STUDIES ON THE ECOLOGY AND SYSTEMATICS OF THE TERRESTRIAL MOLLUSCS OF THE LAKE SIBAYA AREA OF ZULULAND, SOUTH AFRICA

by

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With 10 text-figures and 4 plates

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1. GENERAL INTRODUCTION

Lake Sibaya (sometimes misspelt Sibayi) is a freshwater lake on the subtropical coastal plain of Zululand, the northeastern part of the province of Natal, South Africa. Northern Zululand, usually called Tongaland, a fairly narrow stretch of country wedged between the Indian Ocean and the eastern border of Swaziland and bounded to the north by Mozambique, is particularly interesting from biogeographical and ecological points of view. The area harbours a rich terrestrial malacofauna, which has been partly discussed by Van Bruggen (1969), while some early data are also recorded

in Connolly's monograph (1939). The junior author (Appleton) was privileged to be able to spend a year in 1972/3 at the Lake Sibaya Research Station of Rhodes University (Grahamstown) on the eastern shore of the lake, during which period as a sideline he studied the ecology of and generally surveyed the land molluscs of the wide surroundings of the station. He subsequently sent his extensive collection to the senior author (Van Bruggen) for identification (or confirmation of identification). The wealth of collected material and large amount of field data more than warrant publication of the joint results. Additional data were obtained by the junior author during a short visit in May 1976 (samples numbered as from 79E). Part 2, containing data on the ecology of the snails in the broad context of available habitats in the Lake Sibaya area has been written mainly by the junior author. Part 3, containing a critical checklist of material studied in Leiden has been composed mainly by the senior author. A meeting on neutral ground in the Transvaal in April, 1975, has done much to establish personal contact leading to fruitful co-operation. This meeting was realized for the senior author as part of a trip financially supported by the Nederlandse Organisatie voor Zuiver-Wetenschappelijk Onderzoek (Z.W.O., The Hague).

The material has been deposited in the Rijksmuseum van Natuurlijke Historie, Leiden; the slugs, however, are in the Naturhistorisches Museum, Bâle, Switzerland.

The senior author gratefully acknowledges the continued free use of the facilities of the Rijksmuseum van Natuurlijke Historie due to the gracious co-operation of the director and particularly of the Curator of Molluscs, Dr. E. Gittenberger. Furthermore he owes a debt of gratitude to Mr. J. F. Peake and his staff of the Mollusca Section of the British Museum (Natural History), London, for assistance during a sojourn at the museum in May, 1974. Prof. A. R. Mead of the Department of Biological Sciences of the University of Arizona, Tucson, U.S.A., has very kindly dissected certain achatinid material and has contributed notes on the genital anatomy of these snails. Dr. L. Forcart of Bâle, Switzerland, has identified the slugs for Appleton, thereby supplying essential data. Mr. R. N. Kilburn of the Natal Museum, Pietermaritzburg, South Africa, has loaned certain material described by Van Bruggen in 1969. The junior author is indebted to Prof. B. R. Allanson (Rhodes University, Grahamstown) and Dr. R. J. Pitchford (Bilharzia Field Research Unit, Nelspruit), for providing the opportunity of living and working at Lake Sibaya Research Station, and to Mr. M. N. Bruton (until recently officer-in-charge of the Lake Sibaya Research Station) for making available climatic data recorded there. Finally the permission of the South African Medical Research Council to publish this paper is also

acknowledged. All the above-mentioned persons have contributed to make this study possible.

2. Notes on the climate, ecology and isolation of the coastal dune forest at Lake Sibaya, pertinent to its molluscan fauna

2a. Introduction

The bulk of the present mollusc collection is from a small part of the indigenous coastal dune forest lying between the eastern shore of Lake Sibaya and the Indian Ocean, on the Tongaland coastal plain (N.E. Natal) (fig. 1), and was made from December 1972 to November 1973. This plain, a southern extension of the broad Mozambique lowlands, consists of unconsolidated Pliocene marine deposits overlying Cretaceous sandstones and shales. The soil throughout the area is light-brown and sandy though not very porous. The coastal dune forest is situated on a long range of stabilized sand dunes which form the eastern margin of the Tongaland plain (the 'dune or coastal area', of Van Bruggen, 1967b) and as aptly remarked by Tinley (1958, published in 1976) "has a black appearance from afar, enough to excite any naturalist's imagination". This longshore dune range is virtually the only topographical feature of the entire plain, except the Lebombo Mountains in the extreme west, which rise above an altitude of 107 m. The intervening landscape is featureless.

The main collection area of approximately 1,500 square meters lies near the base of the steep western (inland-facing) aspect of the dune forest, immediately behind Lake Sibaya Research Station (27°23'S 32°43'E). This c o a s t a l d u n e f o r e s t which is situated on dunes parallel to the sea, should not be confused with the patches of c o a s t a l f o r e s t which have a different plant community (Tinley, 1958; Breen & Jones, 1971). The latter occurs around Lake Sibaya, chiefly along the lake's western arm and is separated from the dune forest by grassland.

Aspects of plant ecology in the dune forest have been discussed by Tinley (1958), Breen (1971), and Breen & Jones (1971). From the lake shore in the vicinity of Lake Sibaya Research Station (21.4 m above sea level) to the base of the dune is a narrow, grassy fringe dominated by *Acacia karroo* scrub. Eastwards of this the heavily afforested dune rises steeply, at a slope of approximately 30° (Breen, 1971) to a maximum altitude of 162 m. The crown undulates for about 1.6 km before descending gently to the sea. The *A. karroo* fringe can be seen as the line of low trees nearest the camera in pl. 1. Behind them the tallest canopy trees of the forest proper are clearly shown: they mark the beginning of the slope of the dune.

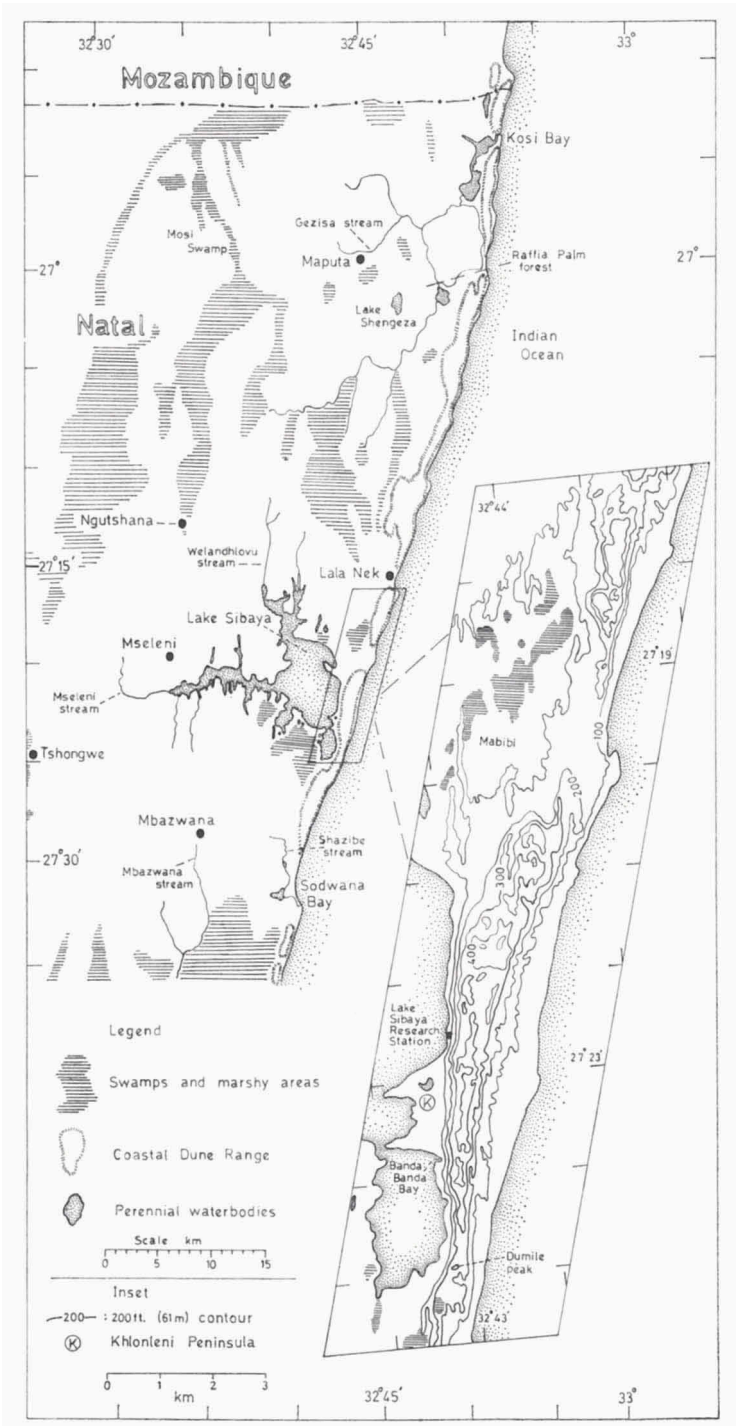

Fig. 1. Map of the eastern half of the Tongaland coastal plain (NE. Natal) showing the principal features and places mentioned in the text. The main portion was taken from the 1:250,000 trigonometrical survey map of the area and the detailed inset from the corresponding 1:50,000 map. C. C. Appleton del.

Though most snails were collected from the forest and the *A. karroo* fringe, some were found in fairly extensive patches of rolling grassland or savanna such as at Mabibi, and around Empayeni pond on the Khlonleni peninsula between the *A. karroo* fringe and the lake. A few species were also taken amongst the marginal vegetation of perennial waterbodies, most of which are associated with Lake Sibaya. Pl. 2 shows typical open grassland at Mabibi, which is continuous with that covering much of the Tongaland plain. Where locality data refer to "forest", the main collection site in the coastal dune forest on the eastern shore of Lake Sibaya is intended, excepting of course the Raphia palm forest (*Raphia australis* Oberm. & Strey) (27°01'S 32°49'E) which is situated near Kosi Bay.

2b. Climate

The climate here is very hot and humid with predominantly summer rainfall although some rain does fall each month, even in winter. According to Köppen's (1931) climatic classification, the Lake Sibaya area of Tongaland belongs to the extreme southerly end of the Tropical Savanna type of climate which embraces much of the Mozambique coastal plain (Schulze, 1947), and is characterized by the coldest month (July) having a mean temperature above 18°C. Schulze also applies the Thornthwaite (1931) classification based on rainfall deficit in relation to evapo-transpiration, a system placing emphasis on humidity which may be expected to be an important ecological factor to terrestrial molluscs. The Lake Sibaya area belongs to the sub-humid warm climatic type, with sufficient moisture in all seasons. This type covers much of Natal and the southern Mozambique lowlands. The dune forest under consideration here, which is too narrow an area to be treated separately by Schulze, should possibly on account of its localized high rainfall and temperatures belong to the humid warm type which prevails elsewhere in Natal, both on the coast and inland. Effective Temperature (ET) isolines are considered by Stuckenberg (1969) to have greater zoogeographical significance than classical isotherms since the former emphasize the biologically important warmer months of the year (austral summer). This variable, which stresses the seasonal activity of poikilothermous animals (during rainy months) should hold good for terrestrial molluscs since they usually enter a state of diapause during prolonged dry periods. Lake Sibaya Research Station has an ET value of 17.9°C. The 18°C ET isoline, which includes almost all of southern Mozambique, penetrates the Tongaland plain to a point near Sodwana Bay, only 19 km south-west of the main collection site so that the forest fauna may be expected to contain many tropical forms, perhaps at the southernmost limits of their distribution.

In Tongaland this isoline is roughly coincident with the southerly boundary of Köppen's Tropical Savanna climatic type.

Since few measurements of climatic factors exist from the forest itself, records from Lake Sibaya Research Station are used. The proximity of the collection area to the station (about 100 m) renders these data particularly valuable.

Rainfall. — Rainfall is high, with a mean annual total of 1,130 mm for the six years from 1968 to 1974. Mean monthly values are given in fig. 2, and together with the number of rainy days per month in table 1. During the whole rainy season, from September to March, rainfall exceeds a mean of 80 mm per month; most precipitation falls as heavy showers during thunderstorms. The drier months (April to August) do not experience less than 20 mm rain each distributed over five days.

Air temperatures. — These are fairly high with a mean annual temperature during 1973 of 21.6°C which is perhaps slightly below average. Mean monthly maxima and minima measured inside a Stevenson Screen are given in fig. 3

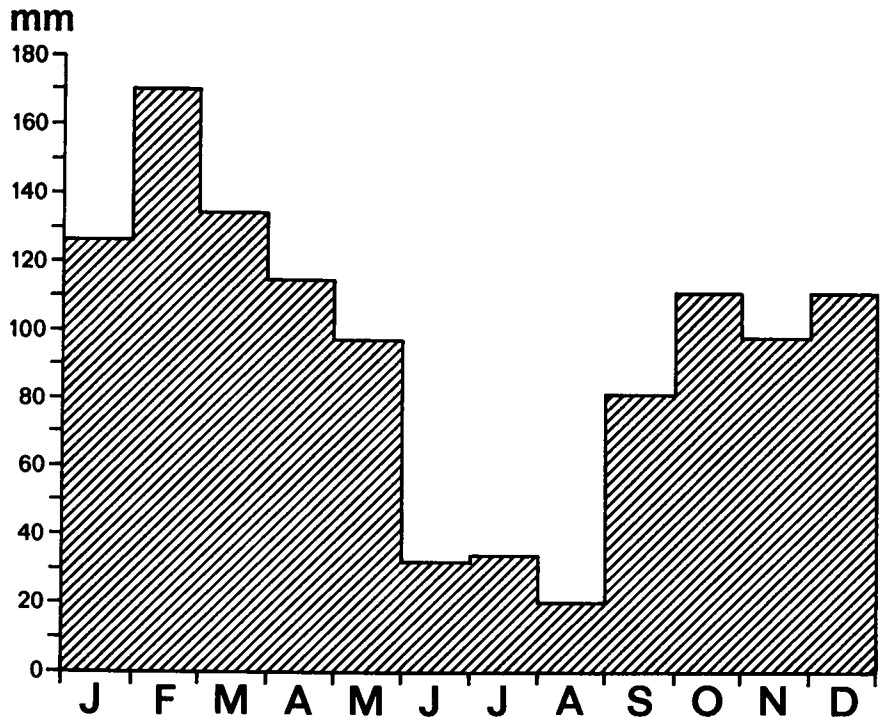

Fig. 2. Mean monthly rainfall at Lake Sibaya Research Station over six years. For details see table 1. C. C. Appleton & H. Heijn del.

and table 2. Diurnal temperatures in 1973 did not exceed 38.0°C while nocturnal values did not drop below 9.0°C. Frosts are unknown here.

TABLE 1

Mean monthly rainfall and mean number of rainy days per month at Lake Sibaya Research Station during the years 1968-1974. Cf. fig. 2.

Month	Mean monthly rainfall	Mean number of rainy days
January	126.5 mm	13
February	169.6 mm	11
March	133.8 mm	15
April	115.3 mm	11
May	96.5 mm	9
June	32.7 mm	7
July	33.8 mm	5
August	20.3 mm	6
September	81.8 mm	8
October	112.1 mm	7
November	95.3 mm	13
December	112.2 mm	11

TABLE 2

Air temperatures in °C at Lake Sibaya Research Station during 1973. Cf. fig. 3.

Month	Minimum	Maximum
January	22.8	28.7
February	21.0	28.5
March	21.7	29.2
April	17.9	25.0
May	16.0	24.2
June	14.3	23.6
July	11.5	23.8
August	14.0	22.3
September	16.7	23.0
October	17.2	24.0
November	19.1	26.1
December	21.0	25.6

Humidity. — Humidity expressed as % relative humidity, measured by a thermohydrograph also inside a Stevenson Screen, reached mean maxima and minima of 88 and 56% respectively during the 1973 winter months (April to September) and 83 and 60% during the summer months (October to March).

Evaporation. — This was measured in a Symon's Tank, and during 1973 ranged from a maximum mean monthly rate of 5.8 mm/day in January to a minimum of 2.0 mm/day in June (mean annual rate 4.1 mm/day). Individual rates of up to 10.7 mm/day are, however, known to occur during summer. Mean monthly rates are given in table 3.

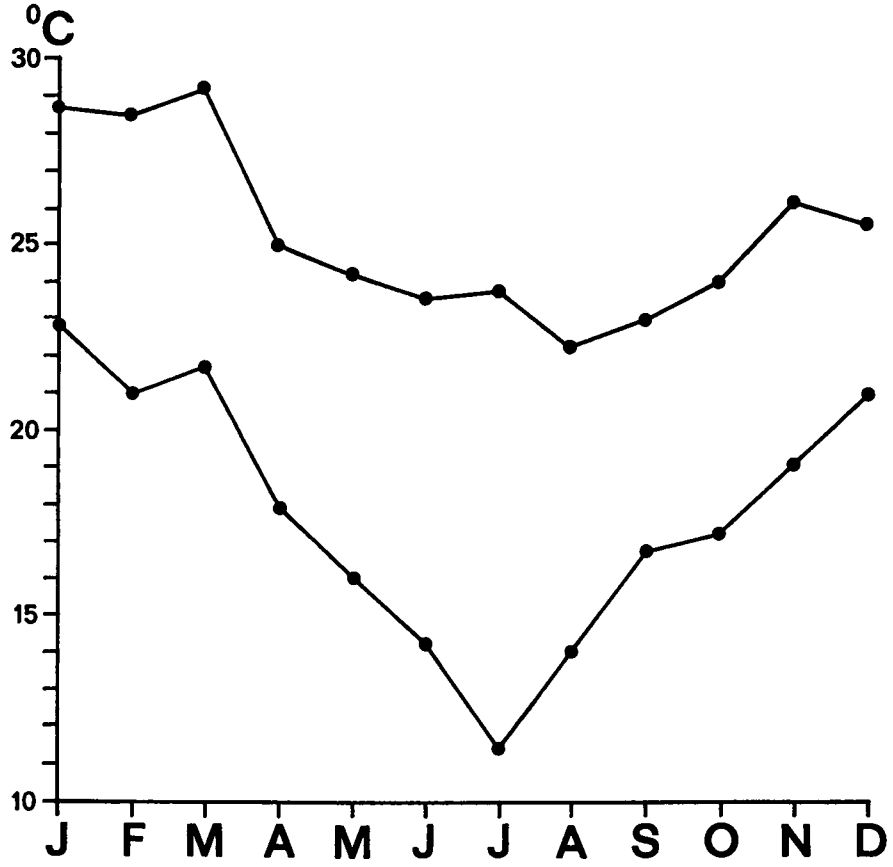

Fig. 3. Mean monthly maximum (upper graph) and minimum (lower graph) air temperatures at Lake Sibaya Research Station during 1973. For details see table 2. C. C. Appleton & H. Heijn del.

Allee et al. (1950) point out that temperature variation during both the annual and day-night cycle within a forest is less than in more exposed situations outside and Lawrence (1964) refers to investigations made by Phillips (1931) showing that temperature becomes still less variable closer to the ground. Relative humidity within the forest will however be slightly greater and evaporation lower than that outside while foliage will reduce the light intensity. Temperature conditions beneath the leaf-litter are even more stable and humidity is constantly high. Measurements of climatic factors within the forest are available only for May 1976 but nevertheless indicate the extent to which the forest cover modifies the outside climate (table 4). There is a marked decrease in daily temperature range, especially close to the

TABLE 3

Evaporation rates at Lake Sibaya Research Station over six years (May 1968-April 1974).

Month	Mean monthly evaporation rate in mm/day
January	5.8
February	5.3
March	5.1
April	3.3
May	3.0
June	2.0
July	2.3
August	3.1
September	4.1
October	4.6
November	5.3
December	5.6

forest floor, an increase in relative humidity to near saturation and severe light extinction. The investigated area lies on the westward-facing slope of the dune and did not receive direct sunlight until 09h00. Only after this time did light intensities exceed 340 and 20 lux at 3 m and ground level respectively on clear days and 490 and 100 lux on cloudy days. Temperature maxima and minima recorded at Lake Sibaya Research Station should be regarded therefore as somewhat too high in summer and too low in winter while relative humidity would be a little too low generally, if they are to be considered

TABLE 4

Selected environmental factors measured from 6-31 May, 1976, at Lake Sibaya Research Station and in two dune forest strata (at a height of 3 m in the subcanopy 1.4 m above the stand of *Isoglossa woodii* which forms the lowest stratum) and at ground level beneath *I. woodii*. Temperatures were measured with maximum and minimum thermometers, relative humidity with a wet and dry bulb hygrometer and light intensity with a Li-cor LI 185 photometer.

	Lake Sibaya Research Station	forest canopy at 3 m	forest ground level
maximum temperature (°C)	21.5	22.3	21.2
minimum temperature (°C)	12.2	15.8	17.7
mean temperature (°C)	16.8	19.1	19.5
daily temperature range (°C)	9.3	6.5	3.5
relative humidity (%)	71-100	no data	92-100
maximum light intensity at 14h00 (lux)	40000-53000	1000-1600	250-310
available light (%)	100	2.5-3.0	0.6-0.7

pertinent to the dune forest environment and especially to the microclimate of the lowest stratum. Wind velocities will be significantly reduced by the interference of forest foliage, in the present situation perhaps by up to 20-30% according to the criteria given by Allee et al.

2c. Description of the habitats

Snails were collected from three different environments, (1) coastal dune forest, (2) the *A. karroo* fringe at the foot of the dunes and (3) open grassland. Habitats nos. 1 and 2 are contiguous and share a number of species; however, the special climatic conditions inside the forest itself will not be as distinctive in the *A. karroo* fringe which is less well protected. Collection areas in forest and grassland environments correspond respectively to areas 1 (Dune Forest) and 3 (Savanna) of Breen & Jones (1971).

(1) Coastal dune forest (pl. 1). — Breen (1971) considers this to be a climax forest formation in which the tallest canopy trees reach 17 m. He recognizes three strata within the forest, (a) canopy, up to 17 m, (b) subcanopy, up to approximately 7 m, and (c) a shrub and herbaceous layer, below approximately 3 m. From the results of sampling, Breen lists the following plant species as being the most abundant in each stratum.

canopy	subcanopy
Acacia karroo Hayne	*Drypetes natalensis* Hutch.
Mimusops caffra E. Mey. ex A. DC.	*Teclea natalensis* (Sond.) Engl.
Drypetes natalensis Hutch.	*Cassipourea gerradrii* Alston
Croton gratissimus Burch.	*Plectroniella armata* (K. Schum.) Robyns
Cassipourea gerradrii Alston	*Mimusops caffra* E. Mey. ex A. DC.
Euclea natalensis A. DC.	*Croton gratissimus* Burch.
Celtis africana Burm. f.	*Clausena anisata* (Willd.) Hook f. ex Benth.
Zizyphus mucronata Willd.	*Acacia karroo* Hayne
	Acalypha glabrata Thunb.
	Clerodendrum glabrum E. Mey.

Young canopy-forming trees, shrubs such as *P. armata, A. glabrata, C. anisata* and *Cassine aethiopica* Thunb., and the herb *Isoglossa woodii* C.B.Cl. dominate the shrub and herbaceous layer. *I. woodii* is particularly dense beneath broken canopy cover, especially near the base of the dune where it dominates the undergrowth (pl. 2). A thin layer of organic leaf-litter covers much of the forest floor. Large quantities of this autochthonous debris are washed out of the forest into the *A. karroo* fringe and the lake after heavy summer rainstorms. Pl. 2 shows the forest interior, particularly the lowest stratum, the shrub and herbaceous layer. This layer, as well as the leaf-litter beneath it, yielded the majority of mollusc species from the forest.

(2) *Acacia karroo* fringe (pl. 1). — Breen (1971) suggested that it may be a subclimax stage distributed along the drainage of the dune range. Floor vegetation consists largely of grasses such as *Andropogon eucomus* Nees and *Leersia hexandra* Sw., the sedges *Juncus maritimus* Lam. and *Scirpus litoralis* Schrad., the reed *Phragmites mauritianus* Kunth., and the dicotyledon *Hydrocotyle bonariensis* Lam. Considerable shade cover is afforded by impenetrable thickets of *A. karroo*.

(3) Savanna (pl. 2). — This abuts on the *A. karroo* fringe and incorporates several perennial waterbodies and some ephemeral marshy terrain. Dominant grass species include *Imperata cylindrica* (L.) Beauv. and *Eragrostis ciliaris* (L.) R. Br., with *Dactylotenium geminatum* Hack. and *Rhynchelystrum repens* (Willd.) C. E. Hubb. less common. Breen & Jones (1971) and Moll (1972) list many other plants, chiefly grasses, from this environment which provides low, though dense, cover to a height of about 0.8-1.2 m. Scattered trees, usually *Syzygium cordatum* Hochst., *Phoenix reclinata* Jacq. and *Hyphaene natalensis* Kunze also occur here.

2d. Ecological observations on the Mollusca [1]

Most species from the dune forest were collected beneath the canopy between floor level and about 2 m on tree-trunks, saplings and plants of the shrub and herbaceous layer. Only *Edouardia meridionalis, E. natalensis, E. spadicea,* and *Rhachidina dubiosa* occurred higher, and were observed up to about 7 m from the ground on tree-trunks. Live *R. dubiosa* were found only in a large tree (*Ficus polita* Vahl) growing at the edge of the forest 0.8 km north of Banda Banda Bay. The majority of minute cryptofaunal species (55% of the total number of species recorded from the forest proper) were recovered from samples of leaf-litter from the forest floor, while larger species such as *Metachatina kraussi* and the carnivore *Natalina wesseliana* were recorded only on this debris. *Sheldonia poeppigii* and *Laevicaulis* spp. were seldom seen above ground level.

The *A. karroo* provides shelter to a height of some 3 m which, although it will moderate the comparatively more extreme physical conditions of the grassland environment, will still be more variable and severe than in the forest itself. This fringe, which is found only on the edge of the dune forest where this abuts directly on the lake, represents a temporary transition between the marginal vegetation of the lake and the forest. During inundative phases

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[1]) For notes on ecology see also Van Bruggen (1966b: 390-395; 1969: 53; in the press). Generally literature on the ecology of African terrestrial molluscs is almost non-existent; the main reference is Pilsbry & Bequaert [1927: 458-479 (-519)].

of the lake such as 1975-1976, which Pitman & Hutchison (1975) show to have occurred at least once before during this century (1943-1944), this fringe becomes flooded and the *A. karroo* die. Its molluscan community is largely composed of forest dwelling species (since they appeared most common in the forest). These include *Tropidophora* spp., *Laevicaulis natalensis* (slug), *Urocyclus flavescens* (slug), *Archachatina vestita, Natalina wesseliana, Gulella kosiensis, G. triglochis,* and *G. zuluensis.* Others such as *Laevicaulis alte* (slug), *Nata vernicosa,* and *Apera gibbonsi* (slug) seemed more common in the fringe or were found only there. Some forest dwelling elements might of course simply be washed out of the forest amongst floor debris during heavy rains. Bleached *Archachatina vestita* and *Metachatina kraussi* shells were in fact frequently found washed up on the sandy eastern shore of Lake Sibaya. *Archachatina zuluensis* and *Succinea striata* appear to be grassland dwelling species and approach afforested areas via small grassland inclusions which change abruptly to forest, but were not recorded at all within the forest. This abruptness is most unnatural and reports by early travellers suggest that coastal woodland once extended some 8 km inland from the dune forest. Today, however, this has been forced eastwards by veld fires and cattle and only small patches of woodland adjacent to the dune forest remain, grassland having taken its place. A few species, *'Guppya' rumrutiensis, Kaliella barrakporensis, Succinea striata, Oxyloma patentissima* and *Urocyclus flavescens,* were found over water, on marginal vegetation of sheltered parts of Lake Sibaya and other perennial pans, ponds and streams in grassland areas. This vegetation consists predominantly of emergent monocotyledons such as *Scirpus litoralis, Typha latifolia* L. and *Leersia hexandra;* except for *S. striata* and *O. patentissima,* these molluscs were also recorded from the dune forest.

2e. The origin and isolation of the dune forest environment

The formation of the coastal plain of south-east Africa has been discussed by King (1972). He considered it to have been cut by a Pliocene marine transgression which at its maximum stage reached the Lebombo foothills. During late Pliocene or perhaps early Pleistocene times the sea retreated and as the plain became exposed, the marine deposits were broken up and redistributed as the present sand and dune sediments. Conspicuous sandy ridges lying parallel to the present coastline but stranded at various distances inland are evidence of halting stages of the sea level during this and subsequent lesser regressions. These remnants were presumably once longshore dunes similar to the present seaward range and also afforested. It is possible that the forest community migrated eastward across the emerging plain with

these successive dune cordons to its now almost completely isolated situation on the eastern margin. It might be expected therefore that there are some common elements between the malacofaunae of the coastal dune forest and the forests of the Lebombo mountains (see also Van Bruggen, 1969: 74).

The absence of dateable material makes it difficult to assign meaningful dates to the formation of dune cordons in Tongaland. Davies (1976) has suggested however from archaeological evidence uncovered further south and from a consideration of associated marine terraces that the coastal dune cordon was formed during a late Pleistocene regression (post Eem — the last interglacial). Cordons lying further inland are older and the most westerly may be of Pliocene age. According to Prof. Davies (personal communication) an age of the order of 60,000 to 70,000 years is probably indicated for the present seaward dune on whose inland slope most of the mollusc collection under discussion was made. Prof. L. C. King (in litt. to M. N. Bruton at Lake Sibaya Research Station, 1975) suggested a more recent date, about 40,000 to 50,000 years B.P.

The dune forest community may thus have been isolated since late Pleistocene times though this might have been subject to oscillation in climate, particularly of rainfall, as tentatively proposed by Cooke (1964). Rainfall is an important limiting factor to terrestrial molluscs (Van Bruggen, 1964, 1966b). They are generally active when humidity is high, particularly close to the forest floor, at night and while rain is falling. Although the broad rainfall pattern during the Pleistocene is not thought to have altered much or to have been very different from the present one (Cooke, 1964), considerable increases and decreases did occur in the quantity and intensity of precipitation, accompanied by temperature fluctuations. These probably caused expansion and contraction of the forest/woodland communities within the forest-savanna mosaic of the Tongaland plain and may have influenced the fixation of the dune cordons by vegetation. Although the magnitude or extent of these movements is unknown, there seems little doubt that they did take place (Cooke, 1964; Van Zinderen Bakker, 1964).

Today the mean annual rainfall decreases across the plain from the coastal dune area but rises again over the Lebombo mountains (fig. 4 and table 5). This steep westward gradient in annual precipitation (approximately 10.2 mm/km) renders the dune forest environment a very restricted one to moisture-loving animals such as the majority of its Mollusca. It is confined by no less a barrier than the 48-60 km wide semi-arid Tongaland coastal plain to the west and the Indian Ocean to the east. Today coastal dune forest continuous with that under discussion still occurs to the north and south (Acocks, 1953) along the eastern margin of the plain shown by King (1972) to have been ex-

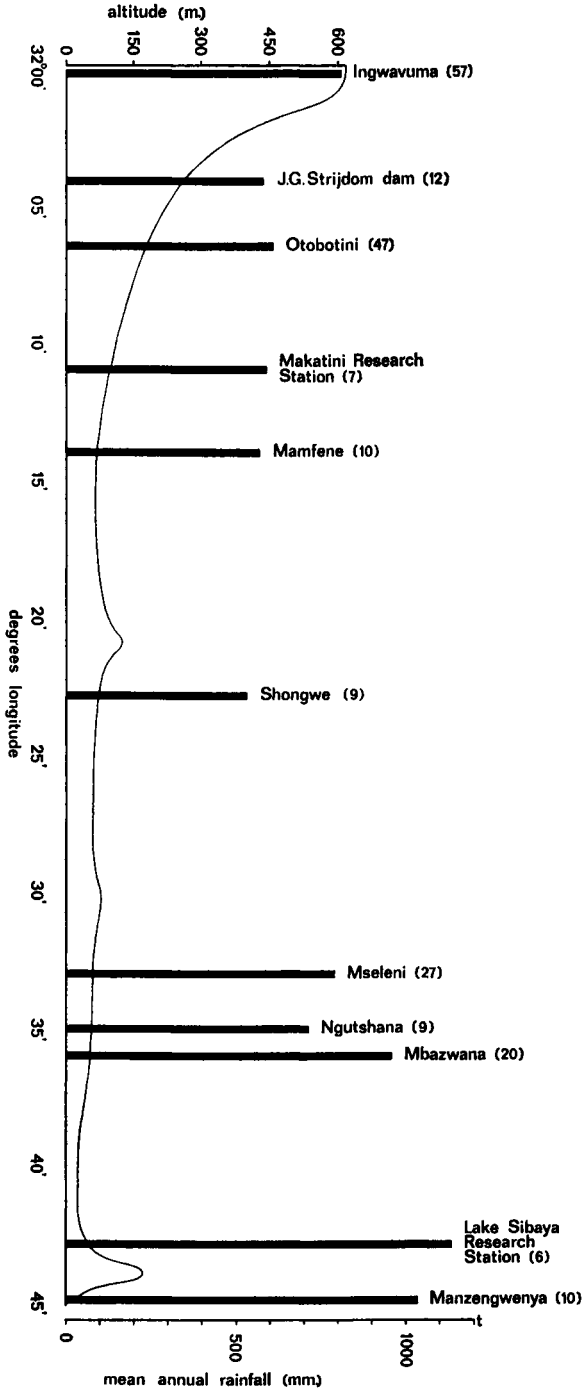

Fig. 4. Diagrammatic section of the Tongaland coastal peneplain between 27°08' and 27°30'S showing the decrease in mean annual rainfall from the coastal dune area in the east to the semi-arid central flats and subsequent increase over the Lebombo Mountains in the west. Bracketed figures indicate the numbers of years involved in the calculation of the means at the eleven stations used. For details see table 5. C. C. Appleton & H. Heijn del.

TABLE 5

Mean annual rainfall figures of eleven stations in Tongaland; the number of years involved in the calculation of the means is also shown. Cf. fig. 4.

Station	Rainfall	Years
Ingwavuma	812 mm	57
J. G. Strijdom Dam	581 mm	12
Otobotini	605 mm	47
Makatini Research Station	589 mm	7
Mamfene	567 mm	10
Shongwe	530 mm	9
Mseleni	757 mm	27
Ngutshana	710 mm	9
Mbazwana	953 mm	20
Lake Sibaya Research Station	1130 mm	6
Manzengwenya	1031 mm	10

posed by the same marine regression from beyond Lourenço Marques (= Maputo) to the south-western Cape Province. This narrow north-south corridor must effectively isolate many of the forest-dwelling snail populations from their confrères living further inland.

Since the area around Lake Sibaya is one which has seen little modern development so far except forestry, the observed distribution of terrestrial molluscs must be associated primarily with past climatic fluctuations with minimal human disturbance. Ecological changes, especially the 'slash and burn' agricultural practices of the local Thonga tribesmen are now gathering momentum, however, and if not countered could have tragic effects on for instance, the dune forest and its most interesting biological community.

3. SYSTEMATIC PART

Two new taxa, *Gulella appletoni* and *G. peakei continentalis,* have been introduced in a paper partly preliminary to the present article (Van Bruggen, 1975). The sequence of the enumeration of the families is mainly that of Taylor & Sohl (1962), while the nomenclature closely follows Zilch (1959-1960) with only a few exceptions. A number of samples has not been included in the list because the specimens so far have defied attempts at identification, either on account of the fact that many of these are juveniles not yet exhibiting diagnostic characters (e.g., many juvenile specimens of the genus *Gulella*; see also sub Subulinidae below), because of poor state of preservation, or otherwise.

The numbers quoted with the material are Appleton's field numbers; notes between inverted commas have been contributed by him.

The following abbreviations have been used below: BM — British Museum

(Natural History), London, U.K.; NM — Natal Museum, Pietermaritzburg, South Africa; NMB — Naturhistorisches Museum, Bâle, Switzerland; RMNH — Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; l/d — ratio length/major diameter of shells, thereby describing the shape of the specimen in question.

3a. Gastropoda Prosobranchia

Family Maizaniidae (one species)

Maizania (Maizania) wahlbergi (Benson, 1852)

Connolly, 1939: 535; Verdcourt, 1964: 4; Van Bruggen, 1969: 53.
No. 18T (shells only), "On slopes of Dumile Peak in dune forest", abundant, 22.IV.1973.

In southern Africa from the Eastern Cape (Port St. Johns) to northern Zululand (Gwaliweni Forest and Dumile Peak); elsewhere in coastal areas of continental Tanzania and of Kenya (see Verdcourt, 1964). Van Bruggen (1969: 54) writes "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".

Family Pomatiasidae (two species)

Tropidophora (Ligatella) ligata (Müller, 1774)

Connolly, 1939: 541; Van Bruggen, 1969: 24; Van Bruggen, 1970b: 446.
No. 18C (alcohol), "abundant in forest".

Tropidophora (Ligatella) insularis (Pfeiffer, 1852)

Connolly, 1939: 546; Van Bruggen, 1969: 24.
No. 13A (alcohol), "abundant in forest".

The subgenus *Ligatella* Von Martens, 1880, in southern Africa (and elsewhere) is in need of revision. Connolly (1939: 541-552) enumerates 15 species, which is obviously far too many. Really reliable characters for distinguishing the taxa here are hardly available, particularly because of frequent local variation. Anatomical details may assist in separating the taxa; preservation suitable for genital anatomy is generally not easy because the difficulty of satisfactorily relaxing and stretching of the live snails. Undoubtedly there are only two widely distributed forms in southern Africa, viz., *T.* (*L.*) *ligata* from the Cape Peninsula to the Zambezi River (and very probably further north), perhaps occurring inland as far west as Griqualand West, and *T.* (*L.*) *insularis* from the Eastern Cape province to as far north as Beira in Mozambique with also an inland distribution westward (and also possibly north of the Zambezi R.). In what respects these are ecologically separated (if at all) is to be investigated. Obviously there is a wide ecological tolerance

because both forms are known from a variety of habitats from arid savanna to tropical forest. In forest *Tropidophora* is usually found fairly low on the stems of trees.

3b. Gastropoda Pulmonata

Family Chrondrinidae (one species)

Gastrocopta damarica (Ancey, 1888)

Haas, 1936: 23; Connolly, 1939: 374; Adam, 1954: 796; Van Bruggen, 1966a: 104; Van Bruggen, 1966b: 325; Van Bruggen, 1970a: 45.

No. 49Z (shells only), "from leaf-litter of forest", 7; No. 79J (shell only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 1.

A widely distributed species, known from all provinces, South West Africa, Botswana, and Rhodesia; in Natal otherwise only known from Mfongosi (Zululand, Tugela R. valley) and the western shore of Lake St. Lucia (Haas, 1936).

Gastrocopta damarica has a minute shell; very small snails seem to be easily dispersed and usually show a remarkably wide distribution (Waldén, 1963: 162). *Gastrocopta* species in southern Africa are known to live in (forest) leaf-litter where they actively crawl on fallen twigs and leaves.

Family Valloniidae (one species)

Pupisoma orcula (Benson, 1850)

Connolly, 1939: 412; Adam, 1954: 807; Adam, 1957: 24.

No. 49R (shell only), "in leaf-litter on floor of coastal dune forest at Lake Sibaya", 1; No. 76N (shells only), "from leaf-litter of forest", 4.

Connolly (1916: 186) originally considered the genus *Pupisoma* Stoliczka, 1873, to be an alien in the fauna of Africa. Subsequent records (Connolly, 1939: 412-414; Adam, 1954: 807-808; Van Benthem Jutting, 1964: 6) have shown that the pattern obviously is a natural one, stretching discontinuously from the Eastern Cape through Africa and Asia as far east as Japan and New Guinea. *Pupisoma orcula* is now known to occur from Port Elizabeth to Japan, the Philippines and New Guinea. The above record is the first for Zululand. *Pupisoma* is an arboricolous genus, which is particularly well demonstrated by the localities from which representatives have been collected in southern Africa. One of the above specimens (loc. no. 76N) is closed by means of an epiphragm in exactly the same brown colour as shown by the shell.

Family Enidae (six species)

Rachis jejuna (Melvill & Ponsonby, 1893)

Connolly, 1939: 436; Van Bruggen 1969: 25.

No. 68L (alcohol), "near Bumbeni on Lower Mkuzi-Hluhluwe road", "on *Euphorbia* sp.", 28.VI.1973, 3.

Only three juvenile specimens of the species have been obtained. *Rachis jejuna* is very widely distributed (Van Bruggen, 1969: 25-27, 31-32, fig. 10) and the above record naturally fits into the known pattern. Most known localities are from within the 500 mm mean annual rainfall isohyet, although Zululand is outside this area. Ecological data as given by Tinley (in Van Bruggen, 1969: 31) show that the species is associated with thicket, woodland or forest on sandy soil, obviously avoiding seemingly suitable thicket on clayey soils.

Edouardia natalensis (Pfeiffer, 1846)

Connolly, 1939: 422; Van Bruggen, 1969: 54.
No. 49A (alcohol), "on trees in forest", 4 (inclusive of 2 empty shells).

Second record for Zululand, otherwise known from Kwa-Mbonambi. A tree dweller from the eastern coastal area from Knysna to northern Zululand and inland as far west as Pietermaritzburg.

Edouardia spadicea (Pfeiffer, 1846)

Connolly, 1939: 423; Van Bruggen, 1969: 54.
No. 49U (shells only), "found on forest floor", 4.

Second record for Zululand, otherwise known from Kwa-Mbonambi. A tree dweller from the eastern coastal area from Port Elizabeth to Barberton in the eastern Transvaal and inland as far west as Somerset East; there are, however, no records from the large area between Kentani (N. of East London) and northern Zululand.

Edouardia meridionalis (Pfeiffer, 1848)

Connolly, 1939: 428; Van Bruggen, 1969: 28.
No. 49B (alcohol), "on trees in forest", 7 (inclusive of one empty shell).

Second record for Zululand, here otherwise known from Mkuzi Game Reserve. A tree dweller from the eastern coastal area from Maitland River mouth to Matolla and the Marracuene district [2] in southern Mozambique.

Edouardia metuloides (Smith, 1899)

Connolly, 1939: 433; Van Bruggen, 1966b: 333; Van Bruggen, 1969: 55.
No. 8B (alcohol), "found on land-rover after trip over grassveld between forest and lake", 11.XII.1972, 1.

Second record for Zululand (specimen, 7.4 × 4.1 mm, l/d 1.80, compared to type material in BM, 1974), here otherwise known from Imfamanzi River near the junction of the Black and White Umfolosi Rivers. The few other

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2) At the mouth of the Incomati River (surroundings of Vila Luiza); Connolly (1925) gives two different spellings: Marrakwen (p. 111) and Morakwen (p. 153).

known localities are all further north: Kruger National Park, Mtisherra River valley (Mozambique), Victoria Falls (Rhodesia), Zomba (Malawi), Broken Hill (Zambia). This is another tree dweller collecting dirt on its shell, which presumably gives protection against visual predators such as birds; once found under the bark of a tree (Van Bruggen, 1966b: 334).

Rhachidina dubiosa (Sturany, 1898)

Connolly, 1939: 417.

No. 49P (alcohol), "collected on large *Ficus polita* in forest", 1.

Second record for Zululand, here otherwise known from Mazimba Hill on the Black Umfolosi River. Obviously rare but widely distributed in southern Africa, the only other records being Matolla (type locality), Dondo (Forest), and Chiluvo Forest (between Gondola and Beira, new record: NM, RMNH), all in Mozambique. This somewhat obscure, but otherwise well characterized species, may be allied to the East and Central African enid *Rhachidina braunsii* (Von Martens, 1869). *R. dubiosa* is a tree dweller in various types of forest.

Family Succineidae (two species)

Succinea striata Krauss, 1848

Quick, 1936: 34; Connolly, 1939: 441; Van Bruggen, 1969: 31; Van Bruggen, 1970b: 454; Allanson et al., 1974: 513, 521.

No. 7T (alcohol), "marginal vegetation of Empayeni pond on lake's eastern shore", 27.IV.1973, 2 (compared in the BM, 1974); No. 63B (alcohol, "in gutter of Research Stn. building after rain", 16.VI.1973, and "after heavy mist", 20.XI.1973, 3 (inclusive of two empty shells).

A widely distributed species known from all provinces, South West Africa, Botswana, Lesotho, Rhodesia, and Mozambique. Specimen no. 7T is dirt-encrusted, a phenomenon not unusual for the species. Sample no. 63B consists of a juvenile shell, an adult shell and an adult specimen, which latter two belong to the well-marked var. *piscinalis* Melvill & Ponsonby, 1898; the adult specimen is also dirt-encrusted. The wide distribution over a variety of habitats varying from semi-desert to almost amphibian conditions testifies to the ecological tolerance of the species.

Oxyloma patentissima (Pfeiffer, 1853)

Quick, 1936: 28; Connolly, 1939: 445; Wright, 1963: 500; Oberholzer & Van Eeden, 1967: 26; Allanson et al., 1974: 521; Lloyd-Evans, 1974: 344 (all s.n. *Succinea patentissima*); Bruton & Appleton, 1975: 289-290, 292.

No. 6C (alcohol), "on marginal vegetation of Mbazwane stream", 22.XI.1972, 1; No. 7L (alcohol), "marginal vegetation of Empayeni pond on lake's eastern shore", 20.I.1973, 1; No. 9A (alcohol), "marginal vegetation of Ishumayela pan, Mabibi area (eastern shore of lake)", 13.XII.1972, 2; No. 14D (alcohol), "Bundlwini pan (Mabibi

area as above)", 19.XII.1972, 7; No. 15G (alcohol), "on *Thelypteris* leaf along Mseleni stream, on western shore of lake", 13.VIII.1973, 2; No. 23H (alcohol), "marginal vegetation of small pan on southern shore of lake", 27.VIII.1973, 1; No. 43B (alcohol), marginal vegetation "of Welandhlovu stream which flows into northern arm of lake", 23.III.1973, 1; No. 61L (alcohol), marginal vegetation "of Shazibe stream, near Sodwana Bay", 28.VIII.1973, 1; No. 70E (alcohol), marginal vegetation "of Kumnyana [now: Gezisa] stream, Maputa", 29.VIII.1973, 1; No. 72F (alcohol), marginal vegetation "of Vasa pan (north of Lake Sibaya)", 7.IX.1973, 2; No. 73V (alcohol), "from mangroves at Sodwana Bay", 11.XI.1973, 2.

All material has been compared with authentic specimens in the British Museum (Natural History). The largest available specimens (sample no. 73V) have shells of 8.9 × 5.1 mm and 10.4 × 5.3 mm respectively. The specimen with the smallest shell, which animal has a length of ca. 13 mm in alcohol, has been dissected in order to check the genitalia. These are in complete agreement with the figures given by Quick (1936), Wright (1963) and Lloyd-Evans (1974). The reproductive organs are very swollen and almost completely fill the body cavity. The specimens were obtained on 11 November when the austral spring is already quite advanced so that the mating season is then probably at its height.

This species has already been recorded from Lake Sibaya early in this century by the Natal Museum's collector F. Toppin. It is now known to occur in Luanda province (Angola, see Wright, 1963) and from southern Natal (Park Rynie) to southern Mozambique (Magude District), with two inland localities, viz., Potchefstroom and the Victoria Falls. No material from these two localities has been checked by the senior author and it is possible that these records are based on wrong identifications. Victoria Falls specimens of juvenile *Oxyloma connollyi* (Preston, 1912), a closely allied species, albeit with a much larger shell, which is quite common in the Victoria Falls Rain Forest on the south bank of the Zambezi R., may have been misidentified as *O. patentissima*. Beyond southern Africa the species has recently been identified in the Lake Chad area (Lloyd-Evans, 1974), which is an indication of a much wider distribution. The latter record is completely reliable since it is based on anatomical data.

O. patentissima obviously has a preference for very wet habitats and frequently is considered a freshwater mollusc (e.g., Bruton & Appleton, 1975: 289, 292). It leads an amphibious life alongside and partly in streams, ponds and lakes. In this process it may come very close to the sea shore, sometimes occurring within feet of mangrove vegetation (Sodwana Bay, sample no. 73V, see above). Five other records suggest that this is perhaps not of uncommon occurrence (Port Natal, Umgeni R. lagoon, Cable Station near Umgeni R. mouth, Park Rynie, Illovo R. lagoon). In Angola the species also appears to lead an amphibian life on the edges of various

freshwater lakes (Wright, 1963: 501, "The inclusion of *Succinea* in a work on freshwater gastropods is questionable from the systematic point of view but fully justified ecologically because of the frequency with which these snails are found when searching for purely aquatic forms."). The Lake Chad material (Lloyd-Evans, 1974) was also collected on the wet fringe of the lake. Representatives of the family Succineidae are known to occupy an almost endless variety of habitats, which ecological tolerance may have caused the family to become cosmopolitan in its distribution.

Family Ferrussaciidae (one species)

Cecilioides gokweanus (Boettger, 1870)

Connolly, 1939: 370; Van Bruggen, 1966b: 351; Van Bruggen 1970a: 49.

No. 49X (shells only), "from leaf-litter on forest floor", 5; No. 79H (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 3.

Cecilioides gokweanus, a blind, usually subterranean [3]), snail, is widely distributed in southern Africa; it is now known from South West Africa, Botswana, the Transvaal, and Zululand (new record). It is somewhat surprising to record it from Zululand from leaf-litter in forest, because the known localities seemingly indicate the species to be adapted to semi-arid conditions. On the other hand, the species of *Cecilioides* are usually widely distributed where there are suitable micro-habitats, such as e.g., a bit of moist humus in a sheltered situation among rocks in an otherwise semi-arid environment.

Family Subulinidae (four species)

Hypolysia florentiae Melvill & Ponsonby, 1901

Connolly, 1939: 358; Van Bruggen, 1969: 57 (*Curvella florentiae*).

No. 49W (shells only), "from leaf-litter in forest", abundant; No. 76B (alcohol), "from leaf-litter of forest", 10.X.1973, 5; No. 79R (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 3.

Hypolysia florentiae occurs in the coastal belt from Knysna to Kosi Bay; the only known inland locality is Rustenburg in the Transvaal. This again is a species of sheltering types of vegetation; it lives in the humus on the forest floor.

Zilch (1959) considers *Hypolysia* Melvill & Ponsonby, 1901, to be a subgenus of *Curvella* Chaper, 1885. However, on account of shell characters such as shape and last whorl, it is perhaps better to keep *Hypolysia* as a separate genus of its own rather than classifying it with either *Curvella* or *Opeas* Albers, 1850.

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[3]) In the Kruger National Park a live specimen was collected under a log (Van Bruggen, 1966b).

Euonyma tugelensis (Melvill & Ponsonby, 1897)

Connolly, 1939: 344; Van Bruggen, 1969: 35.

No. 49V (shells only), "from leaf-litter in forest", abundant; No. 79R (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 2.

Euonyma tugelensis is another forest dweller, so far only known from six localities on the east coast of southern Africa: Illovo River, Pietermaritzburg, Lower Tugela River, Lake Sibaya area, Ndumu Game Reserve, Delagoa Bay.

Subulinidae spec. 1 and spec. 2

No. 49Y, shells only, "from leaf-litter in the forest", spec. 1:4, spec. 2:9.

Sample no. 49Y contains juveniles of two species of Subulinidae, viz., four very small and nine somewhat larger specimens. Both were compared to all southern African subulinids, e.g., in the collections of the British Museum (Natural History). It appears that the present material does not match any of the southern African species. The fact that all are juvenile is a complicating factor here. The very small material may even represent a new species with a small shell. For the time being it is impossible to venture an opinion on this material.

Family Achatinidae (four species)

Archachatina (Tholachatina) parthenia Melvill & Ponsonby, 1903

Connolly, 1939: 310; Bequaert, 1950: 48; Van Bruggen, 1965: 80 (all s.n. *Achatina parthenia*).

No. 18S (alcohol, dry), "on trees in forest", 22.II.1973 (alcohol 3, shell only 1).

"Achatina" parthenia has been described from Zululand (Lower Umfolosi Drift; for discussion of locality see Van Bruggen, 1969: 51-52) and has so far never been found outside this area. Apart from the type locality the species is now known from Makowe, Ubombo, and the Lake Sibaya area. According to the collector it is a tree dweller in forest.

The present material has been compared with the type in the British Museum (Natural History); this is the largest specimen known. Two shells from Makowe collected by Burnup (BM) are smaller; the largest Appleton specimen (dry) measures 24.8 mm and has only five whorls.

Bequaert (1950) has classified this species with *Achatina* Lamarck, 1799, subgenus *Pintoa* Bourguignat, 1889. In view of the broad, dome-shaped summit of the shell of *A. parthenia* it is perhaps more appropriate to consider the species to belong to the genus *Archachatina* Albers, 1850, subgenus *Tholachatina* Bequaert, 1950.

Prof. Mead has dissected the largest Appleton specimen and he comments as follows (in litt., 4.II.1975): "I examined only the largest specimen and it was so immature that it was virtually embryonic; hence, no relationships

could be discovered; the very attenuate nature of the immature genital system gives no clue as to what the mature system is like — ...". Therefore the problem of the identity of *"Achatina" parthenia* remains as yet unsolved. So far these shells have not been matched to any known southern African species of Achatinidae and only further field studies may reveal essential details.

Archachatina (Tholachatina) vestita (Pfeiffer, 1855) (pl. 3)

Connolly, 1939: 314; Van Bruggen, 1966a: 102.

No. 18A (alcohol, dry), "on forest trees", 23.XII.1973 (alcohol 1, shells only 2); No. 63J (shell only), "Research Stn. grounds", 1 juv.

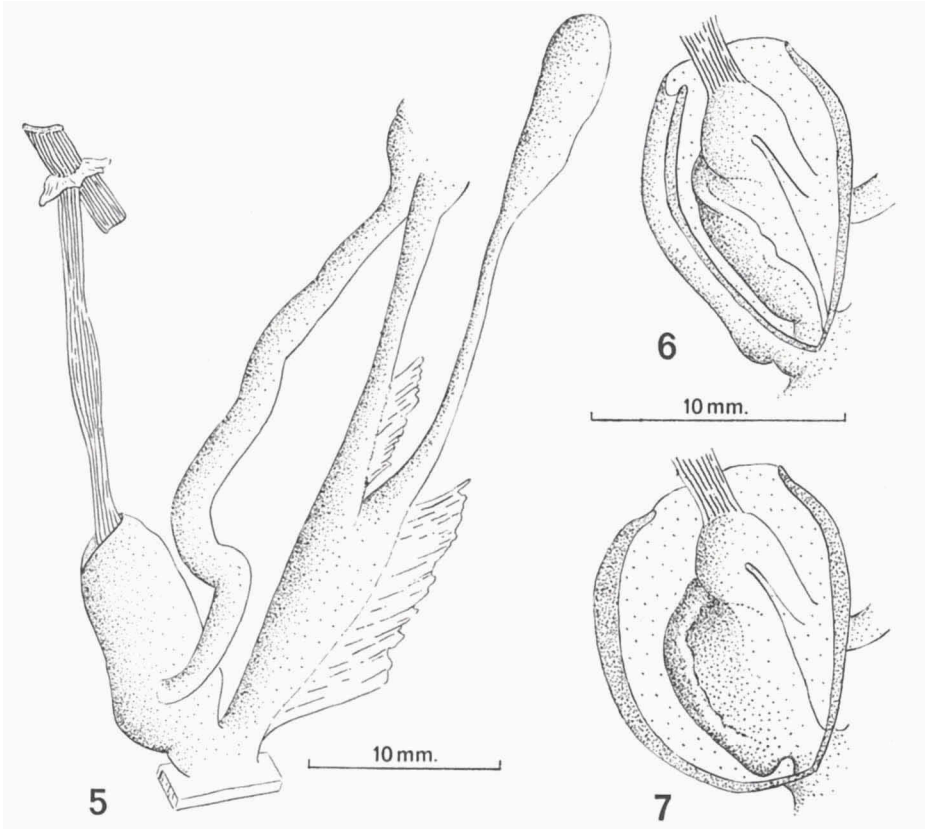
This is only the second record for the species in Zululand; Connolly (1939) reports it from Kosi Bay. It now appears to be distributed from Port St. Johns in the south northward to Chimonzo in Mozambique; it is limited to coastal forest and nowhere occurs further inland than about 10 km from the shores of the Indian Ocean. The largest Appleton shell (dry specimens) measures 76.5 × 34.3 mm. The species has been discussed in detail by Van Bruggen (1966a: 102-103).

Archachatina (Tholachatina) zuluensis (Connolly, 1939) (figs. 5-7)

Connolly, 1939: 308; Bequaert, 1950: 202; Van Bruggen, 1965: 80; Van Bruggen, 1969: 35 (s.n. *Achatina craveni)*, 36.

No. 4K (alcohol), "from grassveld between southern end of lake and Mbazwana", 20.II.1973, 1; No. 60A (shells only), "from Raffia palm forest at Kosi Bay", 2.V.1973, 3; No. 67B (alcohol, dry), "found aestivating in sand at ca. 5 cm, grassveld between forest and lake", 5.IX.1973 (alcohol 1, shell only 1); No. 73K (shells only), "on recently burnt palm-veld near Sodwana Bay", 13.VI.1973, 3; No. 75D (alcohol), "from grassveld in Mabibi area (between eastern shore of lake and sea)", 27.IX.1973, 1; No. 75G (shells only), "Mabibi grassveld", 2.

As mentioned before (Van Bruggen, 1969: 36), in Zululand *Achatina craveni* Smith, 1881, and *Archachatina zuluensis* are difficult to separate, although the species seem to be restricted to different areas. A close study in the British Museum (Natural History) has revealed that *Achatina craveni* is not represented in Zululand; all specimens belong to *Archachatina zuluensis.* This species varies quite considerably, particularly in contour of the shell. Connolly (1939: 308) gives measurements of three specimens: 75.0 × 40.0 mm, l/d 1.88; 67.0 × 37.5 mm, l/d 1.79; 68.0 × 32.2 mm, l/d 2.11. Most specimens of Appleton's material belong to the slender form, such as no. 67B (empty shell): 43.5 × 22.0 mm, l/d 1.98. The largest specimen (no. 4K) has a somewhat damaged, rather thin, shell measuring 62.5 × 33.7 mm, l/d 1.85, with seven whorls, obviously representing the less slender type of shell. The background colour of shells of *Archachatina zuluensis* is a striking straw-yellow, while that of shells of *Achatina craveni* is a deep buff. This may be an aid in separating shells of the taxa involved.



Figs. 5-7. *Archachatina* (*Tholachatina*) *zuluensis* (Connolly, 1939). Lake Sibaya area, collector's no. 4K, from grassveld between southern end of lake and Mbazwana, 20 February 1973, details of genitalia. 5. Basal genitalia. 6. Basal male conduit showing the penis in its peculiar folded manner. 7. Basal male conduit showing the penis in the unfolded condition. A. R. Mead del.

A shell in the British Museum (Natural History), originally in the McAndrew collection and obtained from H. B. Preston in 1904 s.n. *Achatina schinziana* Mousson, 1887, represents an extension of the distribution of *Archachatina zuluensis*. It is labelled as having been obtained at Rikatla (north of Lourenço Marques = Maputo), Mozambique, and it matches the holotype beautifully. The measurements are 72.7 × 36.7 mm, l/d 1.98, last whorl 52.5 mm, aperture 41.5 × 21.0 mm. The specimen was discovered and recognized by Prof. A. R. Mead.

Prof. Mead has dissected and figured the genitalia of specimen no. 4K (figs. 5-7, for measurements of shell see above); specimen no. 75D (shell 53.5 × 32.2 mm, l/d 1.66) was checked and found to agree in all details, although the shell is much smaller. Attention should be drawn to a few parti-

culars; Prof. Mead will later discuss these specimens in more detail elsewhere. The penis is completely ensheathed and upon opening shows a very peculiar organ. The penis has a folded, ear-like extension on one side (figs. 6-7); it appears to be literally folded around itself. Dissection of *Archachatina* (*Tholachatina*) *dimidiata* (Smith, 1879) by Prof. Mead showed that the penis in that species is similarly large, flat and folded upon itself — only it was folded from both sides so that it appeared to be dicotyledonous. Obviously the two species are fairly closely allied despite the great differences in the respective shells. The large, bulbous penis and sheath and the prominent band of muscle tissue between the vagina, spermathecal duct and body wall strongly suggested the conditions in *A. zuluensis* (cf. fig. 5, tissue shown on the right).

This immediately leads to comparison with the material described and figured by Van Bruggen (1969: 35-36, fig. 11) and with some slight doubt attributed to *Achatina craveni*. This specimen from the Ndumu Game Reserve has a shell of 63.5 × 35.0 mm, l/d 1.66, and Van Bruggen's (1969) fig. 11 agrees remarkably well with fig. 5 in the present paper. Unfortunately Van Bruggen failed to open the penial sheath. The material in question was borrowed from the Natal Museum and checked by Prof. Mead, who found it to agree with the material figured here (figs. 5-7). Moreover he managed to dissect the real *Achatina craveni* and found this to be completely different. The reproductive system is basically that of other species he has examined in the subgenus *Achatina*.

The conclusions of the above data are, (1) that Van Bruggen (1969) recorded *Archachatina zuluensis* s.n. *Achatina craveni*, and (2) that consequently *Achatina craveni* has so far not been reliably reported from Zululand. This is an illustration of the importance of the genital anatomy of the Achatinidae in assisting specific identification.

Metachatina kraussi (Pfeiffer, 1846) (pl. 4)

Connolly, 1939: 294; Van Bruggen, 1969: 6-20 (monographic revision); Van Bruggen, 1970b: 467.

No. 49E (shells only), "from forest floor", 4; No. 75F (alcohol), "on forest floor", 1 juv.

The two largest, but by no means fully adult, specimens in sample no. 49E still retain part of their periostracum. The monotypic genus is endemic to a restricted area in southeastern Africa (Van Bruggen, 1969: 15, fig. 4). This snail is usually found in lightly to well wooded areas.

Family Streptaxidae (twelve species)

The family Streptaxidae consists of micropredators which sometimes are locally common; almost all species are ground dwellers occurring in a variety

of habitats varying from forest to semi-desert. Southern Africa harbours at least 130 species of which approximately 125 belong to the very widely distributed genus *Gulella* L. Pfeiffer, 1856 (see Van Bruggen, 1973: 419). Twelve species have been found among the Appleton material, among which two striking novelties (Van Bruggen, 1975). Pending a complete revision of the genus in southern Africa data given here are somewhat summary.

Gulella zuluensis Connolly, 1932

Connolly, 1939: 25; Van Bruggen, 1973: 423.

No. 8V (alcohol), "Research Stn. grounds", 6.V.1973, 2; No. 49D (alcohol), "on trees in forest", IV. 1973, 5; No. 76S (shells only), "from leaf-litter from the forest", 15; No. 76Z (shells only), "from leaf-litter from the forest", 7; No. 79Q (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 13.

According to unpublished data *Gulella zuluensis* is distributed in a narrow stretch of country along the coast of Natal and Zululand from Stanger to the Mozambique border. Obviously the species is restricted to dune forest, dune scrub or coastal forest. After rains they tend to crawl low onto tree trunks and walls of houses.

Gulella triglochis (Melvill & Ponsonby, 1903)

Connolly, 1939: 26; Van Bruggen, 1969: 38.

No. 63L (alcohol), "Research Stn. grounds", 10.XI.1973, 1; No. 76Q (shells only), "from leaf-litter from the forest", 15; No. 76Z (shells only), "from leaf-litter from the forest", 2; No. 79C (alcohol), "on low, herbaceous plants of the forest's lowest stratum", 18.IX.1973, 1; No. 79G (shell only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 1.

Gulella triglochis is another inhabitant of various types of indigenous bush along the coast of Natal, Zululand, and Mozambique; its range stretches from Botha's Hill in the south to Ponta de Ouro (Mozambique, at the coast on Zululand border, colln. D. W. Aiken, new record), and it also occurs on Inhaca Island. Inland it ranges as far west as southern Swaziland. *G. zuluensis* and and *G. triglochis* are therefore largely sympatric and are frequently found occurring together.

Gulella infans (Craven, 1880)

Connolly, 1939: 26; Van Bruggen, 1966b: 386; Van Bruggen, 1973: 422, 424.

No. 76M (shell only), "from forest leaf-litter", 10.X.1973, 1.

The *Gulella infans* complex enjoys a very wide distribution from the eastern Cape Province to Rhodesia and southern Mozambique; throughout its range it varies considerably as regards sculpture, size and form, the dentition usually being fairly constant. The relation to *G. johannesburgensis* (Melvill & Ponsonby, 1907) is not quite clear as the taxa do not seem to be completely separated. Ecologically the *G. infans* complex, which thus may contain more

than one taxon, is very widely tolerant, records being known from semi-arid areas such as the Kruger National Park (Van Bruggen, 1966b: 387) as well as indigenous high forest in Rhodesia and Mozambique.

Gulella perspicuaeformis (Sturany, 1898)

Connolly, 1939: 37.

No. 76V (shells only), "from leaf-litter from the forest", 16; No. 79K (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 4.

According to Connolly (1939) *Gulella perspicuaeformis* is only known from its type locality Lourenço Marques, Mozambique. However, in the Natal Museum there is additional material from Kosi Bay (leg. F. Toppin) and from Enkwalini (= Nkwalini) (leg. H. J. Puzey); in the British Museum (Natural History) there is a sample from Mtimona (leg. H. J. Puzey). All are new records for Zululand; Nkwalini and Mtimona are close together (28 31 DA, Nkandla area, see Leistner & Morris, 1976). This is a distribution pattern into which the Appleton records easily fit. As far as is known this species is a ground dweller in sheltering types of vegetation.

Gulella kosiensis (Melvill & Ponsonby, 1908)

Connolly, 1939: 50.

No. 8K (alcohol), "in leaf beneath shrubs etc. in garden of Lake Sibaya Research Station", 7.I.1973, 3; No. 13B (alcohol), "in grass close to forest, amongst *Acacia* trees", 18.XII.1973, 4; No. 63G (alcohol), "Research Stn. grounds", 18.IX.1973, 2; No. 76R (shells only), "from leaf-litter from the forest", abundant; No. 79P (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", abundant.

Gulella kosiensis is known to occur in the coastal area of Natal and Zululand from Durban in the south to as far north as Kosi Bay. This is also a ground dweller in sheltering types of vegetation. There is a considerable variation in size of the adult shells. Specimens in sample no. 79P are 4.4-6.1 mm long; Connolly (1939: 50) gives as size range for the species 5.2-7.0 mm.

Gulella bushmanensis Burnup, 1926

Connolly, 1939: 57.

No. 79D (shells only), "in leaf-litter on forest floor", 18.IX.1973, 21; No. 79S (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 7.

Connolly (1939: 57) records the following localities for *Gulella bushmanensis:* "Weenen Hill" "and several localities in Weenen District", and Mfongosi (Zululand). In the Natal Museum there are specimens from St. Lucia Bay and the above record confirms the presence of the species in the Zululand coastal area. Nevertheless it is somewhat surprising to find a

species originally described from mountainous areas (Weenen 2841 ft. = 866 m; Mfongosi 600-750 m) to occur in the coastal lowlands of Zululand with its utterly different climate. However, *Metachatina kraussi* (Pfr.) has been found to occur from sea level in Natal, Zululand, and Mozambique to an altitude of ca. 1300 m near Glencoe (Van Bruggen, 1969: 16-17). It is therefore not unlikely that there are more species of snails and indeed of other animals and of plants that show such a type of distribution pattern.

Gulella linguidens Connolly, 1939

Connolly, 1939: 76; Van Bruggen, 1969: 63.
No. 76W (shells only), "from leaf-litter from the forest", 3; No. 79M (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 6.

Until recently *Gulella linguidens* has been very rare in collections. So far only four specimens have been recorded, viz., holotype (NM), paratype (BM), and two Lake Sibaya shells (BM, RMNH) (cf. Van Bruggen, 1969: 63). The Appleton material consists of nine specimens:

4.7 × 2.2 mm, l/d 2.08
4.6 × 2.4 mm, l/d 1.92
4.5 × 2.4 mm, l/d 1.89
4.5 × 2.4 mm, l/d 1.89
4.3 × 2.4 mm, l/d 1.82
4.3 × 2.3 mm, l/d 1.87
4.3 × 2.3 mm, l/d 1.87
4.3 × 2.2 mm, l/d 1.92
4.2 × 2.4 mm, l/d 1.79

The material may be summarized as 4.2-4.7 × 2.2-2.4 mm, l/d 1.79-2.08 (l/d values have been calculated from micrometer readings). At present the species has only been recorded from two widely distant localities in Zululand, the Hluhluwe Game Reserve (type locality) and the Lake Sibaya area. Very probably it is a local Zululand endemic.

Gulella daedalea (Melvill & Ponsonby, 1903)

Connolly, 1939: 88; Van Bruggen, 1969: 50.
No. 79A (shells only), "from leaf-litter from the forest", 3.

Gulella daedalea is now only known from three primary localities in northern Zululand (Tongaland), viz., Ndumu Game Reserve, Kosi Lake system, and Lake Sibaya area. The type locality obviously is a secondary locality (see Van Bruggen, 1969: 51-52). Very probably this species is also a ground dweller in sheltering types of vegetation.

Gulella farquhari (Melvill & Ponsonby, 1895)

Connolly, 1939: 95; Van Bruggen, 1975a: 213.
No. 76D (alcohol), "from forest-leaf litter", 10.X.1973, 1; No. 76X (shells only), "from leaf-litter from the forest", 11; No. 79F (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 8.

Gulella farquhari is a very variable species and many varieties have been described. However, none of the described forms can be upheld as a separate

taxon when large series are studied, although clines (particularly size clines) may occur. The here discussed Zululand material has smooth shells with slight remains of subsutural sculpture; an average specimen measures 2.8 × 1.4 mm, l/d 2.00. The species is very widely distributed from the eastern Cape Province to central Mozambique, inland only as far west as Grahamstown and Weenen, Natal (cf. Van Bruggen, 1975a: 214). So far in Zululand it has only been recorded from Mfongosi (Connolly, 1939: 96, BM, NM, RMNH), Eshowe (W. Falcon leg., NM, new record) and the Lake Sibaya area. The Appleton specimens therefore represent the first coastal record for the species north of the Tugela River inclusive of Mozambique where *G. farquhari* is only known to occur at Mount Vengo near Macequece = Vila Manica.

Gulella appletoni Van Bruggen, 1975

Van Bruggen, 1975a: 213.

No. 76Y (shell only), "from leaf-litter from the forest", 1 (holotype); No. 79E (shell only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 1.

Gulella appletoni is one of the striking discoveries made by Appleton in the Lake Sibaya area. The species has been fully discussed (Van Bruggen, 1975a); in 1976 Appleton has obtained a second specimen, which matches the holotype quite well, apart from being even more slender. It measures 1.9 × 0.7 mm, l/d (calculated from micrometer readings) 2.73, last whorl 0.9 mm, aperture 0.5 × 0.4 mm. Dr. H. E. van Hoepen, a Johannesburg neurologist/psychiatrist and amateur malacologist, has also obtained *G. appletoni* at Sodwana Bay. Early in 1976 he collected from samples of leaf-litter about 200 *G. peakei continentalis,* about 30 *G. appletoni* and about 20 *G. browni,* a marked success for a short trip taking into account conditions such as heavy rainfall and poor roads (Van Hoepen, in litt., 18.IV.1976). Five shells of *G. appletoni* have been generously deposited in the Leiden museum; these measure 1.7-1.9 × 0.7 mm, l/d (calculated from micrometer readings) 2.55-2.73. The species appears to be another ground dweller in sheltering types of vegetation.

Gulella browni Van Bruggen, 1969

Van Bruggen, 1969: 69.

No. 76C (alcohol), "from leaf-litter of forest", 10.X.1973, 6; No. 76T (shells only), "from leaf-litter from the forest", abundant; No. 79L (shells only), "coastal Dune Forest on eastern shore of Lake Sibaya (from samples of leaf-litter)", 12.

Since its description *Gulella browni* has again been obtained in the Lake Sibaya area by Mr. B. H. Lamoral of the Natal Museum and now Appleton's material proves it to be common in the area. Dr. Van Hoepen has also obtained this species at Sodwana Bay (see sub *G. appletoni*). So far the

species is only known from this part of Zululand and from the Chiluvo Forest in Mozambique. *G. browni* is a ground dweller in coastal bush in Zululand and in tropical high forest in Mozambique. The characteristic acute apex of this species is conveniently diagnostic for juvenile shells, which as a rule in this genus cannot be identified as to species.

Gulella peakei continentalis Van Bruggen, 1975

Van Bruggen, 1975a: 209.
No. 76U (shells only), "from leaf-litter from the forest", abundant (type material).

Gulella peakei, originally described from Aldabra Island in the western Indian Ocean (Van Bruggen, 1975b: 164), has somewhat surprisingly within a year turned up in Zululand. Continental populations sampled so far seem to indicate that a well delimited subspecies occurs in Zululand. Zululand shells are characterized by the presence of an additional basal denticle and by being "somewhat larger and more slender than the extinct island form, while at the same time both the last whorl and the aperture are comparatively smaller." (Van Bruggen 1975a: 212). Since its description the continental subspecies has also been found to occur abundantly at Sodwana Bay by Dr. Van Hoepen (see sub *G. appletoni*). It belongs to a group of species of northern, tropical derivation, having its closest relatives in East, Central and West Africa. Obviously *G. peakei continentalis* is another inhabitant of forest leaf-litter.

Family Rhytididae (two species)

Nata (Nata) vernicosa (Krauss, 1848)

Connolly, 1939: 99 (*N. vernicosa*), 101 (*N. liparoxantha*); Van Bruggen, 1967a: 29; Van Bruggen, 1969: 37; Van Bruggen, 1970b: 468.
No. 8U (shells only), "Research station grounds", 2.

Nata vernicosa is a very widely distributed rhytidid occupying an almost continuous range from the eastern Cape Province to the Limpopo River, ranging inland as far west as Louis Trichardt (Transvaal) where there is suitable cover combined with humidity. This species is carnivorous and is usually found on the ground or low on herbs and bushes.

Natalina (Natalina) wesseliana (Kobelt, 1876)

Connolly, 1939: 107; Van Bruggen, 1969: 58; Kilburn, 1973: 11.
No. 60B (shell only), "Raffia palm forest at Kosi Bay", 2.V.1973, 1 juv.; No. 63F (alcohol), "Mbazwana area (west of Lake Sibayi)", 1 juv.; No. 76A (shells only), "from forest at Sibayi", 7 (among which only 2 adults); No. 79B (alcohol), "from forest floor", 3.

Natalina wesseliana and *N. cafra* (Férussac, 1821) are not always easily separated, particularly in the young stages; for the time being the present author

is satisfied that all Appleton material belongs to *N. wesseliana.* This species is so far only known from a restricted area in Zululand and southern Mozambique: Makowe, Lake Sibaya area, Kosi Bay, Rikatla. *N. cafra,* however, is known from southern Zululand (Mfongosi, Eshowe, vide Van Bruggen, 1969: 57-58) southward to the eastern Cape Province; its northernmost locality is "Between Lydenburg and Delagoa" (Connolly, 1939: 105), so that the two species appear to be largely or perhaps even completely allopatric. The relation between these two taxa is not at all clear and *N. wesseliana* may only be a variety or perhaps even subspecies of *N. cafra. N. wesseliana* obviously is an inhabitant of sheltering types of vegetation; personal experience has shown that these snails require a good deal of moisture.

Natalina wesseliana is a large carnivorous snail preying on soft invertebrates; stories of species of *Natalina* feeding on human corpses on battle fields (see e.g., Connolly, 1912: 91) have never been properly substantiated. Instances of these snails having been found to scavenge on dead game animals have so far not been reported reliably. Normally the prey of these species would consist of snails such as achatinids and subulinids and possibly any other snail sufficiently common to fall victim to these predators.

Family Aperidae (one species)

Apera gibbonsi (Binney, 1879)

Connolly, 1939: 7; Forcart, 1967: 524.

"A single juvenile found within the grounds of the Research Station, on hard sand", 15.III.1973.

Apera gibbonsi appears to occur in a narrow stretch of country from Pondoland to Zululand; the present record is the northernmost for the species. The Research Station is not built in the forest itself but rather between it and the lake in a narrow fringe dominated by *Acacia karroo.* The known localities show that *A. gibbonsi* is a forest dweller.

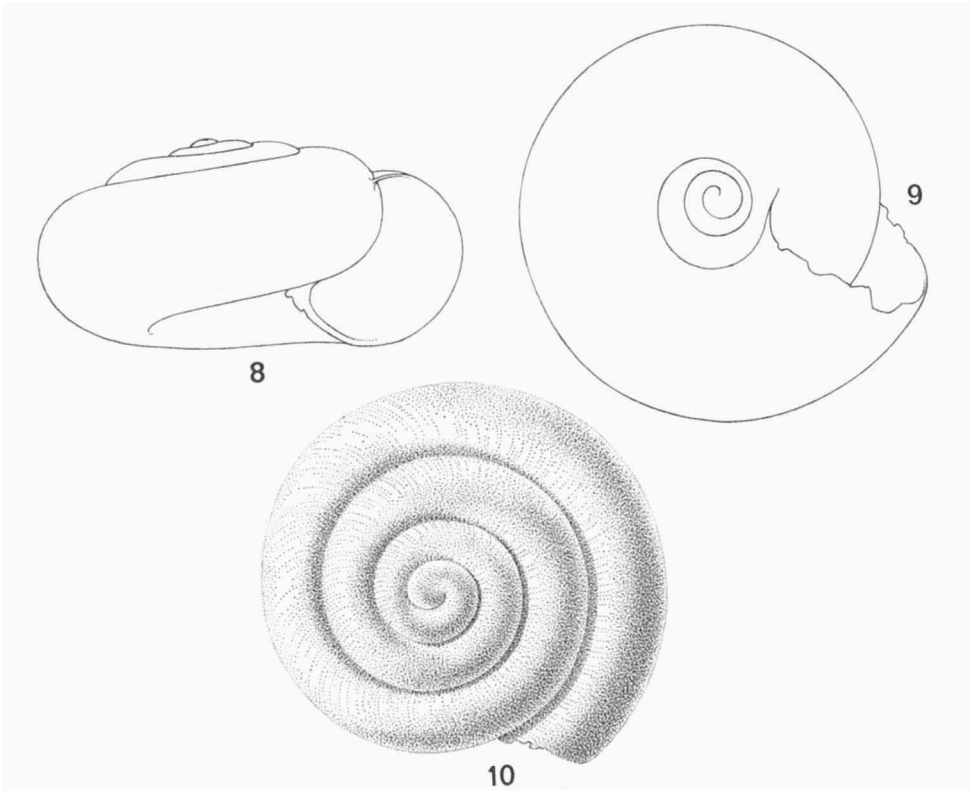
Family Endodontidae (five species)

Afrodonta novemlamellaris Burnup, 1912

Connolly, 1939: 253; Solem, 1970: 350.

No. 49J (shells only), "beneath rotting log on forest floor", 29.VII.1973, 3.

This new record (specimens compared with type in BM) conveniently fills the gap in the known distribution of the species: Eastern Cape Province, Kimberley, Ntimbankulu (Natal), and Mt. Vengo (= Mt. Panga) in Mozambique. The species of the genus *Afrodonta* have minute shells and are bottom dwellers in forest litter.



Figs. 8-10. *Trachycystis mcdowelli* Connolly, 1922, Lake Sibaya area, collector's no. 49J, beneath rotting log on forest floor, 29 July 1973, three views of the same adult shell. 8. Front view, half schematic. 9. Bottom view, half schematic. 10. Top view. Major diameter of shell 1.7 mm. H. Heijn del.

Trachycystis mcdowelli Connolly, 1922 (figs. 8-10)

Connolly, 1939: 221.

No. 49J (shells only), "beneath rotting log on forest floor", 29.VII.1973, 6.

Trachycystis mcdowelli has so far only been recorded from its type locality, Maforga Siding on the Umtali-Beira railway in Mozambique. The six available shells agree well with the holotype in the British Museum (Natural History) (No. 1937.12.30.4662). The species is new to both South Africa and to Zululand. These small species of *Trachycystis* are bottom dwellers in forest environment. Apart from two juvenile shells there are four adult shells, all with four whorls and a major diameter of 1.4-1.7 mm.

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

Connolly, 1939: 194; Van Bruggen, 1969: 33.

No. 49K (alcohol, dry), "on *Isoglossa* sp. in forest", 29.VII.1973 (alcohol 1, shells only 7).

The above material was compared with the type in the British Museum (Natural History). The species is now known to occur in Natal and Zululand only: Pietermaritzburg district, Mazimba Hill (on the Black Umfolosi River, 25.X.1938, leg. L. D. Brongersma, RMNH; new record), Mkuzi and Ndumu Game Reserves, False Bay, and the Lake Sibaya area. Species of the subgenus *Chalcocystis* are forest dwellers that usually occur on low herbs and bushes.

T. burnupi and *T. aenea* (Krauss, 1848) are closely allied and (partly) sympatric in part of their respective ranges. The shells are very close indeed, but particularly in adult and large *T. aenea* the umbilicus is almost invisible. It is small and almost completely covered by the overhanging, reflected columellar margin. *T. aenea* has also been collected in the Lake Sibaya area: "dune forest east shore of Lake Sibayi", 13.VI.1966, leg. D. S. Brown (BM, RMNH, alcohol and dry). However, it is not represented in the Appleton collection.

Trachycystis (Psichion) ariel (Preston, 1910)

Van Bruggen, 1969: 56.

No. 18M (alcohol, dry), "on trees in forest", 16.VI.1973 (alcohol 6, shells only 6); No. 49J (alcohol), "beneath rotting log on forest floor", 29.VII.1973, 1; No. 49H (alcohol), on "trees in forest", 16.VI.1973, 1; No. 49K (shells only), "on *Isoglossa* sp. [*woodii*] in forest", 29.VII.1973, 9; No. 49R (shell only), "from leaf-litter of coastal dune forest", 1.

Trachycystis ariel was first mentioned for Zululand by Van Bruggen (1969: Hluhluwe Game Reserve rest camp [4]) and east of Lake Sibaya); he only recorded two specimens. Now it appears that the species is obviously common around Lake Sibaya. The largest available shell (No. 49K) has $5^1/_2$ whorls and measures 4.6 × 3.5 mm, l/d 1.31; this is the largest known shell. The shape of the shell varies somewhat and the l/d may be as low as 1.22. The sculpture also varies somewhat in sometimes being considerably less well-marked.

T. ariel is a forest and bush dweller to be found low on trees; when conditions are favourable it may temporarily emerge from the bush for short distances as shown by the first South African specimen. The range of the species stretches from the Hluhluwe Game Reserve in Zululand northward to Nairobi, Kenya (Verdcourt, 1953, s.n. *T. ambigua*); it occurs inland as far west as the Eastern Escarpment on the borders of Rhodesia and Mozambique.

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[4]) A search by the senior author in exactly the same place on March 20-21, 1975, failed to reveal further specimens.

Trachycystis (Chilocystis) loveni (Krauss, 1848)

Connolly, 1939: 241; Van Bruggen, 1970b: 457.
No. 18J (alcohol), "on *Isoglossa* sp. (dominant lower storey plant in forest)", 23.XII.1973, 4.

Only second record for Zululand, otherwise known from Kwa-Mbonambi. *Trachycystis loveni* is distributed along the east coast of southern Africa from the Eastern Cape Province to the Lake Sibaya area. This species is a forest dweller, usually found on low herbs and bushes. This is the only species with a hirsute shell in the Lake Sibaya area collections.

Family Limacidae (one alien species)

Limax (Limacus) nyctelius Bourguignat, 1861

Connolly, 1939: 176; Van Regteren Altena, 1966: 290.
"A single juvenile found at Mbazwana Forest Station by Chief Forester Mr. B. H. Groenewald", 28.VIII.1973.

This alien species, originally occurring around the Mediterranean, is now known from a number of localities from the Cape Province, Orange Free State, and Natal (inclusive of Zululand: Hluhluwe Game Reserve and above locality).

Family Euconulidae (one species)

"Guppya" rumrutiensis (Preston, 1911)

Van Bruggen, 1966b: 344; Van Bruggen, 1967a: 10; Van Bruggen, 1969: 33.
No. 7P (alcohol), "on marginal vegetation of Empayeni pond on lake's eastern shore", 5.II.1973, 8 (alcohol 6, shells only 2); No. 49R (shells only), "in leaf-litter on floor of Coastal Dune Forest", IX.1973, 23.

Obviously *"Guppya" rumrutiensis* is a tropical element in the fauna of southern Africa. The species is now known to occur in Zululand (Lake Sibaya area and Ndumu Game Reserve), in the Transvaal (Kruger National Park), in Rhodesia (Khami Ruins near Bulawayo), and further north as far as central Kenya. In southern Africa it has so far only been collected in habitats such as leaf-litter and forest humus; the Empayeni pond marginal vegetation consists of a fairly dense fringe of grasses and sedges.

Verdcourt (1972: 336) has used the name *Guppya* Mörch, 1867, tentatively, suggesting affinity to "certain Pacific genera e.g. *Liardetia*" Gude, 1913 (see Zilch, 1959: 277 sqq.; this author only records one genus in the family Euconulidae as possibly African, viz., *Parasitala* Thiele, 1931: "Indopazifische Inseln. ?Ostafrika.", see p. 282). It is most likely that the present species will have to be classified with another genus or in a new genus of its own.

Family Helicarionidae (one species)

Kaliella barrakporensis (Pfeiffer, 1852)

Connolly, 1939: 164; Van Bruggen, 1967a: 11; Van Bruggen, 1969: 103.

No. 15F (shell only), "on marginal vegetation along Mseleni stream which flows into lake's western arm", 26.I.1973, 1; No. 49R (shells only), "in leaf-litter on floor of Coastal Dune Forest", IX.1973, 2.

Kaliella barrakporensis, originally described from eastern India (type locality Barrackpore, north of Calcutta, West Bengal), is very widely distributed over Africa (inclusive of Madagascar) and Asia (for details see Van Bruggen, 1967a: 11). This is a forest dweller requiring a fair amount of rainfall and/or humidity.

Family Urocyclidae (two species)

The Urocyclidae are an endemic and dominant family in Africa and a fair number of species is known to occur in Zululand; the slug-like Urocyclinae are an important element of this family in Zululand, but are represented in the Appleton collection by one species only.

Sheldonia (Kerkophorus) poeppigii (Pfeiffer, 1846)

Connolly, 1939: 134; Van Bruggen, 1969: 33.

No. 18B (alcohol, dry), "from forest floor" (alcohol 3, shells only 10); No. 18Z (alcohol), "slopes of Dumile peak (part of dune forest, opposite southern shore of lake)", 22.IV.1973, 1; ?No. 49K (alcohol), "on *Isoglossa* sp. in forest", 29.VII.1973, 1.

All above material was compared to authenticated material in the British Museum (Natural History). Specimen No. 49K is a juvenile that probably belongs to the species. *Sheldonia poeppigii* is widely distributed from the eastern Cape Province to southern Mozambique. There is only one inland locality, viz., Mooi River (Transvaal); no material of this locality has been seen and it seems unlikely that specimens from near Potchefstroom belong to this species. The genus *Sheldonia* as a rule consists of forest dwellers requiring a fair deal of humidity; these snails usually inhabit low herbs and bushes and are to be found on the leaves of these.

Urocyclus (Elisolimax) flavescens (Keferstein, 1866) (pl. 4)

Connolly, 1939: 166; Forcart, 1967: 542; Van Bruggen, 1969: 34.

"In the coastal dune forest at Sibaya and in the *Acacia karroo* fringe between the forest and the lake".

Urocyclus flavescens is a very common and variable slug species with the colour ranging from green-yellow to grey. It was also taken in marshy areas of the grassveld environment. This slug is widely distributed in Mozambique, Rhodesia, the Transvaal, and Natal. For further data, particularly on colour

variation, distribution and ecology, the student is referred to Forcart (1967: 542-547).

An interesting record by Mr. M. N. Bruton of the Lake Sibaya Research Station should be included here. Three specimens of this slug were regurgitated by a 320 mm variegated slug-eater snake, *Duberria variegata* (Peters, 1854), after capture; the snake was found under sandy soil near Mabibi village, east shore of Lake Sibaya, on 25 November 1975 (Transvaal Museum No. 47426).

Family Veronicellidae (two species)

Laevicaulis alte (Férussac, 1821)

Connolly, 1939: 451 (*Veronicella maura*); Forcart, 1967: 514.

No. 18R (alcohol), "on dune forest floor".

"Fairly common in the *Acacia karroo* fringe though seemed to be less so in the forest proper. In the forest however a very large specimen measuring 65.5 mm in length and 37.5 mm in width when in a contracted position, was found beneath leaf-litter".

This is a very widely distributed slug in (southern) Africa (see Forcart, 1967: 515). It occurs in a wide variety of habitats from savanna to equatorial forest. *L. alte* in the wake of man has spread over the tropics of the Old World as far east as China, Formosa (Taiwan), New Guinea, Australia (Queensland), New Caledonia, and the Loyalty Islands (vide Forcart, 1953, and Van Benthem Jutting, 1964). A note by the junior author shows how easily this slug is dispersed. "*L. alte* was picked up on a variety of occasions, floating in the water of the lake at the Station. These specimens always recovered after being rescued! I can only assume that they either fell in from overhanging or marginal vegetation or were washed in".

Laevicaulis natalensis natalensis (Krauss, 1848)

Connolly, 1939: 450 (*Veronicella natalensis*); Forcart, 1967: 512; Van Bruggen, 1969: 24.

No. 8D (alcohol), "amongst leaf axils of *Strelitzia alba* in grounds of Lake Sibaya Research Stn."; No. 18P (alcohol), "on undergrowth in dune forest"; No. 49M (alcohol), "beneath rotting log, in dune forest". "Common in both the forest and the *Acacia karroo* fringe. Found beneath rotting logs, in the axils of *Strelitzia alba* leaves and on the gravel road running through the forest".

This species is also very widely distributed; the subspecies occurs from Rhodesia and Mozambique to the southeastern Cape Province (see Forcart, 1967: 513). Like *L. alte* it occurs in a very wide variety of habitats.

3c. Zoogeographical conclusions

The Appleton collection contains 49 species of terrestrial molluscs, viz., 3 prosobranch and 46 pulmonate gastropods, obtained in the Lake Sibaya area

sensu lato [5]). *Limax nyctelius,* a Palaearctic slug, is an alien element in the malacofauna of Zululand. This reduces the total to 48 species of which two (Subulinidae spec. 1 and spec. 2) are not as yet named. Therefore we will have to consider only 46 gastropod species.

Tongaland is well-known as a southern extension of the tropical lowlands of Central Africa; a considerable number of plants and animals [mammals such as the Suni, *Neotragus moschatus* (a small species of antelope), some birds, reptiles such as the Gaboon Adder, *Bitis gabonica,* some anurans, etc.] reach their southern limits in Africa here. There is a considerable literature on this phenomenon and we limit ourselves here to quoting Poynton (1964) and Stuckenberg (1969). Among the Appleton material there are seven species of snails that seem to reach their southern limits more or less in the Lake Sibaya area, viz., *Rachis jejuna* (as far south as the Mkuzi Game Reserve, see Van Bruggen, 1969: 25), *Edouardia metuloides* (only one locality further south: Imfamanzi River near the junction of the Black and White Umfolosi Rivers), *Rhachidina dubiosa* (only one locality further south: Mazimba Hill on the Black Umfolosi River), *Gulella browni* (further south only known from Sodwana Bay), *Trachycystis mcdowelli* (unknown further south), *T. ariel* (only one locality further south: Hluhluwe Game Reserve rest camp), and *Guppya rumrutiensis* (unknown further south).

On the other hand a number of temperate species does not seem to be able to penetrate further north than the Lake Sibaya area. This category comprises a total of five species, viz., *Edouardia natalensis* (unknown further north), *Hypolysia florentiae* (as far north as Kosi Bay, see Van Bruggen, 1969: 57), *Apera gibbonsi* (unknown further north), *Trachycystis burnupi* (as far north as the Ndumu Game Reserve, see Van Bruggen, 1969: 33 [6]), and *T. loveni* (unknown further north).

A third category of species is only known from Natal and Zululand, sometimes occurring as far north as southern Mozambique; these species may be more or less considered endemic to the area. The two new taxa (*Gulella appletoni* and *G. peakei continentalis*) are as yet only known from the Lake Sibaya area, although *G. peakei continentalis* appears to belong to a very widely distributed species. Therefore the endemic group comprises a total

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[5]) Incidentally, this compares reasonably well with 24 species for each of two considerably drier nearby savanna areas, the Mkuzi and Ndumu Game Reserves (vide Van Bruggen, 1969: 72). However, the Appleton collection was gathered in the course of a year; the Mkuzi and Ndumu Game Reserve material (together only 32 species) is the result of a total of only eleven days collecting in January.

[6]) Attention is drawn to a typographical error in the 1969 paper. Instead of "MGR: Banzi Pan bush (NM)." one should read "NGR: Banzi Pan bush (NM)."

of twelve species: *Euonyma tugelensis, *Archachatina parthenia, *A. zuluensis, Metachatina kraussi, Gulella zuluensis, G. triglochis, G. perspicuaeformis, G. kosiensis, G. bushmanensis, *G. linguidens, *G. daedalea,* and *Natalina wesseliana.* The species indicated with an * have not been found beyond the confines of Zululand proper.

The remaining species may be divided into two groups, viz., those that enjoy a wide to very wide distribution in the southern African subregion (i.e., the area south of the Cunene and Zambezi Rivers), and those that enjoy a very wide distribution in southern Africa and beyond the somewhat artificial boundaries of that subregion, sometimes even into Asia. The widely distributed southern African species comprise the following fifteen (or perhaps fourteen only): *Tropidophora ligata, T. insularis, Gastrocopta damarica, Edouardia spadicea, E. meridionalis, Succinea striata, (Cecilioides gokweanus), Archachatina vestita, Gulella infans, G. farquhari, Nata vernicosa, Afrodonta lamellaris, Sheldonia poeppigii, Urocyclus flavescens,* and *Laevicaulis natalensis.*

Cecilioides gokweanus is shown between brackets because it may also occur in Kenya (s.n. *C. tribulationis* Preston, 1911, vide Connolly, 1939: 371, and Verdcourt, 1972: 324); this is the reason why it is also enumerated in the next category. This comprises the species also distributed beyond the Cunene and Zambezi Rivers, a total of six (or possibly five only): *Maizania wahlbergi* (two separate areas, i.e., eastern Cape Province to northern Zululand, and coast of northern continental Tanzania and southern Kenya, see Verdcourt, 1964), *Pupisoma orcula* (as far north as Japan and as far east as the Philippines and New Guinea), *Oxyloma patentissima* (beyond southern Africa also in Angola and Chad), *Kaliella barrakporensis* (as far east as Madagascar and the Indian Peninsula), *Laevicaulis alte* (as far north as Zaire (= Congo-Kinshasa) and Tanzania, see Forcart, 1953: 63), and (*Cecilioides gokweanus,* see above).

The above data may now be summarized as follows:

(a)	alien species	1	2.4%
(b)	species reaching their southern limits here	7	14.3%
(c)	species reaching their northern limits here	5	12.0%
(d)	endemic species (Natal-S. Mozambique)	12	24.5%
(e)	species widely distributed in southern Africa	15 (14)	30.6%
(f)	species widely distributed in and beyond southern Africa	6 (5)	12.2%
(g)	species of which the distribution is not exactly known	4	8.2%
	total species in the area (one species shown under both categories e and f)	49	

In this context the categories e and f are not of direct biogeographical interest. Apart from those, accounting for a total of almost 43%, the most important part of the malacofauna is made up of endemics (12 species or 24.5%). The groups of species reaching their southern or northern limits in the Lake Sibaya area account for 7 (14.3%) and 5 (12.0%) respectively and therefore seem to play a somewhat minor role. Once again this shows that Tongaland is biogeographically of great interest as a meeting place of tropical (category b) and temperate (category c) elements, while at the same time the element endemic to Natal and Zululand is numerically very strong indeed. The background of these phenomena is summarily discussed in chapter 2e on the origin and isolation of the dune forest environment.

4. Summary

An evaluation of the land molluscs of the Lake Sibaya area (Tongaland, N.E. Natal) based on a year's collecting has revealed the occurrence of 49 species (3 prosobranch and 46 pulmonate gastropods). These were obtained in (1) coastal dune forest, (2) *Acacia karroo* fringe at the foot of the dunes, and (3) open grassland. The majority of the species was found in the coastal dune forest; some ecological data on the various species are supplied. Among the species are two novelties, *Gulella appletoni* and *G. peakei continentalis* (vide Van Bruggen, 1975a), one species new to South Africa (and Zululand), *Trachycystis mcdowelli,* and two species new to Zululand, *Cecilioides gokweanus* and *Afrodonta novemlamellaris.* Many species have only been obtained rarely before, resulting in new distribution data. A zoogeographical analysis shows that seven species reach their southern limits in Tongaland, five their northern limits, and twelve appear to be endemic in the area Natal-S. Mozambique. The bulk of the species (fifteen) appear to be widely distributed in southern Africa. Particular attention is drawn to the origin and isolation of the dune forest environment.

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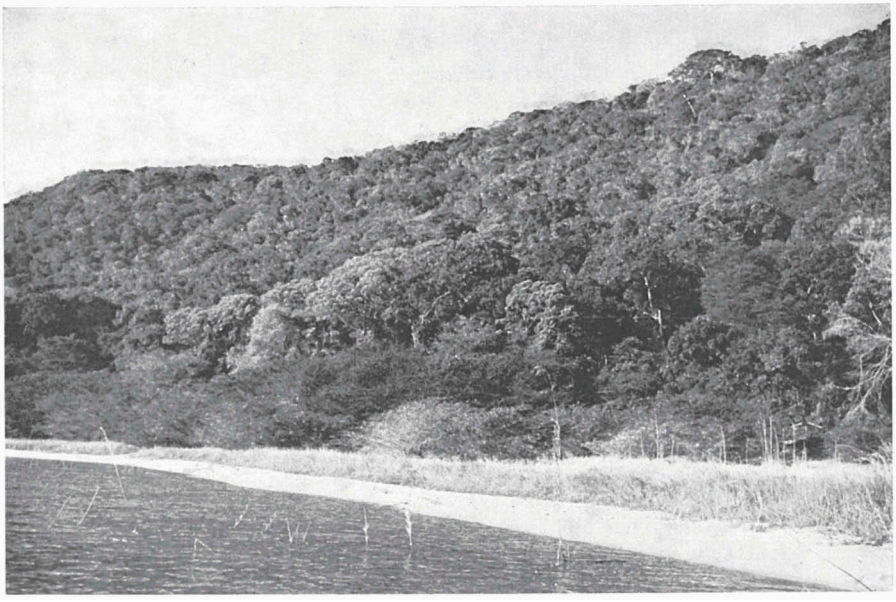
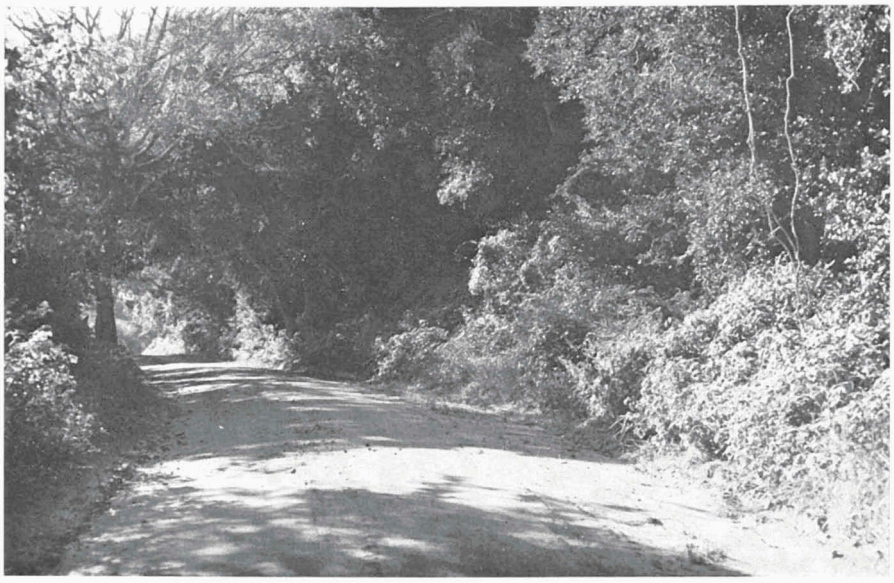
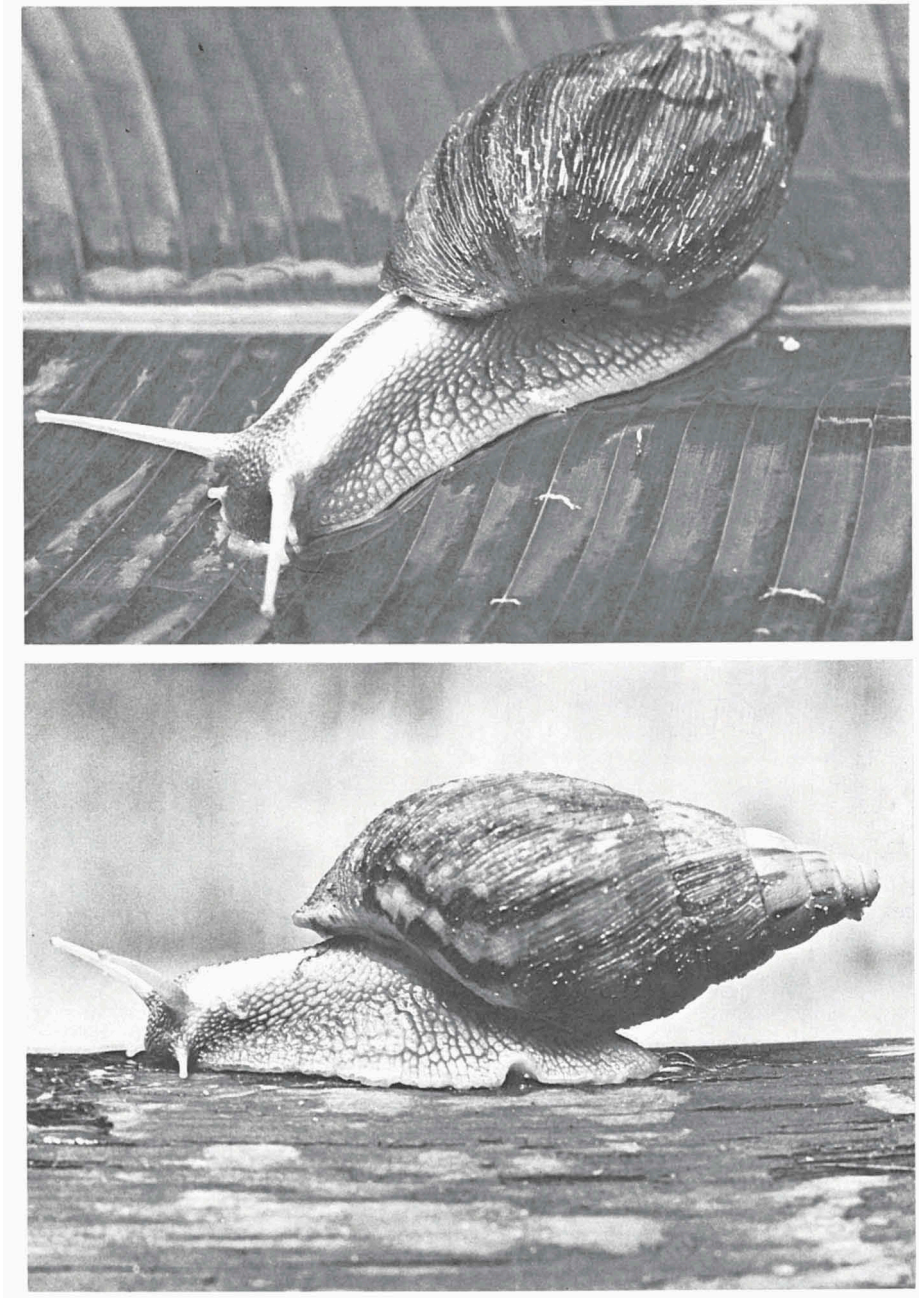


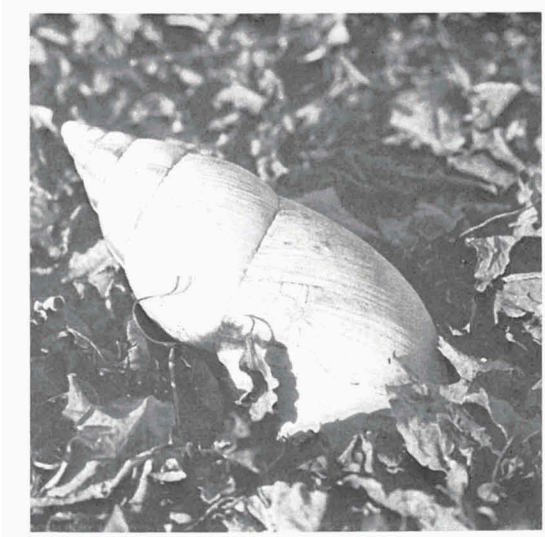
Two views of the main collection area of the coastal dune forest from the eastern shoreline of Lake Sibaya. Note the change from the *Acacia karroo* fringe (up to 3 m high) to the magnificent, tall canopy trees of the forest proper, at the foot of the dune. Most snails were collected from the *A. karroo* fringe and beneath these canopy trees. Photos C. C. Appleton.

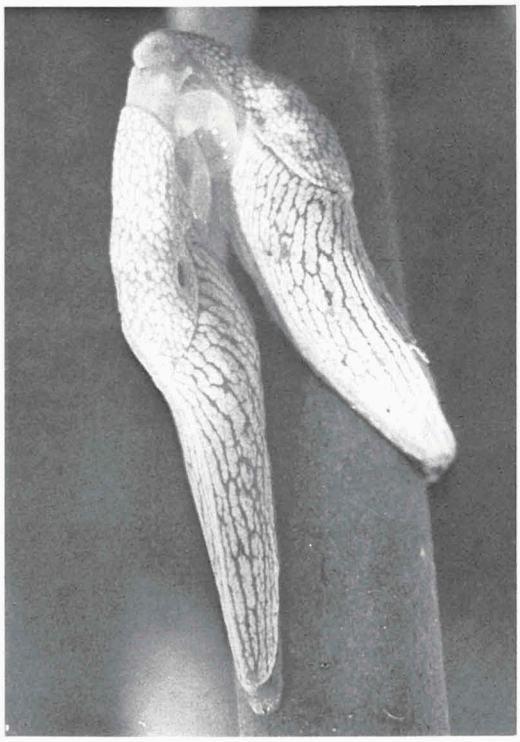


(Above) General view of the savanna or grassland in the Mabibi area. The depression in the centre of the picture is a perennial pan (shallow vegetation-filled waterbody). The scattered trees in the middle distance are *Syzygium cordatum* and *Phoenix reclinata*. The afforested coastal dunes rise in the far distance.
(Below) View of the inside of the coastal dune forest, near the base of the dune. Of particular interest here is the lowest stratum, the shrub and herbaceous layer, dominated by *Isoglossa woodii*, seen on the right hand side of the road. Most molluscs were collected from this stratum and the layer of leaf-litter beneath. Photos C. C. Appleton.



Archachatina (*Tholachatina*) *vestita* (Pfeiffer, 1855), Lake Sibaya Research Station grounds, photographed on a leaf of *Strelitzia nicolai*. Attention is drawn to the peculiar periostracum of the shell. This thin cuticle develops laminae over the whole length of the rib-like growth-striae, recalling velvet or Manchester fabric. The periostracum is usually only preserved on the penultimate and body whorls of the shell, being worn away on the earlier whorls and where the shell touches the substratum when the animal moves around (see also Van Bruggen, 1966a: 102). Approximately natural size. Photos C. C. Appleton.





(Above) *Metachatina kraussi* (Pfeiffer, 1846), Lake Sibaya area, hidden in leaf-litter on forest floor, 15 April 1973; shell 155.6 × 65.0 mm.
(Below) *Urocyclus* (*Elisolimax*) *flavescens* (Keferstein, 1866), Lake Sibaya area, mating on a petiole of *Strelitzia nicolai*. Note colour pattern, tail gland in left hand specimen and extended penes. Approximately 1.25 ×. Photos C. C. Appleton.