SIZE CLINES AND SUBSPECIES IN THE STREPTAXID GENUS *GULELLA* PFR. (MOLLUSCA, GASTROPODA PULMONATA) IN SOUTHERN AFRICA

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With 30 text-figures

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1. INTRODUCTION

The concept of subspecies has been applied to terrestrial molluscs at a comparatively early stage. Mayr (1942) quotes the works of Rossmässler (1826), Kobelt (1881), the Sarasin brothers (1899), Gulick (1905), and particularly Rensch (since 1929) as examples of proponents or precursors of this concept. Since the 1930s the polytypic species has been generally accepted among students of land snails. However, so far it has played a relatively minor role in comprehensive works on African (Afrotropical) land molluscs, such as Pilsbry (1919), Connolly (1939) and Bequaert (1950) [1]. Undoubtedly a fragmented topography (e.g., island areas such as Indonesia) has more attractions to the student of micro-evolution than the more solid continental blocks. Isolation of island subspecies is usually quite evident

[1]) Two recent monographs of a very high standard (Van Mol, 1970; Van Goethem, 1977) do not recognize subspecies, most likely because of (a) poorly delimited and understood taxa, and (b) limited material representing comparatively few distribution records.

and in many cases island subspecies are well established. In continental areas a reduced gene flow may not always be apparent and subspecies may be recognized where no real discontinuity exists. Some seeming discontinuities may be abolished when more material from interlying areas becomes available in which case variation frequently proves to be of a clinal nature. Also, allopatric taxa have sometimes initially been interpreted as having full species status.

Due to its chequered geological history and its multitude of climatic variations resulting in a plethora of vegetation types, southern Africa harbours a very diverse malacofauna (Van Bruggen, 1969, 1978). A glance at geological, topographical, soil, climatic and vegetation (both the latter past and present) maps of southern Africa (e.g., as featured in Werger, 1978) shows that there is ample scope for fragmentation of land mollusc ranges. It is a well-known fact that in mammals, birds and butterflies numerous subspecies have been recognized; indeed, at times the student of biogeography may find that certain of his predecessors have been overenthusiastic in creating subspecies. Nevertheless it is obvious that many animals in this part of Africa have discrete populations separated by natural barriers such as mountain ranges, ancient river valleys, different climatic regions, etc. There is even a certain number of isolated mountain complexes in southern Africa, although perhaps not as markedly isolated as in East and Central Africa. Some of the land snail species are very widely distributed and again some of these have developed isolated, allopatric populations which may be classified as subspecies.

The near-circumtropical pulmonate gastropod family Streptaxidae seems particularly suited for studies on micro-evolution. The family is very diverse and widely distributed in Africa (Van Bruggen, 1967). Many species occupy large ranges and recently much new material has been made available for study. It is now also known that some streptaxids in isolation tend to evolve into local forms which, if allopatric, may be given subspecies status.

The genus *Gulella* L. Pfeiffer, 1856, is the main representative of the Streptaxidae in southern Africa. Ca. 130 species occupy roughly the eastern parts of the subcontinent south of the Zambezi River, few of which are distributed beyond that river (see Van Bruggen, 1973, for general data on the local distribution). North of the Zambezi the genus is even more diverse. Interesting studies on variation in the genus in East and Central Africa have been published by e.g., Verdcourt (1957, 1962, 1970) and Verdcourt & Venmans (1956).

The following cases of subspecies being recognized in southern African *Gulella* have been recorded:

G. caryatis (Melvill & Ponsonby, 1898) — *G. c. caryatis* in a limited area in the Eastern Cape Province (Connolly, 1939: 45); *G. c. diabensis* Connolly, 1939, in South West Africa (Van Bruggen, 1970: 68).

G. crassidens (Pfeiffer, 1859) — *G. c. crassidens* along the Natal coast and some distance inland; *G. c. jonesi* Van Bruggen, 1969, in Zululand (Mfongosi) and possibly another form in the southern Zululand coastal lowlands (Van Bruggen, 1969: 64-69).

G. gouldi (Pfeiffer, 1855) — *G. g. gouldi* from the Eastern Cape Province to southern Zululand; *G. g. discriminanda* Van Bruggen, 1969, in northern Zululand; *G. g. globulosa* Pfeiffer, 1952, in Tanzania (Van Bruggen, 1969: 39-46).

G. peakei Van Bruggen, 1975 — *G. p. peakei* on Aldabra Island in the western Indian Ocean (extinct); *G. p. continentalis* Van Bruggen, 1975, in northern Zululand (Van Bruggen, 1975a, 1975b).

Size clines have so far been discerned among southern African *Gulella* in *G. perissodonta* (Sturany, 1898) (Van Bruggen, 1969: 46-50) and in *G. triglochis* (Melvill & Ponsonby, 1903) (Van Bruggen, 1969: 38). *G. g. gouldi* (see above) also exhibits clinal variation.

The present study on geographical variation in southern African *Gulella* treats in some detail eight cases, viz., *G. adamsiana* (size cline), *G. darglensis* (subspecies), *G. elliptica* (do.), *G. farquhari* (size cline and probably subspecies), *G. infrendens* (size cline), *G. planti* (do.), *G. vicina* (subspecies), and *G. zuluensis* (size cline). The treatment is strictly conchological because so far anatomical data have yielded little of direct taxonomic importance. Studies on the genitalia together with investigation of the radula are to be conducted at a future date.

The following abbreviations have been employed for collections or other material consulted: BM for British Museum (Natural History), London; CNHM for Field Museum of Natural History, Chicago; DM for Durban Museum and Art Gallery, South Africa; MCZ for Museum of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A.; MMK for Alexander McGregor Memorial Museum, Kimberley, South Africa; NM for Natal Museum, Pietermaritzburg, South Africa; RMNH for Rijksmuseum van Natuurlijke Historie, Leiden; SAM for South African Museum, Cape Town; TP for T. Pain collection, London; vH for H. E. van Hoepen collection, Johannesburg; ZMA for Zoölogisch Museum, Amsterdam. Other abbreviations are alc. for alcohol material and l/d for the ratio length/major diameter of shells, which gives an impression of the shape of the shell (for small specimens these have been calculated from micrometer readings).

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It should be emphasized here that without the valuable collections of the Pietermaritzburg and London museums this study would have been impossible. The Rijksmuseum van Natuurlijke Historie contains some valuable southern African material. First of all, a large number of samples from the W. Falcon collection in the possession of Mrs. Helen Boswell (Valhalla, Pretoria) was very kindly donated to the present author, who passed the material on to the Leiden museum. Much of this material duplicates samples in the Natal Museum although there are additional records. Mrs. Boswell deserves due credit for her generous gift. Moreover, the Leiden museum has some material bought from H. B. Preston, who also sold duplicates obtained from H. C. Burnup. Dr. H. E. van Hoepen (Johannesburg), neurologist/psychiatrist and amateur malacologist of note, has contributed a host of valuable data; his enthusiastic and knowledgeable cooperation is particularly gratefully acknowledged here. Much of the success of the field work is, of course, due to my wife Mrs. Wendy H. van Bruggen-Gorter.

2. Systematic part

The species have been treated in alphabetical order. Zululand, although administratively part of Natal, is usually taken as a separate geographical entity. It encompasses the area north of the Tugela River. The localities have been generally enumerated from south to north and east to west, if and when feasible. All names not to be found in The Times Atlas of the World, comprehensive edition, London, 1967, have been related to names shown in this atlas or have been indicated by their latitude and longitude.

Gulella adamsiana (Pfeiffer, 1859) (figs. 1, 3)

Ennea adamsiana Pfeiffer, 1859, Novit. Conch., 1: 114, pl. 32 figs. 9-11 [2]); Pfeiffer, 1859, Monogr. Helic. Viv., 4: 339; Pfeiffer, 1868, Monogr. Helic Viv., 5: 454; Pfeiffer, 1876, Monogr. Helic. Viv., 7: 504; Nevill, 1878, Hand List Moll. Ind. Mus., 1: 5; Pfeiffer & Clessin, 1878, Nomencl. Helic. Viv.: 19; Tryon, 1885, Man. Conch., (2) 1: 98, pl. 19 fig. 85; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 166; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 546 (10), 558 (22); Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 192, pl. 24 fig. 8; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 159; Connolly, 1912, Ann. S. Afr. Mus., 11: 65.

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

Gulella adamsiana; Connolly, 1932, Ann. Natal Mus., 7: 74; Warren, 1933, Ann. Natal Mus., 7: 295, figs. 1-2; Connolly, 1939, Ann. S. Afr. Mus., 33: 84, fig. 5; Van Bruggen, 1978, Biogeogr. Ecol. S. Afr., (2): 882, 883, fig. 2B.

Ennea socratica Melvill & Ponsonby, 1893, Ann. Mag. Nat. Hist., (6) 12: 109, pl. 3 fig. 14; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 169; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 542 (6), 554 (18); Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 198, pl. 24 fig. 20; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 55; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 162; Connolly, 1912, Ann. S. Afr. Mus., 11: 86.

Ennea impervia Melvill & Ponsonby, 1896, Ann. Mag. Nat. Hist., (6) 18: 315, pl. 16 fig. 1; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 168; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 546 (10), 558 (22); Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 233, pl. 32 fig. 21; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 161.

Ennea adamsiana Pfeiffer var. *impervia*; Connolly, 1912, Ann. S. Afr. Mus., 11: 65.

Gulella adamsiana (Pfeiffer) var. *impervia*; Connolly, 1939, Ann. S. Afr. Mus., 33: 85.

Ennea auris-leporis Melvill & Ponsonby, 1898, Ann. Mag. Nat. Hist., (7) 1: 25, pl. 8 fig. 3; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 167; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 546 (10), 561 (25); Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 182, pl. 23 fig. 10; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 159 (without hyphen); Connolly, 1912, Ann. S. Afr. Mus., 11: 12.

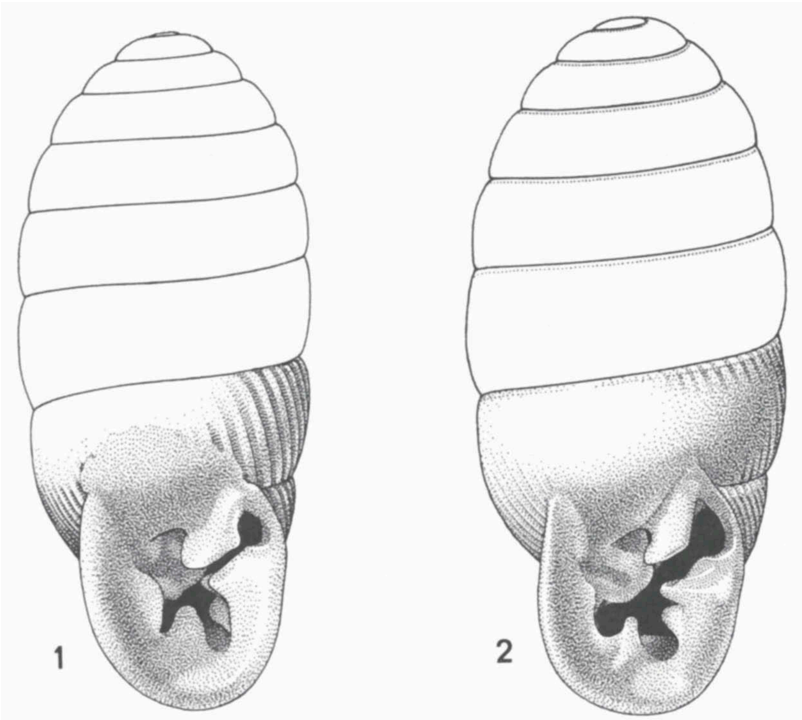
Gulella auris-leporis; Connolly, 1939, Ann. S. Afr. Mus., 33: 86.

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

Description of shell. — Shell (fig. 1) medium-sized to large, from cylindrical to ovate, rimate. Spire produced, sides slightly convex, subparallel, apex obtusely conical. Whorls 6½-8, flattened, sculptured with coarse, oblique costulae; sutures shallow, crenellate. Aperture much obstructed by six-fold dentition: a large, oblique angular lamella connected with apex of labrum;

[2]) Pfeiffer refers to an earlier description in the Proceedings of the Zoological Society of London, 1856, which, however, does not exist, nor in the volumes for 1857 and 1858. Obviously the species has to be dated 1859. Pfeiffer also writes "Aus meiner Sammlung", although Connolly has taken as lectotype a specimen from Hugh Cuming's collection in the British Museum (Natural History). Connolly has been followed here because it is believed that he had good reasons for doing so.

upper labral process a ridge, parallel to angular lamella, terminating in well-differentiated cusp, lower labral process a deeply set denticle below the upper labral denticle, labral complex corresponding to extensive shallow outside depression; basal process left of the base, varying from triangular to squarish in shape, corresponding to shallow outside depression; outer columellar lamella an elongated tubercle, frequently reduced in size, although never completely absent, inner columellar process large with a deep depression in its centre.



Figs. 1-2. Shells of 1, *Gulella adamsiana* (Pfr.) (length 8.4 mm, Pietermaritzburg, Villiers Drive, RMNH), and for comparison 2, *G. wahlbergi* (Krss.) (length 10.2 mm, Durban, NM).

Measurements of shell: 6.5-11.0 × 3.2-5.1 mm, l/d 1.78-2.55. The lectotype measures 8.5 × 4.0 mm, l/d 2.12. Largest specimen (Port St. Johns, NM) 11.0 × 5.1 mm, l/d 2.15, smallest specimen (Pietermaritzburg, NM) 6.5 × 3.5 mm, l/d 1.89. An average specimen (Pinetown, NM) measures 8.7 × 4.0 mm, l/d 2.19, aperture 2.9 × 2.6 mm, last whorl 4.2 mm.

Distribution (fig. 3). — *G. adamsiana* occurs from Pondoland (Transkei) to north of Durban and inland as far west as Bulwer in Natal.

CAPE PROVINCE: Dwes(s)a (also spelled Dweza) Forest Reserve, ca. 30 km S. of Bashee River mouth, H. E. van Hoepen (vH, in litt., non vidi); Bashee River, H. J. Puzey (NM); Port St. Johns, W. Falcon (NM; RMNH); do., R. F. Lawrence (NM, NM alc.); do., H. J. Puzey (BM 1937.12.30.665-7; NM); do., W. G. Rump (NM) (all TRANSKEI). NATAL: Port Shepstone, H. C. Burnup (NM); do., W. Falcon (RMNH); do., R. F. Lawrence (NM); Kelso (Junction), W. Falcon (NM); do., R. F. Lawrence (NM alc.); Equeefa, ca. 5 km SW. of Umzinto, H. C. Burnup (NM); do., V. Wager (NM); Clansthal, between Scottburgh and Umkomaas, W. Falcon (NM; RMNH); do., G. E. Pennington (NM); (Lower) Umkomaas, H. C. Burnup (NM 1448, NM; TP); do., Miss M. F. Hickey (NM); Winkelspruit, between Illovo Beach and Amanzimtoti, H. C. Burnup (NM); Isipingo, C. W. Alexander (NM); Durban (including Burman Bush, Salisbury Island, Wyebank), W. Falcon (RMNH); do., O. Bourquin (NM, NM alc.); do., H. J. Puzey (BM 1937.12.30.668-9); do. (SAM); "Port Natal" (= Durban), Cuming colln. (BM, lectotype and paralectotype); Umhlanga Rocks, D. W. Aiken (D. W. Aiken colln.); Pinetown, H. C. Burnup (NM); Tyeloti (also spelled Tshloti), near Botha's Hill, H. C. Burnup (NM); Krantzkloof, near Kloof, H. W. Bell-Marley (NM); Drummond, ca. 45 km W. of Durban, R. F. Lawrence (NM alc.); do., Umgeni R. valley, R. F. Lawrence (NM alc.); do., Nagle Dam, R. F. Lawrence (NM alc.); Inchanga, between Cato Ridge and Botha's Hill, R. F. Lawrence (NM alc.); Cato Ridge, Umgeni R. valley, R. F. Lawrence (NM alc.); 13 km NE. of Pietermaritzburg on Greytown road (vH); farm Samvula on road D 245 off Table Mountain road, A. C. and W. H. van Bruggen (RMNH alc.); Table Mountain on the Umgeni R., ca. 48 km E. of Pietermaritzburg, H. C. Burnup (NM); Pietermaritzburg (including Alexandra Park, Botanic Gardens, De Villiers Drive, Durban Road, Ellis's, Fox Hill, Howick Road gardens, Jesmond, Otto's Bluff, Otto's View, Richmond Road, Scottsville), O. Bourquin (NM); do., A. C. and W. H. van Bruggen (NM alc.; RMNH, RMNH alc.); do., H. C. Burnup (NM 1449, NM 1451, NM); do., M. Connolly (BM); do., W. Falcon (RMNH); do., R. F. Lawrence (NM alc.); do., Macandrew colln. (BM); do., Ponsonby colln. (BM 1903.3.11.78, holotype of *Ennea socratica*); do., Price-Jones colln. (BM); do., W. G. Rump (NM 3859, NM; RMNH; TP); Pentrich, near Pietermaritzburg, H. C. Burnup (NM); Bisley, near Pietermaritzburg, R. F. Lawrence (NM alc.; RMNH alc.); Thornville (= Thorny Bush), H. C. Burnup (NM 1451, NM); Hilton (Road), W. Falcon (NM); Albert Falls, H. C. Burnup (NM); Impolweni, between Albert Falls and New Hannover, W. G. Rump (NM); Waterkloof, ca. 32 km W. of Pietermaritzburg, O. Bourquin (NM); Midmar Dam near Howick, A. C. and W. H. van Bruggen (RMNH); Balgowan, farm Yellowwoods, ca. 1300 m (4400 ft.), A. C. and W. H. van Bruggen (NM alc.; RMNH alc.); Deepdale, Umkomaas R. valley, ca. 1200 m (4000 ft.), A. C. and W. H. van Bruggen (NM); do., R. F. Lawrence (NM alc.); Bulwer, R. F. Lawrence (NM alc.); "Natal" (BM 1903.3.11.69, holotype of *Ennea auris-leporis*); do., Ponsonby colln. (BM 1903.3.11.85-6, holotype and paratype of *Ennea impervia*); do., ex H. B. Preston (RMNH); do., Puzey colln. 68 (DM). ZULULAND: J. G. Strijdom (= Josini) Dam wall (Pongola R.), H. E. van Hoepen (RMNH; vH); "Zululand", F. Toppin (NM).

Type locality: Port Natal (= Durban), where first obtained for Hugh Cuming by an unknown collector in the period 1824-1858.

The Port Elizabeth record (see, e.g., Connolly, 1912, 1939) has been deleted as it is highly unlikely that the species occurs in that part of southern Africa.

G. adamsiana occurs over a large area and it is to be expected that some

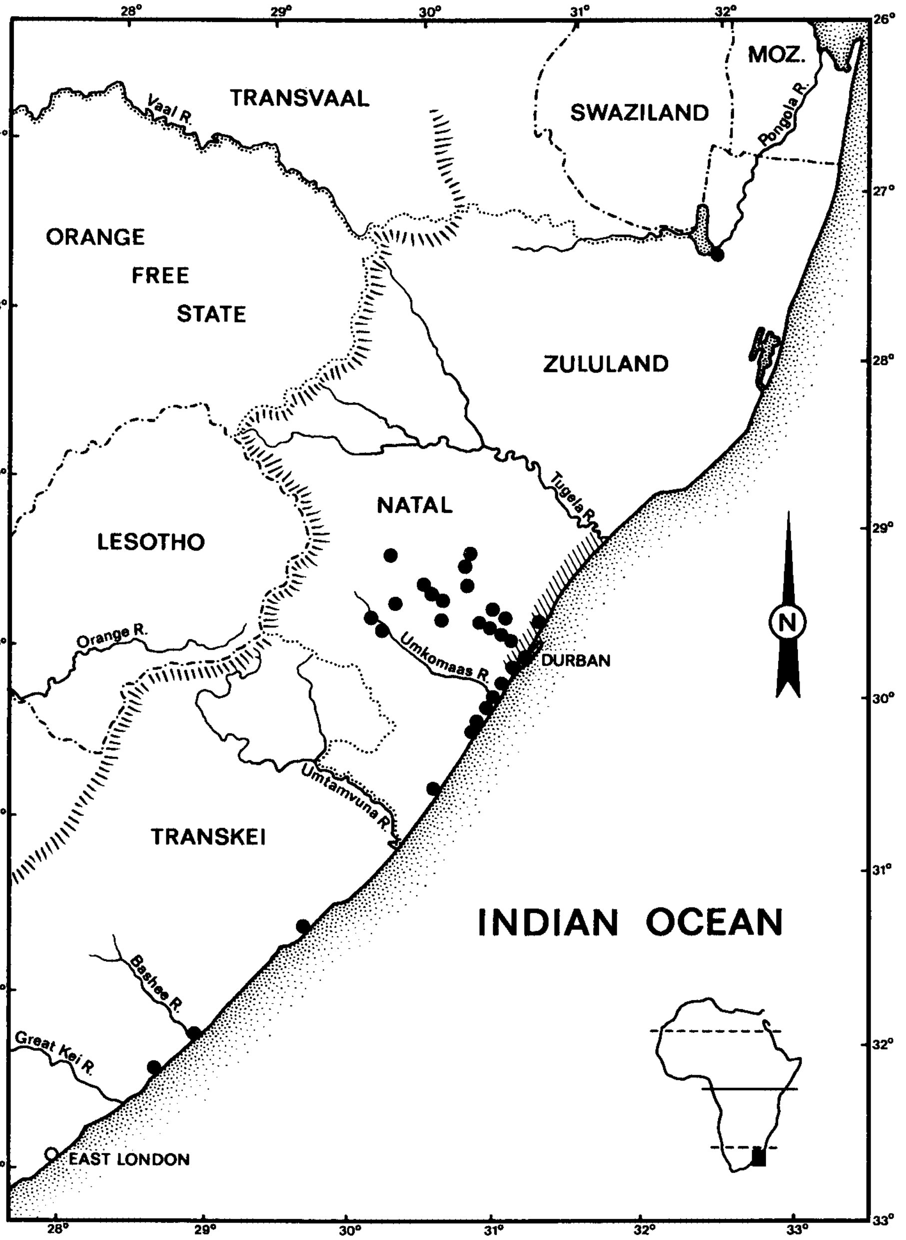


Fig. 3. Distribution of *Gulella adamsiana* (Pfr.); shaded area is that occupied by *G. wahlbergi* (Krss.). The Great Escarpment has been indicated by cross-hatching.

variation occurs as most populations are not by any means contiguous. The measurements of shells in the various areas may be compared as follows:

(1)	Bashee River-Port Shepstone	6.9-11.0 × 3.5-5.1 mm, l/d 1.82-2.30
(2)	Kelso-Winkelspruit	6.7-9.7 × 3.4-4.5 mm, l/d 1.78-2.28
(3)	Isipingo-Drummond	6.9-10.1 × 3.4-4.9 mm, l/d 1.82-2.40
(4)	Inchanga-Pietermaritzburg and district	6.5-9.2 × 3.2-4.0 mm, l/d 1.83-2.55
(5)	Balgowan-Bulwer	7.0-7.7 × 3.5-3.7 mm, l/d 1.87-2.21
(6)	Impolweni	6.9-7.9 × 3.5-3.6 mm, l/d 1.96-2.17
(7)	Zululand	8.9-9.0 × 4.5 mm, l/d 1.97-2.00

The localities have been arranged from south to north and west. In this sequence the shells may be described as large and obese (1), smaller and even more obese (2), about the same in size but less obese (3), smaller and much more slender (4), and smaller and more obese (5 and 6). The two Zululand specimens (7) will be discussed separately below. Thus there is a steady decrease in mean length from south to north and west: 8.9 (1), 8.2 (2), 8.5 (3), 7.8 (4), 7.3 (5) and 7.4 mm (6). This is correlated to a steady decrease of mean major diameter (4.3, 3.9, 4.1, 3.6, 3.6, 3.5 mm). As a result of this one would expect an increase in mean l/d, which, however, is not the case: 2.06, 2.03, 2.11, 2.19, 2.04, 2.06. The two Zululand shells from the northermost limits of the species are as large as those from Transkei and southern Natal at the southermost limits of the species. For their size they are comparatively obese; their apertures and last whorls (lw) are also relatively large:

average shell (see above)	8.7 × 4.0 mm, l/d 2.19, aperture 2.9 × 2.6 mm, lw 4.2 mm
Zululand shells	8.9 × 4.5 mm, l/d 1.97, aperture 3.1 × 3.3 mm, lw 4.5 mm
	9.0 × 4.5 mm, l/d 2.00, aperture 3.1 × 3.1 mm, lw 4.6 mm

The populations in the south and in the north are examples of peripherally isolated populations as discussed by Mayr (1976: 191).

Throughout the area the dentition is essentially identical except for the size of the outer columellar process, which even may be so small as to be hardly noticeable, and the shape of the basal denticle. The latter is subject to a considerable amount of variation; in the south it is rather squarish, while further north it is definitely triangular. In this context it is interesting to note that the three Drummond samples collected by Dr. Lawrence have obviously been taken from three different populations as shown by the size of the shells and the shape of the basal process.

Among the hundreds of specimens examined there are very few shells exhibiting dental abnormalities. Repaired damage occurs regularly, but seldom influences the apertural dentition. In one case the repairs have resulted in angulate last two whorls (Bisley, RMNH). Another abnormality, which is rather frequently seen, is an abnormally oblique aperture; however, because of intermediate forms it is difficult to draw the line between normal and abnormal here.

Warren (1933) has described an abnormal population from near Pietermaritzburg; this material (NM 3859) has been examined by the present author. It consists of 13 normal and 13 abnormal specimens, although the one series smoothly merges into the other through intermediate forms. The former series measures 7.4-8.6 × 3.6-3.7 mm, l/d 2.03-2.30, and the latter 9.3-11.5 × 3.3-3.5 mm, l/d 2.70-3.32. In some of the abnormal series the aperture is quite oblique, but the dentition is normal throughout. The only real difference is in the much higher number of whorls (8½-10) and consequently a much higher l/d, because the major diameter is the same as in normal specimens. For further particulars see Warren (1933).

Apart from the above and the type of *Ennea socratica* as described by Connolly (1932) the following abnormalities have been established: one shell (Pietermaritzburg, Botanic Gardens, NM) with a divided outer columellar process, one shell (Albert Falls, NM) with an additional denticle between the basal and somewhat reduced outer columellar process, one shell (Kelso, NM alc.) with the basal and outer columellar processes fused resulting in a thinner area in between, and one shell (Pietermaritzburg, NM 1449) with a minute sinular denticle. The latter feature, if well-developed, is considered diagnostic in a number of species, but vague indications of such a process are present in very many of the southern African *Gulella*. The other three cases with abnormal dentition all show discrepancies in the area of basal and outer columellar processes. It is interesting to reflect on the fact that these processes themselves are subject to a good deal of variation (see above), so that at least in *G. adamsiana* the basal-columellar area of the aperture is obviously unstable.

In this context it is also worth while to mention that the main differences of *G. adamsiana* and its nearest ally, *G. wahlbergi* (Krauss, 1848), are precisely in this area. The basal denticle of *G. wahlbergi* is an inrunning lamella from the surface of the labrum (fig. 2); in *G. adamsiana* (fig. 1) this process is flattened in front view and not superficial. Apart from this difference, the aperture of *G. wahlbergi* is much less obstructed by dental processes, which in fact are comparatively much smaller. Differences in size of the shell (*G. adamsiana* mean 8.7 × 4.1 mm, *G. wahlbergi* 10.7 ×

5.1 mm) and shape (*G. adamsiana* mean l/d 2.16, *G. wahlbergi* 2.13) add to the separation of the species. Moreover, where they occur together (Durban area; *G. wahlbergi* occurs along the coast of Natal from Isipingo to Sinkwazi — vague records from Zululand and Mozambique need confirmation) the species are easily separated by their different size:

G. adamsiana (Durban area)	6.9-10.1 × 3.4-4.9 mm, l/d 1.82-2.40
G. wahlbergi (Durban area)	9.8-11.6 × 4.7-5.6 mm, l/d 1.89-2.37

The var. *impervia* has not been deemed worth retaining. The dentition of *G. adamsiana* is subject to a good deal of variation, but all extremes are connected by intermediate forms. Therefore, it is impossible to define the var. *impervia* as such. *Ennea auris-leporis* is simply an aberrant specimen of *G. adamsiana*, so that the name becomes a synonym of the latter. The above conclusions are based on personal examination of the types in the British Museum (Natural History).

Connolly (1939: 84, 630) considers *Helix fanulus* Pfeiffer, 1856, to be a synonym of *G. adamsiana*; a re-examination of the types (Hugh Cuming colln., BM) has revealed that these are indeed juveniles of a costulate species of *Gulella*. Obviously Connolly could not make up his mind as regards this question as witnessed by his remarks on p. 84 ("? 1856. *Helix fanulus* Pfr." under the synonymy of *G. adamsiana*), on p. 85 ("*H. fanulus* is unquestionably the top of either this species or its var. *impervia*, ..." while discussing *G. adamsiana)* and on p. 630 ("The tip of a *Gulella* of the group of *adamsiana* q.v." while discussing *Helix fanulus* under the species dubiae). The type locality of *H. fanulus* is Port Natal = Durban. At the moment it is virtually impossible to name separately collected juveniles of the genus *Gulella*. In view of the fact that there is more than one species with a medium-sized to large costulate shell in the Durban area, the present author feels that he cannot support Connolly in his synonymy as regards *H. fanulus*. *H. fanulus* has three years priority over *G. adamsiana*, so that by considering it a nomen dubium and virtually ignoring it undue nomenclatorial difficulties may be avoided.

G. adamsiana inhabits a number of different habitats, although on the whole obviously preferring a fairly high rainfall. The following data have been extracted from labels and field notes: "in well tended garden with compost heap and a few logs", "coastal bush", "underneath one end of fallen trunk of wattle", "in thin layer of comparatively dry and poor wattle humus in neglected wattle plantation with some indigenous undergrowth and a few indigenous trees", "under stones on grassy slope", under stones on comparatively dry grassy slope, "on the ground among herbs and grass on shale", montane forest at 4000 ft. (= ca. 1200 m), and "ex termitarium". The latter record is probably a winter record; the uniformly humid conditions of a termitarium are eminently suitable for a diapause during the dry season. The species occurs from sea level to ca. 1300 m.

A glance at the distribution map (fig. 3) shows that the pattern is a typical collector's pattern. All localities are situated near main roads leading from the cities of Pietermaritzburg and Durban to the holiday resorts on the Natal south coast and the Drakensberg range. Nevertheless it gives an impression of the true distribution and allows one to extrapolate that very probably *G. adamsiana* occurs along the valleys of most rivers draining the Natal midlands and discharging their water into the Indian Ocean.

Gulella darglensis (Melvill & Ponsonby, 1908) (figs. 4-7)

Ennea darglensis Melvill & Ponsonby, 1908, Ann. Mag. Nat. Hist., (8) 1: 130, pl. 7 fig. 1; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 160; Connolly, 1912, Ann. S. Afr. Mus., 11: 71; Burnup, 1914, Ann. Natal Mus., 3: 48, pl. 4 fig. 32.

Gulella darglensis; Connolly, 1939, Ann. S. Afr. Mus., 33: 72; Van Bruggen, 1973, Malacologia, 14: 421.

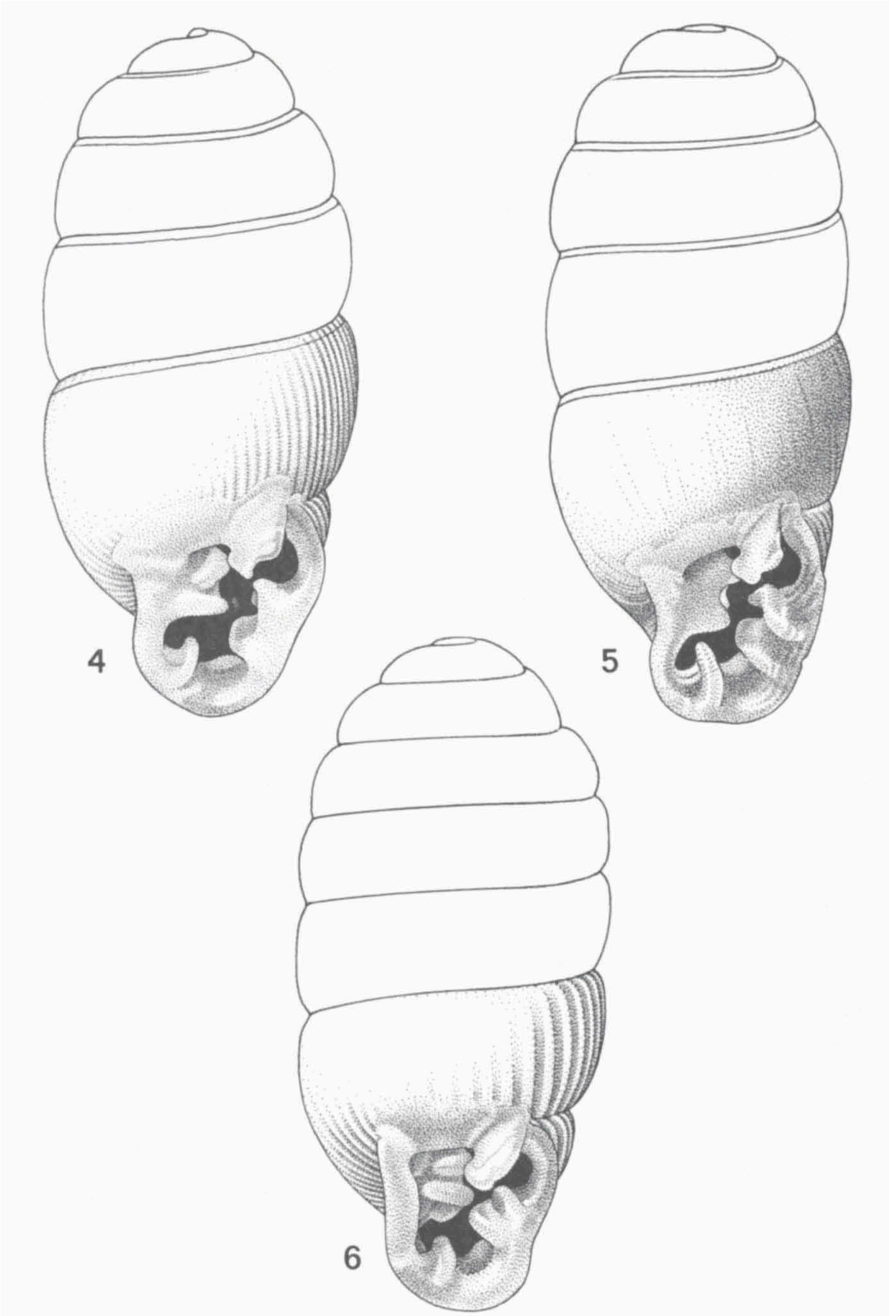
Diagnostic characters. — A minute, smooth to costulate species with sixfold dentition consisting of angular lamella, two labral processes, basal process and duplex columellar lamella.

Description of shell. — Shell minute, subcylindriform, with fairly open umbilicus. Spire produced, sides subparallel, apex flattened, obtusely conical. Whorls 5-6½, very slightly convex, from practically smooth with some costulation around the umbilicus to sculptured with close, regular, somewhat oblique costulae; sutures shallow, simple to subcrenellate. Aperture with sixfold dentition: almost vertical angular lamella, scarcely connected with apex of labrum; labral processes consisting of two subequal lamellae, the upper sometimes angulate on the outside, complex corresponding to shallow outside depression; an inrunning lamella to the left of the base; duplex columellar lamella consisting of superficial, horizontal slab and smaller, more deeply and higher situated denticle.

Measurements of shell: 2.2-3.1 × 1.1-1.4 mm, l/d 1.84-2.28.

Distribution (fig. 7). — *G. darglensis* occurs from the Eastern Cape Province to the Natal midlands and foothills of the Drakensberg range.

G. darglensis may be divided into three well-marked subspecies. The following key serves to distinguish between these:



Figs. 4-6. Shells of *Gulella darglensis*; 4, *G. d. darglensis* (M. & P.) (length 2.6 mm, Inhluzane, RMNH); 5, *G. d. illovoensis* (Bnp.) (length 3.1 mm, Ntimbankulu, NM 2560); 6, *G. d. benthodon* nov. subsp. (holotype, length 2.9 mm, Pirie Forest, BM).

1a Shell costulate, columellar processes either superficial or deeper situated 2
b Shell practically smooth, columellar processes superficial (Natal south coast) . . . . *G. d. illovoensis*
2a Columellar processes superficial (Pondoland, Natal midlands and Drakensberg foothills) . . . . *G. d. darglensis*
b Columellar processes more deeply situated (Ciskei) . *G. d. benthodon*

Gulella darglensis darglensis (Melvill & Ponsonby, 1908)

Diagnostic characters — Shell (fig. 4) costulate, columellar processes superficial.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Measurements of shell: 2.2-2.9 × 1.1-1.4 mm, l/d 1.84-2.28. The type measures 2.6 × 1.2 mm, l/d 2.17. Smallest shell (Tonti Forest, NM) 2.2 × 1.2 mm, l/d 1.84, largest shell (Karkloof, NM) 2.9 × 1.4 mm, l/d 2.14. An average specimen (Dargle, NM) measures 2.6 × 1.2 mm, l/d 2.16, aperture 0.8 × 0.7 mm, last whorl 1.4 mm.

Distribution (fig. 7). — *G. d. darglensis* occurs in Pondoland, the Natal midlands and the foothills of the Drakensberg range.

CAPE PROVINCE: Tonti Forest near Mt. Ayliff (Pondoland, TRANSKEI), W. Falcon (NM); Mhlozana (Pondoland, TRANSKEI), H. J. Puzey (BM 1931.6.3.1-4). NATAL: Enon Bush, Richmond, H. C. Burnup (NM type 545, three paratypes); Bulwer, C. W. Alexander (NM); do., E. Warren (NM); Dargle, H. C. Burnup (BM 1908.12.14.40, holotype; BM 1937.12.30.778-80, three paratypes; NM type 545, two paratypes; NM 2170, four "part of original lot"; NM); (Furth) Inhluzani (Hill) near Dargle, H. C. Burnup (BM 1914.12.19.41-4; NM; RMNH); Nottingham Road, A. J. Taynton (NM); Karkloof (NE. of Howick: 29°25'S 30°20'E), A. J. Taynton (NM); do., Cascade Falls, W. Falcon (NM).

Type locality: Dargle, where first collected by H. C. Burnup in January, 1907.

Gulella darglensis illovoensis (Burnup, 1914)

Ennea darglensis Melvill & Ponsonby var. *illovoensis* Burnup, 1914, Ann. Natal Mus., 3: 49, pl. 4 figs. 33-35.
Guella darglensis (Melvill & Ponsonby) var. *illovoensis*; Connolly, 1939, Ann. S. Afr. Mus., 33: 72.

Diagnostic characters. — Shell (fig. 5) practically smooth, columellar processes superficial.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Measurements of shell: 2.6-3.1 × 1.3-1.4 mm, l/d 2.00-2.27. The type measures 2.9 × 1.4 mm, l/d 2.04. Smallest shell (NM) 2.6 × 1.3 mm, l/d

2.00, largest shell (NM) 3.1 × 1.4 mm, l/d 2.27. An average specimen (NM) measures 2.9 × 1.4 mm, l/d 2.09, aperture 0.9 × 0.8 mm, last whorl 1.5 mm.

Distribution (fig. 7). — *G. darglensis illovoensis* is so far only known from Ntimbankulu (Mid-Illovo) on the Natal south coast.

NATAL: (Backworth) Ntimbankulu, H. C. Burnup (BM 1914.12.19.14, holotype; BM 1914.12.19.37-40, four paratypes; BM 1937.12.30.783-4, two paratypes; NM 2560, type 546, five paratypes; NM; RMNH; SAM, six paratypes).

Type locality: Ntimbankulu, where first collected by Burnup some time before 1914.

Gulella darglensis benthodon nov. subspec.

Diagnostic characters. — Shell (fig. 6) costulate, with somewhat coarser dentition and the columellar processes more deeply situated than in the nominate form.

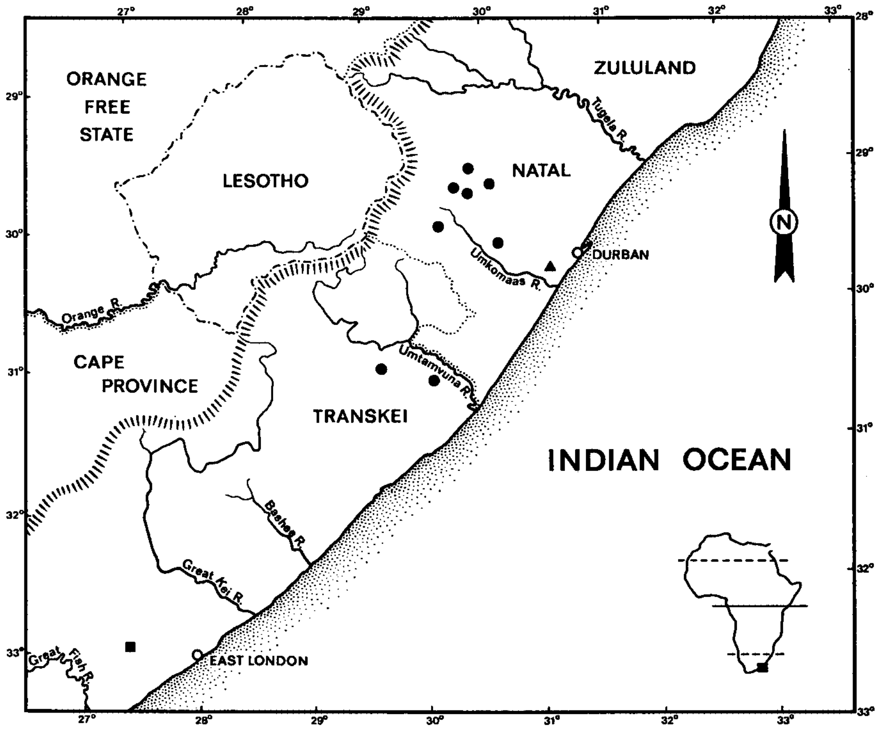


Fig. 7. Distribution of *Gulella darglensis*; dots — *G. d. darglensis* (M. & P.), triangle — *G. d. illovoensis* (Bnp.), square — *G. d. benthodon* nov. subsp. The Great Escarpment has been indicated by cross-hatching.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Measurements of shell: 2.9-3.0 × 1.3-1.4 mm, l/d 2.09-2.28. The type (fig. 6) measures 2.9 × 1.4 mm, l/d 2.09, aperture 0.9 × 0.8 mm, last whorl 1.4 mm, 6½ whorls; the paratype measures 3.0 × 1.3 mm, l/d 2.28.

Distribution (fig. 7). — *G. darglensis benthodon* is so far only known from the Pirie Forest in the Kingwilliamstown district, Eastern Cape Province.

CAPE PROVINCE: Pirie Forest near Kingwilliamstown, R. Godfrey (BM 1937.12.30.781-2, holotype and paratype).

Type locality: Pirie Forest, where first collected by the Rev. R. Godfrey, probably around 1920.

The newly described subspecies has been named after its most typical character, the deeply situated columellar teeth (*benthodon*, Greek, deep tooth).

On the average the shells of the subspecies *illovoensis* are somewhat larger and more slender than those of the nominate subspecies. Unfortunately only two shells of the subspecies *benthodon* are available and only one population of *illovoensis* has been sampled. The subspecies *benthodon* has seemingly even larger and more slender shells. The following data may be compared:

G. d. darglensis	2.2-2.9 × 1.1-1.4 mm, l/d 1.84-2.28 (72 shells)
G. d. illovoensis	2.6-3.1 × 1.3-1.4 mm, l/d 2.00-2.27 (54 shells)
G. d. benthodon	2.9-3.0 × 1.3-1.4 mm, l/d 2.09-2.28 (2 shells)

While the material of *G. d. illovoensis* (one population) is fairly uniform, the populations of *G. d. darglensis* show a size cline, i.e. an increase in length of the shell from south to north:

Tonti Forest	2.2-2.4 × 1.1-1.2 mm, l/d 1.84-2.17
Richmond	2.2-2.6 × 1.2 mm, l/d 1.89-2.15
Bulwer	2.2-2.7 × 1.1-1.2 mm, l/d 2.11-2.15
Dargle and district	2.3-2.7 × 1.1-1.2 mm, l/d 1.85-2.28
Nottingham Road-Karkloof	2.6-2.9 × 1.2-1.4 mm, l/d 2.05-2.20

Obviously the greatest size is reached in the mountains in the north; the hypsometric distribution of the nominate subspecies reaches from ca. 900 m (ca. 2800 ft.: Richmond) to ca. 1500 m (4800-5000 ft.: Nottingham Road and Bulwer). The subspecies *benthodon* is so far only only known from ca. 400 m (ca. 1200 ft.) and the subspecies *illovoensis* from between 500 and 900 m (ca. 1600-3000 ft.). A glance at the distribution map (fig. 7) combined with the size data may lead to the conviction that *G. darglensis* only really thrives in somewhat temperate climates.

G. darglensis is subject to little variation in its apertural dentition. Rarely a vestige of a sinular swelling may be detected. In Dargle populations of the nominate subspecies the upper labral lamella now and then may be slightly bifid. One shell from Furth (Inhluzani Hill, NM) has its columellar processes fused into one squarish slab; another specimen from Dargle (NM) has a repaired aperture with all processes present, but much reduced in size.

G. d. illovoensis and *G. d. benthodon* are examples of peripherally isolated populations as discussed by Mayr (1976: 191).

Gulella elliptica (Melvill & Ponsonby, 1898) (figs. 8-12)

Ennea elliptica Melvill & Ponsonby, 1898, Ann. Mag. Nat. Hist., (7) 2: 126, pl. 7 fig. 2; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 167; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 180, pl. 23 fig. 4; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 160; Connolly, 1912, Ann. S. Afr. Mus., 11: 73; Burnup, 1914, Ann. Natal Mus., 3: 38, pl. 3 figs. 7-12.

Gulella elliptica; Connolly, 1939, Ann. S. Afr. Mus., 33: 82; Van Bruggen, 1973, Malacologia, 14: 421.

Ennea elliptica Melvill & Ponsonby var. *manca* Burnup, 1914, Ann. Natal Mus., 3: 39, pl. 3 figs. 13-14.

Gulella elliptica (Melvill & Ponsonby) var. *manca*; Connolly, 1939, Ann. S. Afr. Mus., 33: 83.

Ennea elliptica Melvill & Ponsonby var. *caelata* Burnup, 1914, Ann .Natal Mus., 3: 40, pl. 3 figs. 15-17.

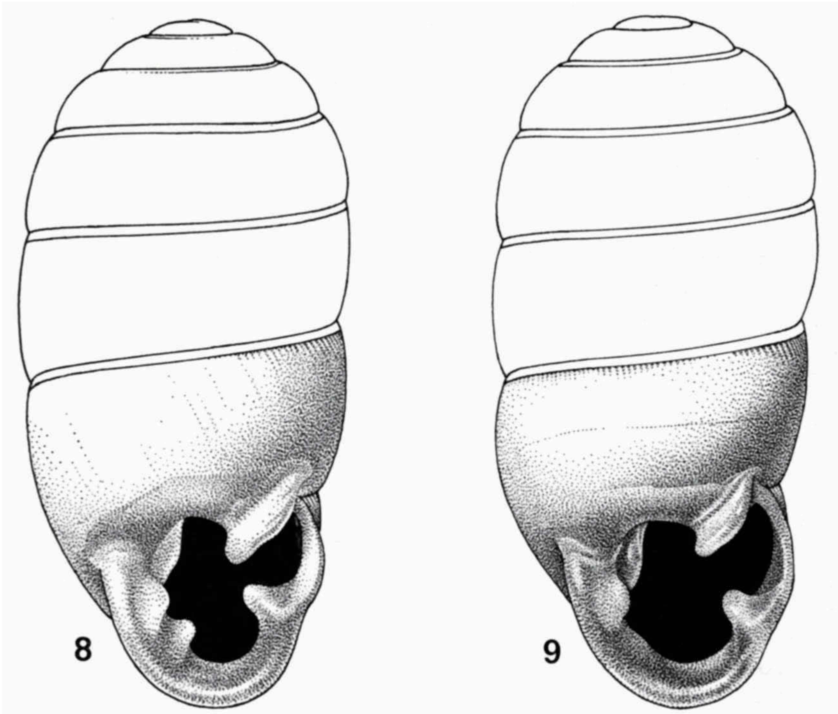
Gulella elliptica (Melvill & Ponsonby) var. *caelata*; Connolly, 1939, Ann. S. Afr. Mus., 33: 83.

Diagnostic characters. — A small, smooth to costulate species with four- to five-fold dentition consisting of angular lamella, labral process, one or two outer columellar denticles, and an inner columellar lamella.

Description of shell. — Shell smal, cylindrical to elliptical, rimate. Spire produced, sides parallel to slightly convex, apex flattened to bluntly rounded. Whorls 6-7¼, flat to slightly convex, from almost completely smooth to costulate, in which latter case the shell is sculptured with fine, close, regular and almost straight costulae; sutures shallow to somewhat impressed, simple. Aperture with four- to five-fold dentition: strong, oblique angular lamella, distant from or scarcely connected with apex of labrum; strong mid-labral denticle, corresponding to small outside pit; two subequal, more or less superficial tubercles on the columellar lip, of which the lower may be reduced in size to complete absence; inner columellar lamella weak and shelf-like.

Measurements of shell: 2.9-4.7 × 1.6-2.4 mm, l/d 1.75-2.28.

Distribution (fig. 12). — *G. elliptica* occurs from Pondoland (Transkei) to the Natal midlands and north coast as far north as East-Central Zululand.



Figs. 8-9. Shells of *Gulella elliptica*; 8. *G. e. elliptica* (M. & P.) (length 3.7 mm, Pietermaritzburg, NM); 9, *G. e. elliptica* var. *manca* Bnp. (length 3.9 mm, Curry's Post, NM).

G. elliptica may be divided into three subspecies, which may be distinguished as follows:

1a Shell smooth, at most with growth lines below the sutures, length 2.9-4.4 mm, labral denticle bluntly acuminate or square, outer columellar tubercles subequal in size or the lower much reduced in size . . 2

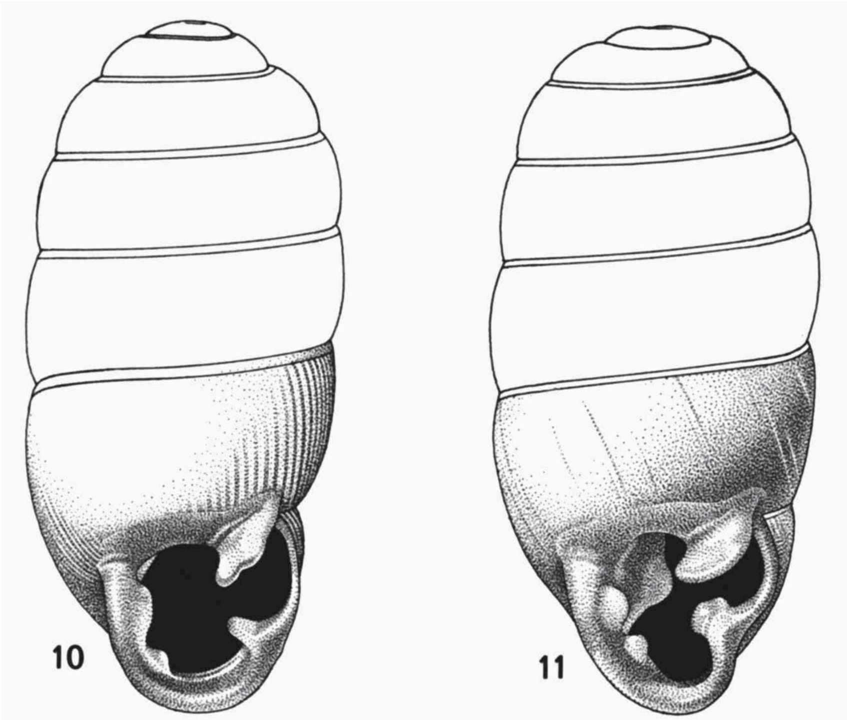
b Shell costulate, length 4.2-4.7 mm, labral denticle bluntly acuminate, outer columellar tubercles subequal in size (Pondoland) *G. elliptica caelatior*

2a Labral denticle bluntly acuminate, lower outer columellar tubercle usually reduced in size (may be completely absent), shell 3.0-4.4 mm long (Natal midlands to Drakensberg foothills and Natal north coast to southeastern Zululand) . . . . *G. ellipitica elliptica*

b Labral denticle square, outer columellar tubercles subequal in size, shell 2.9-4.1 mm long (East-Central Zululand) . . *G. elliptica tesserula*

Gulella elliptica elliptica (Melvill & Ponsonby, 1898)

Diagnostic characters. — Shell (fig. 8) 3.0-4.4 mm long, sculpture confined to growth lines below the sutures and on the body whorl behind the



Figs. 10-11. 10, *G. e. caelatior* Conn. (length 4.5 mm, Port St. Johns, NM); 11, *G. e. tesserula* nov. subsp. (holotype, length 4.1 mm, Hlabisa, NM).

labrum, labral denticle bluntly acuminate, lower outer columellar tubercle may be reduced in size to almost complete absence.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Measurements of shell: 3.0-4.4 × 1.6-2.1 mm, l/d 1.75-2.28. The type measures 3.2 × 1.7 mm, l/d 1.88. Smallest shells (Tongaat, NM) 3.0 × 1.6 mm, l/d 1.84 and (Dargle, NM) 3.0 × 1.7 mm, l/d 1.78, largest shell (Eshowe, NM) 4.4 × 2.1 mm, l/d 2.12. An average specimen (Eshowe, NM) measures 3.7 × 1.9 mm, l/d 1.93, aperture 1.1 × 1.1 mm, last whorl 2.1 mm.

Distribution (fig. 12). — *G. e. elliptica* occurs in the Natal midlands to the foothills of the Drakensberg range and along the Natal north coast into southeastern Zululand.

NATAL: Enon Bush, Richmond, H. C. Burnup (NM); Henley (SW. of Pietermaritzburg), E. Warren (NM); Taylors (SW. of Pietermaritzburg), W. Falcon (NM); Edendale Falls (SW. of Pietermaritzburg), H. C. Burnup (NM); Pietermaritzburg (includes Botanic Gardens, Chase Krantzes, Chase Valley and Town Bush), H. C. Burnup (BM 1903.3.11.71, holotype; BM 1937.12.30.791-8; NM, three paratypes; NM

2257; NM); do., W. Falcon (NM; RMNH); do., R. F. Lawrence (NM alc.); do., ex H. B. Preston (RMNH); Zwartkop (= Swartkop, NW. of Pietermaritzburg) (Connolly, 1939); Hilton Road, H. C. Burnup (NM); Karkloof (NE. of Howick: 29°25'S 30°20'E) (BM 1937.12.30.801); Curry's Post (E. of Balgowan), A. J. Taynton (NM 2552, type 548, two paratypes of var. *manca*; NM, paratype of var. *manca*; SAM, paratype of var. *manca*); Lidgetton, W. G. Rump (NM); Dargle, H. C. Burnup (BM 1914.12.19.8-9; BM 1937.12.30.799-800; NM); Fort Nottingham, A. J. Taynton (BM 1914.12.19.10, holotype of var. *manca*; BM 1914.12.19.23-4, two paratypes of var. *manca*; NM 2547, type 548, two paratypes of var. *manca*); do., Miss M. F. Hickey (NM); Lion's Bush, Nottingham Road, R. F. Lawrence (NM alc.); Balgowan (Connolly, 1939); Dragon's Peak resort near Champagne Castle, H. E. van Hoepen (RMNH; vH); Kranskop, W. Falcon (NM); Zimbaba Bush (Kranskop), H. C. Burnup (NM); Botha's Hill (BM, Macandrew colln.); Tyeloti (Tshloti) (near Botha's Hill) (Connolly, 1939); Tongaat (Beach Bush), H. C. Burnup (NM); Umhlali (Beach, includes Sheffield Beach), H. C. Burnup (NM); do., R. F. Lawrence (NM alc.); do., W. G. Rump (NM); Stanger (Connolly, 1939); Blythdale Beach near Stanger, H. E. van Hoepen (RMNH; vH); Sinkwazi (S. of Tugela R. mouth), H. C. Burnup (NM; RMNH); "Natal" (TP). ZULULAND: Mfongosi (W. of Jameson's Drift), W. G. Jones (DM, Puzey colln. 24); Eshowe, H. C. Burnup (NM 3555); do., W. Falcon (NM); do., Lady Saunders (BM 1914.12.19.2, holotype of var. *caelata*; NM type 547, paratype of var. *caelata*); Richards Bay, W. Falcon (NM).

Type locality: Pietermaritzburg, Botanic Gardens, "a bush-clad hill within the boundaries of the gardens but not disturbed by cultivation" (Burnup, 1914: 38), where first collected by Burnup some time before 1898.

Gulella elliptica caelatior Connolly, 1939

Gulella elliptica (Melvill & Ponsonby) var. *caelatior* Connolly, 1939, Ann. S. Afr. Mus., 33: 83, pl. 1 fig. 5.

Diagnostic characters. — Shell (fig. 10) compartively large and slender (4.3-4.7 mm long), completely costulate, labral denticle bluntly acuminate, outer columellar tubercles subequal in size.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Measurements of shell: 4.2-4.7 × 1.9-2.4 mm, l/d 1.96-2.19. The type measures 4.7 × 2.4 mm, l/d 1.96. Smallest shell (Hole in the Wall, RMNH) 4.2 × 1.9 mm, l/d 2.19, largest shell (type, see above). An average specimen (Port St. Johns, NM, fig. 10) measures 4.5 × 2.1 mm, l/d 2.12, aperture 1.4 × 1.3 mm, last whorl 2.2 mm.

Distribution (fig. 12). — *G. elliptica caelatior* is so far only known from three localities in Pondoland (Transkei).

CAPE PROVINCE: Hole in the Wall (near Coffee Bay, TRANSKEI), H. E. van Hoepen (RMNH; vH); Port St. Johns, W. Falcon (BM 1937.12.30.802-4, holotype and two paratypes; NM, four, probably paratypes; NM); do., E. Warren (NM) (TRANSKEI); Makwa [Magwa] Falls (near Lusikisiki) (Connolly, 1939) (TRANSKEI).

Type locality: Port St. Johns, Pondoland (Transkei), where first collected by Dr. Ernest Warren (director of the Natal Museum, 1903-1936) in January 1913. Warren's single worn shell was labelled "Ennea ? n. sp." by Burnup. Connolly subsequently described what he took to be a variety of *G. elliptica* on material gathered by W. Falcon in February 1934.

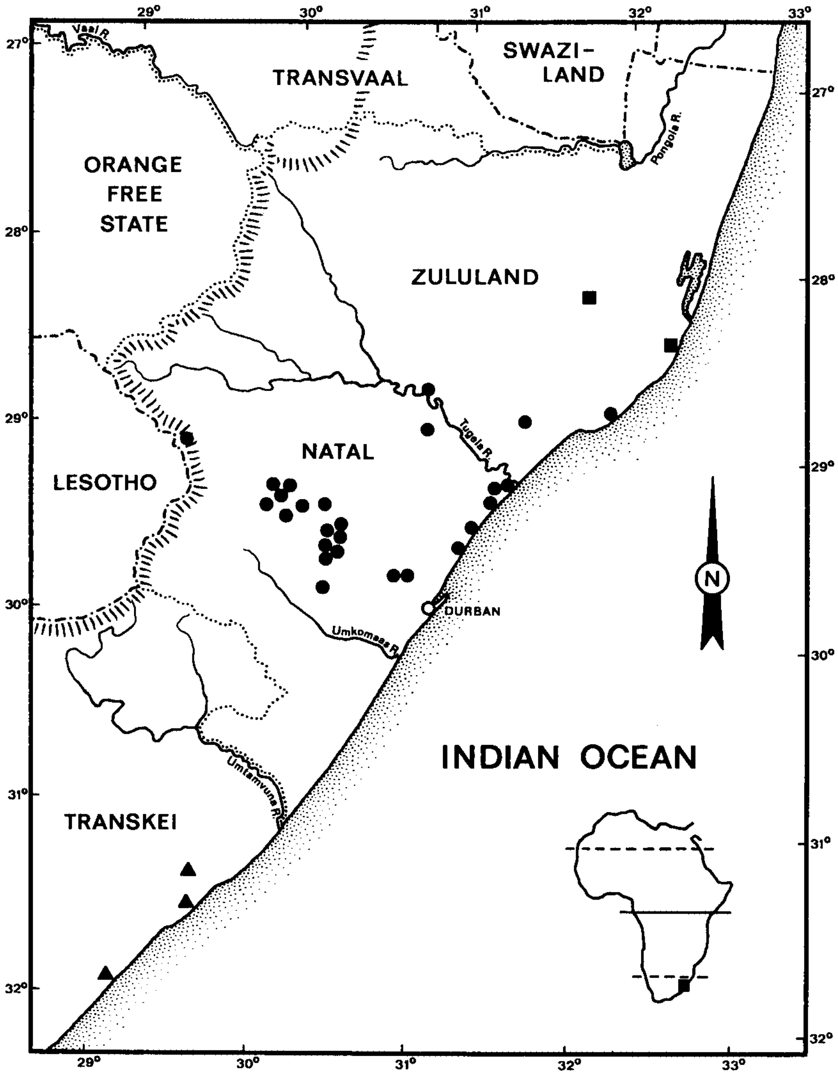


Fig. 12. Distribution of *Gulella elliptica*; dots — *G. e. elliptica* (M. & P.), triangles — *G. e. caelatior* Conn., squares — *G. e. tesserula* nov. subsp. The Great Escarpment has been indicated by cross-hatching.

Gulella elliptica tesserula nov. subspec.

Diagnostic characters. — Shell (fig. 11) 2.9-4.1 mm long, almost completely smooth, labral denticle square, outer columellar tubercles subequal in size.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Measurements of shell: 2.9-4.1 × 1.6-2.0 mm, l/d 1.81-2.13. The type (fig. 11) measures 4.1 × 1.9 mm, l/d 2.13, aperture 1.2 × 1.2 mm, last whorl 2.1 mm, 7 whorls. Smallest shell (St. Lucia Bay, NM) 2.9 × 1.6 mm, l/d 1.81, largest shell (type, see above).

Distribution (fig. 12). — *G. elliptica tesserula* is so far only known from two localities in East-Central Zululand north of the Umfolosi River.

ZULULAND: Hlabisa, F. Toppin (NM, holotype and paratype); St. Lucia Bay, H. J. Puzey (BM 1956.6.8.24-6, three paratypes; DM, Puzey colln. 18, five paratypes; NM, three paratypes).

Type locality: Hlabisa, west of the railway line, Zululand, where first obtained by Fred Toppin (collector for the Natal Museum) in the first decade of the twentieth century.

G. elliptica is subject to a good deal of variation, mainly expressed in the size, sculpture and apertural dentition of the shell. A reconsideration of the abundant material available for this study has led to the recognition of three, reasonably easily separated subspecies, and the synonymizing of the varieties *manca* (fig. 9) and *caelata* with the nominate form. These varieties are not sharply delimited from the latter and are probably only examples of clinal variation. The southern subspecies, *G. elliptica caelatior*, is at once recognized by its costulate shell and the northern subspecies, *G. elliptica tesserula*, by its square labral tooth.

There is a sample of the typical subspecies labelled "Port Natal" (= Durban) in the British Museum (McKen colln., BM). It is hightly unlikely that *G. elliptica* occurs in Durban, otherwise it would not have escaped the attention of a host of collectors, who locally have abundantly obtained many smaller species. Therefore this record has been ignored.

The typical form shows a lot of variation in size, which may be the result of geographical variation. Measurements may be tabulated as on p. 25. This shows that the shells of the Kranskop populations are comparatively small, while those of the Zululand hills are large and somewhat squat.

The lower outer columellar denticle tends to disappear in shells of populations northwest of Pietermaritzburg. The form with only the upper denticle was separated by Burnup (1914) as the var. *manca*; it appears, however, to be extremely difficult (if not impossible) to draw the line here. Both the

area	measurements in mm	l/d	measurements in mm (mean)	l/d (mean)
Natal midlands and Drakensberg foothills	3.0-4.2 × 1.6-1.9	1.78-2.27	3.6 × 1.7	2.02
Kranskop	3.1-3.4 × 1.6-1.7	1.92-2.11	3.2 × 1.6	2.01
Natal north coast and Richards Bay	3.0-4.0 × 1.6-1.9	1.75-2.28	3.5 × 1.7	2.01
Zululand hills	3.1-4.4 × 1.6-2.1	1.81-2.12	3.7 × 1.8	1.96

typical and the above forms are known to occur in populations in and around Pietermaritzburg (Town Bush, Edendale Falls, etc.); towards the west (foothills of the Drakensberg range) the var. *manca* tends to dominate, even to the exclusion of the typical form. Shells from coastal localities usually have a complete dentition, although in a large sample from Sinkwazi (>350 shells, NM and RMNH) there are a few specimens with a reduced lower outer columellar denticle. Kranskop and Zululand shells all show two well-developed outer columellar denticles.

Only seven shells of the southern subspecies, *G. elliptica caelatior*, have been examined; as far as can be judged from such limited material this subspecies is remarkably uniform in size, sculpture and dentition [3]).

The same cannot be said for the northern subspecies, *G. elliptica tesserula*. Although easily recognized by the square labral process (*tesserula*, Lat. = small squarish block used in mosaic) and the almost complete absence of sculpture, the two populations sampled show great discrepancies in the size of the shells. The two Hlabisa shells measure 3.8-4.1 × 1.9-2.0 mm, l/d 1.91-2.13, while the eight St. Lucia Bay shells are exact miniatures of these: 2.9-3.3 × 1.6-1.7 mm, l/d 1.81-2.04.

A general survey of the above data reveals that in reasonably cool areas the species reaches its greatest size. The largest specimens known belong to the southernmost subspecies (Port St. Johns); other populations with large shells are those from the Zululand hills (Mfongosi, Eshowe: *G. e. elliptica*; Hlabisa: *G. elliptica tesserula*) and from around Pietermaritzburg. On the other hand the smallest specimens are known from St. Lucia Bay (*G. elliptica tesserula*), the Natal north and Zululand south coasts and the Kranskop area (all nominate subspecies). Undoubtedly St. Lucia Bay is the hottest of these localities and this is seemingly correlated with the smallest shells.

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[3]) The Van Hoepen specimen in RMNH is somewhat worn and only shows faint costulae.

The species is confined to coastal bush, montane forest and intermediate types of sheltering vegetation up to approximately 1500 m (ca. 5000 ft). Apparently the species is somewhat sensitive to a decrease in relative humidity as witnessed by the thick epiphragms of many specimens in diapause collected on 24 May 1919 (Pietermaritzburg, Town Bush, NM and RMNH). In southern Africa May is one of the dry winter months and even in forest types of vegetation the relative humidity shows a considerable decrease as compared to that of the wet or intermediate seasons.

It is a well-known fact that juvenile and subadult shells of *Gulella* have apertural dentitions different from those of adult specimens. Shell material is continually deposited until such time as labrum and dentition have acquired their final form and thickness. In many cases it is difficult to judge when exactly specimens are really fully-grown, i.e., when they are not expected to add any more to their apertural dentition. There is a distinct possibility that some obscure species with a thin labrum, and particularly thin denticles and processes widely separated from each other, in fact are subadults of another species, which e.g. may explain why they have never been found or recognized again. In this context attention should be drawn to two shells from the Zululand coast, St. Lucia Bay, H. J. Puzey leg. (BM, ex Connolly colln.). These shells key out and seemingly belong to *G. e. elliptica*, being without a trace of sculpture on their whorls and as regards apertural dentition with a somewhat acute labral process and the outer columellar tubercles unequal in size (the upper process is well developed, the lower minute). The measurements of these specimens are as follows:

3.5 × 1.7 mm, l/d 2.00, last whorl 1.7 mm, aperture 1.1 × 1.2 mm,
3.2 × 1.7 mm, l/d 1.93, last whorl 1.6 mm, aperture 1.1 × 1.1 mm.

The largest shell has 6½ whorls. However, a close scrutiny reveals that in these specimens the lip is still thin and the denticles obviously still are in the process of formation. A somewhat acute labral process may well later become square by addition of more shell material. Also, the general habitus of the shells in question is that of *G. e. tesserula* rather than that of the nominate form; it is extremely difficult to define this exactly and it may be pure conjecture. In the present author's opinion these shells are indeed subadult specimens of *G. e. tesserula*. If true, this shows that (a) in *G. elliptica* probably all subspecies pass through a generalized stage, in this case resembling the nominate form, and (b) *G. e. tesserula* is indeed a subspecies of *G. elliptica* and not a separate allopatric species of its own. There are indications that the first of these conclusions may apply more generally to other (and perhaps all) Streptaxidae. In the present case the nominate form may also be the ancestral form having given rise to the two peripheral subspecies *G. e. caelatior* and *G. e. tesserula* (see Mayr, 1976: 191).

Gulella farquhari (Melvill & Ponsonby, 1895) (figs. 13-16)

Ennea farquhari Melvill & Ponsonby, 1895, Ann. Mag. Nat. Hist., (6) 16: 478, pl. 18 figs. 3-5; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 167; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 548 (12), 564 (28); Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 186, pl. 23 fig. 17; Connolly, 1912, Ann. S. Afr. Mus., 11: 74; Burnup, 1914, Ann. Natal Mus., 3: 41, pl. 4 fig. 24.

Gulella farquhari; Connolly, 1925, Trans. Roy. Soc. S. Afr., 12: 119; Germain, 1935, Mem. Estud. Mus. Zool. Univ. Coimbra, (1) 80: 5; Connolly, 1939, Ann. S. Afr. Mus., 33: 95; Zilch, 1961, Arch. Molluskenk., 90: 94; Van Bruggen, 1975, Zool. Meded. Leiden, 49: 213; Van Bruggen & Appleton, 1977, Zool. Verh. Leiden, 154: 30, 40; Verdcourt, 1978, Basteria, 42: 22, fig. 5.

Ennea farqhari; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 160.

Ennea labyrinthea Melvill & Ponsonby, 1895, Ann. Mag. Nat. Hist., (6) 16: 479, pl. 18 figs. 7-8; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 168; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 224, pl. 28 figs. 2-3; Connolly, 1912, Ann. S. Afr. Mus., 11: 78.

Ennea labyrinthica; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 550 (14), 565 (29); Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 161.

Ennea microthauma Melvill & Ponsonby, 1899, Ann. Mag. Nat. Hist., (7) 4: 194, pl. 3 fig. 1; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 234, pl. 32 fig. 13; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 161; Connolly, 1912, Ann. S. Afr. Mus., 11: 80.

Ennea berthae Melvill & Ponsonby, 1901, Ann. Mag. Nat. Hist., (7) 8: 315, pl. 2 fig. 1; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 235, pl. 32 fig. 20; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 159; Connolly, 1912, Ann. S. Afr. Mus., 11: 67.

Ennea farquhari Melvill & Ponsonby var. *berthae*; Burnup, 1914, Ann. Natal. Mus., 3: 44, pl. 4 figs. 25-27.

Gulella farquhari (Melvill & Ponsonby) var. *berthae*; Connolly, 1939, Ann. S. Afr. Mus., 33: 96.

Ennea hypsoma Melvill & Ponsonby, 1909, Ann. Mag. Nat. Hist., (8) 4: 488, pl. 8 fig. 7; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 160; Connolly, 1912, Ann. S. Afr. Mus., 11: 75.

Ennea oppugnans Melvill & Ponsonby, 1909, Ann. Mag. Nat. Hist., (8) 4: 488, pl. 8 fig. 8 [4]); Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 161; Connolly, 1912, Ann. S. Afr. Mus., 11: 82.

Ennea periploca Melvill & Ponsonby, 1909, Ann. Mag. Nat. Hist., (8) 4: 489, pl. 8 fig. 10; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 161; Connolly, 1912, Ann. S. Afr. Mus., 11: 82.

Ennea farquhari Melvill & Ponsonby var. *avena* Burnup, 1914, Ann. Natal Mus., 3: 46, pl. 4 figs. 28-31.

Gulella farquhari (Melvill & Ponsonby) var. *avena*; Connolly, 1939, Ann. S. Afr. Mus., 33: 96.

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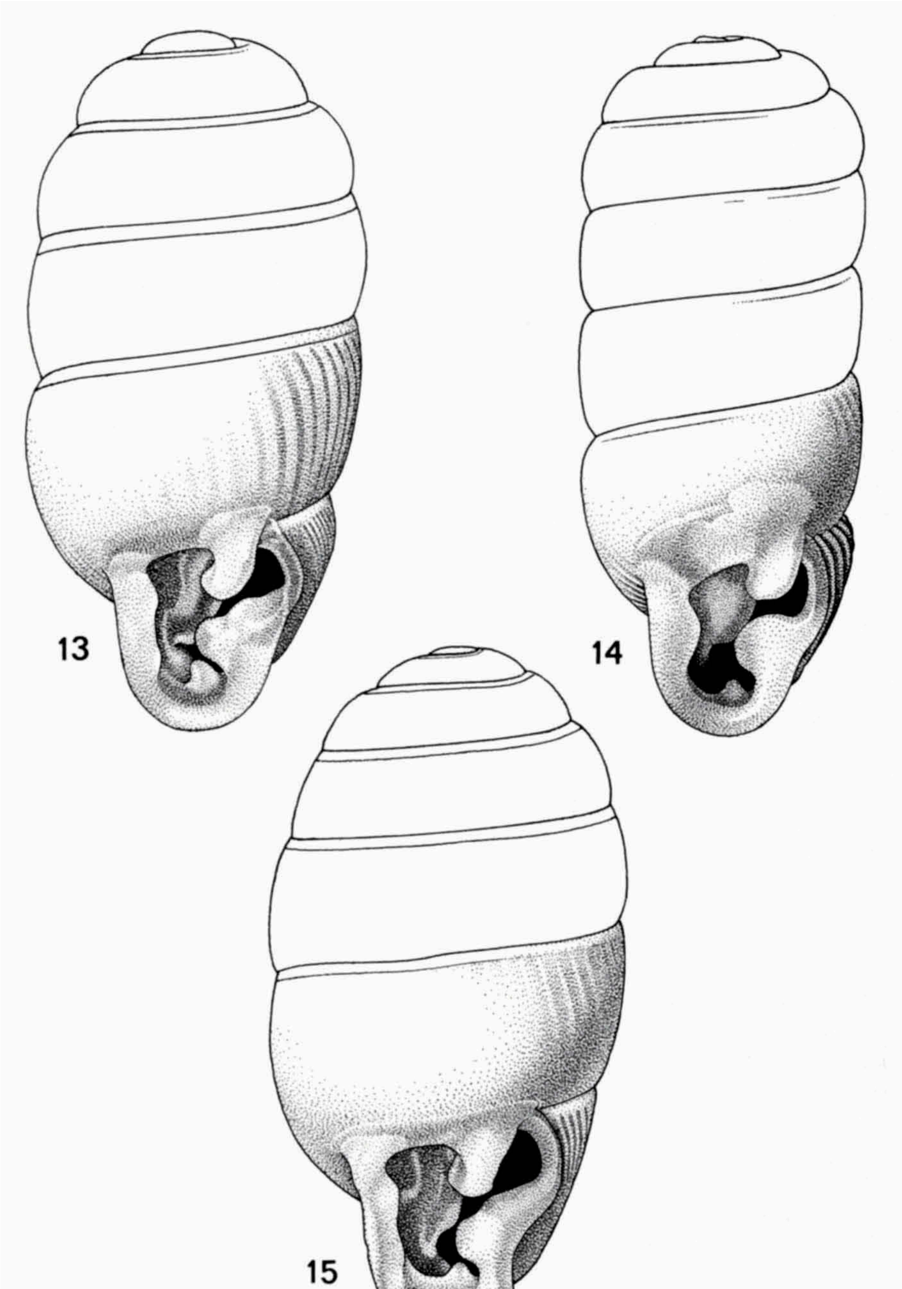
[4]) The type locality, Boschberg Mountain, Somerset East, Cape Province, is incorrect; it should be "Dassy Krantz, Grahamstown" (fide Burnup, 1914: 41, 61).



Figs. 13-15. Shells of *Gulella farquhari* (M. & P.); 13, Grahamstown (length 2.1 mm, NM); 14, Durban (length 3.6 mm, NM 2559); 15, Karkloof (length 2.9 mm, NM 2549).

Diagnostic characters. — A minute, striate to almost smooth, species with five-fold dentition consisting of angular lamella, labral slab (sometimes bicuspid), basal denticle and duplex columellar lamella.

Description of shell. — Shell (figs. 13-15) minute, (sub)cylindrical to elliptical, narrowly rimate. Spire produced, sides subparallel to convex, apex flattened, obtusely conical. Whorls 4¾-8, slightly convex, sculptured with coarse, fairly distant, nearly vertical and straight striae or costulae, most prominent below the sutures and behind the labrum around the umbilicus, to almost completely smooth (always except for the area behind the labrum around the umbilicus); sutures shallow, subcrenellate to simple. Aperture with five-fold dentition: strong, oblique angular lamella, connected with apex of labrum; labral process a large slab, frequently bilobed or bicuspid [5]), corresponding to deep outside depression; deeply situated, small mid-labral denticle; outer columellar process varies from poorly developed low swelling to vertical process or denticle, inner columellar lamella large and prominent.

Measurements of shell: 1.9-3.8 × 0.9-1.6 mm, l/d 1.80-2.60. The type measures 2.8 × 1.5 mm, l/d 1.87. Smallest specimen (Kowie East, NM) 1.9 × 1.0 mm, l/d 1.87, largest shell (Mfongosi, NM) 3.8 × 1.5 mm, l/d 2.54. An average specimen (Pietermaritzburg, NM) measures 2.8 × 1.2 mm, l/d 2.25, last whorl 1.4 mm, aperture 0.9 × 0.7 mm.

Distribution (fig. 16). — *G. farquhari* occurs over an enormous area in southeastern Africa from Port Alfred (Cape Province) in the south to Vila Manica (Mozambique) in the north, frequently in a discontinuous pattern, and also in the Ukaguru Mountains in East-Central Tanzania.

CAPE PROVINCE: Kowie (RMNH); Kowie East, S. Kincaid (NM); Bathurst (BM 1910.1.5.5, holotype of *Ennea hypsoma*; BM 1910.1.5.6, holotype of *Ennea oppugnans*; BM 1937.12.30.842-4, three paratypes of do.); Trappe's Valley, Bathurst, J. Farquhar (NM 2534); Grahamstown, J. Farquhar (BM 1903.3.11.49-50, holotype and paratype; BM 1914.12.19.11, paratype; BM 1903.3.11.58, holotype of *Ennea labyrinthea*; NM); do., S. Kincaid (NM); do., E. J. Langley (BM 1903.3.11.52-3, two syntypes of *Ennea microthauma*); do., ex H. B. Preston (RMNH); do., Dassie Krantz (BM 1910.1.5.11, holotype of *Ennea periploca*; BM 1937.12.30.845-7, three paratypes of do.); do., Mountain Drive (kloofs), J. Farquhar (NM 2556; NM); do., do., S. Kincaid (NM); do., Paradise Kloof, J. Hewitt (TP); Highlands, near Grahamstown (Connolly, 1939); Katberg forest (Connolly, 1939); Reed River, ca. 13 km E. of Port Alfred, J. L. B. Smith (SAM A 8131); East London, S. Kincaid (BM 1937.12.30.851-7; NM); Bashee River, W. Falcon (NM). NATAL: Backworth, Ntimbankulu, Mid-Illovo, H. C. Burnup (NM 2557); Durban, H. C. Burnup (BM 1914.12.19.13, paratype of var. *avena*; BM 1914.12.19.30-2, two paratypes of do.; BM 1937.12.30.848, paratype of do.; SAM A 3245, two paratypes of do.; SAM, paratype of do.); do., above King's House, H. C. Burnup (NM 2559, type 551, four paratypes of do.); do., W. G. Rump (NM); Pinetown, H. C. Burnup (NM type 551, two paratypes of do.); Pietermaritzburg (in-

[5]) This may lead to interpreting the dentition as six-fold instead of five-fold.

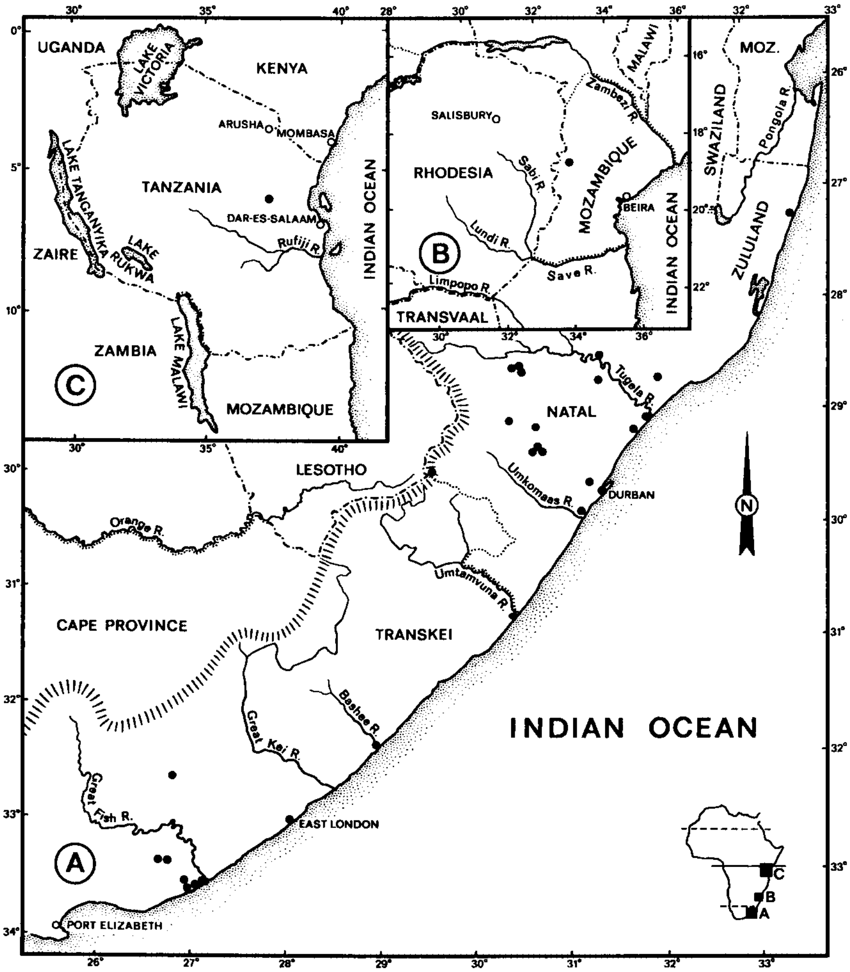


Fig. 16. Distribution of *Gulella farquhari* (M. & P.) in South Africa (A), in Mozambique (B) and in Tanzania (C). The Great (Eastern) Escarpment has been indicated by cross-hatching.

cludes Botanic Gardens), H. C. Burnup (BM 1914.12.19.12, holotype of var. *avena*; BM 1914.12.19.28-9, two paratypes of do.; BM 1937.12.30.849-50, two paratypes of do.; NM 2558, type 551, four paratypes of do.; NM type 551, two paratypes of do.; NM); Swartkop, NW. of Pietermaritzburg, W. Falcon (NM); Hilton, Morton's Bush, W. Falcon (NM); Karkloof (NE. of Howick: 29°25'S 30°20'E) (BM 1903.3.11.81, holotype of *Ennea berthae*); do., W. Falcon (NM, RMNH); do., J. McBean (NM 2549 [6]),

[6]) Not 1441 as recorded by Burnup (1914, specimen figured on pl. 14 figs. 25-27); Burnup had the somewhat exasperating habit of using provisional numbers, later to be replaced by proper catalogue numbers.

type 552, paratype of do.); do., Geikie's Farm, R. F. Lawrence (NM alc.); Nottingham Road, A. J. Taynton (NM type 551, paratype of var. *avena*; NM); Mt. Mkolombe, 28°53'S 30°08'E, H. P. Thomasset (NM); Bushman's River Falls, near Weenen, H. P. Thomasset (NM); do., 'Darkest Africa', ca. 11 km below Weenen, H. P. Thomasset (NM); south slope Platte Rand, Town Lands, Weenen, H. P. Thomasset (NM); Balquidden Farm, Weenen, H. P. Thomasset (NM); Hlonyana River banks, Tugela Estates, near Weenen, H. P. Thomasset (NM); Kranskop, W. Falcon (NM); Zimbaba Bush, Kranskop, H. C. Burnup (NM); Stanger, G. E. Pennington (NM); Sinkwazi (mouth), S. of Tugela River mouth, G. E. Pennington (NM; RMNH; TP). ZULULAND: Mfongosi, W. of Jameson's Drift, W. E. Jones (BM 1931.6.3.111-7; NM; TP); do., ex H. C. Fulton (RMNH); Eshowe, W. Falcon (NM); Lake Sibaya, coastal dune forest, C. C. Appleton (RMNH). MOZAMBIQUE: Mt. Vengo, N. of Vila Manica (formerly Macequece), B. Cressy (BM 1937.12.30.836-41; NM). TANZANIA: Mnyera Ridge, Ukaguru Mts. (near Nguru Mts.), D. J. Mabberley (RMNH).

Type locality: Grahamstown, where first collected by James Farquhar, a tailor's cutter, well-known shell collector and friend of Burnup, probably in the late 1890s.

G. farquhari exhibits a bewildering variability in size, shape, costulation, and number of whorls of the shell as shown by its complicated synonymy. The dentition is subject to some variation, but this is comparatively little. The species occurs from sea level to almost 1500 m in bush and forest in scattered and frequently isolated populations from Port Alfred at 33°36'S in the south to the Ukaguru Mts. at ca. 6°S in the north. The species seemingly prefers a cool, subtropical climate, since it is absent from hot areas such as the Natal south coast and southern Mozambique. The discovery in the Lake Sibaya area in the Zululand lowlands (Van Bruggen & Appleton, 1977: 30) therefore came as somewhat of a surprise. Ostensible absence may be due to it having escaped the attention of collectors by virtue of its small size. Mozambique and Tanzania have indeed not been sufficiently sampled for small terrestrial molluscs, which, however, can by no means be said about the Natal south coast. It is perhaps significant that the only records from Mozambique and Tanzania, generally hot, tropical countries, are from cool mountainous districts.

Very large series from throughout the range of the species have been available for the present study. A close scrutiny has revealed that it is impossible to maintain the varieties *avena* and *berthae*, although a first impression might point to the existence of a number of subspecies. However, the characters on which the varieties have been based are subject to such a large amount of variation, that it is impossible to assign all specimens to either *G. farquhari* s.s., the var. *avena* or the var. *berthae*. Extremes are easily separated, but many specimens are obviously intermediate.

A comparison of the various measurements shows the existence of a size cline from south to north:

Eastern Cape Province	1.9-3.2 × 0.9-1.4 mm, l/d 1.87-2.25, mean 2.06
Natal coast	2.3-3.5 × 1.1-1.6 mm, l/d 1.96-2.54, mean 2.25
Natal inland	2.7-3.6 × 1.2-1.6 mm, l/d 1.80-2.60, mean 2.20
Zululand	2.7-3.8 × 1.2-1.7 mm, l/d 2.00-2.54, mean 2.27
Mount Vengo	2.2-2.7 × 0.9-1.2 mm, l/d 2.25-2.44, mean 2.34
Ukaguru Mountains	3.0-3.6 × 1.3-1.5 mm, l/d 2.31-2.40, mean 2.35

The above table at the same time shows that while the fluctuations in l/d are enormous, the mean is pretty well much the same throughout Natal and Zululand. Mean length of the shell, however, shows a regular increase from south to north, except for the Mt. Vengo specimens: 2.5, 2.9, 3.1, 3.2, 2.4 (Mt. Vengo), and 3.3 mm respectively. The seven Mozambique shells are in more than one respect aberrant as regards measurements; they are not only comparatively small (being within the limits of the southernmost populations) but also very slender indeed, in fact as slender as their nearest relatives in Tanzania more than 1500 km to the north. The Tanzanian specimens smoothly fit into the above size cline, but show a somewhat different dentition (cf. Verdcourt's fig. 5 in his 1978 paper and figs. 13-15 in the present paper). The outer columellar lamella seems particularly poorly developed; Verdcourt (1978: 22) writes "the columella is longitudinally thickened, but it can hardly be said to bear a marginal process". Furthermore the shells are costulate and have a comparatively high number of whorls (7½-8, range for the species 4¾-8, without the Tanzanian specimens the range would be 4¾-7). Eventually both the Mozambique and Tanzania populations might be separated on a subspecific level; however, first of all we need some more material from these countries and the isolation of the populations should also be investigated.

Attention is drawn to a few peculiar specimens. A paratype of *Ennea oppugnans* (Bathurst, BM 1937.12.30.842-4) with 5½ whorls measures 3.5 × 1.3 mm, l/d 2.69; this is indeed abnormally slender, the slenderest shell in the area having an l/d of 2.25 and the next slenderest specimen known (Balquidden Farm, Weenen, NM) an l/d of 2.60. The shell from Bathurst is considered abnormal and it has not been incorporated in the above table. Two specimens from the Karkloof Falls (NM) are without basal process. Another sample from the Karkloof (RMNH, 10 shells), while all being mainly smooth or substriate, clearly demonstrates the variability in size and shape of the shell: 2.7-3.6 × 1.5-1.6 mm, l/d 1.83-2.23.

Gulella infrendens (Von Martens, 1866) (figs. 17, 18, 20)

Pupa infrendens Von Martens, 1866, Malak .Blätt., 13: 110, pl. 3 figs. 10-12.

Ennea infrendens; Pfeiffer, 1868, Monogr. Helic Viv., 5: 454; Pfeiffer, 1876, Monogr. Helic. Viv., 7: 504; Pfeiffer & Clessin, 1878, Nomencl. Helic. Viv.: 19; Tryon, 1885, Man. Conch., (2) 1: 98, pl. 19 fig. 86; Melvill & Ponsonby, 1898, Proc. Malac Soc. London, 3: 168; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 546 (10), 559 (23); Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 215, pl. 27 fig. 1; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 161; Connolly, 1912, Ann. S. Afr. Mus., 11: 76.

Gulella infrendens; Connolly, 1932, Ann. Natal Mus., 7: 75; Connolly, 1939, Ann. S. Afr. Mus., 33: 88; Van Bruggen, 1969, Zool. Verh. Leiden, 103: 51, fig. 18.

Ennea foriclusa Melvill & Ponsonby, 1901, Ann. Mag. Nat. Hist., (7) 8: 316, pl. 2 fig. 3; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 236, pl. 32 fig. 23; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 54; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 160; Connolly, 1912, Ann. S. Afr. Mus., 11: 74.

Ennea claustraria Melvill & Ponsonby, 1903, Ann. Mag. Nat. Hist., (7) 12: 597, pl. 31 fig. 16; Connolly, 1912, Ann. S. Afr. Mus., 11: 69.

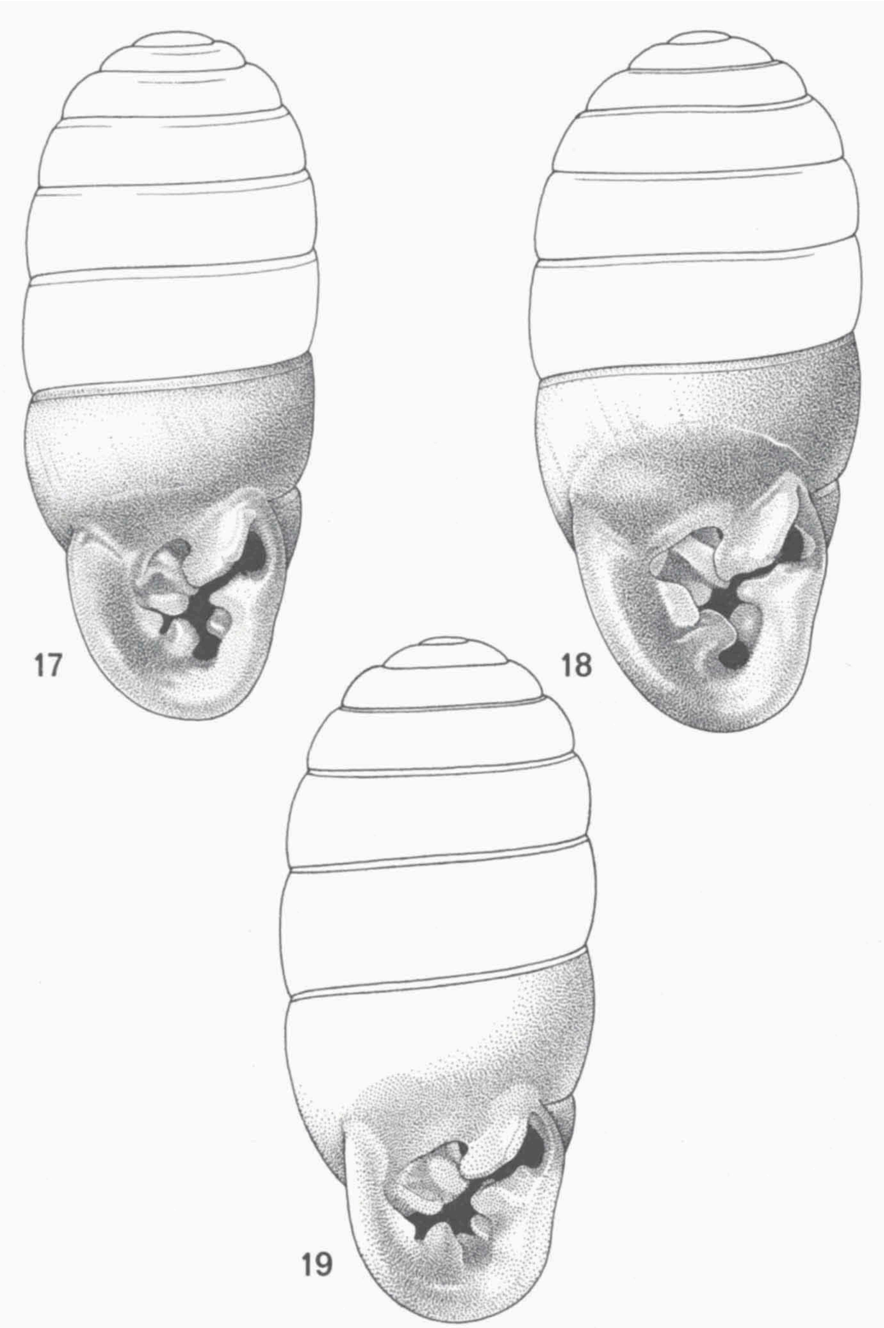
Ennea stauroma Melvill & Ponsonby, 1907, Ann. Mag. Nat. Hist., (7) 19: 96, pl. 6 fig. 4; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 55; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 162.

Diagnostic characters. — A medium-sized, smooth species with six-fold dentition consisting of angular lamella, two labral processes, a basal denticle, outer (frequently absent) and inner columellar lamellae.

Description of shell. — Shell (figs. 17-18) medium-sized, cylindrical to ovate, rimate. Spire produced, sides straight and (sub)parallel to somewhat convex, apex obtusely conical. Whorls 6¼-8, slightly convex, smooth; sutures shallow, simple. Aperture much obstructed by six-fold dentition: strong, oblique angular lamella, connected with apex of labrum; upper labral process an inrunning ridge, angulate at both apices, corresponding to shallow outside depression, lower labral process a squarish, deeply set denticle; basal process a usually squarish denticle to the left of base, corresponding to small outside depression; outer columellar lamella a slab low on the columellar lip, frequently reduced in size to complete absence, inner columellar lamella large and prominent, with at least one plica.

Measurements of shell: 5.2-9.1 × 2.5-4.4 mm, l/d 1.78-2.54. The type was said to be 7.0 × 3.5 mm, l/d 2.00 (Connolly, 1939: 88). Smallest shell (Van Staadens River, NM) 5.2 × 2.5 mm, l/d 2.10, next smallest shell (Kelso, NM alc.) 5.9 × 2.9 mm, l/d 2.04, largest specimen (Table Mountain, NM) 9.1 × 4.4 mm, l/d 2.08. An average specimen (Kelso, RMNH) measures 6.5 × 3.0 mm, l/d 2.17, aperture 2.1 × 2.1 mm, last whorl 3.4 mm.

Distribution (fig. 20). — *G. infrendens* occurs along the coast from the Eastern Cape Province to northern Zululand and also some distance inland.



Figs. 17-19. Shells of 17, *Gulella infrendens* (Mts.) (length 7.9 mm, Durban, Burman Bush, NM); 18, do. (length 7.0 mm, Dimera Dell, Hilton Dist., RMNH); and for comparison 19, *G. daedalea* (M. & P.) (length 7.6 mm, Lower Umfolosi Drift, NM 1474).

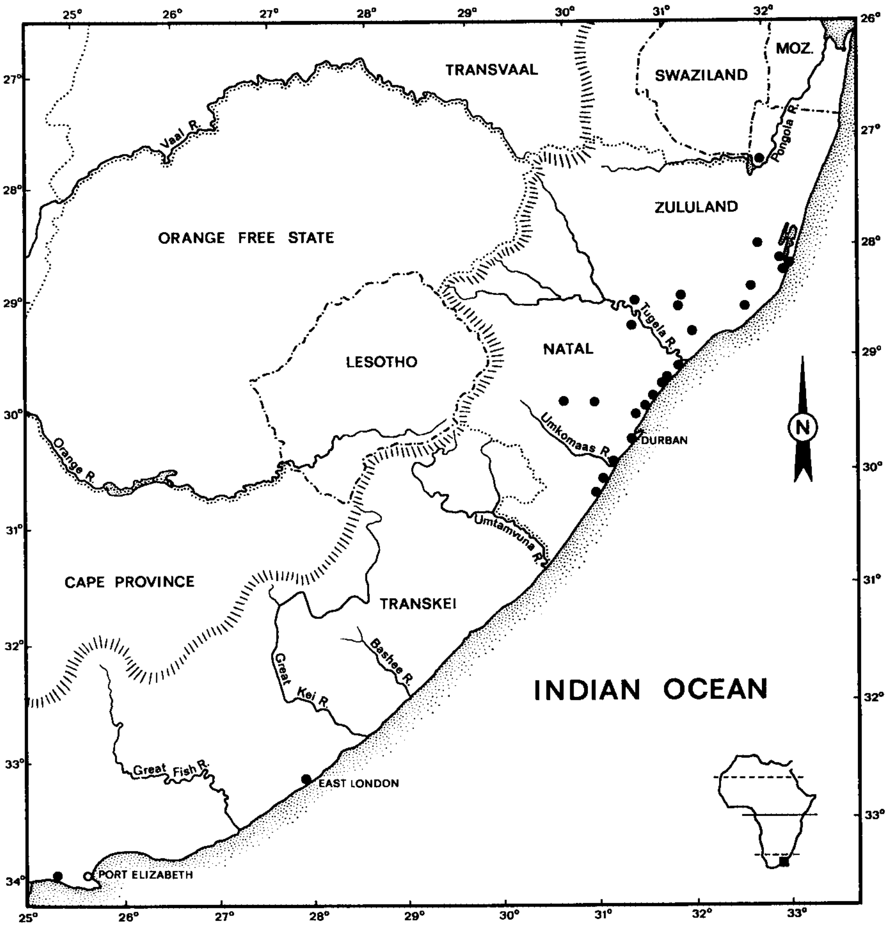


Fig. 20. Distribution of *Gulella infrendens* (Mts.); *G. daedalea* (M. & P.) is restricted to the eastern Zululand lowlands (Van Bruggen, 1969: fig. 18). The Great Escarpment has been indicated by cross-hatching.

CAPE PROVINCE: Gorge near pumping station, Van Staadens River (W. of Port Elizabeth at 33°53'S 25°12'E), J. Farquhar (NM); East London (SAM A 30003). NATAL: Kelso (Junction), W. Falcon (RMNH); do., R. F. Lawrence (NM alc.); Clansthal, between Scottburgh and Umkomaas, W. Falcon (NM); Illovo River c.q. Beach, H. C. Burnup (NM); Durban (includes Beachwood, Burman Bush, Greenwood Park, Morningside, and Westville), O. Bourquin (NM); do., Miss M. F. Hickey (NM); do., H. E. van Hoepen (RMNH; vH); do., R. F. Lawrence (NM alc.); do., H. J. Puzey (BM 1931.6.3.121-4); do., Macandrew colln. (BM); Table Mountain on the Umgeni River, ca. 48 km E. of Pietermaritzburg, H. C. Burnup (BM 1903.3.11.74, holotype of *Ennea foriclusa*; NM 1430, type 553, paratype of do., NM); Hilton (includes Dimera Dell in the Hilton district and Morton's Bush), H. C. Burnup (NM); do., W. Falcon (NM; RMNH); Tongaat, H. C. Burnup (NM; TP); Compensation Beach near Verulam, E. Perks (NM); Umhlali (includes Chaka's Rock and Sheffield Beach), R. F. Lawrence (NM, NM alc.; RMNH alc.); do., A. D. J. Meeuse (NM, NM alc.;

RMNH); do., W. G. Rump (NM); Stanger, G. E. Pennington (NM); Blythdale Beach near Stanger, H. E. van Hoepen (RMNH; vH); Sinkwazi, S. of Tugela River mouth, G. E. Pennington (NM); Kranskop (includes Zimbaba Bush), H. C. Burnup (BM 1937.12.30.963-6; NM, NM alc.); do., W. Falcon (NM); do., R. F. Lawrence (NM alc.); do., E. Warren (NM); "Natal", ex H. B. Preston (RMNH). ZULULAND: Mfongosi (W. of Jameson's Drift), Eshowe, Ngoye Forest (28°50'S 31°42'E), Umhlatuzi Drift (Nkandhla, W. of Melmoth), Melmoth, Kwa-Mbonambi, Lower Umfolosi Drift, Dukuduku Forest (W. of St. Lucia), St. Lucia (Bay), Hluhluwe Game Reserve, Gwaliweni Forest (S. of Ingwavuma), "Zululand" (all fide Van Bruggen, 1969: 51; in BM, DM, NM, NM alc., RMNH, SAM; includes holotypes of both *Ennea claustraria* and *E. stauroma*, both in BM, and a number of paratypes of both taxa in various collections); Charter's Creek, St. Lucia Game Reserve, A. C. and W. H. van Bruggen (RMNH).

Type locality: Natal, here emended to Durban, where first collected by Wilhelm Gueinzius [7]) between 1830 and 1866.

The species was not found in the Lake Sibaya area (Van Bruggen & Appleton, 1977). Before Appleton's survey of this part of Zululand occasional material had been received by the present author, but *G. infrendens* has never been found to be present.

G. infrendens occurs in coastal bush and forest and inland in indigenous forest. One of the Charter's Creek specimens was found inside an otherwise empty *Archachatina* shell (see Van Bruggen, 1966: 393, for the ecological importance of empty shells of achatinids).

The shell of *G. infrendens* is subject to a bewildering variation, particularly in apertural dentition. Surprisingly there are only three synonyms, but this is the kind of terrestrial snail that will make the beginning student want to throw up his cards in despair. However, a closer examination reveals certain regularities. The outer columellar lamella shows the greatest range of variation, from complete absence to a large, superficial slab. It may be as large as or even larger than the adjoining basal process; the latter varies in shape and is sometimes squarish in front view. There is a correlation between geographical distribution and development of the outer columellar lamella as shown below. First of all the localities are enumerated along the coast from south to north:

Van Staadens River-Kelso	poorly developed or absent
Clansthal-Durban	poorly and well developed in about equal proportions
Tongaat-Sinkwazi	well developed (absent in about 1 in 14)
Lower Umfolosi Drift-St. Lucia	absent or rarely poorly developed

7) Spelling according to Gebhardt (1964); also spelled Queinzius, e.g., by Pfeiffer (1868).

This shows that optimal development of this process along the coast is only found between Durban and the Tugela River; in Zululand coastal populations it is close to being absent altogether. The picture of inland lolocalities is as follows:

Table Mountain-Hilton	well developed
Kranskop	well developed
Mfongosi	well developed (absent in about 1 in 14)
Eshowe, Nkandhla, Melmoth	absent
Gwaliweni Forest	absent

Except at Mfongosi in the extreme south no Zululand population has a well developed outer columellar lamella in its shells; in rare cases this process may be poorly developed. A single specimen from the Ngoye Forest near Eshowe (NM) is somewhat aberrant in having basal and outer columellar processes merged into one large slab, squarish in front view.

There is also a good deal of variation in the labral area of the aperture. In one shell (Umhlali, NM) a slightly tripartite angular lamella was found. Sometimes there are indications of a sinular swelling (almost always in Zululand shells only: Melmoth, NM; St. Lucia, DM; Hluhluwe Game Reserve, BM; Gwaliweni Forest, NM), which in one specimen has developed into a sinular denticle (Melmoth, NM). In one case the upper labral process has become tricuspidate (Eshowe, NM); now and then a small swelling superficial to the lower labral process is found, such as e.g., in some Kranskop specimens.

There is a noticeable size cline in the shells from south to north as shown by the following data (localities along the coast from south to north):

Van Staadens River-Kelso	5.9-6.6 × 2.5-3.0 mm, l/d 1.96-2.22
Clansthal-Durban	6.1-7.7 × 3.1-3.4 mm, l/d 1.85-2.30
Tongaat-Sinkwazi	5.7-8.9 × 2.9-3.5 mm, l/d 1.78-2.36
Umfolosi-St. Lucia	6.0-8.1 × 3.2-3.7 mm, l/d 1.81-2.38

Or, expressed in mean values: 6.2 × 2.7 mm, l/d 2.09; 6.9 × 3.2 mm, l/d 2.07; 7.2 × 3.1 mm, l/d 2.07; 7.0 × 3.5 mm, l/d 2.09. This shows that there is a steady increase in length and major diameter of the shells from south to north, while at the same time the l/d is more or less constant.

Inland populations present another picture:

Clansthal-Sinkwazi (coast)	5.7-8.9 × 2.9-3.5 mm, l/d 1.78-2.36
Table Mountain-Hilton	6.9-9.1 × 3.1-4.4 mm, l/d 1.96-2.28
Kranskop	6.9-8.5 × 3.6-3.9 mm, l/d 1.84-2.19
Mfongosi	6.0-7.7 × 3.1-3.6 mm, l/d 1.78-2.14
Eshowe, Ngoye Forest	6.1-8.4 × 3.2-4.3 mm, l/d 1.88-2.17
Nkandhla, Melmoth	6.0-6.6 × 3.0-3.2 mm, l/d 1.85-2.12
(Gwaliweni Forest, 1 shell	7.9 × 3.4 mm, l/d 2.33)

This shows first of all that there is a size cline in the shells from the coast inland (east to west) as demonstrated by the first two groups of localities, showing mean values of 7.3 × 3.2 mm, l/d 2.07 (coast) and 8.0 × 3.7 mm, l/d 2.12 (Table Mountain-Hilton = Pietermaritzburg district) respectively. Obviously the inland shells are not only larger, but also more slender than their coastal counterparts. Kranskop shells are on the average smaller and more obese: mean 7.7 × 3.7 mm, l/d 2.01. On the other hand, specimens from Mfongosi (opposite Kranskop on the north bank of the Tugela River) are little different from coastal ones, except perhaps in being a bit more obese: mean 6.8 × 3.3 mm, l/d 1.96. Data from other inland localities in Zululand are somewhat confusing; the single shell from the Gwaliweni Forest is the largest known inland specimen in Zululand.

A comparison of the above data shows that there is also a correlation of size of the shell and development of the outer columellar lamella, viz., Table Mountain-Hilton (largest known shells of the species, well developed lamella), Kranskop (second largest shells, well developed lamella) and Tongaat-Sinkwazi (largest shells on the coast, well developed lamella). The only remaining population with shells with a well developed outer columellar lamella, viz., those from Mfongosi, is on the other hand characterized by comparatively small shells. As has been shown above the material from Mfongosi is obviously somewhat aberrant in more than one respect. Dr. H. E. van Hoepen has also collected in this district and has obtained some peculiar material, which may not even belong to the species under discussion. More data are needed and a survey of what is left of undisturbed habitat on both sides of the lower Tugela River is certainly bound to be of great interest. In this respect reference should be made to an important paper by Benson, Irwin & White (1962) on the significance of river valleys as avian zoogeographical barriers. Looking at the shells of *G. infrendens* from both sides of the Tugela River one might surmise for both sets of populations dispersal from the coast (east to west) rather than across the river (south to north).

G. infrendens is not easily differentiated from *G. daedalea* (Melvill & Ponsonby, 1903); this is treated in detail in Van Bruggen (1969: 50-53).

Details are not repeated here; the most essential character in the shell is the presence of an inner basal denticle (shown in fig. 19 behind and slightly to the left of the basal process) in *G. daedalea*. Fig. 19 as compared to figs. 17 and 18 shows *G. daedalea* to have a triangular rather than squarish (outer) basal denticle; this character, however, is not completely reliable. *G. infrendens* and *G. daedalea* are largely allopatric in their distribution, *G. daedalea* being restricted to the eastern Zululand lowlands (Van Bruggen, 1969: fig. 18, p. 52).

Gulella planti (Pfeiffer, 1856) (figs. 21-24)

Ennea planti Pfeiffer, 1856, Malakozool, Blätt., 2: 173; Pfeiffer, 1856, Novit. Conch., 1: 72, pl. 20 figs. 5-6; Pfeiffer, 1859, Monogr. Helic. Viv., 4: 337; Pfeiffer, 1868, Monogr. Helic. Viv., 5: 452; Pfeiffer, 1876, Monogr. Helic. Viv., 7: 500; Pfeiffer & Clessin, 1878, Nomencl. Helic. Viv.: 18; Kobelt, 1879, Ill. Conchylienb., 2: 209, pl. 64 fig. 19; Tryon, 1885, Man. Conch., (2) 1: 90, pl. 17 fig. 25; Melvill & Ponsonby, 1898, Proc. Malac. Soc. London, 3: 168; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Wien Math.-Naturw. Cl., 67: 542 (6), 552 (16), pl. 1 fig. 1; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 178, pl. 22 figs. 23-24; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 53; Connolly, 1912, Ann. S. Afr. Mus., 11: 83; Dautzenberg & Germain, 1914, Rev. Zool. Afr., 4: 11; Germain, 1920, Voy. Babault Afr. Or. Angl.: 65.

Pupa planti; Sowerby, 1875, Conch. Icon., 20, *Pupa*: pl. 18 fig. 169.

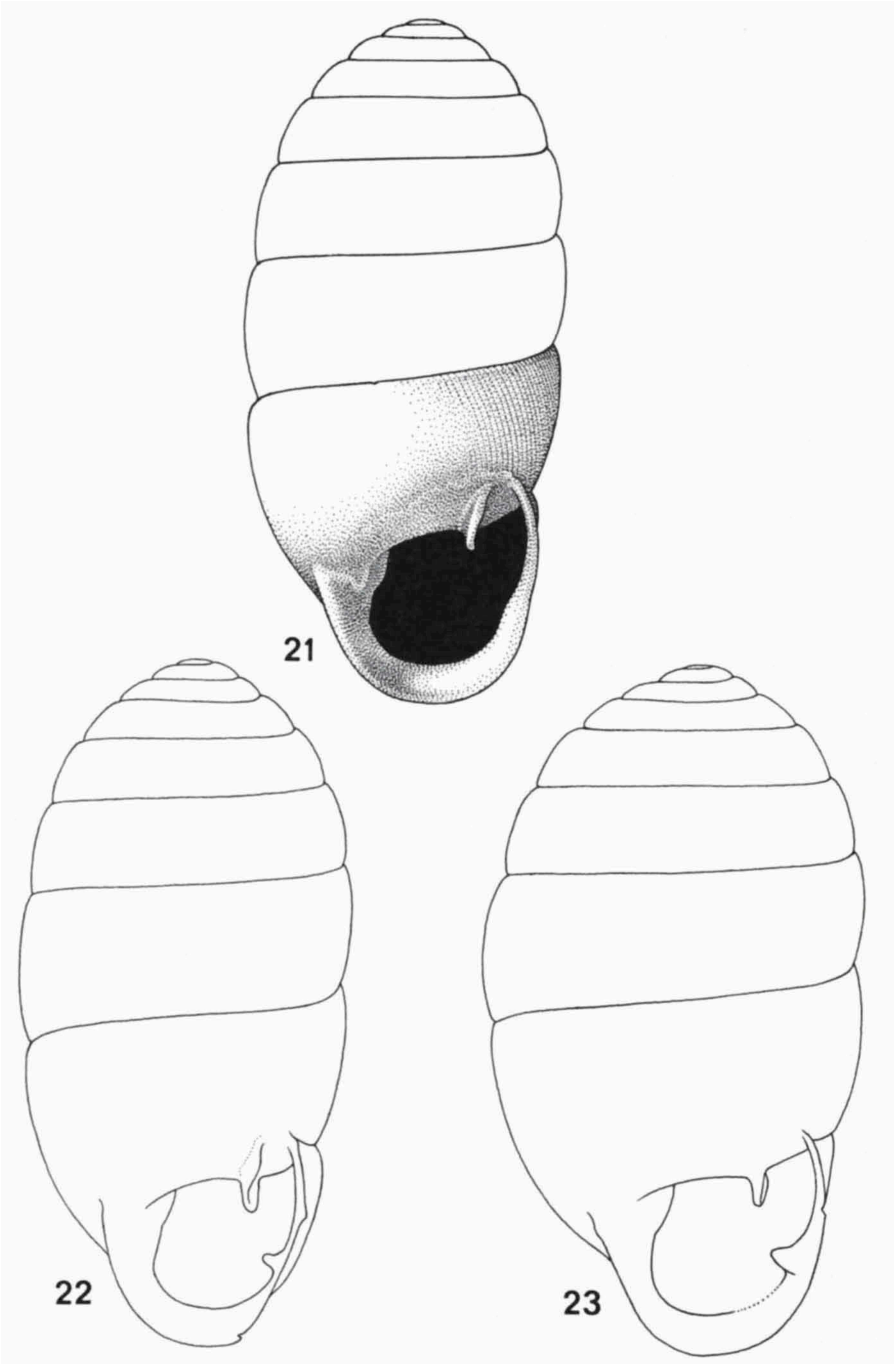
Enneastrum planti; Bourguignat, 1889, Moll. Afr. Équat.: 127.

Gulella planti; Pilsbry & Cockerell, 1933, Proc. Zool. Soc. London, 1933: 365; Connolly, 1939, Ann. S. Afr. Mus., 33: 23; Barnard, (1951), Beginner's Guide S. Afr. Shells: pl. 21 fig. 4; Krauss, 1964, Nautilus, 78: 23 ("*Gulella* sp. probably *G. planti*"); Van Bruggen, 1969, Zool. Verh. Leiden, 103: 58; Van Bruggen, 1973, Malacologia, 14: 423; Van Bruggen, 1978, Biogeogr. Ecol. S. Afr., (2): 902; Mead, 1979, in Fretter & Peake, eds., Pulmonates, 2B: 57.

Diagnostic characters. — Largest species south of the Zambesi River, shell weakly costulate with little obstructed aperture with normally two-fold dentition consisting of single angular lamella and columellar processes.

Description of shell. — Shell (figs. 21-23) large, acuminate ovate or subcylindriform, rimate or with closed umbilicus, smooth and glossy. Spire produced, sides convex, apex blunt, broadly rounded. Whorls 7¼-8½, almost flat, sculptured with weak oblique costulae; sutures shallow, simple, subcrenellate. Aperture large and open, little obstructed by two or rarely three processes: a comparatively thin angular lamella, widely distant from apex of labrum, rarely a small and acute labral process, and a poorly developed shelf-like columellar lamella.

Measurements of shell: 12.7-21.5 × 7.0-10.0 mm, l/d 1.74-2.22. The type was said to measure 16.0 × 9.0 mm (fide original description). Smallest shells (Amahlongwa-Widenham, MMK) 12.7 × 7.0 mm, l/d 1.81, and



Figs. 21-23. Shells of *Gulella planti* (Pfr.); 21, Durban (length 18.2 mm, NM 2091); 22-23, Amahlongwa-Widenham (length 14.5 and 12.7 mm respectively, MMK).

(Natal, RMNH) 14.3 × 8.2 mm, l/d 1.74, largest shell (Zimbaba Bush, NM) 21.5 × 9.7 mm, l/d 2.22. An average specimen (Durban, NM) measures 17.8 × 9.0 mm, l/d 1.98, aperture 5.8 × 6.2 mm, last whorl 8.6 mm.

Distribution (fig. 24). — *G. planti* occurs in a somewhat restricted area on the coast of Natal and Zululand from south of Durban to north of the Tugela River and some distance inland.

NATAL: Railway cutting near Amahlongwa-Widenham (S. of Umkomaas), J. A. Swan (MMK; RMNH); Durban (includes Burman Bush, Stamford Hill, Stella Bush, The Bluff, Umbilo Road), O. Bourquin (NM); do., H. C. Burnup (BM; NM, NM alc.; RMNH); do., W. Falcon (NM); do., R. F. Lawrence (NM); do., H. J. Puzey, Falcon colln. (NM); do., J. F. Quekett (NM 1425; NM); do., F. Toppin (NM alc.); do., Mrs. M. Trotter (NM 2091); do., no collector (BM; MCZ; NM); Drummond, Valley of a Thousand Hills, R. F. Lawrence (NM); Tongaat (Connolly, 1912); Kranskop, W. Falcon (DM, Puzey colln. 80; NM); do., R. F. Lawrence (NM); Untunjambili (Kranskop), H. C. Burnup (NM); Zimbaba Bush (Kranskop), H. C. Burnup (NM

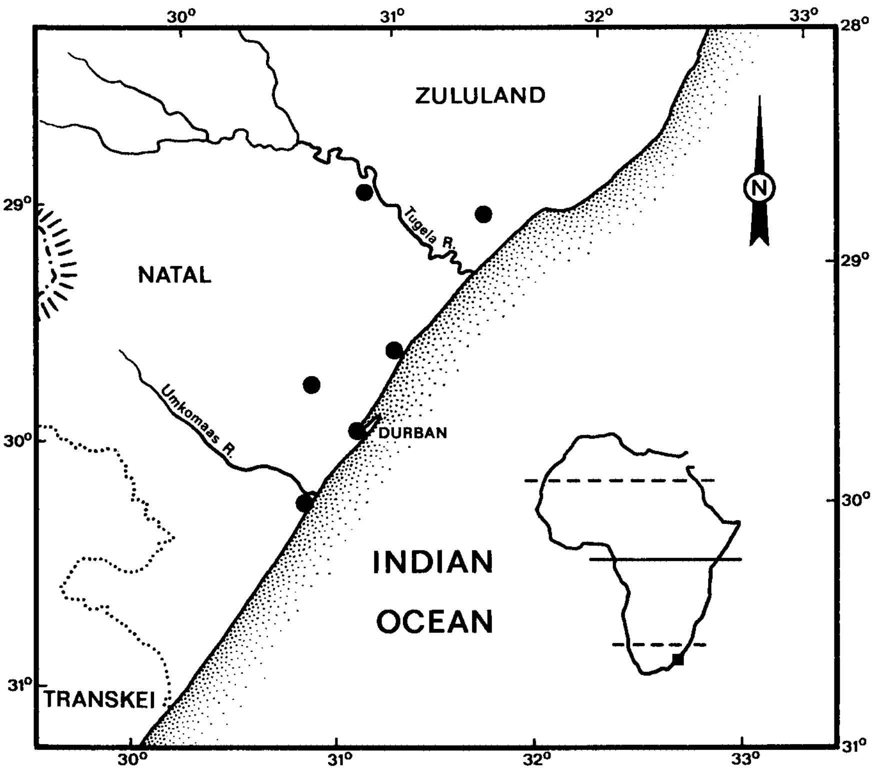


Fig. 24. Distribution of *Gulella planti* (Pfr.). The two Zululand localities are close together and are indicated by one dot only. The Great Escarpment has been indicated by cross-hatching.

3349, 3404, 3405; NM); "Natal" (BM 1929.2.27.1-7; BM; NM; RMNH; TP; ZMA). ZULULAND: Umhlatuzi near Eshowe, H. W. Bell-Marley (NM); Mtimona (28°42'S 31°42'E, E. of Melmoth), H. J. Puzey (BM 1956.6.8.34-41).

Type locality: "Natal", here restricted to Durban, The Bluff, where first collected early in the second half of the 19th century (by R. W. Plant?) and possibly still locally extant.

A record from Port Elizabeth (Germain, 1920: 65) has been ignored; very probably Durban, formerly known as Port Natal, is meant here, because the collector Guy Babault obviously travelled by steamer around the Cape, calling at the various ports on the way to East Africa. Two shells (CNHM 36776) are labelled "Vaal River Colony"; these specimens are from the W. F. Webb collection and the reverse side of the original label reads "from Burnup". The name 'Vaal River Colony' would refer to the Transvaal, which South African province borders on Natal; the only area which may be considered in the context of the known distribution of the species under discussion is the Pongola corridor near the southeastern tip of Swaziland. This area, however, is very far from the nearest known localities in Zululand; moreover, if the material indeed derived from Burnup there would have been other specimens in e.g., the Natal Museum. Therefore this record has also been ignored.

G. planti, southern Africa's largest species of the genus, was originally described in a footnote. The name is usually dated 1855. This is incorrect, because Pfeiffer's paper was published in two parts in 1855-1856; the description of *G. planti* appears in the pages published in 1856. The species was named after Robert William Plant, curator of the Durban Botanic Gardens, 1854-1856. According to Connolly (1939: 24) Pfeiffer's type was in the Stettin museum, where it was destroyed in the Second World War (Dance, 1966; see also Van Bruggen, 1969: 67).

Even outside southern Africa few species are larger than *G. planti*. Among these are *G. grossa* (Mts.) (continental Tanzania, shell up to 22 mm long) and *G. porcina* Conn. (Uganda, shell up to 22 mm long). A few species equal *G. planti* in size, such as *G. hector* (Prest.) (Kenya, shell up to 20 mm long).

The continued existence of *G. planti* is much threatened because of bush clearance on the coast of Natal, which in view of its restricted range may become fatal to the species. Connolly's sweeping statement (1939: 24) "Widely distributed over the southern districts [i.e., in Natal]" is not confirmed by the localities of the material here studied.

G. planti is subject to comparatively little variation in the shell. The sculpture varies from fairly well marked to close on complete absence. The dentition shows somewhat more variation. Two specimens are noticeable for a poorly developed (Natal, RMNH) and a curiously divided angular lamella (Durban, NM 1425) respectively. In a sample labelled 'Natal' (RMNH, ex Falcon colln.) many shells have a faint indication of a swelling on the labrum. Only in the population sampled by Swan at Amahlongwa-Widenham (MMK, duplicates in RMNH, figs. 22-23) a small and acute labral denticle at about the middle of the labrum is consistently present among the ten adult shells studied.

A well-marked size cline may be discerned from south to north:

Umkomaas area	12.7-14.6 × 7.0-7.3 mm, l/d 1.81-2.09 (mean 1.95)
Durban area	15.1-19.0 × 8.1-9.1 mm, l/d 1.76-2.16 (mean 1.96)
Kranskop area	18.8-21.5 × 9.4-10.0 mm, l/d 1.96-2.22 (mean 2.09)

The increase in length (mean 13.6, 17.0 and 20.1 mm respectively) and width (mean 7.1, 8.6 and 9.7 mm respectively) is noticeable, particularly because the overlap of the range of measurements is very small indeed. In fact, only the maximum length of Durban area shells slightly overlaps (i.e., 0.2 mm only) the minimum length of Kranskop specimens. Values for the l/d are different; the ranges of both Umkomaas and Durban areas show a complete overlap without difference in mean values. The overlap for the Kranskop area shells is considerably smaller and the mean value noticeably higher, which means that Kranskop specimens are not only relatively larger, but also comparatively more slender than specimens from elsewhere.

The combination of differences in numerical data and apertural dentition (albeit in dentition only for the southernmost form) raises the question whether one should distinguish the three forms as subspecies or not. Size clines imply contiguous populations, subspecies on the other hand discontinuous populations. The Umkomaas and Durban sensu lato populations presumably must have been or still are in contact, the Kranskop populations are certainly now isolated and may have been so for some considerable time. The odd fact is that, apart from size differences, the Kranskop material cannot be separated from that from other localities, while the Umkomaas area specimens may be distinguished by both numerical data and the presence of an additional denticle. The few Zululand specimens are close to those from the Durban area. For the time being this question is best left in abeyance. In view of the environmental threats to this particularly interesting species its status should be investigated throughout its range; such studies should yield additional material that may throw more light on the above problem.

Many species of the genus *Gulella* appear to have restricted ranges (cf. Van Bruggen, 1973). In many cases this is probably due to insufficient material because of a combination of factors such as remote localities, small size and a cryptic life, etc. *G. planti*, however, has a comparatively very large size and its range cannot be considered to be remote at all. Therefore its natural range is obviously very restricted and must have covered parts of what is now the sprawling city of Durban. Attention should be drawn to two aspects of the species, viz., its limited apertural dentition and its large size. A large aperture little obstructed by dental processes may be an ancestral feature (see Van Bruggen, 1967, 1973: 423); on the other hand the large size is possibly a derived character. A narrowly restricted range is usually associated with an isolated location or adaptation to a unique local situation. Extinction elsewhere may also have contributed to the size of the present range. Finally new taxa that have not yet had the time to expand also occupy a restricted area (cf. Mayr, 1949: 159). None of these factors seems to apply to the case of *G. planti*, although it may be adapted to a unique local situation — after all, it shares its habitat (coastal bush and kindred types of vegetation) with a number of other species of *Gulella*, very few of which have shells of over 12 mm long.

Gulella vicina (Smith, 1899) (figs. 25-27)

Ennea (*Gulella*) *vicina* E. A. Smith, 1899, Proc. Zool. Soc. London, 1899: 580, pl. 33 figs. 1-2; Kobelt, 1904, Syst. Conch. Cab., 1, 12B (1): 225, pl. 28 figs. 4-5; Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 55; Kobelt, 1910, Jahrb. Nass. Ver. Naturk. Wiesbaden, 63: 162.

Gulella vicina; Connolly, 1922, Ann. Mag. Nat. Hist., (9) 10: 499; Connolly, 1939, Ann. S. Afr. Mus., 33: 72; Verdcourt, 1957, Rev. Zool. Bot. Afr., 55: 125 sqq., fig. 1; Verdcourt, 1962, Ann. Mus. Roy. Afr. Centr. (8°) Sci. Zool., 106: 35; Van Bruggen, 1973, Malacologia, 14: 421, 425.

Diagnostic characters. — A medium-sized to large species with eleven-fold dentition consisting of parietal process, angular lamella, three labral processes, three basal processes and triplicate columellar lamella.

Description of shell. — Shell medium-sized to large, cylindrical, rimate. Spire produced, sides straight to slightly convex, (sub)parallel, apex obtusely conical. Whorls 6¼-7, slightly convex, sculpture varying from strong, regular and close costulae to weak striolae below the sutures, behind the labrum and around the umbilicus; sutures shallow, simple to crenellate. Aperture with eleven-fold dentition: a small, mid-parietal denticle; medium-large, oblique angular lamella, connected with apex of labrum; labral complex consisting of three processes on a common base, upper denticle a mere cusp, middle denticle larger and opposite upper columellar denticle, lower denticle largest and most prominent, complex corresponding to deep and extensive outside depression; three basal denticles, left one less deeply set than others; prominent, triplicate columellar lamella.

Measurements of shell: 5.1-9.0 × 2.3-4.6 mm, l/d 1.96-2.30. The lectotype, selected from BM 96.12.31.7-16 (syntypes from Mt. Chiradzulu, Malawi, Sir H. H. Johnston) measures 6.9 × 3.3 mm, l/d 2.09, 6 whorls; this is closest to Smith's description giving 7.0 × 3.5 mm, 6½ whorls.

Distribution. — *G. vicina* occurs from eastern Rhodesia to Samburu and the Taru Desert in central-northern Kenya and as far west as eastern Zaïre.

Type locality (see lectotype designation sub Measurements): Mount Chiradzulu, where first collected between 1893 and 1896 at 5000 ft. (= ca. 1500 m) by Alexander Whyte for Sir Harry Johnston [8]).

G. vicina reaches its southernmost limits in the Rhodesian Eastern Escarpment south of the Zambezi River. These southern populations are characterized by large, slender shells with strong costulation, apical spiral sculpture, and apertural dentition without a mid-parietal process. These characters correlated with the comparative isolation of the localities, strongly suggest the case of a separable subspecies, particularly in view of the differences of the material from the nearest known localities. The distance between Umtali (Mt. Vumba) and Mt. Chiradzulu (Malawi, type locality and southermost known record north of the Zambesi) is about 475 km and the species almost certainly does not occur in the interlying hot and dry Zambesi valley. This wide low-lying valley generally has a low rainfall (400-800 mm mean annual rainfall) and enjoys comparatively high temperatures resulting in a type of vegetation utterly different from that of the Rhodesian Eastern Escarpment and that of the mountains in southern Malawi. These mountainous areas show close similarities in climate and vegetation and also in fauna. The significance of the Zambezi valley as a faunal barrier has been discussed by, e.g. Benson, Irwin & White (1962). Related data are found in other relevant papers referring to, e.g. the climate (Schulze & McGee, 1978), the afromontane forest (White, 1978), the avifauna (Winterbottom, 1978); see also most other chapters in the treatise edited by Werger (1978).

Malawi material of *G. vicina* examined by the present author (BM, NM, RMNH) may be summarized as 6.0-7.0 × 3.2-3.4 mm, l/d 1.96-2.09; all specimens show the mid-parietal process and only have a weak costulation. Malawi and Rhodesia specimens are thus easily separated. Large shells are also known from further north (see, e.g. Verdcourt, 1962: 35, Mfwangano Island, Lake Victoria, Kenya, 8.5-9.0 × 4.0 mm, l/d 2.12-2.25), but these

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8) Sir Harry Hamilton Johnston (1858-1927), eminent "administrator/soldier/explorer/naturalist/author and painter" (church tablet in Poling near Arundel, Sussex, England), discoverer of the okapi and at that time officially "Commissioner and Consul-General for the territories under British influence to the north of the Zambezi" (Oliver, 1957: 10), resident at Zomba, Nyasaland (now Malawi).

usually have a noticeably different dentition. An average Malawi shell is shown in fig. 25.

It is now proposed to consider the material from south of the Zambezi to represent a new subspecies:

Gulella vicina luci nov. subspec. (figs. 26-27)

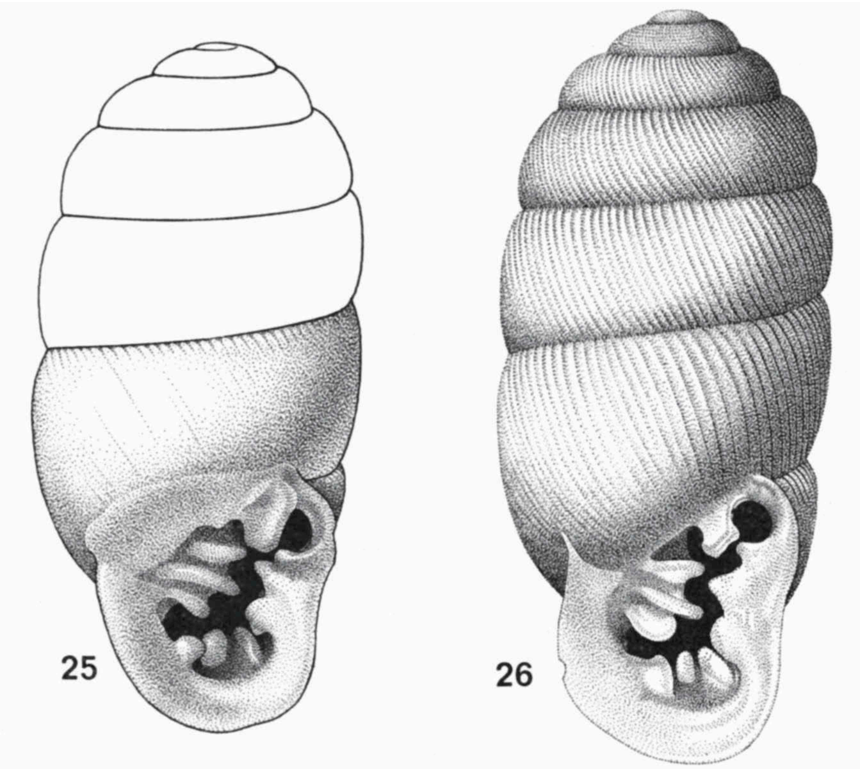
Gulella vicina; Connolly, 1939, Ann. S. Afr. Mus., 33: 72.

Diagnostic characters. — A large, strongly costulate, subspecies of *Gulella vicina* with apical spiral sculpture and without mid-parietal process.

Description of shell. — See sub Description of shell for the species, Diagnostic characters (see above) and Measurements of shell (see below).

Animal yellow (field notes).

Measurements of shell: 7.9-8.9 × 3.6-3.9 mm, l/d 2.17-2.30. The type measures 8.4 × 3.7 mm, l/d 2.23, aperture 3.1 × 2.9 mm, last whorl 5.0 mm,



Figs. 25-26. Shells of *Gulella vicina*; 25, *G. v. vicina* (Smith) (length 6.6 mm, Nyasaland = Malawi, RMNH); 26, *G. v. luci* nov. subsp. (holotype, length 8.4 mm, Mt. Selinda, NM).

6¼ whorls. Smallest shell (Vumba, NM alc.) 7.9 × 3.6 mm, l/d 2.17, largest shell (Mount Selinda, NM alc.) 8.9 × 3.9 mm, l/d 2.29.

Distribution (fig. 27). — *G. vicina luci* is so far only known from the Rhodesian Eastern Escarpment.

RHODESIA: Mount Selinda, Chirinda Forest, V. Fitzsimons (NM alc., holotype, one paratype); Mount Vumba (near Umtali), B. R. Stuckenberg (NM alc., one paratype); do., Laurenceville, ca. 1400 m (4500 ft.), A. C. and W. H. van Bruggen (NM alc., two paratypes; RMNH alc., one paratype).

Type locality: Mount Selinda, Chirinda Forest (see Van Bruggen, 1961), where first collected by the late Dr. Vivian F. M. Fitzsimons, noted herpetologist and director of the Transvaal Museum (1947-1966), in December 1937.

The species was first collected south of the Zambezi at Mount Vumba by Dr. George Arnold, entomologist and director of the National Museum, Bulawayo (Rhodesia), 1911-1947, probably early in the thirties (Connolly, 1939: 72, material not traced).

G. vicina luci in Rhodesia occurs in heavy forest (*lucus*, Lat., sacred forest), which may be considered transitional rain forest (White, 1978: 484) or the southernmost outliers of the tropical rain forest in Africa (Van Bruggen, 1961). The Chirinda Forest is situated at ca. 1100 m (3600 ft.), the locality on Mount Vumba at ca. 1400 m (4500 ft.); at the latter spot the specimens were collected on rotting leaves on top of large boulders in the forest. Elsewhere in Africa the species is also known to occur in high rainfall areas with forest type vegetation, although it has been recorded from a semi-arid area in northern Kenya at the northern limits of its distribution. In the latter area, however, there are small pockets of suitable habitat.

G. vicina is a very widely distributed species; particularly in East Africa it exhibits an almost bewildering variation in shell morphology. Verdcourt (1957) has attempted to sort out the various forms and recognizes four subspecies and a variety: *G. v. vicina* ("widespread") with the var. *sambourouensis* (Dautzenberg, 1908) (eastern Kenya), *G. v. adelpha* (Preston, 1913) (Uganda), *G. v. salutationis* Connolly, 1922 [9]) (Tanzania: Dar es Salaam), and *G. v. mediafricana* Pilsbry, 1919 (eastern Zaïre: Semliki R. area west of Ruwenzori complex). In the same area a number of (closely) allied species is found. Fortunately in southern Africa the problem is comparatively simple, because only one, well-marked subspecies occurs south of

9) In his description of *G. salutationis* Connolly (1922: 499) gives as measurements 5.1 × 1.4 mm, l/d 3.64; this is incorrect, the type (BM) actually measures 5.3 × 2.4 mm, l/d 2.28.

the Zambesi. Aberrant forms at both the northern (Kenya) and southern (Rhodesia) limits of the distribution of the species may be illustrations of the influence of peripherally isolated populations (Mayr, 1976: 191).

Apical spiral sculpture, well-marked in the new subspecies, is very weak or altogether absent in specimens from Malawi and further north.

So far *G. vicina* has not been recorded from Mozambique. Seeing that the Rhodesian localities of *G. vicina luci* are close to the Mozambique border and that suitable habitat is abundantly available in that country, one might confidently predict the local occurrence of the here described subspecies. Because of the sheer size of Mozambique other forms of *G. vicina* may be expected to occur further north, e.g., east of Malawi. Dr. H. E. van Hoepen (Johannesburg, in litt. 25.V.1979) has seen Mozambique material, however, without locality data.

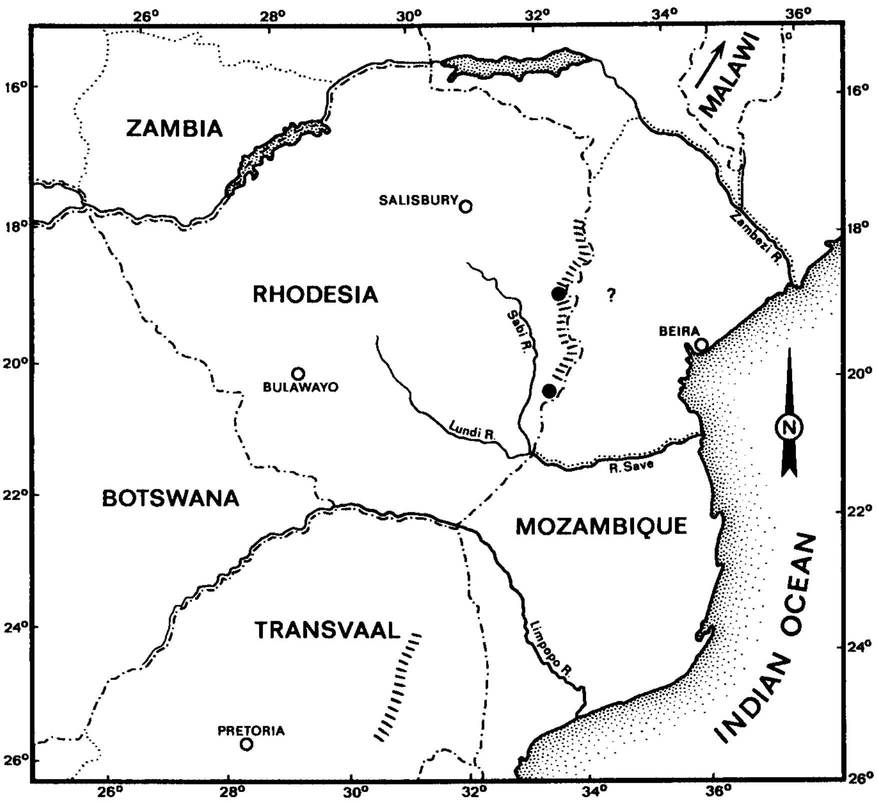


Fig. 27. Southern African distribution of *Gulella vicina* (Smith). South of the Zambezi River only *G. v. luci* nov. subsp. is known to occur; nearest known occurrence (*G. v. vicina*) in Malawi (arrow). The Eastern Escarpment has been indicated by cross-hatching.

G. vicina belongs to the subgenus (or section) *Plicigulella* Pilsbry, 1919. The shells of the species belonging to this group are mainly characterized by the presence of a triplicate columellar lamella. Verdcourt (1957, with additions in 1962: 35-36) has reviewed the (East African) species. The only other species in southern Africa is *G. aprosdoketa* Connolly, 1939. This form occurs in a very limited area in Pondoland (Transkei, eastern Cape Province). It has a very much smaller shell than *G. vicina* and also differs in many other characters.

The subdivision of the genus *Gulella* as featured by Zilch (1960: 570-573) is still open to considerable revision, particularly because it is solely based on shell data. Many of the seventeen subgenera do not seem to be natural units. It is doubtful whether *Plicigulella,* although ostensibly quite distinct, forms a natural group. The distribution of the taxa included here, however, is quite coherent and seemingly natural. The species range from eastern Zaïre (ex-Belgian Congo) through Uganda to Kenya and continental Tanzania (with a marked concentration in the East African highlands), with only two species reaching southward, viz., the widely distributed *G. vicina* (south to Rhodesia and possibly Mozambique) and the completely isolated *G. aprosdoketa* far south in Pondoland.

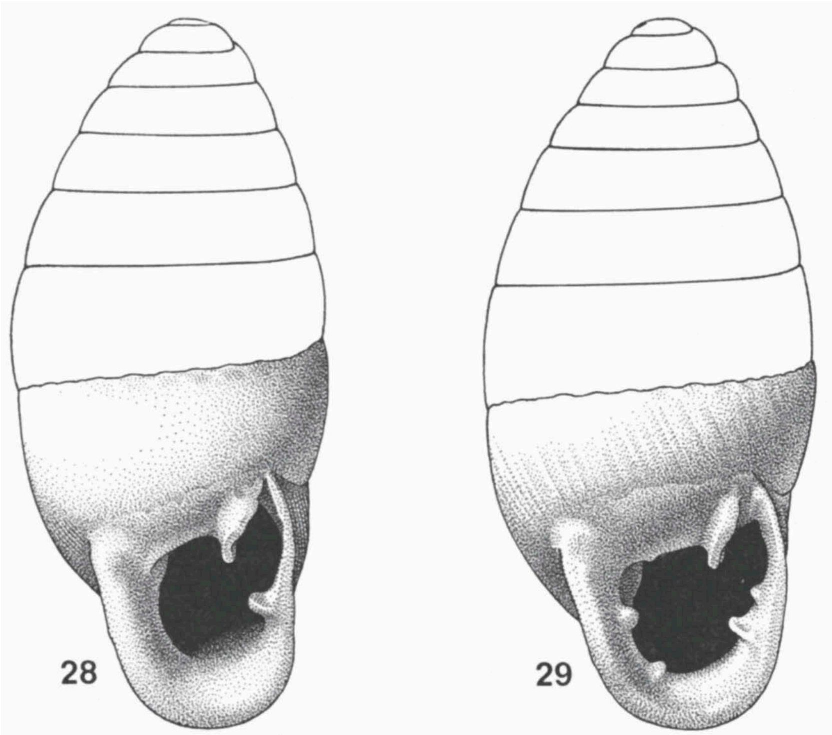
As regards the validity of the subgenera of *Gulella* one should keep in mind that not even the genus itself appears to be sufficiently well defined. Recently Adam & Van Goethem (1978) have drawn attention to the unsatisfactory delimitation of *Gulella* and *Ptychotrema,* at least in Central and East Africa. In southern Africa the pupoid Streptaxidae are only represented by the genera *Streptostele* and *Gulella.* The cautionary concluding remarks of these knowledgeable authors may be repeated here in full (Adam & Van Goethem, 1978: 63): "...actuellement les limites entre des genres comme *Gulella* et *Ptychotrema* et entre leurs sous-genres, établis uniquement sur les caractères de la coquille, sont devenus trop vagues pour pourvoir leur attribuer une valeur systématique réelle."

Gulella zuluensis Connolly, 1932 (figs. 28, 30)

Gulella zuluensis Connolly, 1932, Ann. Natal Mus., 7: 81, pl. 4 fig. 13; Connolly, 1939, Ann. S. Afr. Mus., 33: 25; Van Bruggen, 1973, Malacologia, 14: 423; Van Bruggen & Appleton, 1977, Zool. Verh. Leiden, 154: 14, 28, 40.

Diagnostic characters. — A faintly costulate, fairly large species with tapering apex and three-fold dentition consisting of angular lamella and single labral and columellar processes.

Description of shell. — Shell (fig. 28) fairly large, acuminate ovate, rimate or with closed umbilicus. Spire produced, sides convex, tapering to a blunt apex. Whorls 8-8½, nearly flat, sculptured with weak but noticeable, oblique costulae; sutures shallow, somewhat crenellate. Aperture little obstructed by three processes: a well-developed angular lamella (almost) touching the apex of the labrum; a superficial small tubercle slightly above the middle of the labrum, corresponding to a poorly differentiated shallow outside pit; and an almost invisible shelf-like columellar lamella. Peristome usually well reflected, outer lip somewhat expanded.



Figs. 28-29. Shells of 28, *Gulella zuluensis* Conn. (paratype, length 10.5 mm, Sinkwazi, NM), and for comparison 29, *G. natalensis* (Crvn) (length 9.7 mm, Isipingo, NM).

Measurements of shell: 9.1-12.0 × 4.4-5.3 mm, l/d 2.04-2.39. The type measures 10.8 × 5.0 mm, l/d 2.16, aperture 2.6 × 1.9 mm, last whorl 6.1 mm. Smallest shell (east shore of Lake Sibaya, RMNH) 9.1 × 4.4 mm, l/d 2.07, largest shell (St. Lucia, DM) 12.0 × 5.3 mm, l/d 2.26. The latter specimen is slightly abnormal with a somewhat elongate aperture, which measures 2.9 × 4.0 mm. The next largest shell has the following measurements: 11.5 × 5.3 mm, l/d 2.15 (Sinkwazi, NM).

Animal. — According to field observations at Charter's Creek the body is yellow, while feelers and retractor muscles are orange.

Distribution (fig. 30). — *G. zuluensis* is distributed in a narrow stretch of country along the coast of Natal and Zululand from Stanger to the Mozambique border.

NATAL: Stanger, G. E. Pennington (NM, s.n. *G. natalensis*, det. H. C. Burnup); Sinkwazi, S. of Tugela River mouth, G. E. Pennington (BM 1929.10.10.1, holotype; BM 1937.12.30.1286-8, three paratypes; NM, possibly also from original lot; W. Falcon colln., NM type 591, five paratypes, label in Connolly's handwriting reads "Type came from this box"). ZULULAND: Richards Bay, D. W. Aiken (in litt., non vidi); Dukuduku Forest (W. of St. Lucia), F. Toppin (NM); St. Lucia, H. W. Bell-Marley (NM); do., H. J. Puzey (Falcon colln., NM; Puzey colln. 63, DM); do., W. G. Rump (NM); "St. Lucia & False Bay", H. W. Bell-Marley (NM, probably paratypes); Charter's Creek, St. Lucia Game Reserve, A. C. van Bruggen (NM); do., along road to Fanie's Island, Mrs. W. H. van Bruggen (NM); east shore of Lake Sibaya, D. S. Brown (BM; RMNH; Zoology Department of Potchefstroom University); do., B. H. Lamoral (NM); do., R. F. Lawrence (NM; RMNH); various localities around Lake Sibaya, C. C. Appleton (RMNH, RMNH alc., vide Van Bruggen & Appleton, 1977: 28); Kosi Bay area, Bhanga Nek ca. 15 miles S. of Mozambique border, O. Bourquin (NM); Kosi Lake system, Nkovugeni estuary, A. C. and W. H. van Bruggen (NM; RMNH); do., K. L. Tinley (K. L. Tinley colln.).

Type locality: Sinkwazi, Natal, where first collected by Archdeacon Pennington in July 1924. Sinkwazi is situated between Stanger and the Tugela River, outside Zululand, which makes the name seem somewhat inappropriate. However, in the original description Connolly (1932: 81) also made mention of St. Lucia and False Bay and from the above data it appears that the species has its headquarters in Zululand.

Although widely distributed, *G. zuluensis* was described only in 1932 on specimens collected in 1924; F. Toppin appears to have been the first collector, having obtained specimens in the Dukuduku Forest as early as August 1905. Compared to other parts of southern Africa the zoology of Zululand has made a comparatively very late start. Obviously the Toppin specimens (NM) have escaped the attention of both Burnup and Connolly.

G. zuluensis is chiefly recognized by its tapering apex and little obstructed aperture, characters which it shares with *G. natalensis* (Craven, 1880). A tapering apex is uncommon among southern African *Gulella* (cf. e.g., *G. browni* Van Bruggen, 1969). *G. natalensis* occurs south of *G. zuluensis*; the species are, however, sympatric in a limited area on the borders of Natal and Zululand. Both species occur together in the Dukuduku Forest (Connolly, 1939: 24). The aperture of *G. natalensis* is characterized by the presence of three processes which are always present (angular lamella, labral tooth, and columellar lamella) and which also occur in much the same form in *G. zuluensis*. In addition *G. natalensis* has a single upper labral, two basal and a single superficial columellar process(es), which vary from all

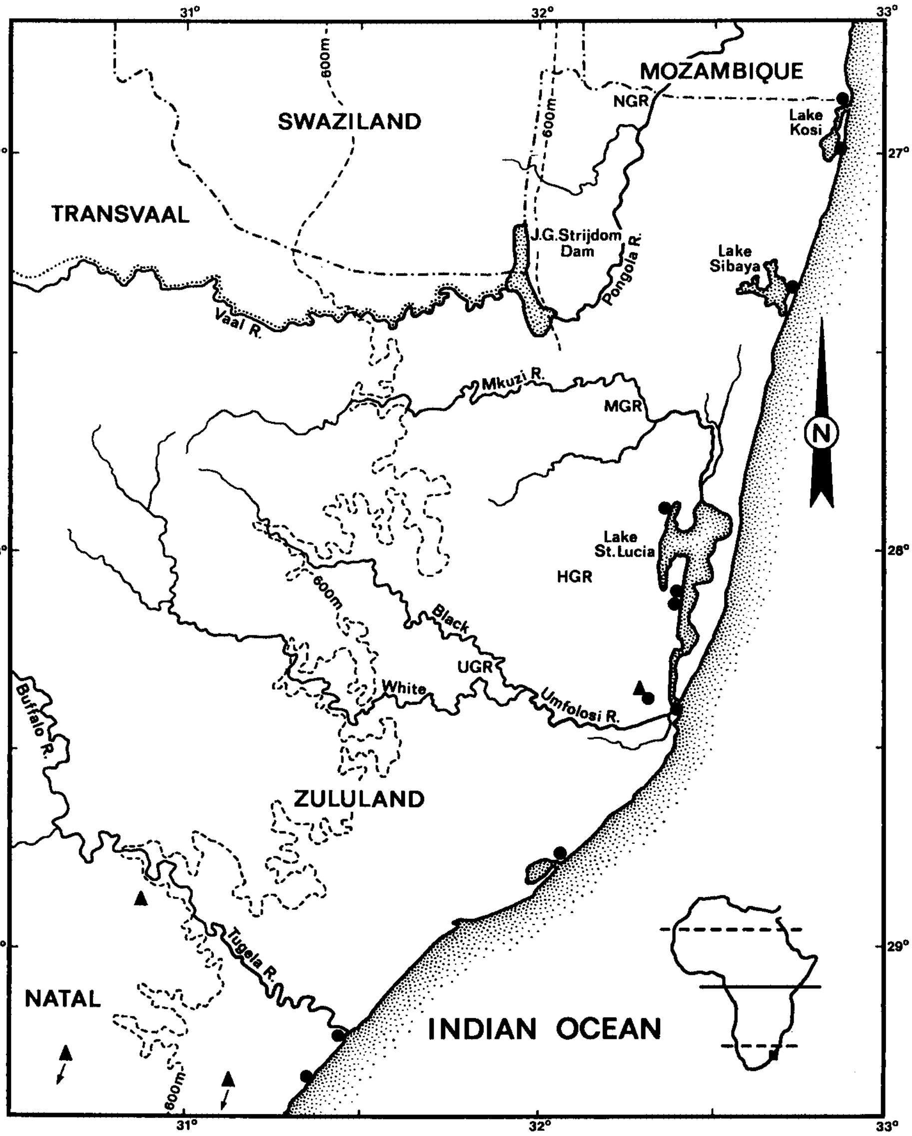


Fig. 30. Distribution of *Gulella zuluensis* Conn. (dots); sympatric occurrence of *G. natalensis* (Crvn) indicated by triangles. HGR = Hluhluwe Game Reserve, MGR = Mkuzi Game Reserve, NGR = Ndumu Game Reserve, UGR = Umfolosi Game Reserve.

present to all absent with all intermediates. Fig. 29 shows a shell with complete dentition. Connolly (1932: 80) has discussed the various additional denticles and shows that the mid-basal process "is the most frequently absent, and occurs only when all the others are present." This is confirmed by 66 specimens examined; only 15 of these have a complete set of apertural processes (in Connolly's material 8 in 35). Only one specimen has but a single additional denticle, viz., the upper labral process (Isipingo, NM). Another shell (Port St. Johns, NM) has no additional denticles and thus has come to resemble *G. zuluensis*. However, it was found in a sample of *G. natalensis* and appears to have a repaired labrum; moreover *G. zuluensis* does not occur anywhere near Port St. Johns, which is situated in the Eastern Cape Province (Transkei) and constitutes the southernmost record for *G. natalensis*. As regards size of the shell and shape there is a considerable overlap between *G. natalensis* and *G. zuluensis:*

G. natalensis	8.5-10.8 × 4.2-5.5 mm, l/d 1.88-2.41
G. zuluensis	9.1-12.0 × 4.4-5.3 mm, l/d 2.04-2.39

G. zuluensis lives close to the shores of the Indian Ocean because it is restricted to what is called on various labels dune forest, dune scrub or coastal forest. "After rains they tend to crawl low onto tree trunks and walls of houses" (Van Bruggen & Appleton, 1977: 28). The only time the species was observed alive by the present author, was at Charter's Creek, where specimens were found on whitewashed outside walls of the rest huts, mainly on the east side. This rest camp adjoins the coastal forest and the snails were probably surprised by the sunrise after having crawled onto these walls, possibly in search of a source of calcium.

In this species the columellar lamella is almost invisible; also, the outer lip is sometimes somewhat flaring. Otherwise it is subject to little variation, except in size and shape of the shell as demonstrated by the following table:

Natal	10.5-11.5 × 4.8-5.3 mm, l/d 2.14-2.22, mean 2.18
S. Zululand	9.8-12.0 × 4.7-5.3 mm, l/d 2.04-2.26, mean 2.15
Tongaland	9.0-10.3 × 4.4-4.6 mm, l/d 2.06-2.39, mean 2.22

This shows that from south to north there is a slight, but noticeable, decrease in length (mean length 11.0, 10.9 and 9.6 mm respectively). The shells of the Tongaland populations have a particularly low major diameter as compared to the length, which, of course, accounts for the increase in l/d, which means that the shells in that area on the average are much more slender than farther south.

3. Concluding remarks

The above eight cases of subspecies and size clines in *Gulella* together with the six treated elsewhere (see Introduction) may be considered within a more general context in order to discover whether there is a general pattern in variation and whether any correlation with biotic and/or abiotic factors exists. Patterns of variation may be complicated at times, because e.g., size clines as regards length might not be correlated to size clines of major diameter of shells, thus resulting in aberrant patterns of variation.

Eight of the species are largely sympatric in an enormous area from the Eastern Cape Province to northern Zululand, another is largely sympatric with these but has a more northern inland distribution pattern (*G. perissodonta*, as far west as the Transvaal), while another two are sympatric but more widely distributed, i.e. as far north as Tanzania (*G. farquhari* and *G. gouldi*). The species are treated from south to north.

G. infrendens exhibits a size cline from south to north; mean length and major diameter show a regular and correlated increase (6.2 × 2.7 mm to 7.0 × 3.5 mm), while the l/d is more or less constant (mean values around 2.08). Another size cline follows an east-west direction from the coast to the foothills (mean 7.2 × 3.1 to 8.0 × 3.7 mm), while the l/d also increases (mean 2.07 to 2.12). Seemingly isolated populations present another picture. All this is further complicated by clinal variation in apertural dentition, particularly in the development of the outer columellar lamella, which ranges from poorly developed in the south through poorly and well developed in about equal proportions in the central area to well developed further north and complete absence even further north. A similar cline exists as regards elevation, the outer columellar lamella being well developed on the coast and absent in the Zululand hills.

G. farquhari shows a steady increase in shell length from south to north (mean 2.5 to 3.2 mm) while retaining its mean l/d. Mozambique specimens are very small (mean length 2.4 mm) and slender, while Tanzania shells are comparatively very large (mean length 3.3 mm) with about the same l/d.

G. g. gouldi shows a decrease in shell length from south to north (mean 9.4 to 8.4 mm and perhaps even less) and also from the coast inland to the Drakensberg foothills (mean 8.1 to 6.0 mm). In the latter populations there is also a correlated decrease in major diameter (mean 3.9 to 2.6 mm), resulting, however, in an increase of l/d (mean 2.06 to 2.13). The northern Zululand subspecies *G. g. discriminanda* also has a small shell, with a mean length of 6.5 mm; it exhibits a size cline showing an increase in shell length and major diameter towards the north (mean 6.0 × 2.7 mm to 6.7 × 2.9 mm), resulting in more slender shells (mean l/d 2.15 to 2.33). The isolated Tanzanian subspecies *G. gouldi globulosa* has small (mean length 5.1 mm) and also comparatively obese shells (mean l/d 1.72; *G. g. gouldi* 2.15; *G. g. discriminanda* 2.25) (all data extracted from Van Bruggen, 1969: 39-46).

G. adamsiana shows a steady decrease in mean shell length from south to north and west (8.9 to 7.4 mm), correlated to a decrease in major diameter (mean 4.3 to 3.5 mm). The few Zululand specimens are aberrant in this respect in being very large and very squat. As regards apertural dentition, the basal denticle is rather squarish in the south and definitely triangular further north.

G. elliptica is divided into three well-marked subspecies, a southern form (*G. e. caelatior*) with a large shell (mean length 4.4 mm), a central form (*G. e. elliptica*) with a somewhat smaller shell (mean length 3.7 mm), and a northern form (*G. e. tesserula*) with again a somewhat smaller shell (mean length 3.5 mm). This looks like a cline of decreasing size from south to north. This is correlated to a decrease in major diameter (mean 2.1, 1.8 and 1.8 mm respectively) and a concomitant decrease in l/d (mean 2.07, 2.01 and 1.97 respectively).

G. darglensis is also divided into three well-marked subspecies, showing a cline of decreasing shell size from south to north: *G. d. benthodon* (southern form, mean 2.9 × 1.3 mm), *G. d. illovoensis* (central form, mean 2.8 × 1.3 mm), and *G. d. darglensis* (northwestern form, mean 2.5 × 1.2 mm). This is correlated with a decrease in mean l/d (2.18, 2.13 and 2.06 respectively). However, this seemingly straight forward pattern is disturbed by a size cline in the typical form. Specimens of this show an increase in length from south to north (i.e., from lowlands to mountains): mean 2.3 to 2.7 mm. Both southern and northern forms have costulate shells, the central form has smooth shells; the southern form has shells with deeply situated columellar processes, the central and northern forms have these more superficial.

G. crassidens may be divided into two (possibly even three) subspecies, a large southern form, *G. c. crassidens* (mean 5.8 × 2.9 mm), and a smaller northern form, *G. c. jonesi* (mean 4.2 × 2.1 mm). There is little difference in shape of the shell. The southern form has a sinular denticle in the aperture, which process is absent in the aperture of the northern subspecies (data from Van Bruggen, 1969: 64-69).

G. planti exhibits a marked size cline from south to north (mean 13.6 × 7.1 to 20.1 × 9.7 mm), correlated to a small increase in l/d (mean 1.95 to 2.09). Southern populations have a labral denticle that is absent in northern populations.

G. triglochis shows a somewhat confused pattern of variation; there are vague indications of a size cline with increasing length of shells from south to north, but the whole pattern is very complicated. Forest dwellers appear to have larger shells than savannah dwellers in about the same area (see Van Bruggen, 1969: 38).

G. zuluensis shows little clinal variation in the form of a slight decrease in shell size from south to north (mean 11.0 × 5.0 mm to 9.7 × 4.5 mm); however, Tongaland specimens at the northern limits of the range are noticeably more slender than the others (mean l/d 2.23, elsewhere 2.15).

G. perissodonta exhibits a size cline from south to north in the Transvaal as regards length and width of the shell: mean 3.9 × 1.9 mm to 5.0 × 2.3 mm. This is correlated to a slight increase in l/d (mean 2.05 to 2.10). Material from Zululand and Swaziland has another pattern of variation (mean 4.2 × 2.0 mm, l/d 2.04); again another pattern is shown by the southern Mozambique material (mean 4.1 × 1.2 mm, l/d 1.87). The latter material is not uniform, consisting of specimens from Maputo (formerly Lourenço Marques) and from Inhaca Island in Delagoa Bay off Maputo (data ex Van Bruggen, 1969: 46-50).

The three remaining cases are somewhat different.

G. caryatis is divided into two well-marked subspecies. The eastern one, *G. c. caryatis*, from a restricted area in the Eastern Cape Province (Martindale, Grahamstown, Cathcart, Cradock, Prieska), is large and slender (2.9-5.0 × 1.1-1.4 mm, l/d 2.59-3.57, mean 3.9 × 1.2 mm, l/d 3.08). The western form, *G. c. diabensis*, widely distributed in midwestern South West Africa (Diab R., Omaruru District, Otavi highlands), has a smaller and more obese shell (2.9-4.1 × 1.1-1.4 mm, l/d 2.48-3.00, mean 3.5 × 1.2 mm, l/d 2.74) (data from Connolly, 1939; Van Bruggen, 1970; Naturmuseum Senckenberg, Frankfurt am Main; unpublished data).

G. vicina has its headquarters beyond the Zambezi River and is only represented in southern Africa by a subspecies with large and costulate shells without a mid-parietal process. The pattern of variation of this species north of the Zambezi is very complicated.

Finally *G. peakei* has a very peculiar distribution. *G. p. peakei*, the extinct form on Aldabra Island, is small and squat (mean 1.9 × 1.4 mm, l/d 1.43), while *G. p. continentalis* from Zululand is larger and somewhat more slender (mean 2.1 × 1.3 mm, l/d 1.55) (data from Van Bruggen, 1975a: 212).

Would it be possible to discern a common pattern in the above, admittedly random, cases? The following table gives a summary of major similar trends:

increase in shell size s.l. from south to north	decrease in shell size s.l. from south to north
G. d. darglensis	*G. adamsiana*
G. farquhari	*G. crassidens*
G. gouldi discriminanda	*G. darglensis* (species as a whole)
G. infrendens	*G. elliptica*
G. perissodonta in the Transvaal	*G. g. gouldi*
G. planti	*G. zuluensis*
(*G. triglochis,* see above)	

Apart from this it is very difficult indeed to distinguish general trends. Usually one species displays a trend and another shows the opposite. One example should suffice here: from the coast to the foothills the shell of *G. infrendens* increases in size and l/d, while *G. g. gouldi* shows the opposite as regards length and diameter, but agrees in the l/d increasing in value. Some species have a more complicated apertural dentition in the north, while others exhibit a similar phenomenon in the south, etc. Isolated populations at the limits of the distribution may have shells smaller or larger than in the main area of the species. It is quite clear, however, that there is no general pattern among the species studied here.

The main area under discussion, the Eastern Cape Province and Natal, displays beautiful gradients in climatic factors (see e.g., Schultze & McGee, 1978), but it seems as if every species individually reacts to these, some shells becoming larger with increasing temperatures, others smaller, etc. General principles as laid down by Rensch (1932, 1966) do not seem to apply here at all. There is a profuse literature on the ecology of the pulmonates in which problems such as possible correlations of shell size, etc. and biotic and/or abiotic factors are dealt with. A good recent summary is that by Peake (1978). Van Bruggen (1973: 424) in a summary general survey of the genus *Gulella* in southern Africa has cast doubt on some of the principles of Rensch, and Peake and others agree. It appears that for the time being as regards the above discussed species no definite pattern can be discerned.

On the other hand one should not conclude that some general rules widely recognized and applied in evolutionary biology do not longer hold. It is probably still quite quite true that most molluscs will reach their maximum size under optimum conditions for the species (Mayr, 1942: 92; locally beautifully illustrated by southern Africa's largest snail, the achatinid *Metachatina kraussi,* see Van Bruggen, 1969: 17-19). On a higher taxonomic level, the genus level, this still applies to *Gulella* (see p. 42). Obviously optimum conditions differ radically even between closely allied species or species in the one genus.

4. Summary

Size clines and subspecies of 14 southern African species of the streptaxid genus *Gulella* have been studied, in many cases based on profuse material. *G. adamsiana*, *G. darglensis*, *G. elliptica*, *G. farquhari*, *G. infrendens*, *G. planti*, *G. vicina*, and *G. zuluensis* are described in detail. The following new subspecies are described: *G. darglensis benthodon* (Kingwilliamstown district), *G. elliptica tesserula* (East-Central Zululand), and *G. vicina luci* (eastern Rhodesia). *G. darglensis* var. *illovoensis* and *G. elliptica* var. *caelatior* appear to represent well-defined subspecies rather than varieties. All named varieties of *G. farquhari* are relegated to the synonymy of the species; the species appears to be very variable indeed.

Most species studied display clines of various types and a number may be divided into well-marked subspecies. Clinal variation is shown in shell features such as length, major diameter, ratio length/major diameter, shell surface sculpture, and details of the apertural dentition. Analysis of clinal variation and subspecies has failed to reveal a common pattern of correlation between shell characters and biotic/abiotic factors. General principles as laid down by Rensch (1932, 1966) do not seem to apply to the above cases.

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6. Index to trivial names in *Gulella*