 22.8 (edge of Khondo Forest) and 23.2 mm (around Nyamiti Pan) long respectively. Recorded by Haas (1936) from "Mkuzi" s.n. *P.* (*K.*) *zulu* Haas.

Curvella saundersae Connolly, 1910

Connolly, 1939: 365.

MGR: Nhlonhlela Pan area (NM).

NGR: Engabatini Forest (NM).

The largest shell measures 10.4 × 3.7 mm, l/d 2.81 (Nhlonhlela Pan area, MGR); the largest shell in the Natal Museum measures 9.9 × 3.5 mm, l/d 2.83 (Mfongosi), while Connolly (1939) gives 7.6 × 3.4 mm, l/d 2.23. The available specimens agree well with material identified by Connolly (NM).

Curvella amicitiae Van Bruggen, 1968

Van Bruggen, 1968: 52, figs. 2-3.

MGR: Mhlala Bush, 1 specimen (NM, paratype).

NGR: not observed.

The species is widely distributed in the Kruger National Park and Rhodesia. It is described in a supplement to the Kruger National Park paper (Van Bruggen, 1968).

Euonyma tugelensis (Melvill & Ponsonby, 1897)

Connolly, 1939: 344.

MGR: not observed.

NGR: Banzi Pan bush (NM, 1 juv.).

Achatinidae

Achatina (Lissachatina) craveni Smith, 1880, fig. 11

Van Bruggen, 1966: 101.

MGR: Nhlonhlela Pan area; rest camp area (juv.) — all striped specimens (NM).

NGR: rest camp area (1 live specimen with striped shell, NM).

Notwithstanding the recent findings of Crowley & Pain (1964) Smith's name has been retained; Crowley & Pain synonymize *A. craveni* with *A. tavaresiana* Morelet, but unfortunately no anatomical data are available as yet. Moreover, the habitat of *A. tavaresiana* s.l. ranges from pure desert to tropical rain forest, which does not seem to support the idea of a single species. The shell varies considerably, which has also accounted for the (perhaps only temporary) retention of the name *A. craveni.* The present specimens fully agree with Natal Museum material recorded by Connolly (1939) and the species occurs in various other localities in Zululand and Swaziland (new for both these areas) as well. These apparently constitute the southernmost records for the species, which clearly is another of the tropical Central and East African elements occurring as far south as Zululand.

The specimen from the rest camp area (NGR) was dissected in order to investigate the genitalia (fig. 11). The shell of this specimen measures 63.5 × 35.0 mm and is thus still immature. The penis is completely ensheathed; the thick vas deferens enters the side of the penis sheath. The spermatheca is very large indeed and is lodged inside a coil of the basal uterus (shaded in fig. 11). The vagina is short and thick. The genitalia on the whole are fairly compact, which is probably caused by the fact that the animal is not yet full-grown. Comparison with anatomical data recorded by Mead (1950) reveals that among the as yet dissected species of *Achatina* there is obviously none which exhibits genitalia that resemble those of the present specimen of *A. craveni*.

Archachatina zuluensis (Connolly) is not always easily distinguished from *Achatina craveni*; usually the sculpture of the former is weaker, particularly on the body whorl, but the difference in the apex of the shell (which is supposed to separate the genera *Achatina* and *Archachatina*) is not always quite evident. There is, however, a marked ecological difference, *Archachatina zuluensis* being restricted to the dune (or coastal) forest and also probably the forests on the Lebombo escarpment, while *Achatina craveni* occurs in the plains in between (see also chapters 4c and 6).

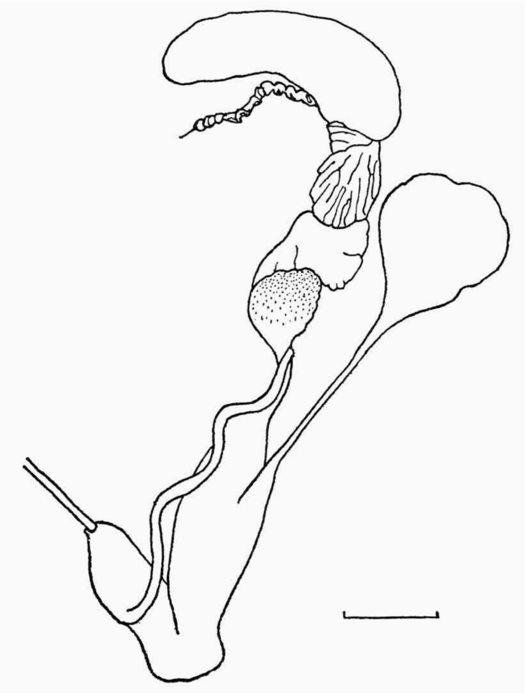


Fig. 11. *Achatina craveni* Smith, rest camp area, Ndumu Game Reserve (NM), genitalia, scale 10 mm.

Achatina (Lissachatina) immaculata Lamarck, 1822

Van Bruggen, 1966: 101, 109; Van Bruggen, 1966a: 371; Van Bruggen, 1967a: 19; Van Bruggen, 1968: 54.

MGR: Nhlonhlela Pan area (common); rest camp area; sand forest, 30-31. V. 1962, leg. D. G. Broadley (all NM).

NGR: Usutu River area; around Nyamiti Pan; Engabatini Forest (all NM).

The status of this species has been fully discussed in the author's Kruger National Park paper (Van Bruggen, 1966a). The species is common on the flats of northeastern Zululand; two live specimens were obtained, which upon dissection proved to conform to the general pattern of the genitalia (looped penis and basal vagina with compound folds) of this variable species. Zululand specimens usually possess heavy and thick shells which reach a fair size; the two largest specimens measure 129+ × 69 mm (Nhlonhlela Pan area, MGR) and 127 × 72 mm (Engabatini Forest, NGR) respectively. In the K. L. Tinley collection is a specimen of 119 × 65 mm from the Ndumu Game Reserve without exact locality.

In more or less weathered shells the pink on the columella tends to fade and specimens with an almost pure white columella have not infrequently been observed. Attention should be drawn to two instances were this has led to incorrect identification. Franca (1960: 87, pl. 17) has recorded and figured *Achatina fulica* Bowd. from Inhaca Island; the photograph clearly shows that *A. immaculata* is meant here. Also, during a visit to the Museu Álvaro de Castro (Lourenço Marques) on 22nd May, 1965, it was found that specimens from Inhambane were exhibited s.n. *A. fulica*.

Rhytididae

Nata vernicosa (Krauss, 1848)

Van Bruggen, 1966a: 376; Van Bruggen, 1967b: 29.

MGR: Nhlonhlela Pan area; rest camp area (all NM).

NGR: around Nyamiti Pan (NM).

Very probably what Haas (1936) referred to as *Natalina caffrula* Melv. & Pons. (fide Connolly, 1939).

Streptaxidae

Gonaxis gwandaensis (Preston, 1912)

Van Bruggen, 1966: 103, 109; Van Bruggen, 1966a: 378; Van Bruggen, 1967b: 30.

MGR: on road from rest camp to gate, 2 juv. (NM).

NGR: not observed.

This is the southernmost record for both genus and species (new for

Zululand, vide Van Bruggen, 1963, fig. 5). Juveniles of this species may be recognized by the crenellate sutures.

Gulella triglochis (Melvill & Ponsonby, 1903)

Connolly, 1939: 26.

MGR: Nhlonhlela Pan area; rest camp area (all NM).

NGR: South bank of Nyamiti Pan (NM).

Gulella triglochis is one of the species recorded from "Mkuzi" by Haas (1936, s.n. *Diaphera triglochis*).

The species is widely distributed from Botha's Hill (Natal) to as far north as Mozambique; the northernmost records are Swaziland, Ingwavuma Road, 900-1000 ft., leg. A. C. and W. H. van Bruggen (NM; new for Swaziland) and Mozambique, Inhaca Island, Punta Tomes Beach, leg. P. H. Boshoff (RMNH; new for Mozambique). *G. triglochis* has its headquarters in coastal Zululand, although it occurs inland as far as Melmoth at over 1500 ft.

G. triglochis exhibits a good deal of variation. The vertical sculpture varies from smooth to weakly costulate, while sometimes there are also indications of spiral sculpture. The dental processes, on the other hand, are fairly constant; only rarely is the basal process poorly developed, such as in the larger paratype (Botha's Hill, Tyeloti Hill, leg. H. C. Burnup, NM 1428, type 581, two paratypes). These specimens are from the southern limits of the range of the species and therefore may show marginal effects because of limited gene flow. The length of the shell is subject to much variation and for the species as a whole may be summarized as follows: 7.5-14.1 × 4.0-7.5 mm, l/d 1.70-2.14 (all l/d have been computed from micrometer readings). This is probably caused by the variety of habitats and microclimate in which this obviously ecologically tolerant species is found. *G. triglochis* inhabits both forest and savanna, as demonstrated by labels such as "dune scrub", "dune forest", "indigenous bush", "forest humus", and its occurrence in notably dry environments such as the Mkuzi and Ndumu Game Reserves. Generally one may say that the larger shells occur in forest (Gwaliweni Forest, leg. K. L. Tinley, KLT and RMNH: 13.6-14.1 × 7.0-7.5 mm, l/d 1.81-2.01) in the northern parts of its range and smaller shells in savanna-like environments and further south. There are vague indications of a size-cline from south to north, but environmental complications obscure the picture. The smallest shell examined (Kosi Bay, leg. F. Toppin, NM: 7.5 × 4.4 mm, l/d 1.70) was obtained in dune scrub, an environment considered favourable for representatives of *Gulella*. There is no satisfactory explanation for these phenomena, but changes in the climate since the Pleistocene may be responsible for these mosaic distribution patterns.

Gulella gouldi (Pfeiffer, 1855), figs. 12-15

Tongaland specimens of this species have necessitated a complete revision of the species, which has resulted in the description of a new subspecies and the sinking into synonymy of a well-known species.

Gulella gouldi may be diagnosed as a medium-sized to large, costulate species with six-fold dentition; the shell measures 4.6-11.7 × 2.3-5.1 mm, l/d 1.78-2.53. *G. gouldi* occurs over a large area in southeastern Africa (Eastern Cape Province to Southern Zululand, nominate subspecies and *discriminanda* nov. subspec.) and also in East Africa (Tanganyika, Usambaras, subspecies *globulosa* Pfr., 1952).

Gulella gouldi gouldi (Pfeiffer, 1855), figs. 14-15

Ennea gouldi Pfeiffer, 1855, Malak. Blätt., 2: 174; Pfeiffer, 1856, Novit. Conch., 1: 72, pl. 20 figs. 7-10; Pfeiffer, 1859, Monogr. Helic. Viv., 4: 339; Pfeiffer, 1868, Monogr. Helic. Viv., 5: 454; Pfeiffer, 1876, Monogr. Helic. Viv., 7: 504; Pfeiffer & Clessin, 1878, Nomencl. Helic. Viv.: 19; Tryon, 1885, Man. Conch. (2), 1: 98, pl. 19 fig. 13; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond., 3: 168; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 542 (6), 554 (18); Kobelt, 1904, Conch. Cab. 1, 12B: 193, pl. 24 figs. 11-12; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nassau. Ver. Naturk., 63: 160 (*gouldii*); Connolly, 1912, Ann. S. Afr. Mus., 11: 75.

Enneastrum gouldi; Bourguignat, 1889, Moll. Afr. Équat.: 127.

Gulella gouldi; Connolly, 1932, Ann. Natal Mus., 7: 82, figs. 3a-d; Pilsbry & Cockerell, 1933, Proc. Zool. Soc. Lond.: 365; Connolly, 1939, Ann. S. Afr. Mus., 33: 58; Barnard, 1951, Beginner's Guide S. Afr. Shells: pl. 21 fig. 5.

Ennea crossleyana Melvill & Ponsonby, 1893, Ann. Mag. Nat. Hist. (6), 12: 106, pl. 3 fig. 8; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond., 3: 167; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 542 (6), 554 (18); Kobelt, 1904, Conch. Cab. 1, 12B: 196, pl. 24 fig. 16; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nassau. Ver. Naturk., 63: 160; Connolly, 1912, Ann. S. Afr. Mus., 11: 71. Nov. syn.

Gulella crossleyana; Connolly, 1932, Ann. Natal Mus., 7: 82, 84, fig. 3e; Connolly, 1939, Ann. S. Afr. Mus., 33: 58; Zilch, 1961, Arch. Moll., 90: 93.

Ennea gouldi var. *excedens* Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 542 (6), 554 (18), pl. 1 fig. 3; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond., 3: 169; Connolly, 1912, Ann. S. Afr. Mus., 11: 75.

Diagnostic characters. — A medium-sized to large, costulate species with six-fold dentition consisting of angular lamella, three labral processes, basal denticle and columellar lamella.

Description of shell. — Shell (fig. 14) medium-sized to large, cylindrical to subcylindriform, rimate. Spire produced, sides straight to slightly convex, (sub)parallel, apex obtusely conical. Whorls 6-8¼, somewhat convex, sculptured with close, regular, oblique costulae; sutures shallow, crenellate. Aperture little obstructed by six-fold dentition: strong, almost vertical, angular lamella, scarcely connected with apex of labrum; three labral denticles, the upper smallest, the other two subequal, corresponding to extensive, shallow, outside depression; basal denticle to the left of base; prominent, mamillate, columellar lamella.

Measurements of shell: 4.6-11.7 × 2.3-5.1 mm, l/d 1.78-2.53. The type, formerly in the Stettin Museum, now lost, was said to measure 8.5 × 4.0 mm, l/d 2.12. Smallest specimen (Pietermaritzburg, NM) 4.7 × 2.6 mm, l/d 1.81, largest shell (Port Shepstone, NM) 11.7 × 5.1 mm, l/d 2.29. Average specimens measure (Pietermaritzburg, NM) 6.0 × 2.7 mm, l/d 2.18, aperture 2.0 × 2.1 mm, last whorl 3.2 mm and (Port Shepstone, NM) 9.2 × 4.4 mm, l/d 2.11, aperture 3.1 × 3.0 mm, last whorl 4.5 mm respectively.

Distribution (fig. 15). — *G. g. gouldi* occurs from the Eastern Cape Province to southern Zululand.

CAPE PROVINCE: Bathurst (Connolly, 1939); Qolora River mouth, R. F. Lawrence (NM); Kentani (SAM); Port St. Johns (includes Second Beach and Umgazi River mouth), H. C. Burnup (NM); do., W. Falcon (NM); do., R. F. Lawrence (NM alc.); do., G. C. Shortridge (SAM); Mbotjie Beach bush (Connolly, 1939); "Cape of Good Hope" (BM). NATAL: Port Edward, R. F. Lawrence (NM); do., W. G. Rump (NM); Trafalgar, R. F. Lawrence (NM, NM alc.); Margate, W. G. Rump (NM); Port Shepstone (includes Beach Terminus), H. C. Burnup (NM 1461, NM); do., W. Falcon (NM, RMNH); do., R. F. Lawrence (NM); do. (BM); Southport, H. J. Puzey (DM, Puzey colln. 67); Umzimkulu (SAM); Ifafa, H. C. Burnup (NM).; Kelso Junction, R. F. Lawrence (NM alc., RMNH alc.); Equeefa, H. C. Burnup (NM); Clansthal, W. Falcon (NM, RMNH); do., G. E. Pennington (NM); Umkomaas, H. C. Burnup (NM 1460, NM, TP); Illovo River, H. C. Burnup (NM, RMNH); Ntimbankulu, H. C. Burnup (NM); Winkelspruit, H. C. Burnup (NM); Isipingo, C. W. Alexander (NM); do. (BM); Durban (includes Bellair, Bluff and Salisbury Island), H. C. Burnup (NM); do., W. Falcon (RMNH); do., Mrs. Nancy Gardiner (NM alc.); do. (BM, SAM); Pinetown, H. C. Burnup (NM); Kranskloof, H. C. Burnup (NM); Gillitts, R. S. Benton (NM); Botha's Hill (includes Tsheloti), H. C. Burnup (NM); Drummond, Nagle Dam, R. F. Lawrence (NM alc.); Inchanga, W. Falcon (NM); do., R. F. Lawrence (NM alc.); Table Mountain, H. C. Burnup (NM); Pietermaritzburg (includes Allerton, Chase Krantzes, Cope's Folley, Scottsville, Slangspruit, Umsinduzi River), A. C. van Bruggen (NM alc.); do., H. C. Burnup (BM 1903.3.11.72, holotype of *Ennea crossleyana*; BM 1937.12.30.769-72, four paratypes of *Ennea crossleyana*; NM 1454, NM, NM alc., RMNH); do., W. Falcon (NM); do., W.

G. Rump (NM); do., B. R. Stuckenberg (NM); Bisley, R. F. Lawrence (NM alc.); Thornybush = Thornville, H. C. Burnup (NM); Hilton, W. Falcon (NM, RMNH); Zwartkops, Pepworth's grounds, H. C. Burnup (NM alc.); Impolweni, W. G. Rump (NM); Umhloti Beach, W. G. Rump (NM); Tongaat, H. C. Burnup (NM); Umhlali (includes Sheffield Beach), H. C. Burnup (NM); do., R. F. Lawrence (NM, NM alc.); do., A. D. J. Meeuse (NM, RMNH); do., W. G. Rump (NM, RMNH); Stanger, G. E. Pennington (NM); Sinkwazi, Miss M. F. Hickey (NM); do., G. E. Pennington (NM); Kranskop (includes Untunjambili and Zimbaba Bush), A. C. and W. H. van Bruggen (NM); do., H. C. Burnup (NM); do., W. Falcon (NM); do., W. G. Rump (NM); "Natal" (BM, NM, RMNH ex H. B. Preston). ZULULAND: Richards Bay (NM); Nkandhla Forest, R. F. Lawrence (NM alc.); "Zululand" (BM 52.1.14.28, NM).

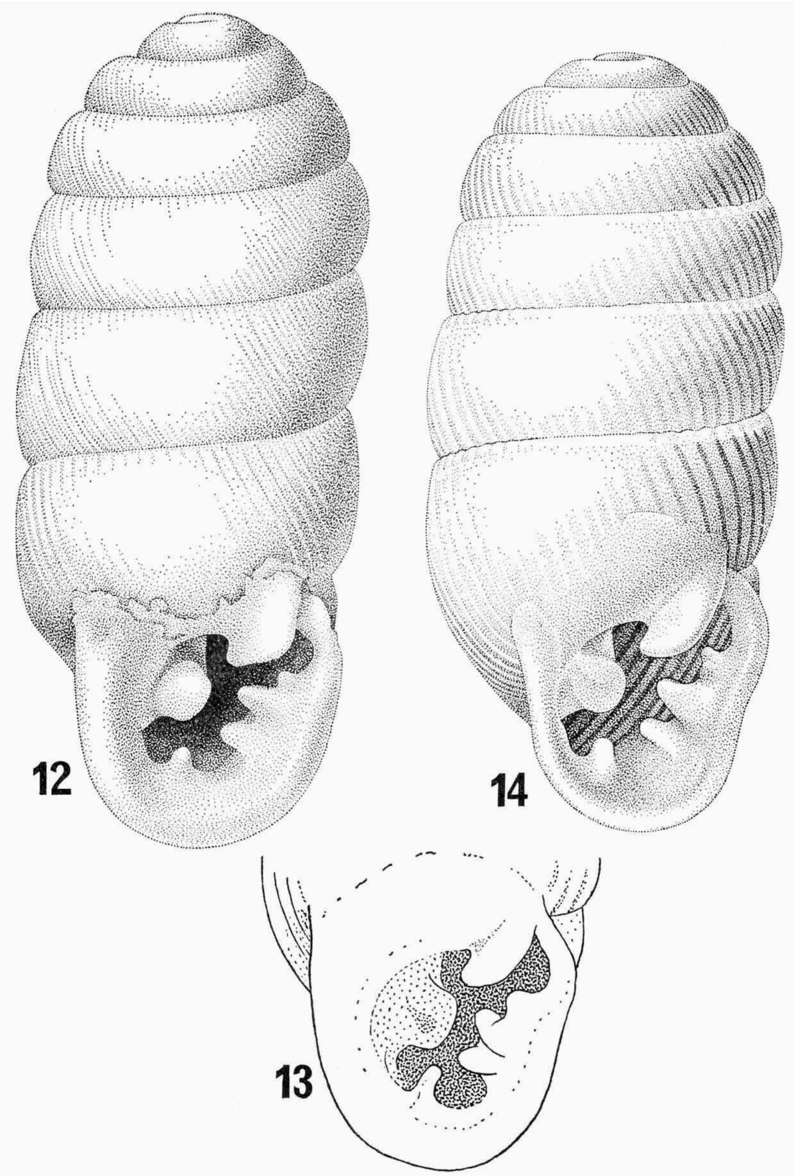
Type locality: "Natal", later emended by Pfeiffer himself (1859) to Port Natal = Durban, where first collected by Plant some time between 1824 and 1855.

G. g. gouldi, originally described in a footnote, occurs over an enormous area in Southern Africa; it is subject to quite a lot of variation in the shell, particularly in size. A superficial examination of the extreme types of shell makes one at once understand why in the past two taxa have been recognised. Only series from throughout the range of the species have enabled the present author to synonymize *G. crossleyana*; both nominal species are connected by intermediates. *G. crossleyana* is nothing but a high altitude variant of *G. gouldi*. Although taxonomically incorrect, the name may be retained for the Pietermaritzburg district populations, i.e. *G. gouldi crossleyana*.

Throughout the range various size clines may be discerned. The coastal pattern is one of a steady decrease in length and width, while the l/d is only subject to minor variations. This is demonstrated by the following table:

Bathurst-Port Shepstone	6.9-11.7 × 3.4-5.1 mm,	l/d 1.84-2.47
Southport-Winkelspruit	7.1-11.5 × 3.5-5.1 mm,	l/d 1.89-2.41
Isipingo-Tongaat	7.1- 9.1 × 3.6-4.2 mm,	l/d 1.90-2.23
Umhlali-Sinkwazi	6.7-10.1 × 3.5-4.5 mm,	l/d 1.86-2.53
(Richards Bay, 1 shell	7.6 × 4.0 mm,	l/d 1.91)

The various areas have been enumerated from south to north along the coast; the point is perhaps best demonstrated by giving the mean values: 9.3 × 4.2 mm, l/d 2.15; 9.3 × 4.3 mm, l/d 2.15; 8.1 × 3.9 mm, l/d 2.06; 8.4 × 4.0 mm, l/d 2.19. The above figures show that initially, i.e. from Bathurst to about Winkelspruit or a distance of over 500 km with a noticeable increase in both



Figs. 12-14. Shells of 12, *Gulella gouldi discriminanda* n. ssp., paratype, edge of Khondo Forest, Ndumu Game Reserve (RMNH), actual length 6.7 mm; 13, aperture of holotype (NM), highly enlarged; 14, *Gulella gouldi gouldi* (Pfeiffer), Pietermaritzburg, leg. H. C. Burnup (RMNH, ex NM 1454), actual length 6.4 mm. N.B. The costulae of *Gulella gouldi discriminanda* are not very pronounced because of wear of the shell; see also plate 4.

temperature and rainfall, there is no increase in length or major diameter. Only north of about Winkelspruit do the shells become appreciably smaller. No explanation is attempted here.

There is also a size-cline from the coast to inland localities; this may be explained by the effects of rapidly increasing altitude.

Isipingo-Tongaat	7.1-9.1 × 3.6-4.2 mm, l/d 1.90-2.23
Pinetown-Table Mountain	6.2-8.7 × 3.0-3.7 mm, l/d 1.84-2.39
Pietermaritzburg dist.	4.6-7.4 × 2.2-3.0 mm, l/d 1.78-2.48

Or, expressed in mean values: 8.1 × 3.9 mm, l/d 2.06; 7.5 × 3.4 mm, l/d 2.11; 6.0 × 2.6 mm, l/d 2.13. There is also obviously a tendency for the shells to grow more slender inland.

The populations from Impolweni and Kranskop are somewhat confusing, the shells measuring 5.1-6.7 × 2.7-3.0 mm, l/d 1.86-2.25 and 5.5-8.7 × 2.9-4.0 mm, l/d 1.91-2.33 (mean values 5.9 × 2.9 mm, l/d 2.05 and 7.1 × 3.4 mm, l/d 2.12) respectively. Both are inland localities considerably higher than Pietermaritzburg. The single shell from the Nkandhla Forest (NM alc.), at approximately the same elevation as Impolweni and Kranskop, measures 7.9 × 3.7 mm, l/d 2.10.

The apertural dentition is subject to some variation, but the number of aberrant shells found among approximately 570 specimens is surprisingly small. The labral processes may be weakly developed, in one specimen the upper process is even completely absent (Umhlali, NM); a large shell (Southport, DM) has an additional tubercle between the upper two processes and in another specimen (Allerton, Pietermaritzburg, NM) the upper process is connected with the median process by a ridge. The single specimen from the Nkandhla Forest (NM alc.) has a basal denticle that is an inrunning ridge rather than a denticle; this may be a local variant rather than an abnormality.

Connolly (1932, 1939) already drew attention to the swelling or tubercle on the columellar lip, which may be interpreted as an outer columellar lamella; this author knew examples of this from Hilton (NM, RMNH). Obviously only one or two populations from that area show this peculiarity, because certain other samples from near Hilton (Otto's View, Hilton College grounds) contain no specimens exhibiting this character. Falcon even gave his specimens a manuscript name referring to the locality. It is interesting to mention here that another species, *G. infrendens* (Mts.), normally has an outer columellar lamella, at least in part of its range, and that this process is particularly well developed in populations in the Hilton district. Outside the Hilton district *G. g. gouldi* only very rarely exhibits this additional process, such as in a shell from Durban (RMNH) and from „Zululand" (BM).

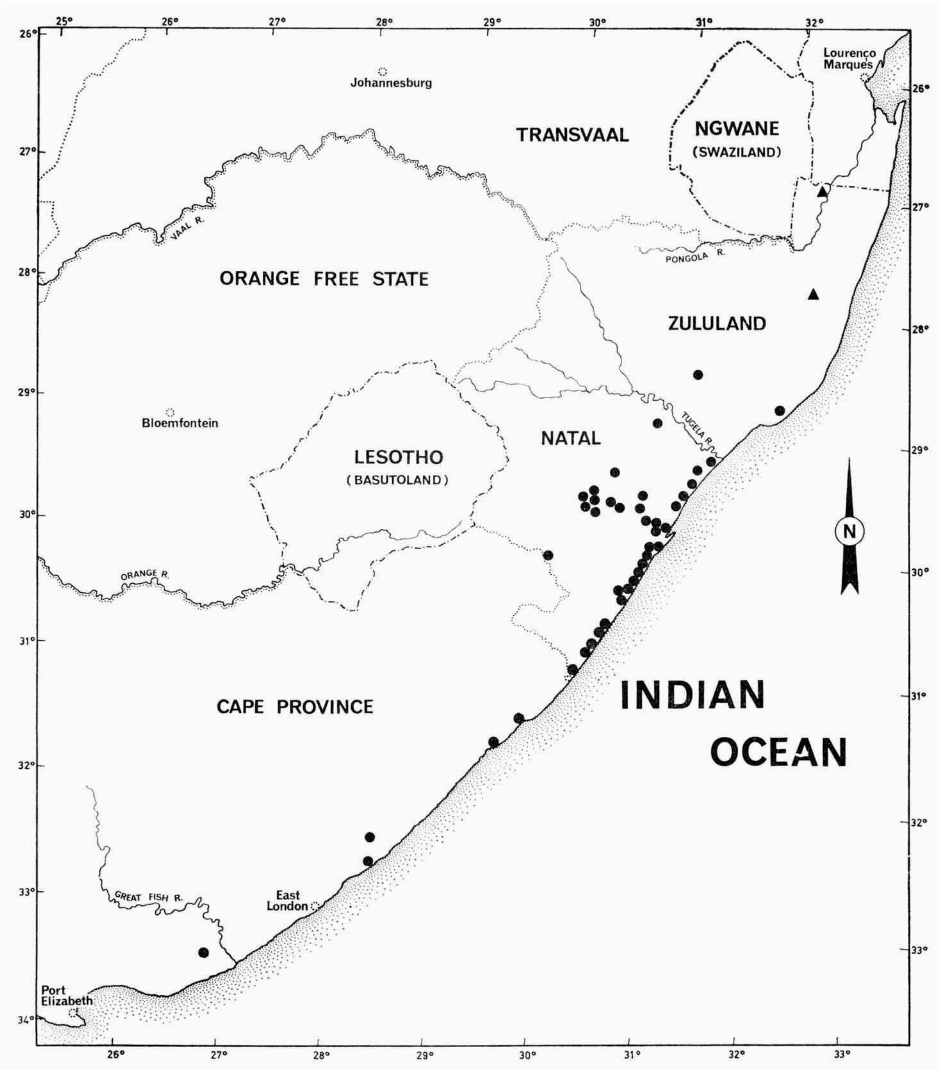


Fig. 15. Southern African distribution of *Gulella gouldi* (Pfeiffer); localities of the nominate subspecies have been indicated by dots and those of *Gulella gouldi discriminanda* n. ssp. by triangles.

G. g. gouldi prefers forest and bush types of vegetation, which is demonstrated by information from labels and field notes: "coastal bush", "in bush near sea", "under rotten log in indigenous bush", "indigenous forest". It has also taken kindly to Man's influence on Nature, particularly in the Pietermaritzburg district: "in garden", "in vegetable compost in garden" (Natal

Museum grounds now occupied by extensions to the original building), "under stones near school" (Hilton College).

Gulella gouldi discriminanda nov. subspec., figs. 12-13, 15, pl. 4

Diagnostic characters. — A dry country subspecies of *G. gouldi* with small, comparatively slender, shell.

Description of shell. — Differing from that of the nominate subspecies in flatter whorls, very thick peristome and somewhat divided columellar process, not connected with the outer lip. The outer columellar lamella is always absent.

Measurements of shell: 5.8-7.3 × 2.6-3.0 mm, l/d 2.07-2.43. The holotype measures 6.6 × 2.9 mm, l/d 2.28, aperture 2.2 × 2.3 mm, last whorl 3.3 mm. Smallest shell (Mkuzi Game Reserve, NM) 5.8 × 2.6 mm, l/d 2.23, largest specimen (Ndumu Game Reserve, NM) 7.3 × 3.0 mm, l/d 2.43.

Animal yellow.

Distribution (fig. 15). — *G. gouldi discriminanda* only occurs in the dry plains of Tongaland.

ZULULAND: Mkuzi Game Reserve, rest camp area, A. C. and W. H. van Bruggen (NM 4246, type 1122, one paratype); do., on road to gate, A. C. and W. H. van Bruggen (MT, one paratype; NM 4247, type 1123, five paratypes); Ndumu Game Reserve, edge of Khondo Forest, A. C. and W. H. van Bruggen (NM 4244, type 1119, holotype, fig. 13, pl. 4; NM 4244, type 1120, four paratypes; RMNH, one paratype, fig. 12); do., Engabatini Forest, A. C. and W. H. van Bruggen (NM 4245, type 1121, one paratype).

Type locality: Ndumu Game Reserve, edge of Khondo Forest, where first collected by A. C. and W. H. van Bruggen on 12 January, 1964.

G. gouldi discriminanda occurs to the north of the typical form, which so far has not been found north of Richards Bay; obviously this dry country subspecies is an offshoot of the southerly, shade and moisture-loving, *G. g. gouldi*. The latter only rarely occurs in southern Zululand; a mere two specimens (Richards Bay, NM; Nkandhla Forest, NM alc.) are available for study. These shells are comparatively obese. It should be noted that the animal of *G. g. gouldi* is (orange)red and that of *G. g. discriminanda* yellow. It appears for the present that both forms, though undoubtedly closely allied, are ecologically and geographically separated; this in addition to a number of minor morphological characters makes the new status as a subspecies of *G. gouldi*, rather than a species of its own, acceptable at least to the present author.

This taxon also displays a noticeable size-cline from south to north as shown by the following data:

Mkuzi Game Reserve	5.8-6.3 × 2.6-2.9 mm, l/d 2.07-2.23
Ndumu Game Reserve	6.2-7.3 × 2.8-3.0 mm, l/d 2.22-2.43

Both length and major diameter increase from south to north and at the same time the shells become noticeably more slender (mean l/d 2.15 and 2.32 respectively).

G. gouldi is essentially a forest dweller; it must have had an enormous distribution when the climate of Africa was characterized by a much higher precipitation. During the cool-humid pluvial of hypothermal periods in the Pleistocene, the forest of East and Southern Africa must have formed a continuous belt. With the onset of drier conditions the forest was split up and *G. gouldi globulosa* Pfeiffer, 1952, became isolated in the Usambaras in Tanganyika. The latter is a smallish and comparatively obese subspecies (4.7-5.5 × 2.7-3.3 mm, type 5.0 × 2.8 mm, l/d 1.78). In Southern Africa *G. g. gouldi* survived in Natal and southern Zululand in sheltered localities and probably later invaded the dry plains of Tongaland. It is, of course, also possible that the species survived by a rapid adaptation when Tongaland started to dry out and the forests withdrew to the Lebombo escarpment on the west and the dunes on the east. The relation of climate and distribution of the land molluscs is discussed in more detail in chapter 6 on p. 75.

Gulella perissodonta (Sturany, 1898), figs. 16-17

Van Bruggen, 1966a: 389.

MGR: Nhlonhlela Pan area; rest camp area (all NM).

NGR: around Nyamiti Pan (NM).

Gulella perissodonta, new to Zululand and long solely known from the unique type in the Vienna Museum, was rediscovered in 1962 in the Kruger National Park (Van Bruggen, 1966a: 389). A prolonged search in various countries has now revealed the presence of the species in a fairly extensive area in southeastern Africa from the Hluhluwe Game Reserve, Zululand, in the south to the northern districts of the Kruger National Park, Transvaal, in the north (fig. 17). All available material has been revised so that a reconsideration has now become possible.

Diagnostic characters. — A small, costulate species with nine-fold dentition consisting of parietal denticle, angular lamella, two-cusped labral complex, three basal denticles and duplex columellar lamella.

Description of shell. — Shell (fig. 16) small, cylindrical, rimate. Spire produced, sides straight and parallel, apex obtusely flattened. Whorls 5½-7¼, convex, sculptured with close, oblique costulae; sutures from shallow to fairly deep, crenellate. Aperture with nine-fold dentition: a small mid-parietal denticle, which occasionally is shaped like a horizontal lamella, frequently also reduced in size to complete absence; a strong, almost vertical angular lamella, distant from apex of labrum; a minute swelling in the sinus may be interpreted as a remnant of a sinular denticle; labral complex with small upper cusp, frequently reduced, and large, horizontal lower cusp pointing towards inner columellar lamella, complex corresponding to deep outside depression; three basal denticles, largest to the left of base and corresponding to small outside depression, remaining two equal in size, close together and deeply situated between largest basal denticle and labral complex; outer columellar lamella a superficial mid-columellar denticle, inner columellar lamella prominent, large and mamillate.

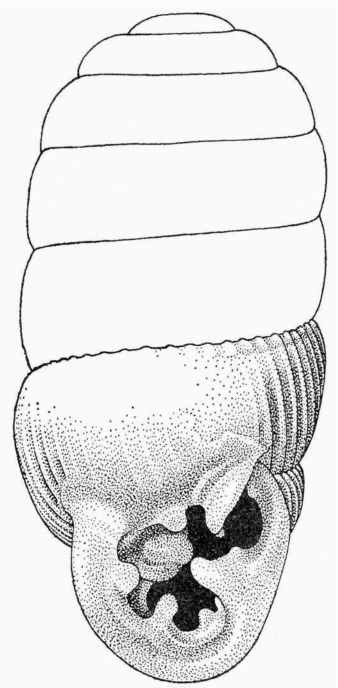


Fig. 16. *Gulella perissodonta* (Sturany), Hluhluwe Game Reserve (NM), actual length 4.6 mm.

Measurements of shell: 3.2-6.2 × 1.6-2.6 mm, l/d 1.74-2.47. The type measures 4.0 × 2.0 mm, l/d 2.00 (fide Dr. O. E. Paget). Smallest specimen (Kruger National Park, Ship Mountain, NM) 3.2 × 1.7 mm, l/d 1.89, largest specimen (Kruger National Park, Shaluka, NM) 6.2 × 2.5 mm, l/d 2.47. An average shell (Kruger National Park, Saselandonga Poort, NM) measures 4.7 × 2.2 mm, l/d 2.17, aperture 1.7 × 1.7 mm, last whorl 2.4 mm. All l/d have been computed from micrometer readings.

Distribution (fig. 17). — ZULULAND: Hluhluwe Game Reserve, central area, near pool on edge of road north of Hlaza River, A. C. and W. H. van Bruggen (NM); Mkuzi Game Reserve, rest camp area, A. C. and W. H. van Bruggen (NM); do., Nhlonhlela Pan area, A. C. and W. H. van Bruggen (NM, RMNH); Ndumu Game Reserve, around Nyamiti Pan, A. C. and W. H. van Bruggen (NM). SWAZILAND: 4 miles from turnoff Ingwavuma Road, A. C. and W. H. van Bruggen (NM); Ingwavuma Road, 900-1200 ft., A. C. and W. H. van Bruggen (NM). MOZAMBIQUE: Lourenço Marques (= Delagoa Bay), A. Penther (MW 33289, holotype); Inhaca Island, Punta Tomes Beach, P. H. Boshoff (RMNH). TRANSVAAL: 13 miles south of Hectorspruit, Mrs. C. Granville (NM alc., RMNH, RMNH alc.); Sabie (SAM A7232); Kruger National Park (29 localities, vide Van Bruggen, 1966a: 389, fig. 67) (KNP, KNP alc., NM, NM alc., RMNH); do., Punda Maria (now called Punda Milia), block N 31 (MT 341111-16).

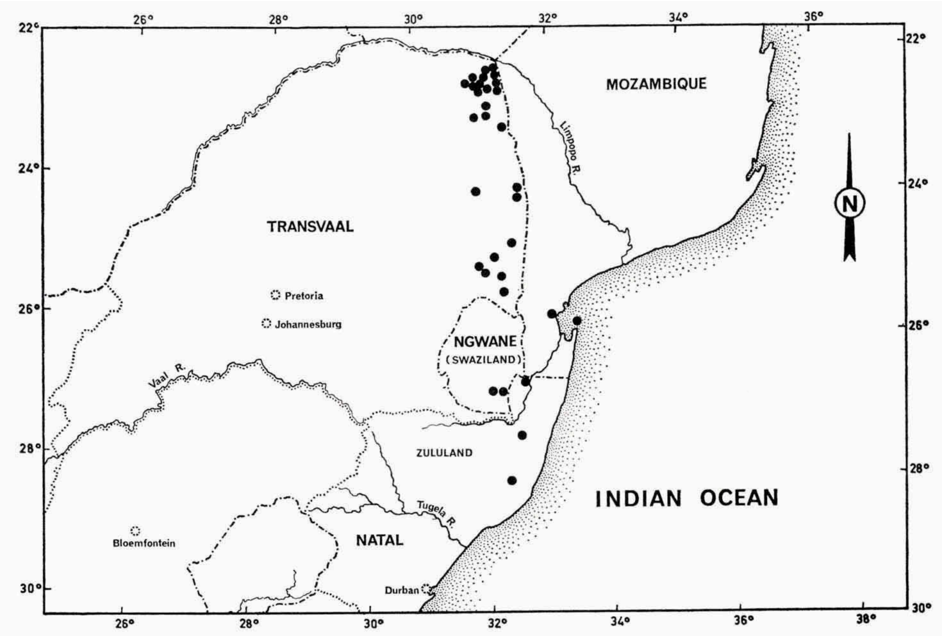


Fig. 17. Distribution of *Gulella perissodonta* (Sturany).

Type locality: Lourenço Marques, Mozambique, where first collected by Dr. Arnold Penther on July 9, 1897 (Sturany, 1898). The holotype in the

Naturhistorisches Museum, Vienna, has been the only specimen known for at least half a century. The next oldest material is a sample from Punda Milia in the Kruger National Park (MT), collected before 1949.

G. perissodonta favours a comparatively dry climate with a sparse vegetation; indeed, it may be considered a typical savanna dweller. From field notes and labels the following information on the habitat has been compiled: under log (Hluhluwe Game Reserve), ex leaf mould under trees in open gallery forest (Pafuri, Kruger National Park), under stones (Shipudze Ridge, Kruger National Park), basalt ridge (road to Shidzivane lookout, Kruger National Park), msimbit forest and groves (northeastern districts of the Kruger National Park). The msimbit tree (*Androstachys johnsonii,* Euphorbiaceae) is deciduous and casts very little shade; msimbit vegetations seem to exclude other species of trees, which may also account for the layer of very dry leaves on the ground. Surprisingly at least seventeen species of terrestrial molluscs were found to occur in this malacologically unattractive habitat (cf. Van Bruggen, 1966a); the area is hot and has a mean annual rainfall of only 15-20 inches.

G. perissodonta varies a lot in apertural dentition. The parietal process varies from a denticle to a horizontal lamella, but may also be reduced in size to complete absence. The upper cusp of the labral complex, in fact nothing more than an obtuse upper angle of the complex, may also disappear completely. In the material available for study it was found that all possibilities actually occur, viz., (a) parietal denticle reduced, (b) upper labral cusp reduced, and (c) both reduced at the same time. In most samples containing more than a few specimens all above mentioned dental variations were found; obviously there is no correlation to climate, subsoil or otherwise in the extensive area of distribution of the present species.

On the other hand it was found that the size of the shell is subject to geographical variation as witnessed by the following table:

	measurements	mean length	number of specimens
1.	3.8-4.6 × 1.9-2.2 mm, l/d 1.91-2.18	4.2 mm	22
2.	3.8-4.4 × 2.0-2.2 mm, l/d 1.74-2.00	4.1 mm	8
3.	3.6-4.2 × 1.8-2.0 mm, l/d 1.93-2.17	3.9 mm	18
4.	3.2-5.7 × 1.6-2.4 mm, l/d 1.77-2.41	4.4 mm	21
5.	4.3-5.4 × 2.1-2.4 mm, l/d 1.94-2.23	4.8 mm	4
6.	3.8-6.2 × 1.9-2.8 mm, l/d 1.74-2.47	5.0 mm	118

1. Zululand, Swaziland; 2. Mozambique; 3. Hectorspruit; 4. Kruger National Park (southern area) including Sabie; 5. do. (central area); 6. do. (northern area).

Unfortunately few areas, except perhaps the northern districts of the Kruger National Park, have been satisfactorily sampled; nevertheless the above table shows that at least in the Transvaal there is a noticeable increase in size from south to north, which undoubtedly may be interpreted to represent a cline.

Gulella daedalea (Melvill & Ponsonby, 1903), fig. 18

Connolly, 1939: 88.

MGR: not observed.

NGR: south bank of Nyamiti Pan (NM, 2 specimens, also KLT); around Nyamiti Pan (common, NM).

Gulella daedalea is only known from a fairly restricted area in the Zululand lowlands. The variation in size and shape of the shell is quite marked. The measurements may be summarized as follows: 6.2-9.1 × 3.1-4.0 mm, l/d 1.67-2.33. The variation in apertural dentition is even more striking. The upper basal tooth is sometimes somewhat squarish (Ndumu Game Reserve, population from around Nyamiti Pan) and the upper columellar lamella may range from well-developed to almost absent. The latter feature was studied in a large sample from Lower Umfolosi Drift (leg. H. C. Burnup, NM, RMNH) and the following transpired here: among a total of 60 shells, two have the upper columellar lamella well-developed, 26 poorly developed and in 32 specimens it is hardly noticeable or absent.

According to Connolly (1939: 88) *G. daedalea* is not easily differentiated from *G. infrendens* (Mts.); Connolly only differentiates the former by its "slightly weaker dentition, the basal tooth, in particular, being more pointed and situate on left centre of base, rather than infringing on the columellar margin". These characters are of extremely doubtful value, particularly in view of the variation in both species. The measurements of *G. infrendens* (5.2-9.1 × 2.5-4.4 mm, l/d 1.78-2.54) differ little from those of *G. daedalea* (see above), except perhaps that the latter is never as small as *G. infrendens* and also a bit more squat. The present author, however, has discovered a character by which the two taxa may be separated with confidence. The inner basal denticle only occurs in *G. daedalea,* and although sometimes somewhat reduced in size, it is never altogether absent. On the other hand it is never present in *G. infrendens;* it is obvious from the literature that both Burnup and Connolly have not been aware of the existence of this process, but somehow have managed to keep both species separate. The differential character was only accidentally discovered and it appeared that the only wrong identification was made by the present author. A close examination reveals a number of additional, but minute differences, which are difficult to describe or figure. An investigation of the radulae has so far not materially contributed to the distinction of the two species.

As shown on the map (fig. 18) *G. daedalea* and *G. infrendens* are allopatric. The Zululand distribution is as follows:

G. daedalea. — Lower Umfolosi Drift, H. C. Burnup (BM 1904.4.29.45, holotype; BM 1937.12.30.773-5, three paratypes; NM 1474, type 554, eight cotypes; NM type 554, three cotypes; NM, RMNH — probably all above material may be considered paratypes); Ndumu Game Reserve, around Nyamiti Pan, A. C. and W. H. van Bruggen (NM); do., south bank Nyamiti Pan, A. C. and W. H. van Bruggen (NM, RMNH); Kosi Lake system, Nkovugeni estuary, A. C. and W. H. van Bruggen (NM); "Zululand", Macandrew colln. (BM).

G. infrendens (syn. *Ennea stauroma* Melvill & Ponsonby, 1903, and *E. claustraria* Melvill & Ponsonby, 1907). — Mfongosi, W. E. Jones (DM, Puzey colln. 53; NM); Eshowe, H. C. Burnup (NM); do., W. Falcon (NM); Ngoye Forest, R. F. Lawrence (NM alc.); Umhlatuzi Drift, Nkandhla, Miss M. F. Hickey (NM); Melmoth, Miss M. F. Hickey (NM 2126, type 580, paratype of *Ennea stauroma*; NM); Umbonambi = Kwa-Mbonambi, H. C. Burnup (SAM); Lower Umfolosi Drift, H. C. Burnup (BM 1904.4.29.41, holotype of *Ennea claustraria*; BM 1937.12.30.776-7, two paratypes of do.; NM 1476, type 538, eight paratypes of do.; NM; RMNH); Dukuduku Forest, F. Toppin (NM); do., R. F. Lawrence (NM alc.); St. Lucia (Bay), W. Falcon (NM); do., H. J. Puzey (DM, Puzey colln. 53); do., W. G. Rump (NM); Hluhluwe Game Reserve, R. F. Lawrence (BM); Gwaliweni Forest, R. F. Lawrence (NM); "Zululand" (BM 1907.7.20.36, holotype of *Ennea stauroma*; BM, Macandrew colln.; BM ex Sowerby and Fulton). Furthermore *G. infrendens* occurs in the Eastern Cape Province in a fairly narrow stretch of country along the coast from the Van Staadens River to Kranskop and Sinkwazi in Natal; the range in Zululand is continuous with that in Natal and the Cape Province.

The two species obviously prefer different environments. *G. daedalea* inhabits the low, dry areas of Zululand with a savanna type vegetation, while *G. infrendens* occurs in coastal bush and forest in the Cape and Natal and inland in indigenous forest, which at higher levels may be considered montane forest. The species have been collected together at the Lower Umfolosi Drift. A "drift" in South Africa is a ford; before the Umfolosi River was bridged it was forded, which was usually only possible without too much trouble in the dry winter season. In the rainy season the river may come down in flood and after retreating to its bed leaves behind large quantities of vegetable debris among which terrestrial molluscs may be well represented.

When Burnup collected at the Lower Umfolosi Drift in June, 1903, the river must have been low and both above species of *Gulella* were very probably obtained from the flood debris. Consequently this is a secondary locality for the species in question and thus does not influence the distribution pattern.

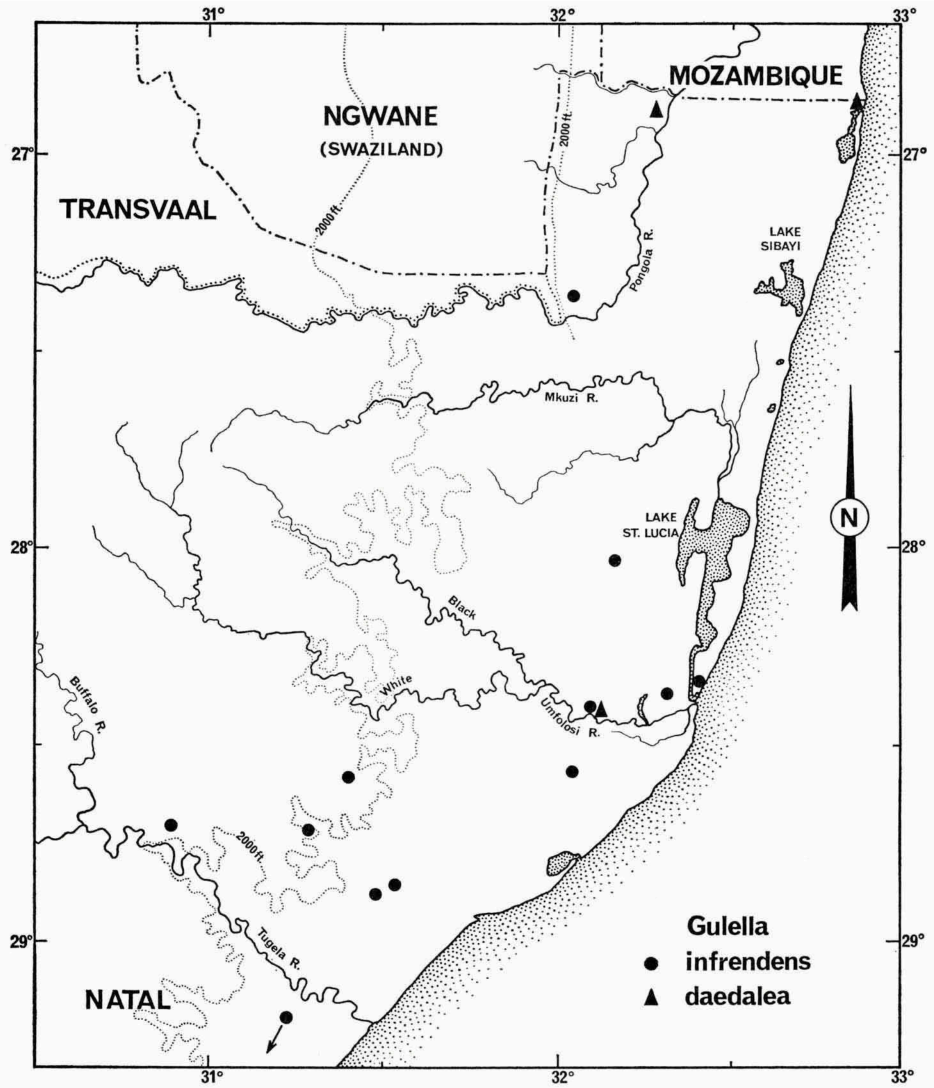


Fig. 18. Distribution of *Gulella daedalea* (Melvill & Ponsonby) and Zululand distribution of *Gulella infrendens* (Von Martens).

Because of the allopatric distribution the possibility that *G. daedalea* is only a subspecies of *G. infrendens* should also be considered here. Although the differences between the species are small, they are constant. The variation in apertural dentition runs more or less parallel, but is definitely clinal in *G. infrendens.* Also there are noticeable size-clines in the latter species; in *G. daedalea* the full range of sizes is found throughout the limited range. In the absence of anatomical data it is proposed to retain the status quo and to provisionally consider *G. daedalea* and *G. infrendens* species rather than subspecies.

4c. Notes on ecology

The only sharply defined community of land molluscs in Tongaland is that of the riverine forest; it consists of *Trachycystis bathycoele, Guppya rumrutiensis* (both minute), *Sheldonia poeppigii* and the slug *Urocyclus flavescens.* Most other species are not confined to certain types of vegetation, but usually occur in a variety of environments outside the riverine forest. As far as microclimate (particularly relative humidity) is concerned, we can distinguish two types, viz., a comparatively humid microclimate confined to the riverine forest and a relatively dry microclimate which covers all other types of vegetation. During summer drought periods much of Tongaland is actually subarid. Obviously terrestrial gastropods are more subject to the influences of microclimate than those of vegetation, although both factors are most intimately connected. The student is also referred to Van Bruggen (1966a: 390-395).

5. OTHER NEW RECORDS FOR ZULULAND

It was thought opportune to discuss here a striking new species and a new subspecies of the family Streptaxidae and various other species formerly unknown to occur in Zululand (eight species altogether, among which one new to South Africa) and to add notes on some species reported from Zululand without exact localities (four species) or from only one locality (two species). Finally two Zululand streptaxids have been raised from varieties to full species, while at the same time one species and its variety have been synonymized.

GASTROPODA PROSOBRANCHIA

Maizaniidae

Maizania wahlbergi (Benson, 1852)

Connolly (1939) gives no records from Zululand, but Verdcourt (1964) mentions specimens in the British Museum from "Zulu country". The occurrence in Zululand is confirmed by specimens from Eshowe (December 1922, leg. W. Falcon; January 1923, leg. H. C. Burnup, all NM) and Gwaliweni Forest, Lebombo Range (1959, leg. K. L. Tinley, NM). The species occurs in two disjunct areas, viz., from the Eastern Cape to Zululand and in the coastal areas of Tanganyika and Kenya.

Verdcourt (1964) has thoroughly studied the genus *Maizania* in East Africa and as regards *M. wahlbergi* concludes that there are no significant differences between East and South African specimens. This was confirmed by the present author at the British Museum (Natural History) and the Natal Museum. Apart from the localities in East Africa and Zululand the species is now known to occur at Port St. Johns, Port Grosvenor (Cape Province), Port Shepstone, Clansthal (leg. W. Falcon, RMNH, new record), Isipingo and Durban (all Natal). All known South African localities are either in coastal tropical forest types ("Coastal Forest and Thornveld", Cape Province and Natal) or in inland tropical forest types ("Lowveld", Zululand, fide Acocks, 1953). This is in accordance with the findings of Verdcourt.

GASTROPODA PULMONATA

Enidae

Edouardia natalensis (Krauss, 1846)

Three specimens from "Umbonambi" = Kwa-Mbonambi, leg. F. Toppin, 28 May 1905 (NM). If Mozambique records are not acceptable (see Connolly, 1939: 423, "Although there is no reason why this species should not occur here, I omit the records of Rikatla and Delagoa Bay, ..., as probably attributable to *meridionalis* Pfr."), this is the northernmost record for the species. New for Zululand.

Edouardia spadicea (Pfeiffer, 1846)

Specimens from "Umbonambi" = Kwa-Mbonambi, leg. F. Toppin, 23 May 1905 (NM) constitute the northernmost records for the species. New for Zululand.

Edouardia arenicola (Benson, 1856)

According to Connolly (1939) this species was in Zululand only known from Dukuduku. The following record extends the distribution northward: St. Lucia Game Reserve, indigenous bush near Charter's Creek, 18-19 May 1965, leg A. C. and W. H. van Bruggen (1 shell, RMNH).

Edouardia metuloides (Smith, 1899)

Four specimens from the banks of the Imfamanzi River (near the junction of Black and White Umfolosi Rivers), leg. H. W. Bell-Marley (NM 2680); the whorls are slightly less convex than those of Victoria Falls specimens (NM 2786). This extends the distribution of the species southward for some considerable distance (see Van Bruggen, 1966a: 333, so far known from Zomba, Malawi = Nyasaland, the type locality; Broken Hill, Zambia = N. Rhodesia; Victoria Falls, Rhodesia; Mtisherra River valley, Mozambique; three localities in the Kruger National Park, Transvaal). New for Zululand.

Rhachidina chiradzuluensis (Smith, 1899)

Rhachidina chiradzuluensis was originally described from Mt. Chiradzulu, Malawi (Nyasaland); subsequently it was found to occur in East Africa as far north as Mombasa and in the Transvaal southward to the Shiluwane District (Connolly, 1939: 417). Meantime the species has also been obtained in Rhodesia (Chisumbanje, Sabi River valley, *Spirostachys* forest on sand, 20 June 1964, leg. D. C. H. Plowes, NM) and now specimens from Zululand have come to light as well. *R. chiradzuluensis* appears to be common at Tete Pan (misspelt Tele Pan), Pongola, Tongaland, where it was collected by A. C. Vause Bell in September, 1927 (NM, duplicates RMNH). The largest available shell is 15.4 mm long. Both varieties, with two or three chestnut bands, occur here. Sometimes a pinkish tinge may be noticed, particularly on the columellar margin, the inside of the aperture, the apex and earlier whorls of the shell. The Tete Pan specimens were originally identified by Connolly, though, surprisingly, not recorded in his monographic survey of 1939. The species is new for Zululand. It is perhaps appropriate here to put on record another new locality for the species: Hanglip Forest, Louis Trichardt, Transvaal, 4500 ft., 8-9 February 1965, leg. A. C. and W. H. van Bruggen (NM, also alcohol specimen; duplicates RMNH).

Rachis vicinus Preston (1910: 532, pl. 8 fig. 17, Shimbi Hills, Kenya) appears to be a synonym of *Rhachidina chiradzuluensis*; there is a note to that effect by Connolly on some of the boxes in the Natal Museum. Although the types are not identical, both "species" are united by intermediates; the Tete Pan material contains both *Rachis vicinus* and *Rhachidina chiradzuluensis*. Apart from the above mentioned specimens the following material was examined: Shiluwane District, Transvaal, leg. A. H. Junod (BM 1937.12.30.

3696-3700, six specimens; NM 3448, 1); Mt. Chiradzulu, Malawi (Nyasaland), leg. A. Whyte (BM 96.12.31.129-134, syntypes of *Buliminus chiradzuluensis* Smith); Shimbi Hills, Kenya, leg. R. Kemp (BM 1937.12.30. 3762-8, paratypes of *Rachis vicinus* Preston); Tana River, Kenya, leg. H. J. A. Turner (BM 1928.10.26.3, length 17+ mm, apex damaged). The largest specimen seen is a paratype of *Rachis vicinus* of 20.2 mm long (BM).

Endodontidae

Trachycystis (Chalcocystis) aenea (Krauss, 1848)

There are specimens from Kosi Bay, leg. F. Toppin, in the Natal Museum. This fills the gap in the distribution between Natal and Mozambique. New for Zululand. The species is closely allied to *T. (C.) burnupi* (M. & P.), which is widely distributed in Zululand.

Trachycystis (Psichion) ariel (Preston, 1910), fig. 19

Phortion ariel Preston, 1910: 531, pl. 8 fig. 15, Shimbi Hills, Kenya.

Trachycystis ambigua Connolly, 1922: 116, headwaters of R. Inyamkarrara, 4500 ft., Mozambique; Connolly, 1925: 141, pl. 4 fig. 9, Lebombo marsh, Rikatla, Mozambique; Mt. Chiradzulu, Malawi (Nyasaland); Vumbu Range, near Umtali, 700 ft., Rhodesia; Connolly, 1939: 215, same localities.

Trachycystis ariel; Verdcourt, 1960: 112, Mrima Hill, Kenya.

Regarding this species Verdcourt (1960: 112) comments as follows: "I feel certain that *T. ariel* (Preston) will prove to be an earlier name for *T. ambigua* Connolly but I found no living specimens". The present author discussed this with Dr. Verdcourt in 1967 and feels justified in synonymizing Connolly's name even in the absence of anatomical data; the types of both were personally examined in the British Museum (Natural History), where they bear the numbers 1911.10.12.76 (*T. ariel,* paratype) and 1925.8.4. 29 (*T. ambigua*). The species may now be added to the South African list, the southernmost record being based on a Zululand specimen from the Hluhluwe Game Reserve, on the low wall of the tea verandah in the rest camp, 23 April 1963, leg. A. C. van Bruggen (RMNH) (fig. 19); the shell has four whorls and measures 3.5 (maj. diam.) × 2.7 (height) mm. Recently Mr. Lamoral obtained another specimen in Tongaland, which is accompanied by the following label: "Humus sieving from soil under *Acacia* trees in area between shore and road on eastern side of lake Sibaya. Approx. 3 miles North of Lala Neck. 25.6.1967." (NM)

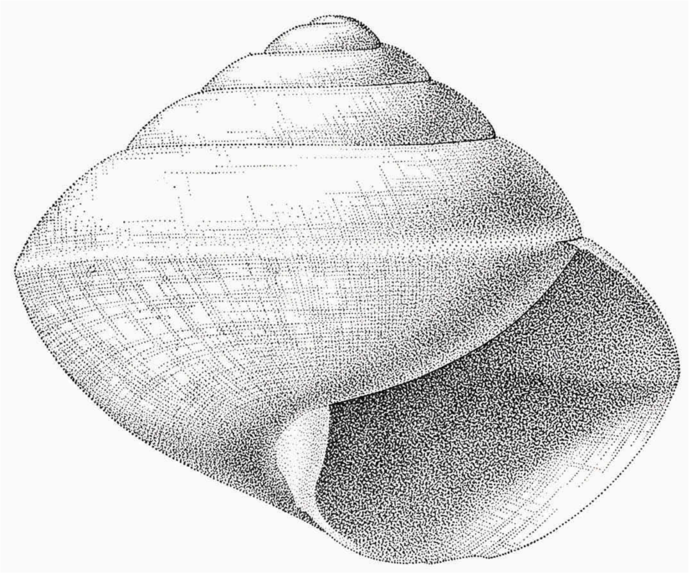


Fig. 19. *Trachycystis ariel* (Preston), rest camp, Hluhluwe Game Reserve (RMNH), diameter 3.5 mm.

Subulinidae

Curvella (Hypolysia) florentiae (Melvill & Ponsonby, 1901)

Connolly's (1939: 358) somewhat vague statement: "Widely distributed ... through Natal into Zululand, ..." is confirmed by specimens in the Natal Museum from "Umbonambi" = Kwa-Mbonambi, leg. F. Toppin, 29 May 1905; Bhanga Nek dune forest, Kosi Bay area, leg. O. Bourquin, December 1964/January 1965; and Hluhluwe Game Reserve, near officers quarters, leg. O. Bourquin, 20 February 1965.

Euonyma lanceolata (Pfeiffer, 1854)

There are three specimens from Zululand in the Natal Museum, viz., St. Lucia Bay; Gwaliweni Forest, Lebombo Range (1959, leg. K. L. Tinley); dune forest between Sordwana Bay and Cape Vidal (15 January 1960, leg. K. L. Tinley). New for Zululand. These fill the gap in distribution records between Natal and Mozambique; see also sub chapter 6.

Rhytididae

Natalina caffra (Férussac, 1821)

So far only recorded from "Zululand". There are two Zululand specimens in the Natal Museum: Mfongosi, leg. W. E. Jones (NM 3365), major diameter 69.5 mm, a repaired fracture in the body whorl makes it seem like an intermediate to *N. wesseliana* (Kob.); Eshowe, leg. W. Falcon.

Natalina wesseliana (Kobelt, 1876)

The following specimens confirm Connolly's somewhat vague record "Zululand" (Connolly, 1939: 107): Kosi Bay, leg. F. Toppin, 1905/06 (3 specimens, NM); Makowe, leg. J. Crosley (NM), a very curious abnormal specimen, of which the shell has the consistency of parchment, being very thin, but not fragile, major diameter 52 mm.

Streptaxidae

Gulella planti (Pfeiffer, 1855)

Gulella planti, Southern Africa's largest species of the genus, occurs in a restricted area on the coast of Natal. Connolly's somewhat sweeping statement (Connolly, 1939: 24, "Widely distributed over the southern districts" of Natal) is not altogether true. Abundant material at the disposal of the present author has revealed that *G. planti* is restricted to an area limited by Durban and Drummond in the south and west respectively to as far north as the Tugela River (Kranskop and surroundings). Specimens from near Eshowe (leg. H. W. Bell-Marley, NM) and Mtimona (leg. H. J. Puzey, BM 1956.6.8.34-41) show that the species also inhabits southern Zululand, another addition to the Zululand list.

A record from Port Elizabeth (Germain, 1920) has been ignored; very probably Durban is meant here, because the collector Guy Babault obviously travelled by steamer around the Cape of Good Hope, calling at the various ports. Moreover, personal experience has proven the absence of the species in this part of South Africa.

A reconsideration of *Gulella isipingoensis* (Sturany, 1898) as understood by Connolly (1939: 46 sqq.) has led to an entirely different interpretation. Connolly recognizes a typical form and five varieties. A critical re-appraisal of the old material augmented by a large number of additional specimens has convinced the present author that the position is as follows:

Connolly, 1939	revised opinion
isipingoensis (typical var.)	*isipingoensis*
var. *sturanyi* (Burnup, 1914)	syn. *sturanyi* (Burnup, 1914)
var. *cathcartensis* Burnup, 1925	syn. *cathcartensis* Burnup, 1925
var. *discrepans* (Sturany, 1898)	*discrepans* (Sturany, 1898)
var. *dextrorsa* Burnup, 1925	*dextrorsa* Burnup, 1925
var. *laevorsa* Burnup, 1925	*laevorsa* Burnup, 1925

G. isipingoensis is herewith restricted to Connolly's typical form and the varieties *sturanyi* and *cathcartensis*. These varieties, although easily separated in their extreme forms, show various intermediates and are not confined to limited parts of the range of the species; consequently it is not necessary to retain the names *sturanyi* and *cathcartensis*. *G. isipingoensis* occurs along the southeast coast of South Africa from Knysna to as far north as Durban, Kranskop, and Nottingham Road; it is also found some distance inland.

Gulella dextrorsa Burnup, 1925, fig. 20

Gulella isipingoënsis var. *dextrorsa* Burnup, 1925, Ann. Natal. Mus., 5: 123, pl. 8 figs. 31-32; Connolly, 1939, Ann. S. Afr. Mus., 33: 38.

Diagnostic characters. — A minute, striate species with oblique aperture with five-fold dentition consisting of angular lamella, labral process with cusp, basal ridge and columellar lamella.

Description of shell. — Shell (fig. 20) minute, elongate-ovate, rimate. Spire produced, sides convex, apex obtusely conical, subacute. Whorls 6¾-7½, convex, sculptured with coarse, regular, almost vertical, costulae; sutures deep, subcrenellate. Aperture obliquely drawn towards the right, with five-fold dentition: strong, vertical columellar lamella, scarcely connected with apex of labrum; labral process a ridge shaped like an inverted V, with a prominent apical cusp, complex corresponding to shallow outside depression; basal process a deeply situated, oblong ridge to the left of base; prominent, blunt columellar lamella.

Measurements of shell: 2.6-3.1 × 1.3-1.5 mm, l/d 1.83-2.14. The type measures 2.6 × 1.4 mm, l/d 1.86. Smallest specimen (Eshowe, NM) 2.6 × 1.3 mm, l/d 2.00, largest shell (Eshowe, NM) 3.0 × 1.5 mm, l/d 2.00. An average specimen (Eshowe, NM) measures 2.8 × 1.4 mm, l/d 2.05, aperture 0.9 × 0.7 mm, last whorl 1.3 mm. All l/d have been computed from micrometer readings.

Distribution. — *G. dextrorsa* is so far only known from Eshowe.

ZULULAND: Eshowe, H. C. Burnup (BM 1937.12.30.974, holotype, BM 1925.4.21.4, paratype); do., W. Falcon (NM 3573, type 562, three paratypes; NM type 562, three paratypes).

Type locality: Eshowe, where first collected at Christmas 1922 by Burnup and Falcon.

G. dextrorsa, originally considered a variety of *G. isipingoensis* (Stur.) (vide Burnup, 1925; Connolly, 1939), is now raised to species level. In many respects *G. dextrorsa* shows considerable differences as compared to *G. isipingoensis*, particularly in the shape of the aperture and its labral complex and basal process, which differences are certainly of a specific rather than a subspecific or even varietal character. *G. dextrorsa* is certainly allied to *G. isipingoensis*. A somewhat bold explanation is that *G. dextrorsa* is an early offshoot of the latter and that *G. laevorsa*, which obviously is much closer to *G. isipingoensis*, is a much later arrival, albeit from the same original stock. In the intervening time *G. dextrorsa* had sufficiently differentiated to prevent interbreeding with the newly arrived form. These migrations may possibly have coincided with the changes in climate during the Pleistocene, when the forest contracted or expanded during dry or wet periods. It is quite conceivable that during one of the hypothermal (wet/cool) periods the types of forest (coastal bush and temperate forest) which shelter *G. isipingoensis* formed a continuous belt from the coast of Natal to the Zululand hinterland and that since both *G. dextrorsa* and later *G. laevorsa* have become isolated at Eshowe. Burnup's views on relationships have been quoted under *G. laevorsa*, which species was also initially considered to represent a variety of *G. isipingoensis*.

In *G. dextrorsa* there is occasionally an indication of a mere trace of a sinular swelling.

The name is presumably given on account of the peculiarly oblique aperture (*dextrorsus*, Lat. = to the right).

Gulella laevorsa Burnup, 1925, fig. 21

Gulella isipingoënsis var. *laevorsa* Burnup, 1925, Ann. Natal Mus., 5: 124, pl. 8 figs. 33-34; Connolly, 1939, Ann. S. Afr. Mus., 33: 49.

Diagnostic characters. — A minute, striate species with six-fold dentition consisting of angular lamella, sinular denticle, two labral processes, basal denticle and columellar lamella.

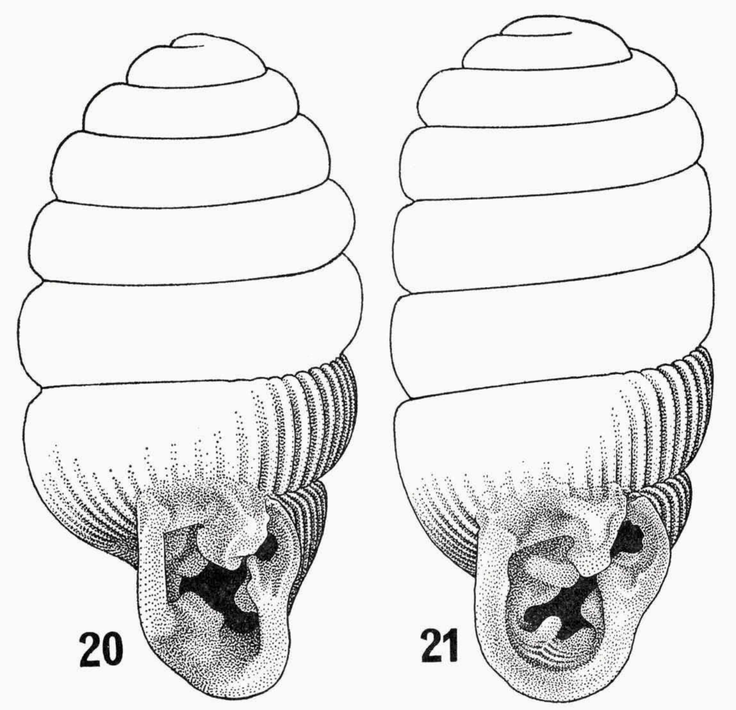
Description of shell. — Shell (fig. 21) minute, (sub)cylindriform, rimate. Spire produced, sides (sub)parallel, hardly convex, apex flattened, obtusely conical. Whorls 7-7¾, flattish to slightly convex, sculptured with coarse, regular, somewhat oblique costulae; sutures deep, subcrenellate. Aperture with six-fold dentition: strong, vertical angular lamella, not connected with apex of labrum; sinular denticle hidden behind angular lamella, with some additional swelling; two inrunning labral ridges, the upper with one or two cusps, complex corresponding to extensive outside depression; basal denticle deeply situated, to the left of base, to the right of this process a hardly discernible swelling; large and prominent mamillate columellar lamella.

Measurements of shell: 2.6-3.1 × 1.3-1.5 mm, l/d 1.83-2.17. The type measures 2.9 × 1.4 mm, l/d 2.07. Smallest specimen (Eshowe, NM) 2.6 ×

1.4 mm, l/d 1.83, largest shell (Eshowe, NM) 3.1 × 1.4 mm, l/d 2.17. An average specimen (Eshowe, NM, fig. 21) measures 2.9 × 1.5 mm, l/d 1.96, aperture 0.9 × 0.9 mm, last whorl 1.4 mm. All l/d have been computed from micrometer readings.

Distribution. — *G. laevorsa* is so far only known from Eshowe.

ZULULAND: Eshowe, H. C. Burnup (BM 1937.12.30.977, holotype; BM 1925.4.21.3, paratype; NM 3574, type 563, two paratypes); do., W. Falcon (NM, type 563, paratype).



Figs. 20-21. Shells of 20, *Gulella dextrorsa* Burnup, paratype, Eshowe (NM 3573), actual length 2.7 mm; 21, *G. laevorsa* Burnup, paratype, Eshowe (NM 3574), actual length 2.9 mm.

Type locality: Eshowe, where first collected at Christmas 1922 by W. Falcon.

G. laevorsa has been considered a variety of *G. isipingoensis* (Stur.) by Burnup (1925) and Connolly (1939) has followed Burnup in this respect. A careful reconsideration of the case has convinced the present author that *G. laevorsa,* although undoubtedly allied to *G. isipingoensis,* is a good species. So far it has only been found at Eshowe in the company of *G. dextrorsa,* which latter was also considered to be a variety of *G. isipingoensis.*

Reasons for considering *G. laevorsa* a good species are mainly the existence of a sinular denticle, accompanied by some curious, additional swellings, and the labral complex; both these dental processes are not known to occur among the many different types of dentition of *G. isipingoensis* and are moreover so utterly different in shape and composition, that one feels confident that *G. laevorsa* should be raised to species level. This is essentially what Burnup meant by writing (Burnup, 1925: 125): "It is with some little diffidence that I nominate this and the preceding form (*dextrorsa*) as varieties of *isipingoensis* (Stur.), for the distinctions are not confined to one or two characters, but can be detected in many. The general appearance of the shells, however, the size, form, swollen whorls, deep suture and strong sculpture suggest a relationship closer than merely generic; so it seems best, until some systematist takes the genus in hand, separating it into sections into which the South African species can conveniently be grouped, to give these forms a status corresponding with that of *discrepans* (Stur.), *sturanyi* (Bnp.), and *cathcartensis* Bnp., as varieties of *isipingoensis*, thus emphasizing their probable affinity with that species."

The derivation of the name is somewhat obscure; probably the name was coined as an opposite to *G. dextrorsa*, although the aperture of *G. laevorsa* is quite normal, particularly so when compared to that of *G. dextrorsa* (*dextrorsus*, Lat. = to the right, *laevorsus*, Lat. = to the left).

Gulella leucocion Connolly, 1929

Gulella leucocion Connolly, 1929, Ann. Natal Mus., 6: 233, pl. 14 fig. 5; Connolly, 1939, Ann. S. Afr. Mus., 33: 84; Zilch, 1961, Arch., Moll., 90: 95.

Gulella tridens Connolly, 1939, Ann. S. Afr. Mus., 33: 59, pl. 1 fig. 13; Zilch, 1961, Arch. Moll., 90: 100 (under subgenus *Molarella*). Nov. syn.

Gulella tridens var. *intermedia* Connolly, 1939, Ann. S. Afr. Mus., 33: 60, pl. 1 fig. 14. Nov. syn.

Diagnostic characters. — A small, costulate species with six- to seven-fold dentition consisting of angular lamella, three-fold labral complex, basal process and duplex columellar lamella of which the outer process is frequently absent.

Description of shell. — Shell small, cylindrical, rimate. Spire produced, sides straight, parallel, apex obtusely conical, flattened. Whorls 6-7, flattish to convex, sculptured with distant, coarse, oblique costulae; sutures shallow, (sub)crenellate. Aperture with seven-fold dentition: almost vertical angular lamella, connected with apex of labrum; three-fold labral complex consisting of small upper cusp and two parallel, subequal inrunning lamellae, complex corresponding to extensive, shallow, outside depression; basal process to the left of base, in shape varying from inrunning lamella to squarish denticle, corresponding to small outside pit; duplex columellar lamella consisting of superficial denticle, frequently reduced in size to complete absence, and large inner process.

Measurements of shell: 4.0-5.6 × 1.7-2.2 mm, l/d 2.17-2.75. The type measures 5.2 × 2.2 (and not 5.2 × 1.8 as given by Connolly, 1929, 1939; see also the original figure, which gives an l/d of 2.36) mm, l/d 2.36. Largest specimen (Mfongosi, BM) 5.6 × 2.2 mm, l/d 2.55, smallest specimen (Mfongosi, NM) 4.0 × 1.7 mm, l/d 2.37. An average specimen (Mfongosi, SAM) measures 4.7 × 2.2 mm, l/d 2.17, aperture 1.7 × 1.6 mm, last whorl 2.5 mm.

Distribution. — *G. leucocion* is so far only known from Mfongosi in Zululand.

ZULULAND: Mfongosi (district), W. Falcon (RMNH); do., ex H. C. Fulton (RMNH); do., W. E. Jones (BM 1931.6.3.67-74, eight paratypes; BM 1937.12.30.1247, holotype of *Gulella tridens*; BM 1931.6.3.60-66, seven paratypes of do.; BM 1937.12.30.1255-9, holotype and four paratypes of *Gulella tridens* var. *intermedia*; NM; RMNH; SAM, holotype of *G. leucocion*; SAM A29997).

Type locality: Mfongosi, where first collected by W. E. Jones before 1929.

A reconsideration of all available material has led to the conclusion that both *G. tridens* and its variety *intermedia* are synonyms of *G. leucocion*. The variation in dentition, particularly in size of the outer columellar and shape and size of the basal processes, is considerable and the one form smoothly merges into the other. The total number of shells checked for the outer columellar process is 32; of these ten or 31 % are without this denticle. The basal process may be a squarish denticle, an inrunning lamella or intermediate between the two. The variation in these processes is best demonstrated by a sample (NM, Falcon colln., ex H. J. Puzey) of ten shells s.n. *G. leucocion*; seven of these have no outer columellar denticle, six have a squarish basal process, two an inrunning lamella in its place and two an intermediate type of basal denticle.

Gulella linguidens Connolly, 1939

So far *Gulella linguidens* was only known from its holotype shell from the Hluhluwe Game Reserve (leg. W. G. Rump, NM type 567); it measures 4.4 × 2.2 mm, l/d 1.97, aperture 1.9 × 1.6 mm, last whorl 2.5 mm (cf. Connolly, 1939: 76, fig. 4). Recently Dr. D. S. Brown has managed to again obtain the species after almost thirty years; two specimens were collected in dune forest on the east shore of Lake Sibayi, Zululand, on 12 June

1966 (BM, RMNH). These specimens closely resemble the type, except that the outer columellar lamella has almost disappeared; in the type it is fairly well developed. This again shows that it is difficult to divide all known species of *Gulella* according to the presence or absence of an outer columellar lamella in addition to the inner one, which, of course, is always present.

G. linguidens is known to occur in dune forest (Lake Sibayi specimens); much of the Hluhluwe Game Reserve has kindred types of vegetation and it is most likely that the original specimen was obtained in such a habitat. By virtue of its dentition *G. linguidens* is an isolated species, which probably occurs over much of Zululand, but so far has been overlooked because of its size.

G. linguidens is not to be confused with *G. linguifera* (Mts.) which is an altogether different species from Uganda.

The discovery of an aberrant form of *Gulella crassidens* (Pfr.) has necessitated a complete revision of the species. It now appears that it may be divided into two or even possibly three subspecies.

Gulella crassidens (Pfeiffer, 1859), figs. 22-24

Ennea crassidens Pfeiffer, 1859, Novit. Conch., 1: 114, pl. 32 figs. 6-8; Pfeiffer, 1859, Monogr. Helic. Viv., 4: 340; Pfeiffer, 1868, Monogr. Helic. Viv., 5: 454; Pfeiffer, 1876, Monogr. Helic. Viv., 7: 504; Nevill, 1878, Hand List Moll. Ind. Mus., 1: 5; Pfeiffer & Clessin, 1878, Nomencl. Helic. Viv.: 19; Tryon, 1885, Man. Conch. (2), 1: 97, pl. 19 fig. 100; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond. 3: 167; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 548 (12), 562 (26); Kobelt, 1904, Conch. Cab., 1, 12B: 192, pl. 24 fig. 7; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nassau. Ver. Naturk., 63: 160; Connolly, 1912, Ann. S. Afr. Mus., 11: 70.

Enneastrum crassidens; Bourguignat, 1889, Moll. Afr. Équat.: 127.

Gulella crassidens; Connolly, 1932, Ann. Natal Mus., 7: 77; Connolly, 1939, Ann. S. Afr. Mus., 33: 91; Zilch, 1961, Arch. Moll., 90: 93.

Ennea scrobiculata Melvill & Ponsonby, 1892, Ann. Mag. Nat. Hist. (6), 9: 93, pl. 6 fig. 8; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond., 3: 169; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 550 (14), 565 (29); Kobelt, 1904, Conch. Cab., 1, 12B: 218, pl. 27 fig. 8; Connolly, 1912, Ann. S. Afr. Mus., 11: 85.

Ennea durbanensis Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 548 (12), 561 (25), pl. 1 fig. 17; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond., 3: 169; Kobelt, 1904, Conch. Cab., 1, 12B: 203, pl. 25 fig. 14; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nassau. Ver. Naturk., 63: 160.

Gulella durbanensis; Zilch, 1961, Arch. Moll., 90: 93.

Diagnostic characters. — A small, costulate species with six-fold dentition consisting of angular lamella, sinular denticle, labral process, basal denticle and duplex columellar lamella.

Description of shell. — Shell small, acuminate elliptical to cylindrical, rimate. Spire produced, sides parallel to convex, apex flattened to slightly acuminate. Whorls 7¼-8¾, (slightly) convex, sculptured with close, regular, almost straight costulae; sutures shallow to somewhat impressed, (sub)crenellate. Aperture with six-fold dentition: strong, oblique angular lamella, connected with apex of labrum; (small) sinular denticle, sometimes (almost) absent, hidden by angular lamella; large, oblong labral slab with minute denticle at its uppermost extremity, complex corresponding to extensive, shallow outside depression; a mid-labral denticle corresponding to small, outside depression; outer columellar process a low marginal swelling, inner columellar lamella large and prominent, mamillate.

Measurements of shell: 3.7-6.9 × 2.0-3.2 mm, l/d 1.58-2.29.

Distribution (fig. 24). — *G. crassidens* occurs in Natal and Zululand from Umzinto in the south to southern Zululand and as far inland as Hilton.

G. crassidens may be divided into two or possibly three subspecies.

Gulella c. crassidens (Pfeiffer, 1859)

Diagnostic characters. — Shell (fig. 22) from 4.7 to 6.9 mm long, acuminate elliptical, apex obtusely conical, sides convex, whorls 7¾-8¾, slightly convex, sinular denticle usually present.

Measurements of shell: 4.7-6.9 × 2.6-3.2 mm, l/d 1.58-2.29. The neotype measures 5.9 × 2.9 mm, l/d 2.03. Smallest specimen (Durban Bluff, DM) 4.7 × 3.0 mm, l/d 1.58, largest shell (Stanger, NM) 6.9 × 3.0 mm, l/d 2.29. An average specimen (Durban, Stella Bush, NM) measures 5.9 × 3.0 mm, l/d 1.96, aperture 1.9 × 1.6 mm, last whorl 2.6 mm. All l/d have been computed from micrometer readings.

Distribution (fig. 24). — *G. c. crassidens* is confined to the coastal strip of Natal from Umzinto to Sinkwazi and as far inland as Hilton.

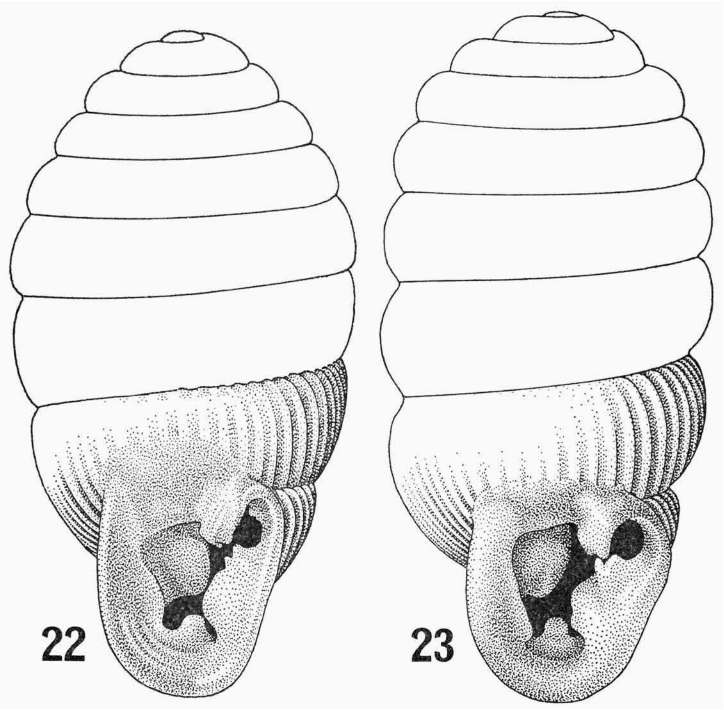
NATAL: Equeefa (Connolly, 1939); Umkomaas, H. C. Burnup (NM); Illovo River, H. C. Burnup (NM); do., A. J. Taynton (NM); Isipingo, C. W. Alexander (NM); do., H. J. Puzey (DM, Puzey colln. 41); Durban (includes Bluff and Stella Bush), H. C. Burnup (NM 1464, NM); do., W. Falcon (NM); do., Goatley (NM); do., A. Penther (BM 1937.12.30.1290, paratype of *Ennea durbanensis*); do., Plant (Cuming colln., BM, neotype and three other specimens); do., Price Jones colln. (BM); do., H. J. Puzey (BM; DM, Puzey colln. 41); do., E. Warren (NM); do. (TP); Natal coast, W. Falcon (RMNH); Pinetown, H. C. Burnup (NM 1462, NM); Spitzkop near Table Mountain, W. G. Rump (NM 3855); Hilton, W. Falcon (NM, NM alc., RMNH); Stanger, G. E. Pennington (NM); Sinkwazi (Connolly, 1939); "Natal", E. L. Layard (BM 1912.8.16.345-6, two syntypes of *Ennea scrobiculata*); do., ex H. C. Fulton (RMNH).

Type locality: Port Natal, now Durban, where first collected by Plant between 1824 and 1859.

Gulella crassidens jonesi nov. subspec.

Diagnostic characters. — A subspecies of *G. crassidens* with the shell (fig. 23) from 3.7 to 4.7 mm long, cylindrical, apex flattened, sides parallel, whorls 7¼-7½, markedly convex, sinular denticle absent.

Measurements of shell: 3.7-4.7 × 2.0-2.2 mm, l/d 1.78-2.19. The holotype measures 4.5 × 2.2 mm, l/d 2.00, aperture 1.4 × 1.4 mm, last whorl 2.0 mm, 7½ whorls. Smallest specimen (Mfongosi, NM) 3.7 × 2.0 mm, l/d 1.87, largest shell (Mfongosi, BM) 4.7 × 2.1 mm, l/d 2.19. An average specimen (Mfongosi, TP) measures 4.1 × 2.1 mm, l/d 1.94, aperture 1.2 × 1.2 mm, last whorl 2.0 mm. All l/d have been computed from micrometer readings.



Figs. 22-23. *Gulella crassidens* (Pfeiffer). 22, nominate subspecies, Durban (NM), actual length 5.9 mm; 23. *G. c. jonesi* n. ssp., holotype, Mfongosi (NM), actual length 4.5 mm.

Distribution (fig. 24). — *G. crassidens jonesi* is so far only known from Mfongosi in Zululand.

Zululand: Mfongosi, W. E. Jones (BM 1931.6.3.75-8, eight paratypes; DM, Puzey colln. 41, eleven paratypes; NM, holotype (fig. 23) and seven paratypes; NM, four paratypes; RMNH, one paratype; TP, two paratypes); "Zululand" (NM, twelve paratypes).

Type locality: Mfongosi, where first collected by W. E. Jones some time before 1932.

The newly described subspecies has been named in honour of its collector, W. E. Jones, a trader at Mfongosi, a collector of some repute and correspondent of Connolly; Jones died in the nineteenfifties and notwithstanding the many species discovered by him so far no terrestrial mollusc has been named after him.

According to available material the subspecies *jonesi* seems to be confined to Mfongosi.

Apart from the above cited material only four other Zululand specimens have come to light. In the British Museum (Natural History) there is a sample of three specimens from "Zululand" (BM 51.1.14.29-30); these shells have the same measurements as Natal specimens. Furthermore there is a single specimen from Kwa-Mbonambi ("Umbonambi"), F. Toppin, in the Natal Museum (NM alc.). This measures 4.9 × 2.7 mm, l/d 1.77 and in many respects is different from the typical form and the Mfongosi subspecies. The shell is more ovate and larger than those from Mfongosi, there is a slight indication of a sinular denticle, the basal denticle is situated more to the left of the base and more superficial, and the inner columellar process is more prominent as compared to those in specimens from Natal and Mfongosi. The Kwa-Mbonambi specimen may therefore represent a third subspecies of *G. crassidens,* a race probably restricted to the southern Zululand coastal lowlands.

According to Connolly (1939) the type of *Ennea crassidens* is preserved in the British Museum (Natural History), although Pfeiffer wrote: "Aus meiner Sammlung". The species was described from "Port Natal" and stated to measure 6 × $3^1/_3$ mm, aperture 2 × $1^2/_3$ mm. No such specimen could be traced in the British Museum. However, two samples of one and three specimens respectively and having belonged to the Hugh Cuming collection were found among old material. Connolly may have considered the single Cuming shell to represent the type; the specimen in question is unfortunately too small and the present author recommends selecting the shell best conforming to the original measurements. One specimen from the sample of three has now been designated neotype; its measurements are 5.9 × 2.9 mm, aperture 2.0 × 1.7 mm. Pfeiffer has worked a good deal on Cuming material and has doubtlessly seen these specimens and may even have made the mistake to attribute them to his own collection.

Louis Pfeiffer's own material was incorporated in the Dohrn collection which subsequently was deposited in the Stettin Museum, where it was completely destroyed in the Second World War (Dance, 1966; Dr. A. Riedel,

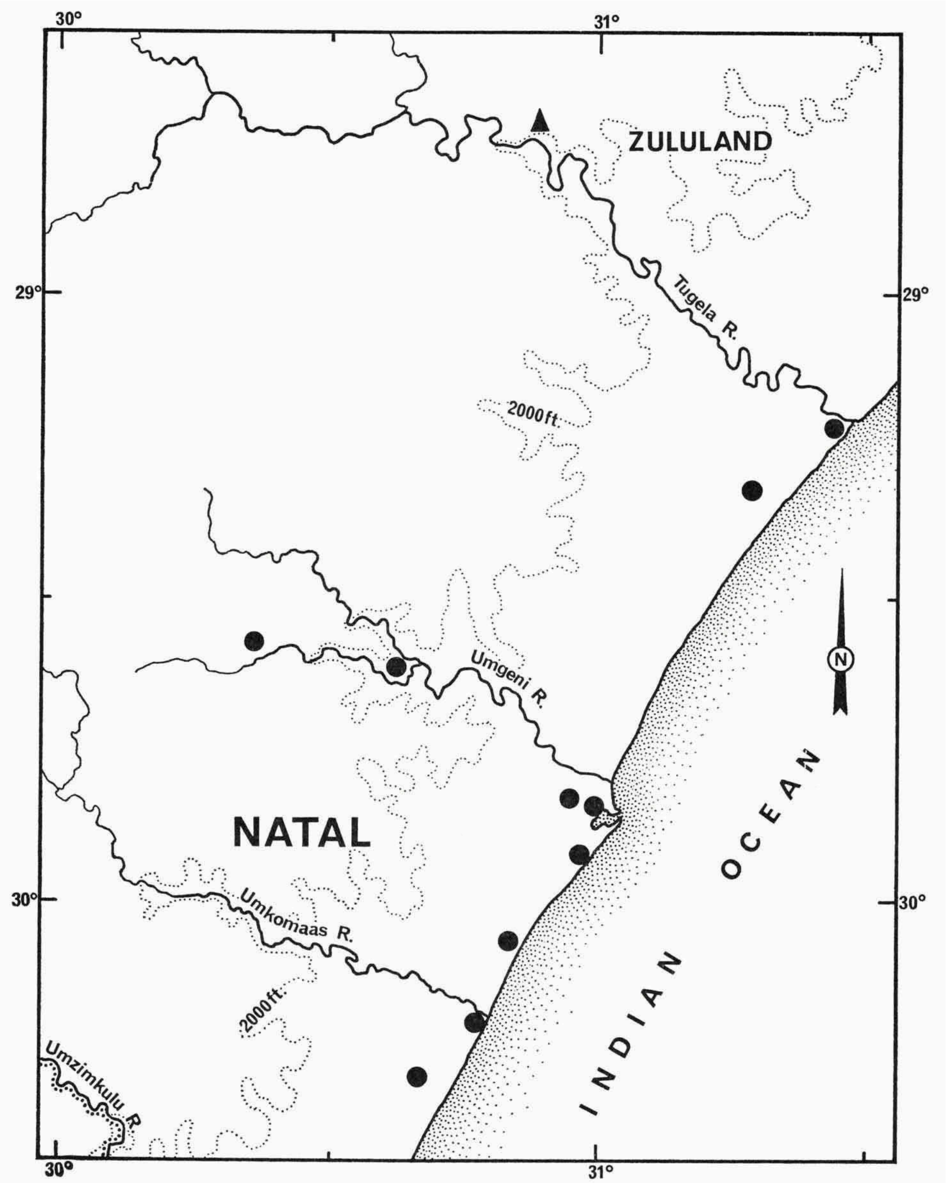


Fig. 24. Distribution of *Gulella crassidens* (Pfeiffer); localities of the nominate subspecies have been indicated by dots and that of *Gulella crassidens jonesi* n. ssp. by a triangle.

in litt.). If Pfeiffer has indeed made the mistake referred to above, the neotype may possibly also be a lectotype.

There is little variation in size, shape and dentition of the subspecies *jonesi*. The nominate race also exhibits few dental variations; attention should be drawn to the Spitzkop specimens (NM), which have very small sinular denticles. This process is hidden behind the large angular lamella, but varies from large and well-developed denticles to mere swellings, although very rarely absent altogether. A shell from Illovo River (NM) shows extensive repaired damage resulting in the aperture now being obliquely drawn to the right. The dentition is fairly normal, except that the outer columellar lamella is absent. Normally this process is not very well developed and occasionally it may be almost completely absent. The repaired shell has 9½ whorls and is also abnormally long: 7.2 × 3.2 mm, l/d 2.23.

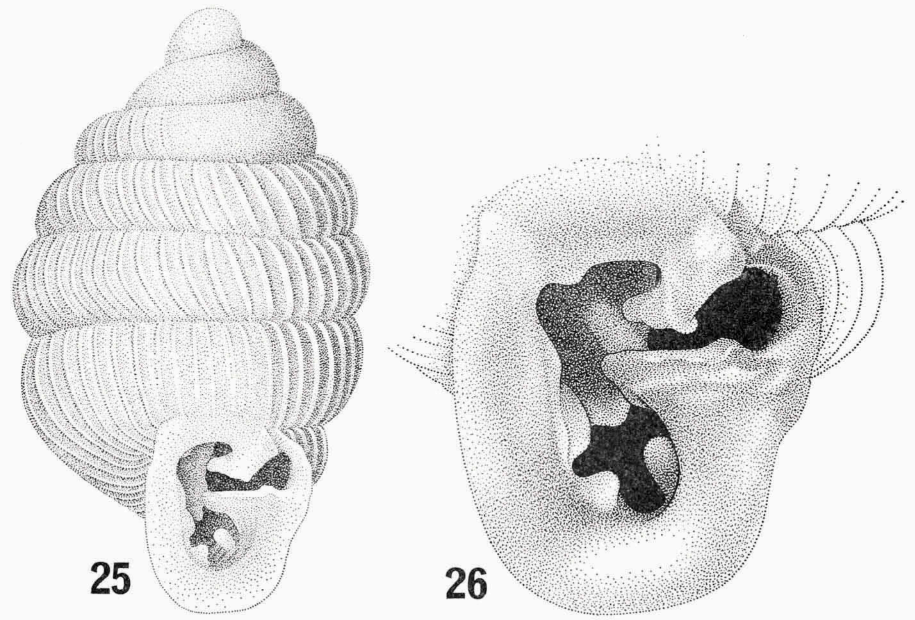
G. crassidens appears to range over a variety of habitats, but seems mainly restricted to coastal bush and associated types of vegetation a little distance away from the coast. Field notes from two labels are worth being put on record, viz., "found inside dead *Achatina* shell" (Umkomaas, NM) and "on veld near old rifle range — in grass roots + under lillies" (Hilton, NM, RMNH). The latter note was made by Falcon and refers to an extensively cultivated area with wattle plantations, grassland, a few remnants of temperate forest and bush, and a spacious residential area with large gardens.

Unfortunately no anatomical details are available, although it is not expected that such data would have helped in understanding the variation in the shell of *G. crassidens*.

Gulella browni nov. spec., figs. 25-26

Diagnostic characters. — A small, striate species of *Gulella* characterized by a markedly tapering apex, an open umbilicus, and a seven-fold dentition consisting of a single angular lamella and two labral, basal and columellar processes.

Description of shell. — Shell (fig. 25) small, acuminate ovate, with fairly open umbilicus, striate, creamy white. Spire produced, sides convex, tapering from penultimate whorl to a blunt, acuminate apex. Whorls 6-6¼, markedly convex, sculptured with comparatively widely spaced, regular, straight, slightly oblique, rather prominent costulae, which may almost be called lamellae (particularly towards the apex), interstices somewhat granulate; sutures deeply impressed, subcrenellate. First two whorls granulate and smooth. Aperture (fig. 26) trapezoid and almost square, rather obstructed by dental processes, peristome somewhat reflected, white and glossy, dentition seven-fold (may even be interpreted as eight-fold). On the right of paries a fairly large, vertical, inrunning angular lamella, the bottom of which is flattened and drawn out to the left resembling a flat shoe when seen in front view (see fig.), scarcely connected with apex of labrum; prominent and comparatively large labral complex above middle of labrum, protruding beyond the centre of the aperture, consisting of two denticles fused into a horizontal slab with a slight outer cusp and hardly discernible inner cusp, labral complex corresponding to shallow outside pit; two basal denticles, left and right of the base respectively, the right one largest, blunt and situated deep inside the aperture beyond the labral complex, the left one smaller and more superficially situated; long and very low outer columellar process with a slight dent in the middle, inside columellar process deeply situated, fairly large, prominent and somewhat mamillate; a very small swelling may be seen on the top left corner, fairly deep inside the aperture and may be termed a supplementary columellar process.



Figs. 25-26. *Gulella browni* n. sp. 25, holotype shell, dune forest on the east shore of Lake Sibayi (RMNH), actual length 3.0 mm; 26, aperture of holotype shell, highly enlarged.

Animal unknown.

Measurements of shell: 3.0-3.2 × 1.7-1.9 mm, l/d 1.70-1.73. The holotype measures 3.0 × 1.7 mm, l/d 1.72, aperture 0.9 × 0.9 mm, last whorl 1.4 mm, 6 whorls. The two paratypes both measure 3.2 × 1.9 mm, l/d 1.70 and 1.73 respectively (all l/d computed from micrometer readings).

Distribution. — *G. browni* is so far known from only two localities in Zululand and Mozambique.

ZULULAND: dune forest on the east shore of Lake Sibayi, leg. D. S. Brown, 12 June 1966 (type locality; holotype, RMNH). MOZAMBIQUE: Chiluvo Forest [4]), Manica e Sofala district (between Gondola and Beira), 700 ft., leg. D. M. Cookson, 15 March 1964 (two paratypes, NM).

This unusually characteristic species has been named after my friend Dr. David Seymour Brown of the Medical Research Council (London) as a tribute to his contributions to African malacology.

The two paratypes are slightly larger than the holotype but are otherwise very similar.

Shape, apex, costulation, and umbilicus make this new species unique among the Southern African species of *Gulella*. *G. browni* may be compared to three East African species, viz., *G. cuspidata* Verdcourt, 1962, *G. radius* (Preston, 1910) and *G. pretiosa* (Preston, 1911). *G. cuspidata* is similar in shape, apex, costulation, and umbilicus; however, it is larger than *G. browni* and moreover has a very different apertural dentition. In this genus the latter complex of characters is usually of great diagnostic value. The species *G. radius* probably consists of a variable complex, but most forms, though similar in shape, apex, and costulation, are characterized by fewer dental processes than in the above new species. *G. pretiosa* is a comparatively much larger species (4.5-5.7 mm) and also has fewer dental processes, particularly in the labral and basal areas.

Undoubtedly *G. browni* is closest to *G. radius*, of which two paratypes were examined at the British Museum (Natural History) (BM 1911.10.12. 146-147, Gazi, Kenya); Dr. B. Verdcourt after having examined the Chiluvo specimens, agreed to this. However, in view of the fact that very little is as yet known about the variability and distribution of *G. radius* (only a few rather diverging specimens from Kenya and Tanganyika being known, see e.g., Verdcourt, 1962), *G. browni* is provisionally given species status. Morphological differences combined with the southern localities for the present seem to justify this view.

6. THE DISTRIBUTION OF LAND MOLLUSCS IN ZULULAND

The composition of the land mollusc fauna of the Mkuzi and Ndumu Game Reserves as a sample of that of the Tongaland plain will first be considered after which the position of *Metachatina kraussi* (Pfr.) will be treated in connection with the above data.

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4) Also spelt Siluvo and Xiluvo.

A total of only 32 species is now known from the Mkuzi and Ndumu Game Reserves. Of these 16 are common to both areas, eight are known either from the one or the other, giving a total of 24 species for each of the two game reserves. There is no reason why most of the species seemingly confined to one of the two areas should not also be found in the other; only those species that occur in habitats restricted to the one place only are not likely to be found in the other game reserve where the habitat in question is absent.

Poynton (1964) has distinguished among the Southern African amphibians three zoogeographical elements: (a) tropical species [Poynton, 1964: 223: "A tropical form is here taken to be a form at least a substantial part of whose range is included in an area experiencing a tropical climate as defined by Köppen, *i.e.* in which the coldest month has a mean temperature of over 18° C (64.4° F)"], (b) Cape or temperate species (non-tropical forms, mainly concentrated in the southwestern Cape Province) and (c) transitional species (Poynton, 1964: 226: "The area carrying the overlapping subtraction margins of the two main faunal groups can be regarded as a transition zone, and the forms endemic to the transition zone can be called 'transitional forms' "). While on the main this system may be applied to terrestrial molluscs as well, a note of caution should be sounded here. Tropical and temperate elements are well defined and give rise to few difficulties. On the other hand the transitional element is less easily disposed of. Many transitional species belong to families and/or genera which are purely tropical in their African distribution (cf. e.g., species discussed by Van Bruggen, 1966a: 397, fig. 70).

An analysis of the land molluscs of the Mkuzi and Ndumu Game Reserves gives a total of 24 tropical species or 75% of the total number known:

Tropidophora ligata
T. insularis
T. plurilirata
Laevicaulis n. natalensis
Pupoides calaharicus
Rachis jejuna
Edouardia meridionalis
E. conulus
E. sordidula
Rhachistia sticta
Trachycystis burnupi
Guppya rumrutiensis
Urocyclus flavescens
Pseudoglessula boivini
Curvella saundersae
C. amicitiae
Euonyma tugelensis
Achatina craveni
A. immaculata
Gonaxis gwandaensis
Gulella triglochis
G. gouldi discriminanda
G. perissodonta
G. daedalea

The remaining seven species or 22% of the total (*Edouardia* spec. indet., which accounts for 3%, not included) are transitional:

Edouardia caffra
E. arenicola
E. cockerelli
Succinea striata
Trachycystis bathycoele
Sheldonia poeppigii
Nata vernicosa

Of these seven species *Succinea striata* is widely distributed south of the Zambezi River while two others are now only known from two localities each, viz., *Edouardia caffra* (Mt. Mohapaani, W. Transvaal; Ndumu Game Reserve, Zululand) and *E. cockerelli* (Durban, Natal; Ndumu Game Reserve, Zululand). *E. arenicola* and *Trachycystis bathycoele* are both known from the Eastern Cape Province, Natal and Zululand; *Nata vernicosa* occurs in the same areas and also in the Transvaal, whereas *Sheldonia poeppigii* covers about the same stretch of country in addition to one locality in Mozambique. Obviously all above species are more or less transitional in the sense of Poynton (1964). However, although these species do not at present show a truly tropical distribution, nevertheless most of them appear to have a tropical origin. The genera *Edouardia* and *Trachycystis* are both represented north of the Zambezi River; the former may be considered tropical. The genera *Sheldonia* and *Nata* are confined to Southern Africa, the latter being a representative of the Rhytididae, one of the families of ancient "Gondwanaland", which cannot be considered tropical at all. *Sheldonia*, on the other hand, is a typically South African offshoot of the tropical family Urocyclidae. Finally one finds that the genus *Succinea* is an almost cosmopolitan representative of a cosmopolitan family. All in all, of the seven transitional species, at least four have definite tropical origins, which on the whole emphasizes the tropical character of the mollusc fauna of the Tongaland plain. After invasion from the north a good deal of speciation apparently took place in the eastern littoral, which might explain the endemism in that area. These findings fully agree with those of Poynton (1964) on amphibians.

It is perhaps appropriate to sound a warning as far as the above zoogeographical data are concerned. Data on terrestrial molluscs are still regrettably few and cannot be compared with e.g., those on amphibians. Poverty of data may thus account for assigning to the transitional group species, which in fact may be tropical in their distribution. The absence of temperate or Cape elements among the land molluscs of Zululand comes as no surprise; if these are present at all, they will only represent a very low percentage of the total number known.

The fauna of the Mkuzi and Ndumu Game Reserves is representative of that of the drier part of the Tongaland plain. Both game reserves are situated in the plain between the coastal dunes on the eastern side and the Lebombo range to the west; the latter is more or less parallel to the Drakensberg escarpment, which itself is situated west of Swaziland. Thus, Tongaland consists of roughly three major areas, viz., the narrow coastal strip, the large central plain, and the eastern escarpment. These areas are ecologically very different, which is mainly caused by a considerable disparity in rainfall. While the dunes and escarpment enjoy a moderate to sometimes even high rainfall, resulting in forest formation (dune and temperate rain forest respectively), the intermediate plain is decidedly semi-arid, resulting in a savanna-type vegetation. It appears that the different types of forest on the dunes and the Lebombos are essentially the same (Tinley, 1967, and in litt.). The land mollusc fauna of both areas shows a remarkable similarity, which makes one conclude that both forest ranges have been connected in the past or received their respective faunas from a common source.

A comparison of what few data are available leads to the following conclusions. The terrestrial molluscs of dune and escarpment forests can be roughly divided into three groups:

(a) Species occurring in both areas without showing any differences at all. These may be termed conservative species, such as *Sheldonia poeppigii.*

(b) Species of which representatives already show measurable differences, having (almost) reached subspecific level. This is well illustrated by the case of *Euonyma lanceolata* (Pfr.) (see also sub chapter 5). Tinley's and the Natal Museum's material are too scanty to allow drawing definite conclusions, but available specimens seem to indicate that the population of the Gwaliweni Forest on the Lebombo escarpment has comparatively short and squat shells, while that of the dune forest between Sordwana Bay and Cape Vidal has longer and more slender shells as shown by the following measurements:

Gwaliweni Forest	47.0 × 14.0 mm, l/d 3.36
dune forest	57.5 × 14.3 mm, l/d 4.02
do.	55.0 × 14.3 mm, l/d 3.82
do.	54.5 × 13.7 mm, l/d 3.98 (average of 3: l/d 3.94)

(c) Species which are different but still show close relationship; these may be called progressive species. Certain Achatinidae probably belong to this group, e.g. *Archachatina zuluensis* (Conn.) of the dune forest as compared to an as yet unidentified species of the escarpment (cf. Van Bruggen, 1967b: 22, end of first paragraph: "An allied flammate species.........").

The fauna of the Tongaland plain shares a small number of species with the areas to the west and east. An example of this phenomenon is the streptaxid *Gulella triglochis* (M. & P.), which in the plains is usually much smaller than in the adjoining forest areas; this may be explained by the influences of a marginal as opposed to a more favourable or even optimum habitat (see also p. 38).

The above discussed mosaic of species is most likely to have had its origin in the history of Tongaland; more particularly, this may have been caused by fluctuations in the climate (mainly precipitation and temperature) during the Pleistocene (see also preliminary note by Van Bruggen, 1967c). Available data on the variation of the Pleistocene climate in Southern Africa have been admirably summarized by Cooke (1964). It appears that "the rainfall ranged from about 60% of the present precipitation in dry periods to about 140% in the wet periods" (Cooke, 1964: 12); this has been caused by a rise or drop in temperature as a sequel of the contraction or expansion of the great ice sheets in the northern hemisphere. These phases have been termed pluvial or hypothermal (cool-humid) and interpluvial or nonpluvial (warm-dry) periods respectively. A change in precipitation and temperature has always been accompanied by a change in the vegetation; the forest belt has contracted and expanded in direct relation to these climatic fluctuations. During the hypothermal periods most of Tongaland must have been covered with a continuous forest (cf. maps in Cooke, 1964: figs. 8-10). At the onset of drier weather towards the end of the Pleistocene this forest belt contracted to its present position east and west of the dry Tongaland plain. This has caused the disappearance of the forest-dwelling species except those that could adapt themselves to a life under marginal conditions. Examples of the latter are the above discussed streptaxid *Gulella triglochis* and also the terrestrial prosobranch gastropod *Tropidophora ligata,* which is an adaptable species, able to survive in sheltered localities in semi-arid areas (riverine forest and even savanna-type vegetations which are so common in e.g., the eastern Transvaal, vide Van Bruggen, 1966a). Differences in rate of evolution among the various families of land molluscs may account for the existence of the three categories of species discussed on p. 74. At the same time the forest withdrew, drier conditions enabled the savanna and dry forest to invade southwards from the Mozambique Plains, thus adding to the separation of dune and escarpment forest fragments. The comparatively poor mollusc fauna of the new habitat also moved southwards occupying the newly available niches. Savanna-adapted species such as *Pupoides calaharicus, Rachis jejuna, Achatina immaculata,* and *Gulella perissodonta* undoubtedly came from the north. The fauna of the plains is evidently an impoverished one; low rainfall, high temperatures and a savanna-type vegetation cannot support a diverse land mollusc fauna, apart from its history as explained above [5]).

Metachatina kraussi fits well into the above described distribution patterns. In Tongaland the species is known to occur on the Lebombo escarpment (locs. nos. 17, 18 and 24, see p. 15) and in the coastal forest (locs. nos. 20-23). However, it is also recorded from one locality in the Tongaland plain, viz., the Sihangwane Bush (loc. no. 19). According to Tinley (in litt.) this is a "DRY FOREST strip near Sihangwane Store". This may either be a remnant of the great Pleistocene forest or the shells in question may have been discarded by natives visiting the shop. In Zululand large achatinids are used for purposes such as hippopotamus scares in cultivated fields, in which case they are usually pierced (specimens mentioned by Connolly, 1939, not traced). It is not impossible that certain remaining pockets of forest in sheltered situations may still harbour forest elements. The general impression is that *Metachatina kraussi* has disappeared from the Tongaland flats, but survived in the fringing areas to the east and west.

7. The distribution of land molluscs in Southern Africa

Little has been published on the zoogeography of the non-marine molluscs of Southern Africa. Although our knowledge of the land molluscs of this part of Africa is now reasonably well advanced, indeed more advanced than that of any other part of Subsaharan Africa, distribution data are still comparatively poor. However, the work done by Connolly (1939) and his successors has given us sufficient data to build up a general picture. Of necessity conclusions based on scanty data must sometimes be bold, but at least the present state of knowledge enables us to draw conclusions.

Pilsbry & Bequaert (1927: 484-486) devote some space to the "South African Subregion"; their list of endemic genera more or less conforms to the one discussed below. Although much of their data has now been superseded by more and more precise information, their general conclusions about derivation and affinities of the Southern African non-marine molluscs are still roughly correct. These authors were among the first to have recognized the main characters of the fauna of Southern Africa as reflected by its land molluscs.

A short and preliminary survey of the distribution of the non-marine molluscs of Africa has been given by Connolly (1931a), who only devoted two

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[5]) Moreau (1966) extensively dwells on the influences of Late Pleistocene climatic changes on the birds of Africa.

pages to his "province" of South Africa. This author has mainly discussed species and groups peculiar to the southern parts of the continent, although mention is made of the obvious absence of tropical genera such as "*Limicolaria, Ledoulxia, Homorus, Pseudopeas, Vitrina, Pseudoglessula* (but for a solitary record in Zululand), and, except for a single species of *Gonaxis*, all of the Streptaxidae but *Gulella*". However, in the last thirty-five years our knowledge of the non-marine molluscs of Africa has greatly increased not in the least due to Connolly's major work (Connolly, 1939). It is now generally realized that the Southern African fauna is decidedly more tropical in facies than has been assumed before and Connolly's above remark has lost much of its strength.

7a. The country (topography, climate, vegetation)

The southern part of Africa is sometimes called a "subcontinent" and is usually limited to the north by the Cunene (also spelt Kunene, in the west) and Zambezi Rivers (in the east), roughly corresponding to 17° S. In the west this is a fairly natural boundary by virtue of the increase in elevation and rainfall in southern Angola. In the centre and east the Zambezi River is largely an artificial boundary accepted for the sake of convenience. This immense country, surrounded from west to east by the Atlantic and Indian Oceans, has an extraordinary variation of geography, climate, and vegetation. Southern Africa encompasses the following countries: South Africa, South West Africa, Botswana (formerly Bechuanaland (Protectorate)), Rhodesia (formerly Southern Rhodesia), Lesotho (formerly Basutoland), Ngwane (formerly Swaziland), and the southern portion of Mozambique or Portuguese East Africa (fig. 27).

Geologically Southern Africa has had a chequered history. The Cape foldings date back to the Mesozoic, while in the Cretaceo-Tertiary strong uplifts were accompanied by climatic variations. The late Tertiary elevation of the continent has led to marked erosion. In the coastal belt this is shown by the deeply-incised river gorges and more inland by plateau-scarps; the Great or Eastern Escarpment thus came into being. Climatic changes before and during the Pleistocene have greatly influenced the vegetation pattern (Cooke, 1964, see also chapter 6).

Probably at one time Africa must have been part of an Antarctic complex of continents; this automatically turns our thoughts to ancient "Gondwanaland". It has now become clear that continents have drifted indeed, that the southern continents have been much closer than they are now and that South America and Africa may even have been united. All continents may have

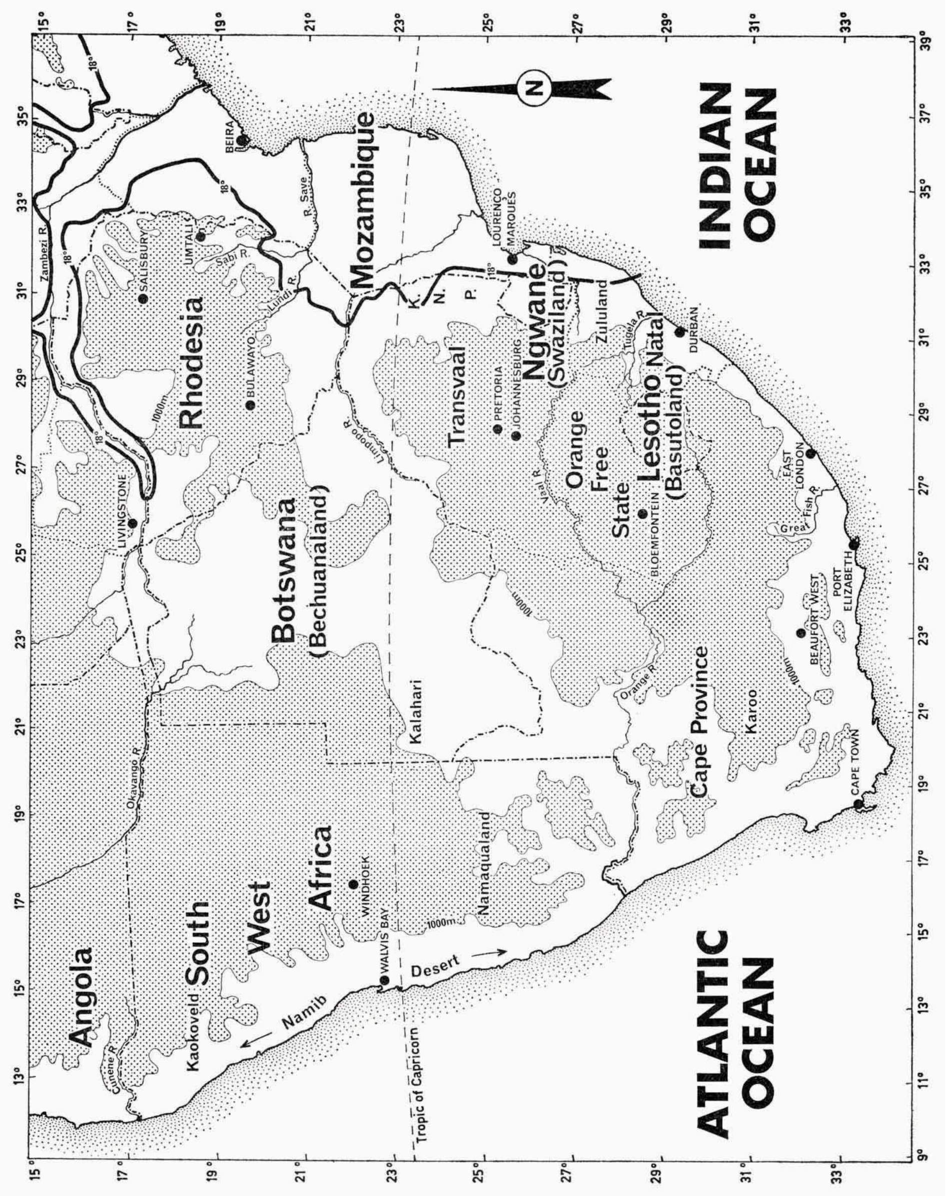

Fig. 27. General map of Southern Africa. Areas over 1000 m have been shaded, while the 18° C. mean July isotherm has been indicated by a line marked with 18°.

been situated farther south than now and Africa and South America probably parted in the Jurassic. The isolation of Madagascar also possibly dates back to that time. Although it is unlikely that there has been a large, closed continent (Gondwanaland), the southern continents must have been sufficiently close for greatly increased possibilities for dispersal over the comparatively narrow sea barriers. Moreover, zonation of climate has always played an important role in causing similarity in southern biota and has indeed been a fundamental factor in the distribution of life on the southern continents. In the past Antarctica has definitely been warmer than today; at times Antarctica must have enjoyed a cold-temperate or even temperate climate, probably in the Permian, Mesozoic and Tertiary. The 'continent' started to drift apart after one or more of these temperate periods, so that at one time a temperate land-sea mosaic may have existed around present-day Antarctica. Darlington (1965) has summarized data from various disciplines of science in his book on the biogeography of the southern continents. This author has particularly studied data derived from paleomagnetic sources and according to him (and many others) we now have fairly good evidence for what has been summarized in the above paragraph. Wegener's theory has long been in discredit, but today a modified version of his interpretation is well on the way to general acceptance.

Undoubtedly the most salient and important feature is the mountain range parallel to and at varying distances from the east coast; this range, the Drakensberg Mountains, reaches a maximum altitude of 3229 m (10822 ft.) in western Natal and is discontinuous in the Transvaal and further north. The Zambezi River is the most important interval and is usually considered to mark the northern limits of the Great or Eastern Escarpment, a more general term for the Drakensberg sensu lato. Much of Southern Africa is elevated country; lowlands (areas under 1500 ft. = 450 m) are only found in a narrow strip bordering the coasts of Natal and Mozambique. The plateaus are extensive and of varying altitude. The greater portion of South Africa is over 3000 ft. (900 m) with an innermost plateau of about 4000 ft. (1200 m), which is called the Highveld and covers much of the Cape Province, the Orange Free State, and the Transvaal. The Middleveld (3000-4000 ft. = 900-1200 m) and Highveld (over 4000 ft. = 1200 m) in Rhodesia are continuations of the Transvaal Highveld, separated by the low-lying Limpopo River valley. The South African plateau is encircled by mountain ranges, such as those of Namaqualand in the west, the Cape fold mountains in the south and the Drakensberg range in the south and east. The highlands are mainly peripheral; much of Lesotho is over 10.000 ft. (3000 m) high. Botswana mainly consists of the relatively low-lying, sand-filled, Kalahari basin

(500-1000 m), which separates the three plateaus of South West Africa, Rhodesia, and South Africa. This separation is partly due to the eastward extension of the Kalahari basin into the Limpopo River valley, an ancient and important interval in the Eastern Escarpment. South West Africa has a comparatively high elevated tableland with an average altitude of about 3600 ft. (1100 m).

The climate is very diverse and mainly follows the chequered topography. The Drakensberg is not only the main watershed but also delimits the areas with good and poor rainfall. Much of the interior and west of Southern Africa is decidedly arid (Karoo, Kalahari, Kaokoveld, Namib Desert, etc). The main precipitation falls on the eastern coastal plain and on the eastern slopes of the mountains. There is a sharp decrease in rainfall from east to west:

east coast	mean annual rainfall	750-1000 mm
forests on the eastern slopes	mean annual rainfall	1000→1500→2500 mm
from Pretoria to the west	mean annual rainfall	750→125 mm (east-west gradient)

In South Africa the mean annual rainfall is 437.5 mm (17.5 inches) and in Botswana the rainfall varies from 450 to 625 mm. South West Africa is mainly very arid indeed, the average annual rainfall varying from 25 mm (coastal belt) to 150 mm (south), 300 mm (central area) and 550 mm (north); Walvis Bay receives on the average only 12.5 mm (0.5 inches) rainfall per annum. The average annual rainfall for Rhodesia is 750 mm, but precipitation varies from 375 to over 1250 mm; the Lowveld with an elevation from 1000 to 2000 ft. (300-600 m), has a rainfall of less than 500 mm, the Middleveld with an elevation of 3000 to 4000 ft. (900-1200 m) from 500 to 750 mm and the Highveld comprising the area of over 4000 ft. (1200 m) from 600 to 1100 mm. Very few areas in Southern Africa enjoy a rainfall of 1750 mm and over (forests on the Rhodesian Eastern Escarpment, see e.g., Van Bruggen, 1961). The rainfall is strongly seasonal and usually concentrated in the period October to February (Summer Rainfall Area); in the southwestern Cape Province the main precipitation falls in the austral winter (Winter Rainfall Area).

The evaporation is great and over the whole of South Africa exceeds the mean annual rainfall. The relative humidity as a rule is higher than expected in an arid country and enables life to exist and diversify in otherwise barren areas.

Temperatures vary much but less than the rainfall. A large part of the southeastern area, although partly south of the Tropic of Capricorn, may be considered to experience a tropical climate in the sense of Köppen (1931).

Köppen defines this as a climate in which the coldest month has a mean temperature of over 18° C.; in Southern Africa July is the coldest month and areas within the mean 18° C. July isotherm are here considered tropical (see fig. 27). The really hot areas with a mean annual temperature of over 21° C. are coastal Zululand, the eastern Transvaal Lowveld, the Limpopo River valley and parts of the Orange River valley. On the whole the plateaus are cool to fairly cool, as shown by the mean annual daily temperature in the following localities from south to north and selected to represent approximately the same latitude:

Plateau		*Coast*	
		Cape Town	16.1° C.
Beaufort West	17.6° C.	East London	18.2° C.
Bloemfontein	15.6° C.	Durban	20.5° C.
Pretoria	17.0° C.	Lourenço Marques	22.0° C.
Salisbury	18.3° C.	Beira	24.5° C.

Windhoek on the South West African plateau has a mean annual daily temperature of 19.4° C. and Umtali on the comparatively low Rhodesian Eastern Escarpment 20.0° C. The temperature of the hot and low-lying Zambezi River valley may be demonstrated by that of Livingstone at 22.2° C.

Seasonal rainfall combined with a high insolation and evaporation results in peculiar environmental conditions, usually considered marginal for terrestrial molluscs.

The vegetation is as diverse as climate and subsoil. Acocks (1953) has given a very good detailed survey of the veld types of South Africa; neighbouring territories have not been covered on the same scale. Forest has become scarce and much of Southern Africa is now grassland and savanna. Tropical rain forest proper is very patchy and unknown south of 21° S.; the best preserved remnants are on the Rhodesian Eastern Escarpment and adjoining parts of Mozambique (see e.g., Van Bruggen, 1961). Riverine forest is common, particularly in savanna country and is ecologically very important for the existence of land molluscs in dry areas such as the Kruger National Park. Various types of temperate forest are mainly found on or east of the watershed. Among the latter the conifer genus *Podocarpus* is particularly important in southeastern Africa.

The most important types of vegetation may be extracted from the maps of Keay (1959) and Cooke (1964). Four types are predominant in Southern Africa and should be summarily discussed here. "Karoo shrub and mixed Karoo" is dominant in the low rainfall zone of up to 375 mm (15 inches) per annum; this mainly covers the southern interior of South Africa and harbours very few land molluscs. "Kalahari grassland or mixed open *Acacia* wooded steppe" is limited by the 500 mm (20 inches) isohyet and covers much of the interior of South West Africa and Botswana; this zone is also poor in land molluscs but less so than the one discussed above. "Temperate mixed grassland" is confined to the South African plateau with a mean annual rainfall in excess of 500 mm and a mean annual temperature of below 18° C. Molluscan life in this zone is generally confined to bush along water courses and on rock formations. Finally "Bushveld and grassland" covers areas with a moderate to high rainfall (15-35 inches = 375-875 mm per annum) and fairly high temperatures (over 20° C.). Bushveld and grassland are subject to periodic, usually seasonal, droughts and the terrestrial molluscs, which are fairly abundant in this area, are adapted to these conditions. Riverine forest in this type of vegetation, which covers much of the Transvaal (e.g., the southern and central districts of the Kruger National Park), is of paramount importance for the distribution of land molluscs (vide Van Bruggen, 1966). With an increase in rainfall bushveld and grassland are being replaced by a forest-savanna mosaic of two varieties. The coastal variety harbours a rich community of molluscs; an additional factor of great importance here is the presence of lime in the soil, which otherwise is quite rare in Southern Africa where many types of soil are decidedly acid. The inland variety of this zone of vegetation is composed of various types of forest, which also harbour very many species of land molluscs. In Southern Africa this forest-savanna mosaic and allied types of vegetation are restricted to the coastal belt and eastern slopes of the escarpment, so that the majority of the species of land molluscs are concentrated in this part of the subcontinent.

In cross-section from east to west one thus notices a gradient in the vegetation closely correlated to the decreasing rainfall: coastal bush (east coast) — grassland (lower slopes) — temperate/montane forest (on the water-shed) — alpine zone (mountains) — bushveld/grassland with gallery forest along the rivers (further west) — savanna/steppe (central part) — semidesert (further west) — desert (west coast).

For more extensive data on topography, climate, and vegetation, the student is referred to the work of Cooke (1964), Keay (1959), Wellington (1955), and others; concise data are supplied by Gordon-Brown (1963).

7b. Composition of the fauna

Southern Africa is known to harbour about 660 species of terrestrial molluscs sensu stricto (i.e., exclusive of semi-marine and semi-aquatic species such as representatives of the families Onchidiidae and Ellobiidae). These species represent 87 genera and 33 families [6]. A total of 23 imported (alien) species belonging to 15 genera of which 14 are alien and to eight families of which six do not otherwise occur in the area, has to be subtracted from this number, leaving roughly 640 indigenous species, representing 73 genera and 27 families. These data have been mainly taken from the following sources: Van Regteren Altena (1966), Van Bruggen (1966 and paper in the press),

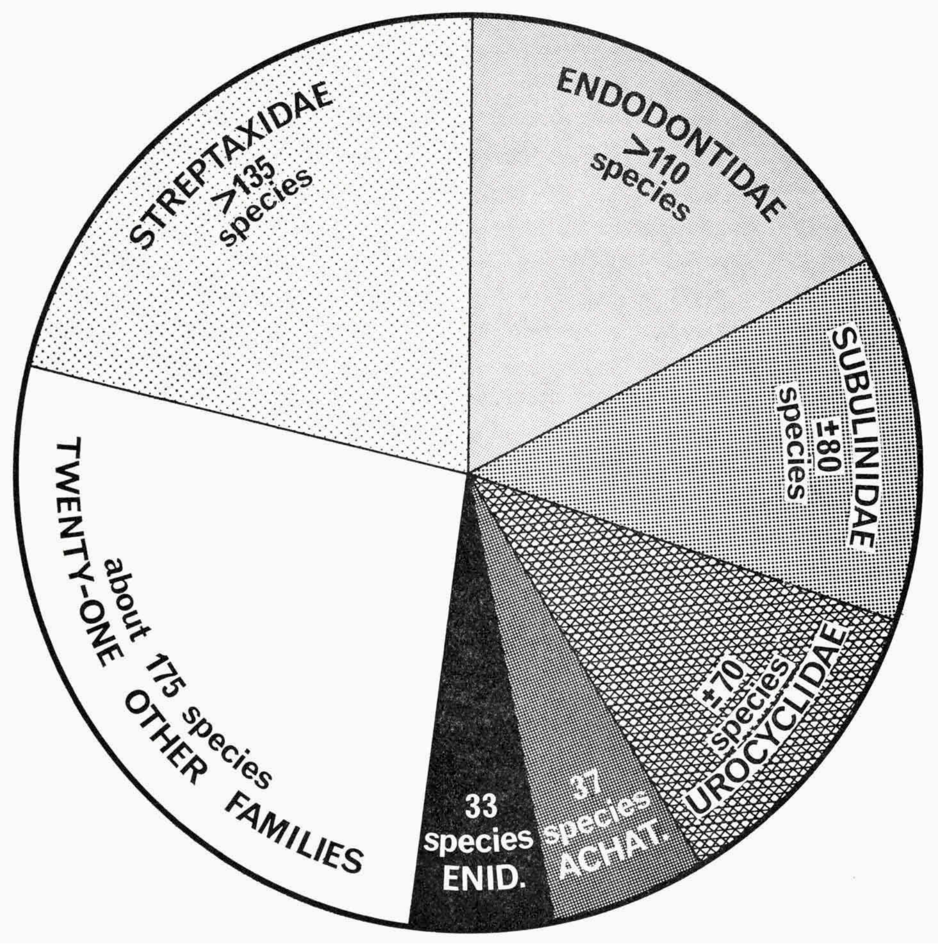

Fig. 28. Composition of the assemblage of Southern African terrestrial molluscs according to families; the six dominant families have been separately indicated.

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[6] All figures are approximate.

Connolly (1939), and Forcart (1967) for the indigenous species and Van Regteren Altena (1966) and Van Bruggen (1964a, 1967) for the alien species.

Fig. 28 graphically depicts the composition of the assemblage of terrestrial molluscs in Southern Africa arranged according to numbers of species in the various families. Counts and/or estimates of the numbers of species are conservative. A glance at the figure shows that there are only six dominant families: Streptaxidae, Endodontidae, Urocyclidae, Subulinidae, Achatinidae and Enidae. In numbers of species these make up almost three-quarters of the total.

The existence of families dominant in certain areas is well established; a mere mention of the position of the family Helicidae in the circum-mediterranean countries suffices here. However, it seems worth while to make some comparisons, particularly with regard to the relative position of the few dominant families in a faunal assemblage. Various data have been calculated for four different areas.

In Central Europe 224 species of land molluscs in 24 families have been recorded. Of these 102 species belong to three dominant families, viz., 48 Helicidae, 31 Clausiliidae, and 23 Zonitidae; the remaining 122 species belong to 21 families. Data have been extracted from Zilch & Jaeckel (1962).

In France 379 species of land molluscs in 25 families have been recorded. Of these 205 species belong to four dominant families, viz., 119 Helicidae, 36 Clausiliidae, 27 Zonitidae, and 23 Chondrinidae; the remaining 174 species belong to 21 families. Data have been extracted from Germain (1930-1931). Incidentally, the position of the Helicidae as a dominant circum-mediterranean family is confirmed by these figures for France.

In the U.S.A. east of the Rocky Mountains 375 species of land molluscs have been recorded. Of these 243 species belong to four dominant families, viz., 104 Polygyridae, 90 Zonitidae, 28 Vertiginidae, and 21 Endodontidae; the remaining 132 species belong to 26 families. Data have been extracted from Burch (1962).

Comparable data from Africa are difficult to procure and in fact are probably almost non-existent. Pilsbry's work on the ex-Belgian Congo (Pilsbry, 1919) has been used here somewhat reluctantly because it is rather out of date. Pilsbry recognizes about 400 species of land molluscs in 15 families. Of these approximately 340 species belong to four dominant families, viz., ± 100 Streptaxidae, ± 100 Subulinidae, ± 75 Urocyclidae, and ± 65 Achatinidae; the remaining ± 60 species belong to 11 families.

Numerically the above data may be compared as follows:

	Southern Africa	Congo	France	Eastern U.S.A.	Central Europe
total number of species	± 640	± 400	379	375	224
number of families	27	15	25	40	24
do. of dominant families	6	4	4	4	3
do. in percentage of total number of families	22%	27%	16%	10%	12%
number of species in dominant families	465	± 340	205	243	102
do. in percentage of total number of species	73%	85%	54%	65%	45%

Obviously (sub)tropical areas harbour proportionally more species belonging to dominant families than temperate regions. Dominance as here understood implies both a plethora of species and large numbers of individuals of those species. This may be caused by adaptability to a particular set of environmental conditions and the genetic potentiality to effect species radiation.

Among the dominant families the Streptaxidae and Subulinidae are circumtropical and the Enidae an Old World family. The Achatinidae and Urocyclidae are Subsaharan or purely African families (Achatinidae with one genus endemic to Madagascar), while only the Endodontidae belong to the Southern Relict fauna (see below). Of these six dominant families four are also dominant elsewhere in Africa (see e.g., above data ex Pilsbry, 1919, for the ex-Belgian Congo); on the other hand the Endodontidae are insignificant as fauna elements north of the Limpopo River.

Southern Africa appears to harbour a comparatively rich assembly of land molluscs. The following comparisons may be made:

area and source	approximate surface in square miles	approximate number of species	approximate number of species per 100.000 square miles
Southern Africa (various sources)	1.300.000	640	49
Congo ex-belge (Pilsbry, 1919)	900.000	400	44
Europe (Waldén, 1963)	3.750.000	> 1500	> 40
Western Australia (Iredale, 1939)	1.000.000	120	12
North America (Waldén, 1963)	7.300.000	700	9

The following comments on this table should be made here. The figures for the Congo are quite out of date; in order to reach the level of Southern Africa only 41 additional species are needed, which indeed have been recorded since 1919 (vide e.g., Adam, 1954, 1957; Pilsbry & Bequaert, 1927; Pilsbry & Cockerell, 1933, and others). Undoubtedly this country should head the above list; among a diversity of habitats the Congo is predominantly covered by equatorial rain forest, which is known to be a centre of evolution, particularity also at its fringes. Unfortunately no reasonably exact data are available for Europe. Western Australia lacks the diversity in habitat exhibited by all other above countries; moreover, it is essentially a rather arid country. Western Australia should perhaps rather be compared to South West Africa; this territory encompasses approximately 318.000 square miles and has a land mollusc fauna of about 65 species (Blume, 1963; Connolly, 1931, 1939, 1941; Zilch, 1939, 1951, 1952; this paper pp. 26, 31). This works out at 20 species per 100.000 square miles, which is considerably higher than the 12 species recorded for Western Australia. However, it is extremely difficult to compare these data; one should take into account the geological history, climate, vegetation, etc. of the countries involved, apart from the fact that the land molluscs of South West Africa are considerably better known and have been more extensively collected than those of the western parts of Australia.

A marked endemism at various levels characterizes the Southern African assemblage of land snails. This may be summarized as follows:

endemic families: 1 (Aperidae: only genus *Apera*); [7]
endemic subfamilies: 1 (Arionidae — Oopeltinae: only genus *Oopelta*);
endemic tribes: 1 (Acavidae — Dorcasieae, composed of the genera *Trigonephrus*, *Tulbaghinia*, and *Dorcasia*);
endemic genera: 16 (*Chondrocyclus*, *Afriboysidia*, *Afrodonta*, *Oopelta*, *Sheldonia*, *Xerocerastus*, *Coeliaxis*, *Metachatina*, *Trigonephrus*, *Tulbaghinia*, *Dorcasia*, *Prestonella*, *Nata*, *Natalina*, *Apera*, *Sculptaria*), of which ten belong to non-endemic higher taxa.

The number of lower categories peculiar to Southern Africa varies; many subgenera seem to be restricted to Southern Africa. These are mainly the subgenera *Tomigerella* and *Fauxulus* s.s. of the genus *Fauxulus* (see Van Bruggen, 1967a: 4-5) and probably ten of the eleven subgenera of *Trachycystis*.

Genera of which the great majority of the (subgenera and) species is restricted to a certain area may be termed near-endemic or subendemic genera in that region. Near-endemics are well-known in various groups of animals and plants, particularly in Africa and its islands. Two examples of Southern African terrestrial molluscs may be called almost classical examples of this phenomenon. In Southern Africa the chondrinid genus *Fauxulus* "occupies

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[7] The list on p. 88 gives details about families and systematic position of genera mentioned here.

a fairly narrow discontinuous area east of the escarpment from the western Cape Province to the Tugela River, Natal" (Van Bruggen, 1967b: 4) with extensions of this range to the west (Kuruman and Kimberley) and to the north (Zoutpansberg District, N. Transvaal). One recently discovered species, *F. milloti* Fischer-Piette & Bedoucha, 1965, was obtained in northern Madagascar, which made South Africa lose one of its oft-quoted endemic genera, which incidentally shows on what a slender base much of our zoogeography rests. However, the Malagasy species undoubtedly belongs to a subgenus widely distributed in South Africa, which country still retains two subgenera and 15 species of *Fauxulus*, so that it may be termed a near-endemic genus in that country. The case has been fully discussed by Van Bruggen (1967b).

The other example of near-endemism is the endodontid genus *Trachycystis*; this extraordinarily diversified genus occurs mainly east of and on the watershed of Southern Africa with at least 106 species [8]) of sometimes very restricted ranges. Zilch (1959) has divided *Trachycystis* into ten subgenera, to which one was added by Van Bruggen & Verdcourt (1965); of these ten are very probably restricted to Southern Africa and many even to certain parts of the Cape Province (see e.g., Van Bruggen, paper in the press). North of the Limpopo River the genus is poorly represented (only about ten species as yet in Rhodesia and Mozambique) and north of the Zambezi there is a decidedly restricted number of species, which do not seem to occur as far north as Ethiopia and the Sudan (Verdcourt, personal communication). Thus, the genus *Trachycystis* in Southern Africa may confidently be considered a near-endemic.

The number of endemic species amounts to approximately 90% of the known species. Of these roughly one-fifth (112 species) belongs to the endemic genera enumerated above, while the great majority of the endemic species has been classified in genera usually widely distributed in Subsaharan Africa (e.g., *Achatina, Curvella, Gulella*) or even beyond the Ethiopian Region (e.g., into southern Asia, such as the enid genera *Rachis* and *Rhachistia*).

Looking at this from another angle, it is interesting to note that only about seventy odd species or roughly 11% of the total are known to occur north of the Zambezi. These mainly belong to four families (17 Enidae, ten Urocyclidae, eight Streptaxidae, six Achatinidae), while twelve others (either tropical or cosmopolitan, such as the Succineidae) are only represented by

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[8]) Connolly, 1939: 100 species; Van Bruggen & Verdcourt, 1965, one species; at least five undescribed species collected by A. C. and W. H. van Bruggen, 1962-1966.

one or a few species. It is obvious that as a rule large areas will have comparatively higher proportions of endemic species than smaller areas and consequently also comparatively lower proportions of more widely distributed species as shown by the above figures. However, this is by no means a general rule in Southern Africa. Among the mammals in particular this is almost the reverse: 184 or 71% of the 258 terrestrial species known to occur in Southern Africa are also found north of the Cunene and Zambezi Rivers and only 74 or 29% of the species are restricted to Southern Africa. On the other hand it should be realised that in many respects it is inopportune to compare the distribution of molluscs and mammals, because of the significant differences in mode and speed of dispersal, let alone their respective phylogeny and evolution. Mammal data were computed from Meester, Davis & Coetzee (1964).

On higher levels the connections of the Southern African terrestrial molluscs with those of Central and East Africa are much more obvious; twenty-one families (78% of the total) and 57 genera (78% of the total) also occur north of the Zambezi.

Recent data on the land molluscs of Madagascar are very scattered 9), but it transpires that the fauna of this island, while showing certain African affinities, has very much a character of its own. Very few species and only a limited number of genera are both known from Madagascar and the African mainland. Endemism is mainly concentrated on the specific level; the number of endemic genera is about the same as in South Africa and there is no endemism at higher levels. Among the Southern Relict families the Acavidae are particularly well represented. The prosobranch genus *Tropidophora,* a well-known South and East African fauna element, is more diverse in species on Madagascar than on the continent.

7c. The endemic genera and their species

The detailed distribution of the endemic genera is as follows (fig. 29-34):

Chondrocyclus (fig. 29) — discontinuous in southeastern South Africa from the Cape Peninsula to the Limpopo River. According to the literature (Connolly, 1939) the genus does not occur north of Mfongosi in Zululand. However, one weathered shell, unidentifiable as to species, but undoubtedly belonging to the genus *Chondrocyclus,* was found in the Hanglip Forest near Louis Trichardt at 4500 ft. (leg. A. C. and W. H. van Bruggen, 8-9.II.1965, NM), which extends the distribution to the Transvaal and almost to the

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9) See numerous papers by Fischer-Piette and collaborators in the Journal de Conchyliologie, the Bulletin and the Mémoires du Muséum National d'Histoire Naturelle, Paris (1948 to date); see summary list in Fischer-Piette, Blanc & Salvat, 1969.

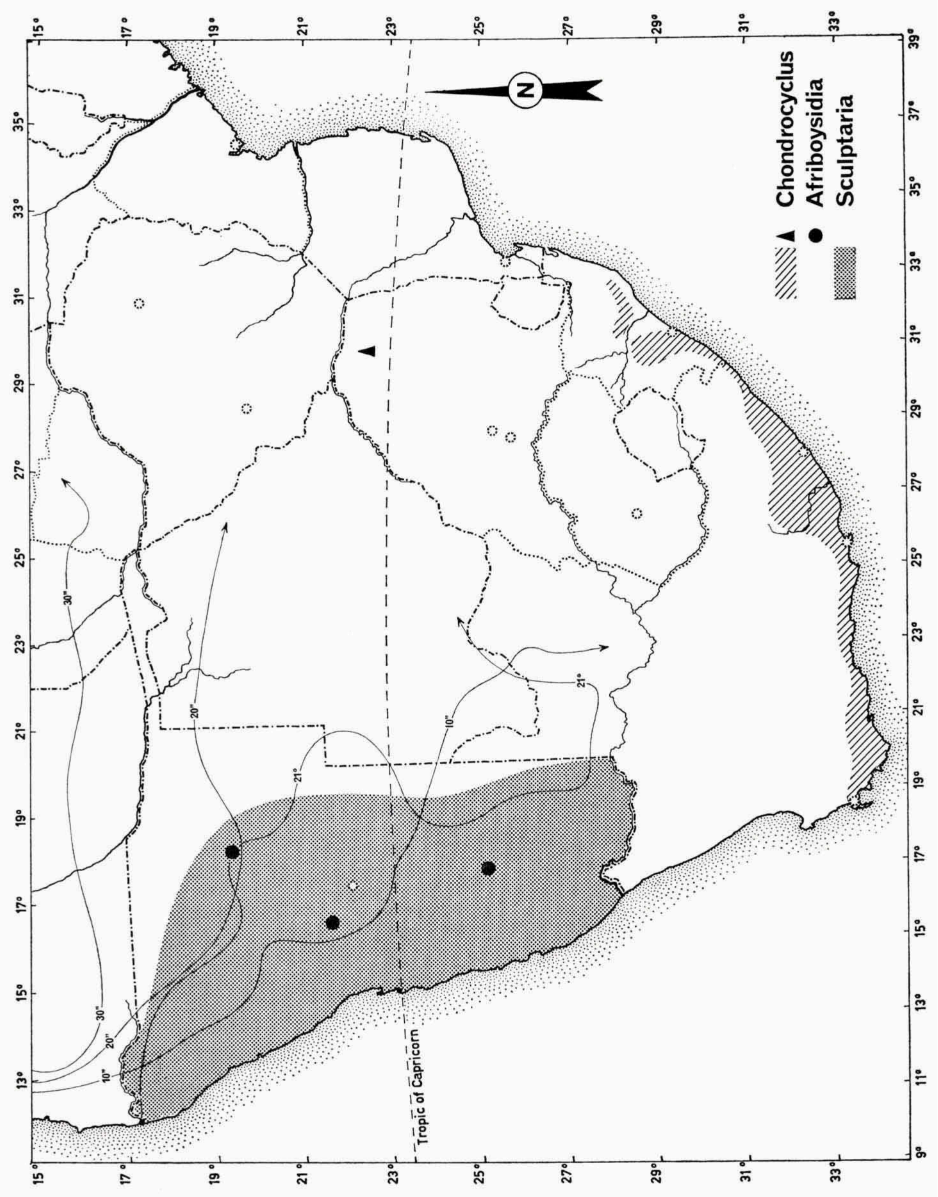


Fig. 29. Distribution of the endemic genera *Chondrocyclus, Afriboysidia,* and *Sculptaria.* Attention is drawn to the new record for *Chondrocyclus* in the N. Transvaal (triangle). The genera *Afriboysidia* and *Sculptaria* seem to prefer low rainfall and high temperatures; the 10 inches = 250 mm, 20 inches = 500 mm and 30 inches = 750 mm isohyets have been indicated by lines with 10", 20" and 30" respectively. The 21° C. isotherm (mean surface temperature) has also been indicated by a marked line.

Limpopo River. Moreover Dr. D. S. Brown obtained a number of *Chondrocyclus isipingoensis* (Stur.) near Lake Futululu, Mtubatuba, Zululand, on 17 September 1966 (BM, RMNH); this is evidence of the species also occurring in the warm Zululand coastal area. At lower latitudes this genus tends to occur in the mountains rather than in the much warmer coastal lowlands. The genus has been doubtfully recorded from Madagascar (Fischer-Piette, Blanc & Salvat, 1969).

Afriboysidia (fig. 29) — South West Africa. The few records known for the three species are widely dispersed throughout the territory (Zilch, 1939).

Afrodonta (fig. 31) — discontinuous along the Drakensberg Range in southeastern Southern Africa from the Keurbooms River to Mount Vengo in Mozambique; outside this area recorded from Kimberley (Connolly, 1939). *Afrodonta* is somewhat temperate in its ecological requirements; in tropical parts of Southern Africa it is only recorded from the mountains, such as Mount Vengo at 5500 ft.

Oopelta (fig. 30) — restricted to the southwestern Cape Province from Niewoudtville to the Albany District (Van Regteren Altena, 1966, fig 9). Slugs of the genus *Oopelta* are adapted to comparatively low temperatures (see 18° C. mean surface isotherm on the map) and could only be kept alive in the laboratory in Pietermaritzburg during the austral winter months (Van Bruggen in Van Regteren Altena, 1966: 280-281).

Sheldonia (fig. 33) — southeastern South Africa from Saldanha Bay to southern Mozambique (surroundings of Lourenço Marques) and the northern Transvaal (Zoutpansberg District) as far inland as Thaba Nchu (Orange Free State). The main distribution is east of and on the escarpment, with a few exceptional species spilling over into Basutoland and the Orange Free State; these species have adapted themselves to the subalpine and alpine conditions of Basutoland, some of the records giving altitudes from 4500-11.000 ft. So far no representatives of the genus *Sheldonia* have been reported from Rhodesia. North of the Limpopo River genera such as *Trochonanina, Zingis,* and *Gymnarion* occupy niches kindred to those inhabited by *Sheldonia* further south. The three above genera have a more northern type of distribution and in fact may be considered tropical in relationships and distribution; only very few species of these occur south of the Limpopo, only one species, *Trochonanina mozambicensis* (Pfr.), occurring as far south as 27° S.

Xerocerastus (fig. 30) — southwestern desert and central area with a westward extension into the Limpopo River valley; outside this area only recorded from Still Bay. The species of this genus are mainly influenced by

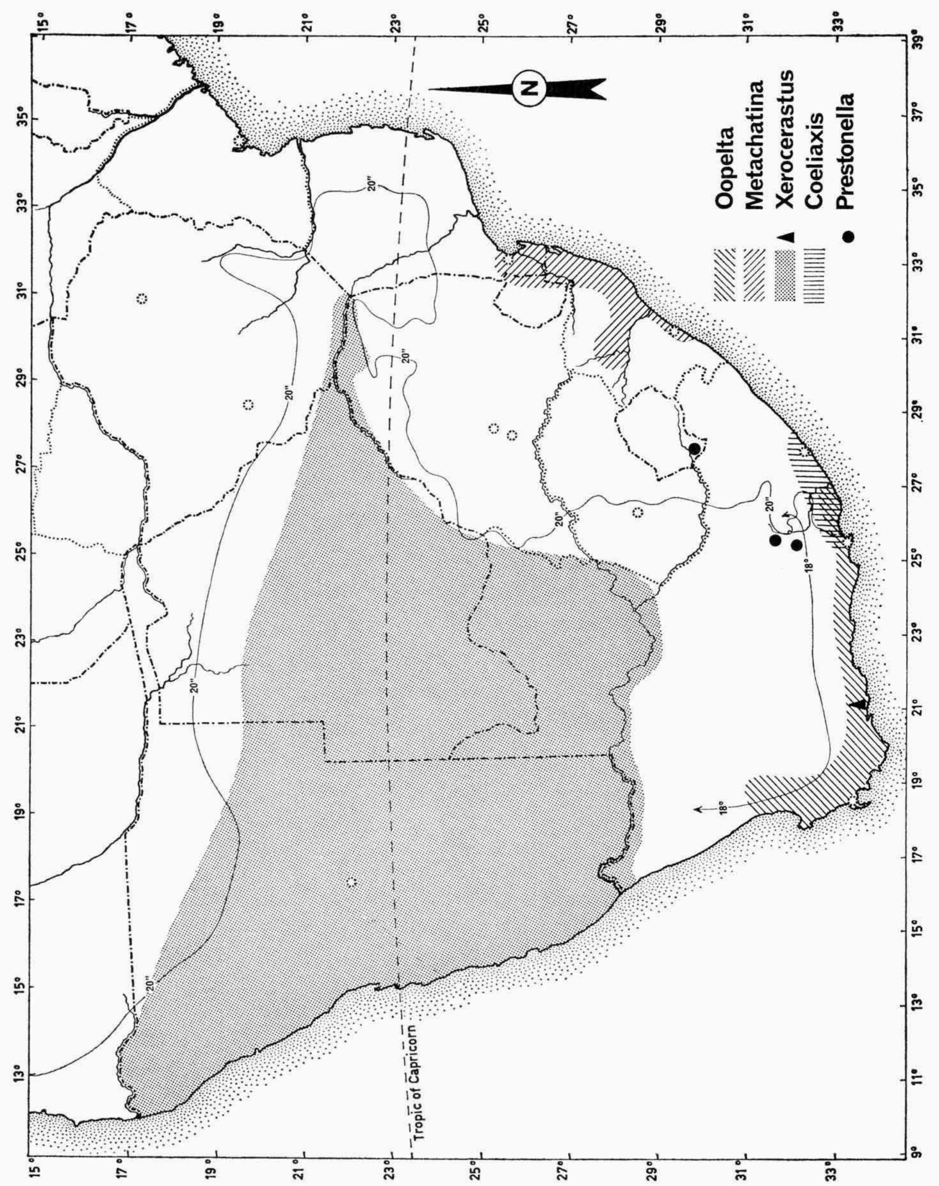


Fig. 30. Distribution of the endemic genera *Oopelta, Metachatina, Xerocerastus, Coeliaxis,* and *Prestonella.* The genus *Xerocerastus* mainly occurs within the 20 inches = 500 mm isohyet (thin line marked with 20"). The single record of *Xerocerastus* outside its continuous range has been indicated by a triangle (see Van Bruggen, 1964). The genus *Oopelta* requires fairly low mean temperatures and its range is roughly encompassed by the 18° C. isotherm (mean surface temperature) in the Cape of Good Hope.

rainfall, probably combined with fairly high temperatures; almost all known localities are encompassed by the twenty inches mean annual rainfall isohyet. This has been discussed at length by Van Bruggen (1964). *Xerocerastus* is the most widely distributed of the endemic genera.

Coeliaxis (fig. 30) — Eastern Cape Province littoral from Port Elizabeth to just north of East London. The genus *Coeliaxis* is monotypic; the species *C. blandi* (Pfeiffer, 1852) has a very restricted distribution in the coastal area of the Eastern Cape Province (Connolly, 1939). Outside this area it has been reported from Mossel Bay, which record in the author's opinion is open to grave doubt; no specimens were seen from this locality. Thus, the genus appears to have a most restricted range; it is unlikely that the species has been overlooked by collectors, because it is usually abundant and moreover the shells have a good size.

Metachatina (fig. 30) — Natal to Southern Mozambique littoral, see chapter 3 (pp. 14-19, fig. 4). A subtropical and tropical monotypic genus preferring high temperatures combined with a fairly high rainfall.

Trigonephrus (fig. 31) — southwestern Cape Province and South West African littoral from George to Lüderitz and inland only in the southwestern Cape and southern Namaqualand about as far west as Upington (Connolly, 1939).

Tulbaghinia (fig. 31) — mountains of the southwestern Cape Province; the single species, *T. isomerioides* (Melvill & Ponsonby, 1898), is only known from three localities over 3000 ft. in a very restricted area north of Worcester (Connolly, 1939). Consequently the genus *Tulbaghinia* as yet has the most restricted range among all Southern African endemic genera of terrestrial molluscs. Undoubtedly it will be found at localities adjoining the known records in the still poorly explored fold mountains of the southwestern Cape of Good Hope. However, important additions to the range as known at present are not expected; *T. isomerioides*, a large snail with a major diameter of over 30 mm, is not easily overlooked.

Dorcasia (fig. 31) — South West Africa as far north as Tsumeb, also in adjoining Little Namaqualand and Bushmanland as far east as about Upington (Connolly, 1939; Zilch, 1939). *Dorcasia* requires high temperatures and low rainfall; most of its range falls within the 21° C. mean surface isotherm and the 500 mm (= 20 inches) isohyet (mean annual rainfall). The three above acavid genera together constitute the endemic tribe Dorcasieae and occupy a continuous range from George to South West Africa, mainly littoral, except for South West Africa and the southern adjoining districts of the Cape Province. In their outline of gastropod classification Taylor & Sohl (1962) consider the tribe Dorcasieae to represent a separate family, the Dor-

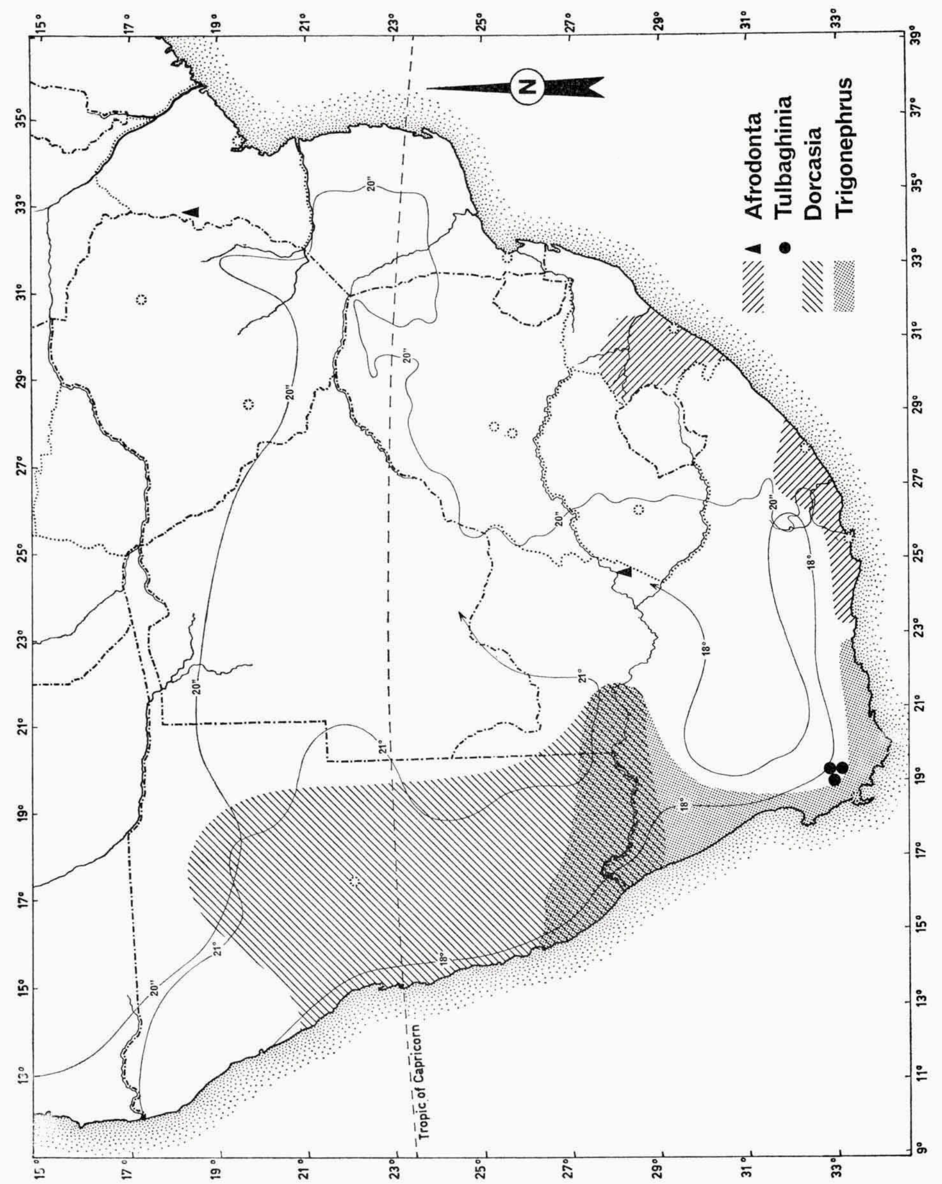


Fig. 31. Distribution of the endemic genus *Afrodonta* and the endemic acavid tribe Dorcasieae. Attention is drawn to the occurrence of *Afrodonta* in the northern Cape Province and Mozambique (triangles). The genus *Dorcasia* seemingly requires low rainfall and fairly high temperatures; the 20 inches = 500 mm isohyet and 18° and 21° C. isotherms (mean surface temperature) have been indicated by lines with 20", 18° and 21° respectively.

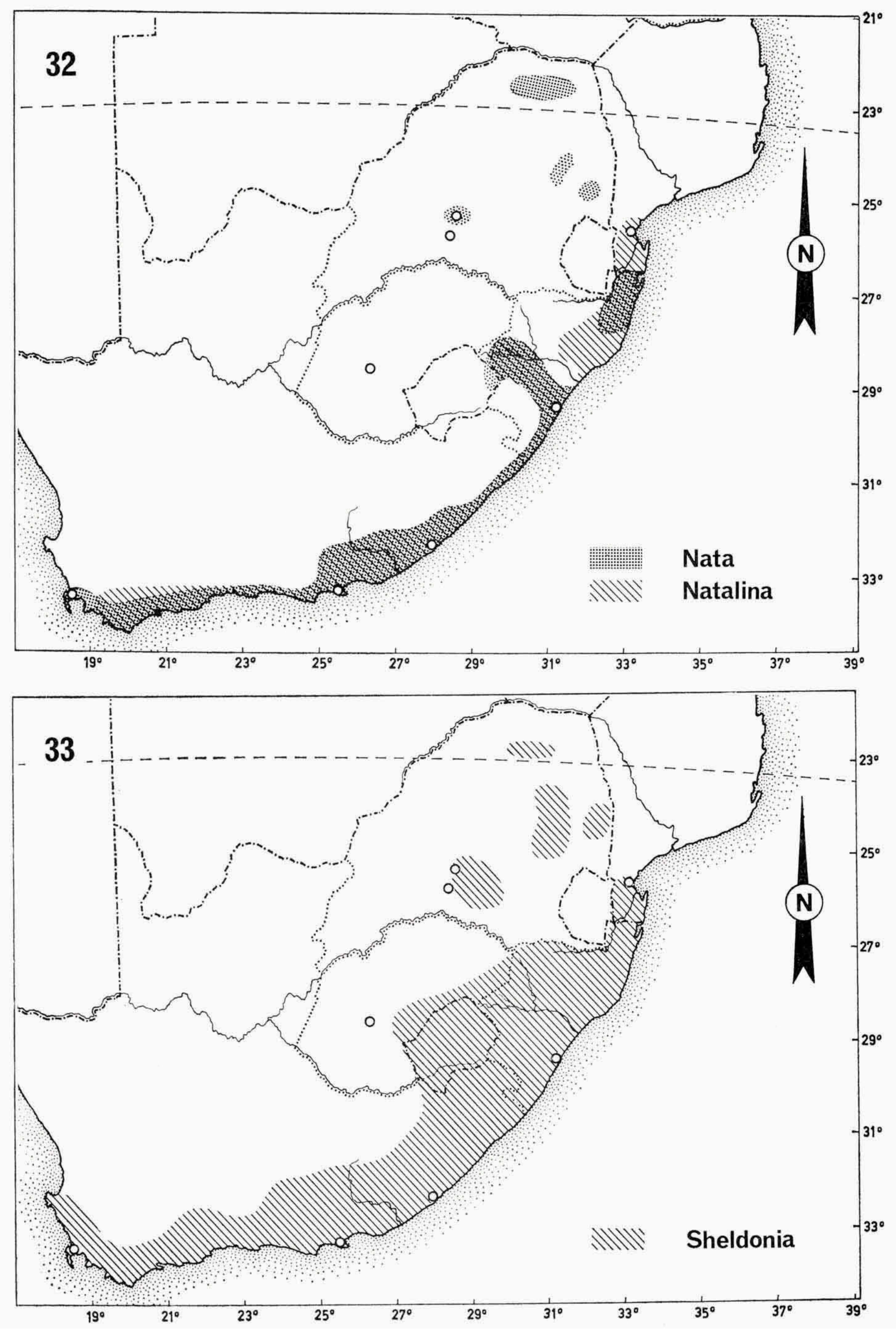
casiidae. This has been done before by Thiele (1931), but they have mainly followed Baker (1955) in dividing the Acavidae sensu Zilch (1960) into Dorcasiidae (Southern Africa) and Strophocheilidae (South America) in the suborder Mesurethra, and Acavidae s.s. (Madagascar, Seychelles, Ceylon, Australian Region, Chile) in the suborder Sigmurethra (see also Franc, 1968). In this case the Dorcasiidae constitute the second pulmonate family endemic to Southern Africa. Zilch has been followed here because his system is more generally accepted (which does not imply that it is the best available) and also more detailed as to genera (see also pp. 98-99).

Prestonella (fig. 30) — discontinuous in the Eastern Cape Province and Lesotho (Basutoland): Somerset East, Cradock, and Quthing (Connolly, 1939), all over 2300 ft. high. Obviously these are species requiring a temperate to cold climate.

Nata (fig. 32) — discontinuous in southeastern South Africa from the Cape Peninsula to the Zoutpansberg District (Transvaal).

Natalina (fig. 32) — discontinuous in southeastern Southern Africa from east of Stellenbosch to Vila Luiza in southern Mozambique. Both *Nata* and *Natalina* live in a variety of usually moist climates on or east of the escarpment in a fairly narrow stretch of country, none of the species far from the shores of the Indian Ocean except in the Transvaal (Van Bruggen, 1967a).

Apera (fig. 34) — discontinuous in southeastern Southern Africa from the Cape Peninsula to Mount Vumba in eastern Rhodesia. North of Zululand *Apera* occurs in mountainous districts so that the genus may be mildly temperate in its ecological requirements. As Southern Africa's only endemic family the Aperidae merit a more detailed discussion (see also Van Bruggen, 1968). Forcart's paper (Forcart, 1967) enumerates a total of twelve species; these are divided into three groups according to Watson (1915). The most primitive of these comprises four species which range from Cape Town to the Kruger National Park (black triangles); the distance between these localities is about 1800 km. The second, intermediate group contains five species which range from Grahamstown to Umtali (black dots), also a distance of about 1800 km. Finally the third, most advanced group comprises only three species ranging from Somerset East to Barberton (open triangles) covering a distance of about 950 km. The map shows that the greatest concentration of species is in Natal, where all three groups are jointly represented by six species or half of the total number known. Obviously this has been an area where a considerable species radiation has occurred and Natal possibly has been the cradle of the genus. *Apera* is probably derived from rhytidid or streptaxid ancestors; both families are abundantly represented in Natal. The



Figs. 32-33. Distribution of the endemic genera 32, *Nata* and *Natalina*, and 33, *Sheldonia*.

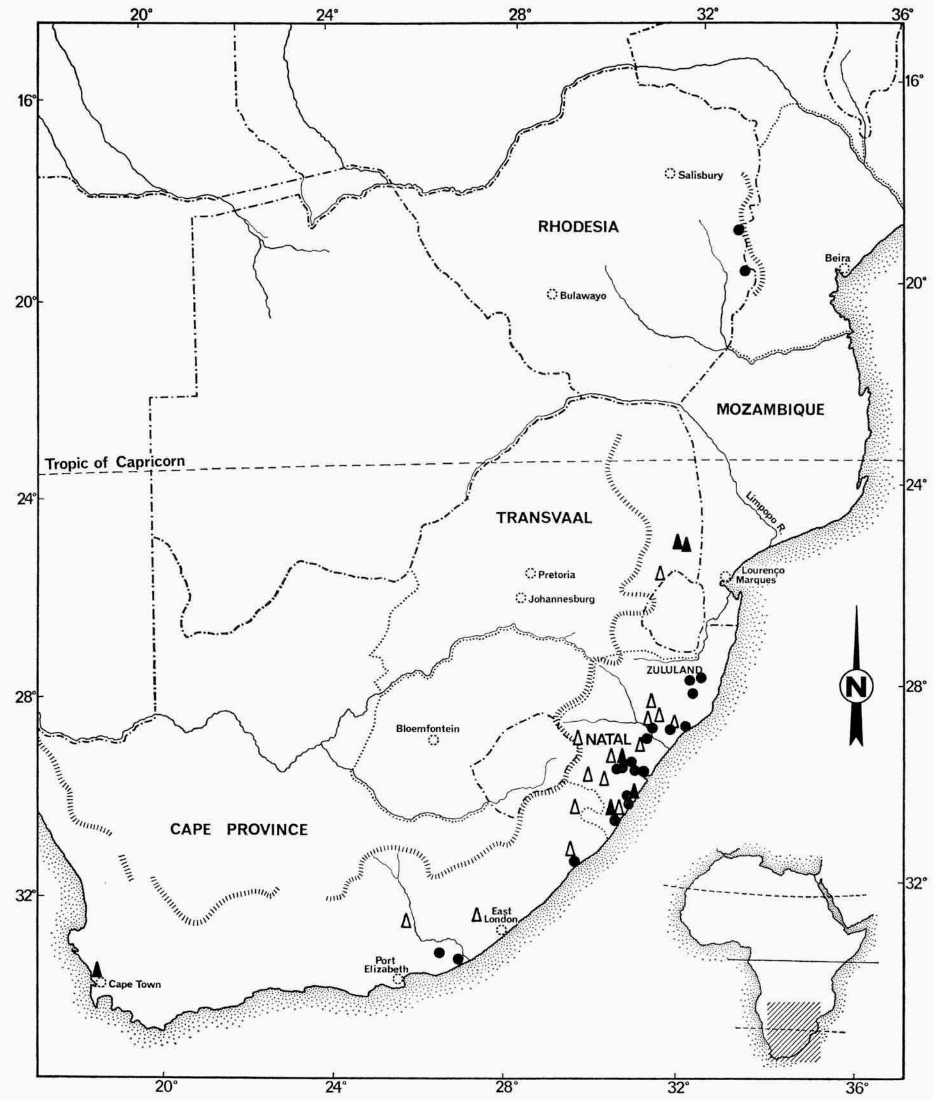


Fig. 34. Distribution of the endemic family Aperidae. The single genus *Apera* is divided into three groups of species, the localities of which have been indicated by black triangles, black dots and open triangles respectively. For further explanation see the text. The Great Escarpment has been indicated by cross hatching.

northeastern Cape Province-southern Natal area even appears to be the main centre of speciation of the rhytidid genus *Natalina* (Van Bruggen, 1967b: 28-29). *Natalina* is the more primitive of the two Southern African genera of Rhytididae.

Sculptaria (fig. 29) — South West Africa. As far as known at present the genus seems to be restricted to within the boundaries of South West Africa. Rumours of species of *Sculptaria* occurring in southern Angola are not to be dismissed lightly. The extreme southern parts of Angola are in many respects very similar to northern South West Africa (Ovamboland or Amboland) and are also within the twenty inches mean annual rainfall isohyet which may well be near the rainfall limit for *Sculptaria*. As shown in the map *Sculptaria* prefers a poor rainfall combined with fairly high temperatures.

According to their distribution three categories may be distinguished among the endemic genera, viz., (1) genera confined to the southern and southwestern Cape of Good Hope (*Oopelta* and *Tulbaghinia*), (2) genera endemic to the western desert area (*Afriboysidia, Xerocerastus, Trigonephrus, Dorcasia, Sculptaria*), and (3) genera with a much wider distribution, sometimes even as large as from Cape Town to the Zambezi, but still confined to the eastern parts of the country (*Chondrocyclus, Afrodonta, Sheldonia, Coeliaxis, Metachatina, Prestonella, Nata, Natalina, Apera*). The above categories are not sharply delimited and do not necessarily reflect the distributional history of these genera. The three acavid genera forming the endemic tribe Dorcasieae have evidently all originated somewhere in the southwestern Cape; however, in the above classification *Trigonephrus* (southern Cape to the Namib Desert) and *Dorcasia* (Orange River to the Namib Desert) obviously belong to category (2), while the closely allied genus *Tulbaghinia* is confined to the southern Cape Province and thus belongs to group (1).

The genera confined to the southern and southwestern Cape Province are remarkably few in number. The southwestern Cape is a well-known centre of endemism for many animals and plants, even to such an extent that some zoogeographers consider it to be a separate subregion. Of a total of about 73 genera of land molluscs, of which sixteen are endemic, only two of the latter are restricted to the southwestern Cape Province (category 1). At lower levels various subgenera, particularly of *Trachycystis* (*Phortion, Liparocystis*), are also restricted to the southwestern Cape.

According to their relationships the endemic genera may be divided into a number of groups. First of all two genera represent families restricted to Subsaharan Africa (or in the case of the Achatinidae to Subsaharan Africa with one genus endemic to Madagascar), viz., *Sheldonia* (family Urocyclidae, a tropical African family) and *Metachatina* (family Achatinidae, a southeastern offshoot of a tropical African family).

The second group encompasses five genera belonging to families with a wider distribution, but still represented in the Ethiopian Region outside Southern Africa: *Chondrocyclus, Afriboysidia, Afrodonta, Xerocerastus,* and *Coeliaxis.* The genus *Chondrocyclus* belongs to the Cyclophoridae, an Old World family which is otherwise very sparingly represented in Africa (Pilsbry,1919; Tielecke, 1940). However, the family Maizaniidae, represented by the genus *Maizania,* discontinuously distributed in southeast and East Africa, is closely allied to the Cyclophoridae and probably is an offshoot from the latter family. *Afriboysidia* is as yet insufficiently known, but probably belongs to the Chondrinidae, a cosmopolitan family concentrated on the northern hemisphere, but with various representatives in Africa; these belong to the almost cosmopolitan (extinct in Europe since the Middle Oligocene) genus *Gastrocopta* and the Southern African-Malagasy genus *Fauxulus.* The minute species of *Afrodonta* have been classified with the Endodontidae, a family belonging to the Southern Relict Fauna of Solem (1959). The Endodontidae are very well represented in Southern Africa (more than 100 species), but also occur, albeit much rarer and less diverse, in East and Central Africa. *Xerocerastus* and *Coeliaxis* are representatives of the Subulinidae, a circumtropical family abundant in genera and species all over Africa.

Finally nine of the endemic genera belong to families, which in the Ethiopian Region are restricted to Southern Africa: *Oopelta, Trigonephrus, Tulbaghinia, Dorcasia, Prestonella, Nata, Natalina, Apera,* and *Sculptaria.* The genus *Oopelta* constitutes the subfamily Oopeltinae, a subdivision of the Arionidae, a family of slugs which is Holarctic in its distribution. *Trigonephrus, Tulbaghinia,* and *Dorcasia* are all genera of the Acavidae, a relict family of so-called "Gondwanaland" being distributed over South America, South Africa, Madagascar, the Seychelles Islands, Ceylon, New Guinea, and Australia. Taylor & Sohl (1962) consider the genera *Trigonephrus, Tulbaghinia,* and *Dorcasia* to constitute the family Dorcasiidae. This family is closely allied to the South American Strophocheilidae, so that the Dorcasiidae are still a Southern Relict family (see also pp. 92, 94). The genera of carnivorous snails, *Natalina* and *Nata,* are representatives of the family Rhytididae, which essentially also has a Gondwana type of distribution, although without the South American sector of this hypothetical ancient continent: South Africa, New Guinea, Australia, New Caledonia, New Zealand, and many groups of islands in the southwest Pacific as far west as Borneo. Southern Africa's most characteristic slugs have been named *Apera,* which genus constitutes the Aperidae, the only endemic family among the non-marine molluscs; these carnivorous slugs are probably allied to the Rhytididae and Streptaxidae and in view of their distribution may therefore also be considered Southern Relict elements. *Sculptaria* is the sole representative of the Corillidae outside Asia; in Asia the family occurs in the southern parts of the continent from India and Ceylon to Tibet, China, and Tonkin. The last of the genera which superficially seem alien to the fauna of the Ethiopian Region is *Prestonella,* a somewhat enigmatic genus, which belongs to the otherwise South and Central American family Amphibulimidae.

The Southern Relict families Acavidae, Rhytididae, and Aperidae are concentrated on the southern hemisphere and more particularly on the southern part of the continents and on the islands near the latter. The above families occur at the very tip of the African continent. The following table (see also figs. 31, 32, 34) shows that in the east the northernmost limit is reached by the Aperidae with one species at 19° 00′ S. and that in the west the same limit is reached at approximately the same latitude: 19° 13′ S. by one species of Acavidae, viz., *Dorcasia alexanderi* Gray.

family	east	west
Acavidae	George District at approximately 34° 00′ S. 22° 30′ E.	Tsumeb, 19° 13′ S. 17° 42′ E. (not east of 22° 00′ E.)
Rhytididae	Louis Trichardt, 23° 01′ S. 29° 43′ E.	——
Aperidae	Mount Vumba, 19° 00′ S. 32° 40′ E.	——

In this respect it is interesting that the Southern Relict families occurring in Southern Africa and not beyond the Zambezi (as is done e.g., by the Endodontidae) are more markedly confined to the southernmost tip of the continent than elsewhere. In Southern Africa none of the above families has been found north of 19° 00′ S., while outside Africa the Acavidae occur as far north as approximately 15° 00′ N. (South America and Ceylon) and the Rhytididae as far as approximately the equator (Borneo and the Moluccas).

The position of the family Corillidae, in the western desert and subdesert of Southern Africa represented by the genus *Sculptaria,* but otherwise confined to Asia, is not quite clear. This mesurethran group is certainly a relict family; Solem (1959) does not treat the Corillidae in detail but does not include them in his Palaeo-Oriental fauna. Unfortunately the total absence of fossils precludes any firm speculation about the origin of the family. In Southern Africa the Corillidae are restricted to an area roughly between the Angola border in the north (approximately 17° 00′ S.), the eastern border of South West Africa (not east of 20° 00′ E.) and the Orange River at about 28° 00′ S. The genus has adapted itself magnificently to the (sub)arid conditions here and not only has radiated into a comparatively large number of species (16), but has also managed to become very abundant locally. Perhaps this distribution relict is in itself again a remnant of a southern distribution connected with Gondwanaland, in which case the family may also be considered to belong to the Southern Relict fauna.

The genus *Prestonella* is the sole African representative of the Amphibulimidae; this somewhat poorly defined family otherwise occurs in northern South America, Central America, the West Indies, and Trinidad. If *Prestonella* indeed belongs to this family, which is by no means certain because of the anatomy only radula data are available (Connolly, 1939), then it definitely shows a relict distribution. It is difficult to decide whether in this case the Amphibulimidae show a Southern Relict distribution or not; the American genera would not normally be classified as Southern Relict elements because of the above-described distribution.

The number of species in the endemic genera varies a great deal, but, except in one case (*Sheldonia*), is usually not large. A marked species radiation has occurred both in and along the southeastern mountains and in the western (semi)deserts:

southeastern mountains		western (semi)deserts	
Afrodonta,	11 species	*Xerocerastus,*	15 species
Sheldonia,	44 species	*Sculptaria,*	16 species
Natalina,	17 species		
Apera,	12 species		

The above genera are confined to the respective areas. All other endemic genera have fewer species. Of the subendemics the endodontid genus *Trachycystis* has more than a hundred species, the great majority of which are again concentrated in the southern mountains. Incidentally, this genus is the second largest in Southern Africa, leaving first place to the streptaxid *Gulella* of which at least 125 species have been found to occur in Southern Africa. As far as endemic species are concerned (i.e., species belonging to endemic and non-endemic genera), it appears that very many of these are again restricted to the southeastern mountain range, which obviously has offered conditions most suitable for extensive speciation.

7d. The temperate element

Temperate elements are taxa requiring a temperate climate with moderate temperatures and rainfall. The temperate zone in Southern Africa is mainly confined to the southwestern Cape and the mountains.

Except for the endemic taxa belonging to the Southern Relict families Endodontidae, Acavidae, Rhytididae, and Aperidae a fair number of other fauna elements may also be considered temperate. The endemic slug genus

Oopelta forms the subfamily Oopeltinae of the otherwise Holarctic Arionidae. Southern Africa's sole representative of the Clausiliidae, *Macroptychia africana* (M. & P.), occurs in a discontinuous pattern in the mountains from the Great Fish River to the northern Transvaal. This interesting species has been extensively treated by Van Bruggen (1967b: 24-28, figs. 12, 13), who concludes that the species is a silvicolous montane palaeogenic element in the fauna of South Africa. Palaeogenic invertebrates have a discontinuous distribution in more than one zoogeographical region, but within the Ethiopian Region are restricted to South Africa. *M. africana* has such a relict distribution; its nearest relatives are relict species inhabiting the mountains of East Africa, Abyssinia, and south Arabia. Very probably the ancestors of the South African clausiliid have reached their southern destination from the north. It is more difficult to speculate on the ancestry of the Oopeltinae, rightly considered palaeogenic by Van Regteren Altena (1966). In view of the modern distribution of the Arionidae the same kind of explanation at once offers itself. Variations in the climate during the Pleistocene certainly will have made contact with the Palaearctic Region for temperate invertebrates somewhat easier than today. It is therefore conceivable that in the other parts of Africa the Arionidae became extinct and that only at the Cape the environment was still sufficiently congenial to these slugs.

A good deal of the temperate species belong to tropical families; an enormous adaptive radiation has resulted in many, mostly endemic, temperate species belonging to tropical families (*Sheldonia*, Urocyclidae; *Achatina, Archachatina*, Achatinidae; *Gulella*, Streptaxidae). See also sub the tropical element.

Two Palaearctic species of terrestrial molluscs have been found in a surface deposit at Tlapings Laagte Well near Vryburg, northern Cape Province. Connolly calls these specimens "subfossil", a somewhat obscure term which does not clarify the position; the age of this deposit is unknown. The species are *Vertigo antivertigo* (Drap.), a minute Palaearctic (or even possibly Holarctic) species, and *Zonitoides africanus* (Bttg.), which latter is also known in "subfossil" condition from Gobabis, South West Africa. *Z. africanus* seems extraordinarily close to the Holarctic *Z. nitidus* (Müll.). Adam (1954) has described other closely related species of *Vertigo* from Central Africa, so that the distribution is possibly not as discontinuous as it seems at first sight. In this respect Waldén (1963: 162) may be quoted: "In all regions it is mainly the minute forms that exhibit wide distribution. This is pertinent on generic as well as specific levels". Passive dispersal, such as via dust storms and seasonal floods, has probably influenced the distribution pattern. Many Southern African species show a scattered or discontinuous distribution pattern. The species may have escaped attention in the intervening areas because of their minute size. The genus *Zonitoides* is not indigenous in the Ethiopian Region; *Z. arboreus* (Say) only occurs as an alien. However, zonitoid types of shells are well-known in entirely different families (e.g., Urocyclidae: *Thapsia, Gudeella*); some of these species have originally been classified with *Zonitoides*. A reconsideration of *Z. africanus* has therefore become imperative.

7e. The tropical element

The tropical element may be defined as the assemblage of species which mainly occur within the 18° C. mean July isotherm or are directly allied to or derived from such species. In the fauna of Southern Africa it is proportionally of great importance: of the dominant families the Streptaxidae, Subulinidae, Urocyclidae, and Achatinidae are tropical. The tropical element in Southern Africa is mainly confined to a rapidly narrowing belt along the coast east of the main watershed; this is particularly well illustrated on map 3 in Poynton (1964). In some groups the southward extension is two-pronged, penetration in a westward direction having been accompanied by adaptation to the (semi)desert conditions of the central and western parts of Southern Africa. The family Achatinidae is an almost classical example of this phenomenon; numerous species are known from southeastern Africa, but also a number from the arid areas in Bechuanaland and adjoining parts of South West Africa. The decreasing numbers of species from north to south may also be illustrated by this family:

south of the Zambezi River	about 40 species in	5 genera
Eastern Cape Province	8 species in	2 genera
south of Port Elizabeth	4 species in	2 genera
Mossel Bay	2 species in	2 genera
Cape Agulhas	—	—

A similar pattern is exhibited by families such as the Veronicellidae, Urocyclidae, Subulinidae, and Streptaxidae. From north to south there is again a sharp decrease in the number of taxa as witnessed by the following table:

	south of Zambesi	Limpopo	Tugela	Greath Fish	Gouritz Rivers
species of Streptaxidae non *Gulella*	9	5	0	0	0
species of Streptaxidae-Streptaxinae	5	2	0	0	0
genera of Subulinidae	11	9	7	6	1

However, many decidedly tropical families penetrate with one or a few species as far as the southern tip of the African continent (Cape Agulhas) or even beyond that point westward to the Cape Peninsula. These species are usually temperate representatives of tropical families, i.e., restricted to the temperate parts of South Africa. The southernmost representatives of the family Achatinidae are *Archachatina ustulata* (Lam.) and *Achatina zebra* (Brug.). The first is an endemic species of the southeastern coastal parts of the Cape Province "from the Gouritz River in the west to the Koega River in the east, without, however, reaching either of these rivers" (Van Bruggen, 1967b: 22). *Achatina zebra* is restricted to the Eastern Cape Province from the George District in the south to the area around East London in the north. Other species are restricted to comparatively high and thus decidedly temperate parts of the country, such as *Archachatina machachensis* (Smith), *A. montistempli* Van Bruggen and *A. omissa* Van Bruggen which are all confined to areas over 4000 ft. in the Drakensberg range (see Van Bruggen, 1965). All these species are typically temperate representatives of the largely tropical family Achatinidae. Very few tropical species per se, probably not more than a dozen, penetrate southward to or beyond the Eastern Cape Province. Examples of these are the veronicellid slug *Laevicaulis n. natalensis* (Krss.) (from eastern Rhodesia and adjoining parts of Mozambique to Port Elizabeth) and the terrestrial prosobranchs *Tropidophora ligata* (Müll.) (from Tete on the Zambezi to the Cape Peninsula, also on Madagascar) and *T. insularis* (Pfr.) (from north of Macequece = Vila Manica, northwest of Beira in Mozambique, to the Alexandria District, northeast of Port Elizabeth). On the whole comparatively few species of Southern African land molluscs show a really wide distribution [e.g., *Pupoides calaharicus* (Bttg.) and *Kaliella barrakporensis* (Pfr.)].

The following examples of progressively penetrating tropical families may be quoted:

	southernmost record	coordinates
Veronicellidae	Port Elizabeth	33° 58′ S. 25° 36′ E.
Achatinidae	Gouritz River	34° 00′ S. 21° 45′ E.
Streptaxidae	Swellendam	34° 01′ S. 20° 26′ E.
Subulinidae	Houw Hoek	34° 10′ S. 19° 03′ E.
Urocyclidae	Cape Point	34° 21′ S. 18° 29′ E.

This picture is, of course, the reverse of that of the Southern Relict or temperate families; few of the species of these cross the Limpopo and only one family, the Endodontidae, the Zambezi. Consequently Natal is the area where both temperate and tropical elements intimately intermingle; towards the north Zululand is almost wholly tropical and southwards the Eastern

Cape Province has a progressively more temperate facies. The bulk of the tropical species thus lives north of Natal; this even more markedly holds good for the genera. Many tropical Central and East African genera reach their southern limits in Rhodesia and adjoining parts of Mozambique (*Limicena, Trochozonites* [10]), *Homorus, Subuliniscus, Burtoa,* and *Gymnarion*), a few do so in the Transvaal (e.g., *Streptostele*), one in Swaziland (*Trochonanina*) and many again in Zululand (*Rachis, Rhachistia, Rhachidina, Pseudoglessula,* and *Gonaxis*). Incidentally, Connolly (1921) as quoted on p. 77 remarked on the absence of the genera *Trochonanina* (s.n. *Ledoulxia*) and *Homorus* and the markedly sparse records of *Pseudoglessula* and *Gonaxis*; these remarks are now out of date. The Great or Eastern Escarpment plays an important role here; the escarpment forests in Rhodesia, Mozambique and to a lesser extent also in the Transvaal have acted as refuges for the fauna of the tropical rain forest when after the Pleistocene Southern Africa gradually became more arid.

7f. Distributional history

The fossil record for Southern African terrestrial molluscs is exceedingly poor and in fact almost non-existent. Of the Southern Relict families only some Eocene fossils of the acavid genera *Trigonephrus* and *Dorcasia* and some doubtfully Palaeocene *Dorcasia* are known (Connolly, 1939; Zilch, 1960). Fossil records of Southern Relict families outside Africa are from or near areas where species of the same genera are still living.

In a recent paper Frankel (1964) has recorded five species of land molluscs in a Plio-Pleistocene Foraminifera-bearing calcareous sandstone exposed in the Burman Bush area, Durban: *Maizania wahlbergi* (Bens.), *Tropidophora insularis* (Pfr.), *Edouardia arenicola* (Bens.), *Euonyma lanceolata* (Pfr.), and *Gulella wahlbergi* (Krss.). Without exception these molluscs still occur locally.

A summary zoogeographical analysis will however be of assistance in trying to explain the complex pattern of today. The Southern Relict families are concentrated in the southern hemisphere and more particularly in the south of the southern continents. The fossil record of these families, scanty though it may be, seems to indicate that these families never were represented

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[10] Based on a specimen of an East African species collected at Mount Selinda in 1965 (RMNH alc.). Connolly (1939: 161) records *Trochozonites dioryx* (M. & P.) from Little Namaqualand; the species is founded on a singleton which according to Connolly is a true *Trochozonites*. The genus is only known to inhabit tropical forest and a record from a semidesert area very remote from the forest districts immediately arouses suspicion. Since its description the species has not been obtained again, although a fair deal of collecting has been done around its type locality.

in the northern hemisphere. The Endodontidae are in this respect exceptional; although largely concentrated in the southern hemisphere, about half a dozen of fifty odd genera are known from the northern hemisphere. Three of these are known from the same parts of the world since the Palaeocene.

Land molluscs are among the earliest terrestrial animals. By virtue of their fragile shells land molluscs make unsatisfactory fossils and much of their early history will probably never be revealed. Primitive forms are known from the Jurassic, but it is well possible that much earlier, i.e. in the Carboniferous, both Opisthobranchia and Pulmonata arose from similar Prosobranch ancestors. Therefore, when the 'continent' Gondwanaland started to fall apart (see p. 79), land molluscs must already have been present throughout this area. The absence of both fossil and Recent northern hemisphere temperate records for the Southern Relict families Acavidae, Amphibulimidae, Rhytididae, Aperidae, and Corillidae indicates in this author's opinion that these families may have arisen in various areas of the southern complex and may have spread from there.

The case of the family Endodontidae is however different. As has already been indicated this family is represented in the northern hemisphere in the temperate zone. Zilch (1959) recognizes a total of 53 genera in seven subfamilies; seven genera partly or exclusively occur in North America, Europe, and northern Asia as far east as Japan. Four of the subfamilies show distribution patterns which for the present study are of no direct interest, viz. the Rotadiscinae (Central America), Helicodiscinae (Northern South America to North America, also Europe), the Stenopylinae (Australian Region, Sumba, Philippines), and the Discinae (Holarctic, Madeira, Canary Is., Cape Verde Is.; in Europe since the Palaeocene, in North America since the Upper Eocene). The three remaining subfamilies show patterns which more or less conform to those discussed by Darlington (1965: 49, fig. 14, stages A-D). The Punctinae have a Holarctic distribution (also in the Upper Oligocene of Europe), but are also widely spread in Southern Africa and the Australian Region including New Zealand; the Endodontinae are very widely spread along the western shores and on the islands of the Indo-Pacific (Japan, Australian Region including New Zealand, Pacific islands as far east as Hawaii and the Society Is., Indonesia, Southern Asia, Mascarene Is., Southern and Central Africa, Antarctic islands), Fernando Po and St. Helena (here also in the Pleistocene). Finally the Amphidoxinae have an exclusively southern distribution: the Australian Region including New Zealand, and Juan Fernandez and South America.

Darlington (1965) in studying distribution patterns of carabid beetles has arrived at a hypothetical pattern of evolution and dispersal for some taxa of these animals, which pattern may apply to other organisms as well. An initial stock evolves in the northern temperate zone and subsequently disperses southwards, finally reaching the southern continents (stage A); this may have been followed by the development of a second northern stock, which later reached the southern continents, perhaps in a different geographical pattern (stage B). Various processes of extinction in both the north and the south may eventually leave seemingly unexplained relicts in both the north and the south (stage C), or only exclusively on the southern continents (stage D). The distribution pattern of the Amphidoxinae as given above more or less conforms to Darlington's stage D; those of the Punctinae and Endodontinae represent various possibilities within the stages A to C. Darlington's conclusions as regards these beetles are well-founded, because of the accumulated knowledge of these animals. However, many of the above Endodontidae are anatomically still unknown and it is not impossible that ultimately the division into subfamilies will be different from the one given by Zilch. A survey of the characters of the species of this family and an evaluation whether these are primitive or advanced will possibly reveal whether the above conformity to Darlington's patterns is indeed acceptable.

The controversy Brundin-Darlington (see Brundin, 1966, e.g., pp. 61-64 and 457-463) is not likely to be solved quickly and easily, but for the present it is perhaps best to accept an austral centre of evolution for the Southern Relict families Acavidae, Amphibulimidae, Rhytididae (with the Aperidae, as a local African offshoot) and Corillidae. The Edondontidae, on the other hand, may originally have evolved in the northern hemisphere and their southern distribution may have come into being as a sequel of a process somewhat like the one described by Darlington; in this case the Endodontidae are no longer to be included among the Southern Relict families. Incidentally, Darlington himself has not discussed land mollusc distribution patterns in the southern continents.

Modern distribution records thus lead to the tentative conclusion that none of the Southern Relict families Acavidae, Amphibulimidae, Rhytididae, and Corillidae has arisen in South Africa. However, the Aperidae, although restricted to Southern Africa, undoubtedly belong to this group of ancient families. The single genus *Apera* represents an ancient type, probably derived from the Rhytididae (Watson, 1915) and also possibly connected with the allied circumtropical Streptaxidae (Van Bruggen, 1967a). Very probably the Aperidae have arisen in South Africa. The Dorcasiidae, if indeed a separate family (see pp. 92, 94, 98-99), have possibly also arisen in South Africa, albeit originally from an acavid ancestor somewhere on the southern 'continent'.

The bulk of the Southern African land molluscs have their origin in tropical Africa, which must have been a great centre of evolution. Both typically African elements such as the Achatinidae, but also circumtropical (e.g., Veronicellidae) and Afro-Oriental elements (*Pupoides*) must have originated north of the Zambezi. A great adaptive radiation has taken place in Southern Africa, both in the arid and subarid areas and in the moist parts east of the watershed, resulting in temperate species derived from tropical ancestors. A large number of species is transitional in the sense of Poynton (1964), i.e. inhabits the overlapping substraction margins of the two faunal groups (tropical and Cape or temperate groups). The majority of the transitional elements are really of tropical extraction.

A very limited number of elements show connections further north beyond Africa and may have reached South Africa during cool-temperate periods; all these show peculiar relict patterns and are either restricted to the southwestern Cape Province (genus *Oopelta*) or to temperate mountain refuges (*Macroptychia africana* (M. & P.)).

By and large the main pattern of the distribution of the Southern African land molluscs is thus essentially bipolar; this bipolarity is also evident in other groups of animals (cf. Poynton, 1964). The literature on zoogeography is vast and South Africa has had its fair share, a good deal of which has been used and enumerated by Poynton; this renders long lists of relevant references superfluous here. Many authors have attempted to divide Southern Africa into zoogeographical provinces, which here has as yet not been deemed opportune. No such subdivisions have been designated or even attempted because of the uncertainty where to draw the boundaries, apart from the fact that zoogeographical boundaries on land are at best doubtful and problematic. Regions such as South West Africa, Natal and the Eastern Cape Province littoral, the southwestern Cape Province, etc. are more or less acceptable subdivisions, but at the moment distribution data are not sufficiently profuse to allow the delimitation of detailed subregions. Moreover minor centres with endemism on a specific rather than a generic level occur over much of Southern Africa. This is particularly the case in the interrupted parts of the Drakensberg range, e.g., in the northern Transvaal (Mariepskop, Woodbush Forest, Zoutpansberg range, etc.) and in eastern Rhodesia (Mount Selinda, Mt. Chimanimani, Mt. Vumba, Mt. Inyanga, etc.). These are usually refuges for tropical forest elements. The above, usually isolated, centres are as a rule surrounded by ecologically totally different areas.

Detailed distributions have been greatly influenced by the climate in the past and present. This is particularly significant in northern Zululand (see chapter 6). That distribution patterns are definitely influenced by rainfall, has been shown in the case of the genus *Xerocerastus* (see Van Bruggen, 1964); this genus has penetrated with one species as far east as the Mozambique border through a dry corridor in the Limpopo River valley. Moreau (1966) extensively dwells upon problems of climate and distribution of the birds of Africa.

These notes should suffice to indicate that, although much basic work remains to be done, the study of the distribution of Southern African land molluscs and its history is a most promising field of research.

8. SYSTEMATIC LIST OF FAMILIES, GENERA, AND SUBGENERA

The list mainly follows the system of Zilch (1959-1960). Some subgenera have been shown between brackets. Where necessary a few synonyms are also given.

Class Gastropoda
  Subclass Prosobranchia (also Streptoneura)
    Order Mesogastropoda
      Families Cyclophoridae: *Chondrocyclus*; Maizaniidae: *Maizania*; Pomatiasidae: *Tropidophora* (*Ligatella*).
  Subclass Pulmonata (sometimes the Opisthobranchia and Pulmonata are united to form the Subclass Euthyneura)
    Order Soleolifera (also known as Ditremata, which is the oldest name available; the name Systellommatophora has been proposed in order to fit into the series of Basommatophora and Stylommatophora)
      Family Veronicellidae: *Laevicaulis*.
    Order Stylommatophora
      Families Vertiginidae: *Vertigo*; Chondrinidae: *Fauxulus (Tomigerella), Gastrocopta, ?Afriboysidia*; Pupillidae: *Pupoides*; Enidae: *Buliminus, Rachis, Conulinus, Edouardia* (see p. 28), *Limicena, Rhachidina, Rhachistia*; Succineidae: *Succinea*; Endodontidae: *Afrodonta* (subgenus of *Ptychodon* in Zilch, 1959), *Trachycystis* (*Chalcocystis, Psichion, Phortion, Liparocystis*); Arionidae: *Oopelta*; Vitrinidae: *Vitrina*; Zonitidae: *Zonitiodes*; Euconulidae: *Guppya*; Helicarionidae: *Kaliella*; Urocyclidae: *Trochonanina* (syn. *Ledoulxia*), *Zingis* (subgenus of *Trochonanina* in Zilch, 1959), *Trochozonites, Sheldonia* (*Kerkophorus*), *Thapsia, Gudeella* (provisionally synonymized with *Thapsia* by Zilch, 1959), *Gymnarion, Urocyclus* (*Elisolimax*, considered a synonym of *Urocyclus* s.s. by Zilch, 1959, but see Forcart, 1967); Subulinidae: *Homorus, Subuliniscus, Pseudoglessula (Kempioconcha), Curvella (Hypolysia), Pseudopeas, Xerocerastus* (includes *Namibiella*, see Van Bruggen, 1964), *Euonyma, Coeliaxis*;

Achatinidae: *Achatina (Lissachatina)*, *Archachatina*, *Metachatina*, *Burtoa* (syn. *Livinhacia*), *Limicolaria*; Clausiliidae: *Macroptychia*; Acavidae: *Trigonephrus*, *Tulbaghinia*, *Dorcasia* (see also p. 92); Amphibulimidae: *Prestonella*; Rhytididae (also Paryphantidae): *Natalina*, *Nata*; Aperidae (in Zilch, 1960 s.n. Chlamydephoridae, but see Forcart, 1963): *Apera*; Streptaxidae: *Gonaxis*, *Streptostele*, *Gulella (Molarella)*, *Diaphera*, *Ennea* (syn. *Enneastrum*); Polygyridae; Corillidae: *Sculptaria*; Helicidae.

9. SUMMARY

Studies on the terrestrial mollucs of Zululand have led to the discovery of a new species of Streptaxidae, viz., *Gulella browni* (near Lake Sibayi, also in southern Mozambique, figs.) and two new subspecies in the same genus: *G. crassidens jonesi* (Mfongosi, fig.) and *G. gouldi discriminanda* (Mkuzi and Ndumu Game Reserves, figs.). *G. dextrorsa* Bnp. (Eshowe, fig.) and *G. laevorsa* (Eshowe, fig.), formerly considered to represent varieties of *G. isipingoensis* (Stur.), have been raised to species rank. One species new to South Africa, *Trachycystis ariel* (Prest.) (*T. ambigua* Connolly, 1929, nov. syn. of *Phortion ariel* Preston, 1910, Hluhluwe Game Reserve, fig.), and sixteen species new to Zululand are recorded. The anatomy of the genitalia of *Edouardia cockerelli* (Pils.) (fig.) and *Achatina craveni* Smith (fig.) is described for the first time. *Rachis vicinus* Preston, 1910, appears to be a synonym of *Buliminus* (now *Rhachidina*) *chiradzuluensis* Smith, 1899. *Gulella crossleyana* (Melvill & Ponsonby, 1893) is now considered to represent a form of *G. g. gouldi* (Pfeiffer, 1855). *Gulella tridens* Connolly, 1939, and its variety *intermedia* Connolly, 1939, are synonymized with *G. leucocion* Connolly, 1929. In a discussion on the distribution of *Rachis jejuna* (M. & P.) and *Rhachistia sticta* (Mts.) both species are reported to be new to South West Africa; these species are partly sympatric and roughly show a sandveld distribution within the 500 mm isohyet (fig.). *Rachis punctata* (Anton) is probably ancestral to *R. jejuna*.

A revision of the aberrant endemic achatinid *Metachatina kraussi* (Pfr.) with special emphasis on clinal variation (figs.), genital anatomy (figs.) and distribution (figs.) has led to the conclusion that it must be considered an advanced offshoot from near the southern limits of the family.

A survey of the Mkuzi and Ndumu Game Reserves in Tongaland has revealed the presence of 32 species of land molluscs; a zoogeographical analysis (categories according to Poynton, 1964) shows that 75% of the species are tropical, 22% transitional and that Cape or temperate elements are altogether absent. The land mollusc fauna of the Tongaland plain differs

significantly from that of the dune forest to the east and the temperate forest on the escarpment to the west; the terrestrial molluscs of dune and escarpment forests are closely allied, but also show certain differences. A possible explanation for this may be found in a drastic reduction of rainfall and resultant changes in the vegetation after the Pleistocene.

An analysis of the distribution of the terrestrial molluscs of Southern Africa shows that the subcontinent south of the Zambezi and Cunene Rivers is inhabited by about 640 indigenous species belonging to 73 genera and 27 families. A marked endemism at various levels characterizes this assemblage of species: endemic families (one: Aperidae), subfamilies (one), tribes (one) and genera (16). Of the latter eight belong to families not otherwise represented in Subsaharan Africa: Arionidae, Acavidae, Rhytididae, Aperidae, and Corillidae. Near-endemic or subendemic genera (i.e., genera of which the majority of species is confined to a certain limited area) are *Fauxulus* (one species on Madagascar) and *Trachycystis* (more than a hundred species in Southern Africa, a few in East and Central Africa).

Twenty-one families (78% of the total) and 57 genera (78% of the total) testify to connections with Central and East Africa, from which areas much of the fauna must have been derived. However, only about seventy species (11% of the total), mainly belonging to four families, are known to occur north of the Zambezi.

Endem centres of great importance are South West Africa, where a specialized fauna with peculiar Subulinidae, Achatinidae, Acavidae, Corillidae, etc. has developed, and the southwest Cape Province with its endemic Endodontidae, Arionidae, Acavidae, and Rhytididae. Minor centres are particularly found in the interrupted parts of the Drakensberg range (N. Transvaal, Rhodesia); endemism here is on a specific rather than generic level.

In the overall picture the dominant families (fig.) are the Streptaxidae (>135 species), Endodontidae (>110 species), Subulinidae (about 80 species) and Urocyclidae (about 70 species); Achatinidae and Enidae are also very well represented. These six families between them account for almost 75% of the known species of the area. Of the above families the Streptaxidae and Subulinidae are circumtropical and the Enidae an Old World family. The Achatinidae and Urocyclidae are African families; the sharply decreasing number of species from north to south indicates that their Southern African representatives have come from north of the Zambezi. The Endodontidae, Acavidae, Aperidae, and Rhytididae belong to the Southern Relict Fauna (Solem, 1959); north of the Great Fish River (Eastern Cape Province) there is a marked decrease in the number of species which is continued north of the Limpopo and Zambezi Rivers, while the Acavidae and

Rhytididae even do not occur beyond the Limpopo River. On the other hand the tropical taxa show a marked decrease in numbers of species from north to south and are mainly restricted to a rapidly narrowing area in southeast Southern Africa. Very few species belonging to tropical genera and families occur so far south as the Cape Peninsula. Consequently from north to south the typically African character of the terrestrial molluscs gradually changes into that of a Southern Relict Fauna, thus emphasizing the essential bipolarity of the fauna of Southern Africa. Distribution patterns of Southern Relict families may have originated via a southern continent, which may subsequently have been forced apart into the components we know nowadays as the southern continents and islands.

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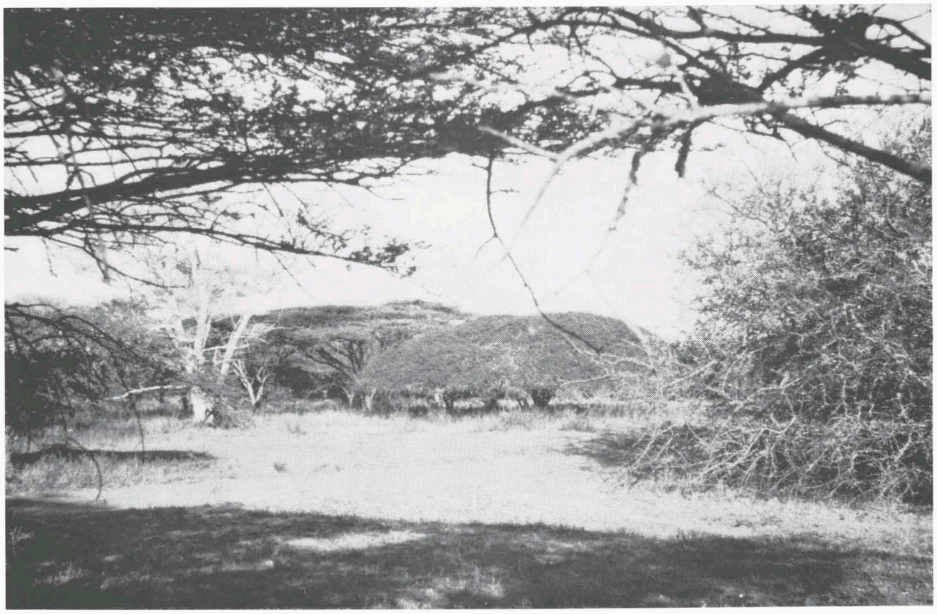
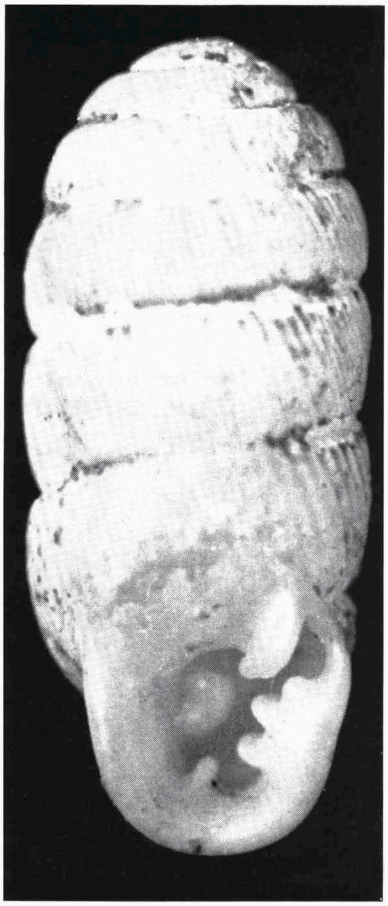
11. INDEX TO GENERA AND SUBGENERA OF MOLLUSCS

Metachatina kraussi (Pfeiffer), holotype shell of *Achatina planti* Pfeiffer (BM 1966276), actual size. Photographs courtesy British Museum (Natural History).

Mkuzi Game Reserve. General views of the scenery with scattered trees alongside the road from the entrance gate to the rest camp, January 1964 (top) and of the vegetation in the interior, May 1965 (bottom). The latter photograph shows a characteristic flat-topped *Acacia*. After colour slides 42m and 47m.



General view of the vegetation of the Mkuzi Game Reserve, May 1965 (top) and view from the rest camp of the Ndumu Game Reserve towards Polwe Pan, January 1964 (bottom). The top photograph shows a low, flattish, thorntree to the right of a specimen of *Acacia xanthophloea* with its pale bark. After colour slides 471 and 42t.



Gulella gouldi discriminanda n. ssp., holotype, edge of Khondo Forest, Ndumu Game Reserve (NM), actual length 6.6 mm. Photograph B. R. Stuckenberg.