Revision of the Larger Cannibal Snails (Natalina s. l.) of Southern Africa — Natalina s. s., Afrorhytida and Capitina (Mollusca: Gastropoda: Rhytididae)

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ABSTRACT

Natalina sensu lato includes some of the largest carnivorous snails in the world and represents an important African radiation of the Gondwanan land snail family Rhytididae. It comprises the taxa *Natalina*, *Afrorhytida* and *Capitina*, all three of which we treat as full genera. We provide a comprehensive revision of each genus, and update the species-level taxonomy extensively in the light of new molecular and morphological data. Detailed comparative morphological observations are provided for the distal reproductive tract (including spermatophores for the first time in this family), pulmonary cavity, mantle edge, radula and suprapedal gland. In addition, we present a summary of biological and ecological data including information on habitat preferences, feeding, prey and mating behaviour. Although the genera are well circumscribed in terms of both morphological and molecular data, morphology is usually highly conserved within genera. Yet surprising cryptic diversity is evident within the described species and restricted-range endemism is more frequent than was previously thought, with significant implications for conservation. The widespread common cannibal snail, *Natalina cafra* (Férussac, 1821), is shown to comprise four cryptic, allopatric lineages. For the most part, we recognise this cryptic diversity at the level of subspecies. In some cases where populations from disjunct, lime-rich habitats exhibit a significantly different shell morphology, it is difficult to evaluate whether and to what extent this is genetically or environmentally determined. Spermatophores exhibit considerable phylogenetically consistent morphological variation and may eventually prove to be an important source of new taxonomic characters. The geographic distributions of the respective lineages are interpreted in the light of phylogenetic data, current regional vegetation patterns, and historical environmental phenomena, so as to identify biogeographic trends. Some lineages are clearly forest-associated specialists and have fragmented, narrowly-endemic distributions resulting from cyclical changes in forest cover during the Plio-Pleistocene, but there is also strong evidence for regional endemism associated with other vegetation types, notably Albany Thicket. Observations on the conservation status of all taxa are provided.

New subgenus: *Natalina* (*Tongalina*). New species: *Afrorhytida burseyae*, *Capitina calcicola*. New subspecies: *Afrorhytida kraussi oraria*, *Natalina cafra amathole*, *Natalina cafra natalensis*, *Natalina quekettiana dracomontana*, *Natalina quekettiana lucaris*, *Natalina quekettiana montistempli*. New synonyms: *Natalina compacta* Connolly, 1939 = *Natalina cafra cafra* (Férussac, 1821); *Natalina coerneyensis* Melvill & Ponsonby, 1894 and *Natalina insignis* Melvill & Ponsonby, 1907 = *Afrorhytida knysnaensis* (Pfeiffer, 1846); *Natalina liliacea* Preston, 1912 = *Afrorhytida kraussi kraussi* (Pfeiffer, 1846); *Natalina arguta* Melvill & Ponsonby, 1907 = *Afrorhytida trimeni* Melvill & Ponsonby, 1892. Revised status: *Helix* (*Aerope*) *eumacta* Melvill & Ponsonby, 1892 is considered a subspecies of *Natalina cafra* (Férussac, 1821). Lectotypes designated for *Aerope beyrichi* Martens, 1890 [= *Natalina*] and *Helix schärfiae* Pfeiffer, 1861 [= *Capitina schaerfiae*].

KEY WORDS: Afrotropical, Mollusca, Rhytididae, cannibal snails, taxonomic revision, new taxa, conservation.

INTRODUCTION

Carnivorous snails of the family Rhytididae represent some of the most spectacular of all lands snails. Historically, species representative of the family have been recorded from eastern and southern Africa, the Seychelles, Madagascar, Indonesia, Melanesia, Australia and New Zealand. However, subsequent studies have shown that the East African species referred by Thiele (1911) to *Rhytida* Martens, 1860 are in fact helicoid

streptaxids belonging to the genus *Tayloria* Bourguignat, 1889 (Pilsbry 1919; Verdcourt 1958). Similarly, Gerlach (1995) has shown that the genus *Priodiscus* Martens, 1898 from the Seychelles is also streptaxid rather than rhytidid. In addition, Emberton's suggestion that the Madagascan *Ampelita covani* (Smith, 1879) is an unrecognised rhytidid rather than an acavid (Emberton 1990) has proved unfounded (Herbert & Moussalli, unpubl. data). Currently the family is thus known only from southern Africa and the Australasian–Austronesian region. Early in the study of the group, Watson (1915) suggested that the present day distribution of the family was strongly suggestive of an origin in Mesozoic Gondwana, a hypothesis which has been broadly accepted by subsequent authors (Solem 1959; Bruggen 1969, 1978; Climo 1977; Smith 1998). Currently, ten genera are recognised in Australia (Smith 1998), and nine or ten in New Zealand (Barker 2005; Spencer *et al*. 2006), and Solem (1959) recorded five in Austronesia. All are endemic to these respective regions. In contrast, until the present study was initiated, all southern African species were referred to only two genera, either *Natalina* Pilsbry, 1893 or *Nata* Watson, 1934.

From a taxonomic perspective, the Rhytididae as a whole were monographed by Möllendorff (1903) in his treatment of the Agnatha. For the southern African species, this brought a degree of order to the piecemeal description of taxa which had occurred up to that point, helping to clarify the generic affinities of the described species. In the absence of anatomical data, however, some errors remained, including the referral of the southern African urocyclid taxa *Sheldonia fuscicolor* (Melvill & Ponsonby, 1892) to *Natalina* and *Zingis morrumbalensis* (Melvill & Ponsonby, 1894) to *Rhytida* (*Afrorhytida*). Two South African charopid taxa, *Trachycystis lightfootiana* (Melvill & Ponsonby, 1909) and *T. oconnori* (Preston, 1912) were later also initially erroneously referred to *Natalina*, and other species have been mistakenly transferred to *Natalina* subsequent to their description [e.g., *Sheldonia capsula* (Benson, 1864), *Trachycystis cosmia* (Pfeiffer, 1852) and *T. somersetensis* (Melvill & Ponsonby, 1893), cf. Melvill & Ponsonby 1898].

Morphological studies on southern African rhytidids initially comprised anatomical descriptions of single species (Pilsbry 1889, 1890; Pace 1895; Woodward 1895) until Watson (1934) undertook a more comprehensive comparative study which led him to recognise six supraspecific taxa, four of which were new. It was upon this more sound generic and subgeneric framework that Connolly (1939) based his subsequent and much more extensive taxonomic revision of the southern African Rhytididae, referring the species to two genera *Natalina* Pilsbry, 1893, and *Nata* Watson, 1934. However, although the endeavours of Watson (1934) and Connolly (1939) greatly improved our knowledge of the group, they were based on relatively little material, and many species remained poorly known and inadequately diagnosed. Distribution data and ecological information were limited, and several nominal species remained of dubious validity. Furthermore, although Watson was able to recognise groups of species identifiable on the basis of shared morphological characters, he provided little phylogenetic interpretation.

As part of a long-term programme of research investigating systematic relationships within this family, we have recently published a phylogeny of the genus *Natalina s.l.* based on molecular data that is strongly supported by congruent information from a suite of morphological characters relating to a number of different anatomical features (Moussalli *et al*. 2009). This is reproduced here in Fig. 1. Whilst this phylogeny supported many of the observations made by Watson (1934), it has called for the reappraisal of the
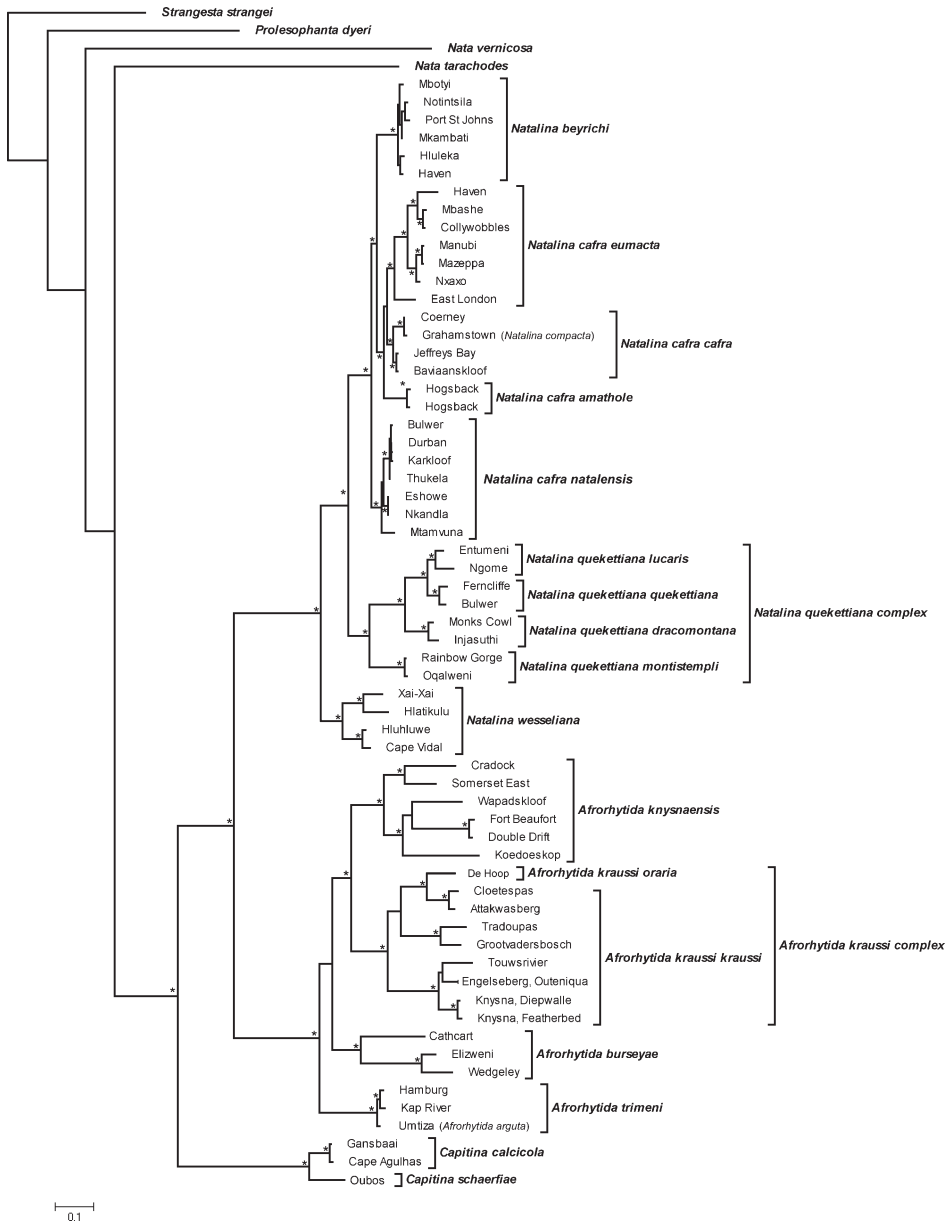
Fig. 1. All compatible Bayesian consensus tree based on mixed model partitioned analysis of the combined nucleotide dataset (16S and COI = GTR + IΓ, ITS2 = GTR+I). Asterisk indicates nodal support >95 % posterior probability (PP); PP below 95 % are not shown. (From Moussalli *et al*. 2009)

ranking of supraspecific taxa within the genus *sensu lato* and has identified a number of highly divergent yet cryptic lineages. From this it is clear that the apparently low generic diversity of rhytidids in southern Africa is an artefact resulting from the conservative approach to supraspecific taxonomy adopted by Watson (1934) and Connolly (1939).

In reality, *Natalina* comprises three deeply divergent lineages each of which merits recognition as a separate genus. Likewise, our preliminary data for *Nata* suggest that this too is an assemblage of highly divergent lineages that need to be re-assessed in terms of their generic referral (Moussalli & Herbert, unpubl. data). The preparatory work undertaken in order to determine the identity of voucher specimens used in our phylogenetic analyses of *Natalina s.l.* necessitated a re-evaluation of both the diagnostic characters of the species and of their distributions. In the light of this work we are now able to present a taxonomic revision of *Natalina s.l.* structured in ac-cordance with our phylogenetic findings, at the same time incorporating our observations on species characters and new distribution data. In addition, we provide more detailed information on the anatomical characters which underpin the morphology dataset used in the phylogenetic analysis of Moussalli *et al*. (2009).

Rhytidid snails represent one of the most characteristic elements of the southern African malacofauna, and have considerable charismatic appeal on account of their large size, often bright skin colours, carnivorous diet and ancient origins. They thus have potential to function as flagship taxa for invertebrate conservation. A number of species and subspecies are narrow-range endemics of conservation concern. As animals with limited capacity for dispersal, their patterns of endemicity also have potential to contribute valuable information to the growing pool of data regarding the evolutionary biogeography of the southern African low-vagility fauna (Griswold 1991; Hamer & Slotow 2000; Tolley *et al*. 2006; Daniels *et al*. 2009). Although this revision is based on a sound phylogenetic framework incorporating a great deal of new data (both molecular and morphological, Moussalli *et al*. 2009), we are acutely aware of the fact that our knowledge of the diversity of larger rhytidids in southern Africa is still embryonic. In New Zealand, where rhytidids are comparatively much more well studied, on-going research continues to result in the discovery of new taxa (Walker *et al*. 2008). It can only be expected that similar unrecognised taxa exist in southern Africa, particularly within the more deeply divergent complexes for which we currently have in-sufficient material.

MATERIAL AND METHODS

The studied material is kept in the following institutions:

ELM   – East London Museum, East London, South Africa;
BMNH – Natural History Museum, London, UK;
MNHN – Muséum National d'Histoire Naturelle, Paris, France;
MNHU – Museum für Naturkunde der Humboldt-Universitat, Berlin, Germany;
MVM   – Museum Victoria, Melbourne, Australia;
NMSA   – Natal Museum, Pietermaritzburg, South Africa;
ISNB   – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
RMNH   – National Museum of Natural History, Leiden, The Netherlands;
SAMC   – South African Museum, Cape Town, South Africa;
SMFD   – Senckenberg Museum, Frankfurt, Germany.

The bulk of the material examined is housed in the NMSA. This material has been accumulated over more than a century of collecting activity, but has been greatly aug-mented by recent field surveys undertaken by the authors in collaboration with Mary Cole (née Bursey) of the ELM. The specimens thus acquired have much more accurate
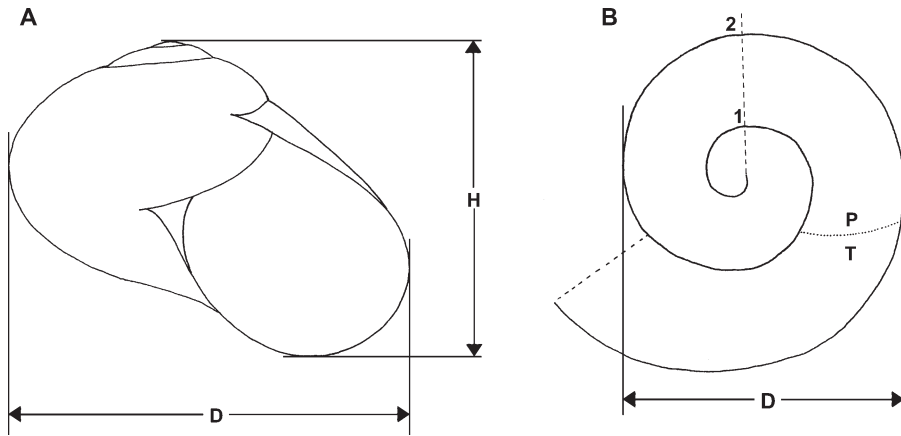
Fig. 2. Diagrams illustrating methods for measuring shell dimensions and protoconch whorls: D – diameter, H – height, P – protoconch, T – teleoconch.

and detailed provenance, including GPS co-ordinates and habitat data. At all times ethical issues relating to the collection of potentially rare or threatened species were considered, and the sampling of living specimens was kept to a minimum. In some cases records are based on photographs and no voucher was taken. Additional material was examined at the ELM, SAMC and BMNH. When not present in the NMSA or SAMC, material cited by Connolly (1939) is generally to be found in the BMNH. For anatomical study, living specimens were drowned overnight in sealed containers and preserved in 75 % ethanol for dissection. Prior to drowning, small fragments of the foot were excised and preserved in 99 % ethanol for molecular work. Details of the molecular techniques and analytical methods used to generate the phylogeny depicted in Fig. 1 were provided by Moussalli *et al*. (2009), together with details of the specimens used and the GenBank numbers of the respective sequences. All dissections were performed under a Wild M4 dissecting microscope with drawing tube. Radulae were extracted by maceration of the buccal mass in dilute NaOH and then rinsed in distilled water. For light microscopy radulae were stained in Shirlastain A [SDLAtlas] and for SEM they were dehydrated in ethanol and air-dried on stubs with double-sided carbon tape. Shells and radulae for SEM examination were coated with gold–palladium and examined at low accelerating voltage (5–10 kv) in a Hitachi S-570 SEM and a Philips XL30 ESEM. Photographs of shells were taken with a Nikon F4 or Nikon D70 camera and those of living specimens with a Nikon CoolPix 8800. Automontage micrographs of protoconchs were taken using a Leica MZ16 stereomicroscope and *Automontage Pro V5.0* [Syncroscopy]. Shell height and diameter measurements were made with the shell held in apertural view with the axis of coiling vertical, as shown in Fig. 2A. Immature shells were excluded from the data used to calculate H:D ratios. The dimensions of the protoconch were measured as shown in Fig. 2B, i.e. the suture to suture diameter of that part of the protoconch visible in apical view in shells with more than one teleoconch whorl. Since the suture usually lies slightly above the periphery this measurement is somewhat smaller than actual periphery to periphery dimension of the protoconch, but the latter cannot be measured in any but the most juvenile individuals.

The following acronyms and abbreviations are used in the paper:

E. Cape – Eastern Cape;
H:D – height:diameter ratio;
IUCN – International Union for Consevation of Nature;
KZN – KwaZulu-Natal;
NPB – Natal Parks Board [now Ezemvelo KZN Wildlife];
W. Cape – Western Cape.

BIOLOGICAL OBSERVATIONS

Ecology

In the broader Australasian region (including Indonesia, Melanesia and New Zealand) rhytidid snails occur mostly in mesic to wet, well vegetated environments, including some habitats with extremely high rainfall, such as the Australian genus *Victaphanta* Iredale, 1933 in the cold temperate *Nothofagus* rainforest of Victoria and Tasmania. In South Africa, species of *Natalina s.l.* are likewise confined to the region south and east of the Great Escarpment where rainfall is higher than in the western and central regions. Even so, there is great variation in the type of habitat in which the various species live, ranging from extremely wet mist-belt forest (e.g., Ngome Forest, mean annual precipitation >1200 mm, Schulze 1997) to surprisingly dry regions. Recent field work has shown that species of *Afrorhytida* extend far further into the dry interior than was previously thought (Bruggen 1978), for example, in the Karoo of the north-western E. Cape (mean annual precipitation 200–400 mm, Schulze 1997). Most species occur in well vegetated habitats, such as forest, woodland and thicket, but some also range into more open grassland and fynbos, particularly near the coast (in the south west) and in mist-belt and montane areas where grass and forb cover is dense, and rainfall higher. In the relatively dry E. Cape interior, *Afrorhytida knysnaensis* is to be found, for example, in Sundays Noorsveld and Great Fish River Thicket (Mucina & Rutherford 2006) as well as in isolated patches of mist-belt forest, where the topography results in a local increase in precipitation and a favourably shaded aspect.

Like most snails, species of *Natalina s.l.* are cryptic, seeking out sheltering microhabitats and are active almost exclusively at night and in warm, damp weather. All species are fully terrestrial, none have been found climbing trees. In forests they live in leaf-litter and beneath fallen logs, whereas in fynbos they seek shelter beneath shrubs, forbs and rocks. In montane grassland they live amongst dense tussocks of grass and in patches of bracken, while in thicket and Karoo type habitats they are to be found beneath fallen aloes, in stands of shrubby *Euphorbia* spp. and beneath bush clumps. In all open habitats, rocky areas and outcrops with sheltering, vegetation-filled cracks and crevices are favoured. During dry periods the snails seek more shaded, well protected sites and bury themselves more deeply, if the soil permits, but we have never encountered any specimens with an epiphragm, even in those living in relatively dry habitats.

At any one locality, only one species is likely to be found. Where two species co-occur they generally belong to different genera or different lineages. For example, single localities in E. Cape thicket habitats may sometimes contain species of both *Natalina* and *Afrorhytida*, and mist-belt forests of KwaZulu-Natal may contain both *N. cafra natalensis* subsp. n. and a subspecies of *N. quekettiana*. Proven instances of microsympatry in closely related species are rare, the only cases we have encountered being the co-

occurrence of *Natalina beyrichi* and *N. cafra eumacta* at localities in the Xora–Dwesa area, E. Cape.

Feeding

One of the most interesting aspects of rhytidid snails is their predatory feeding behaviour, the more so since some are amongst the largest carnivorous snails in the world (in terms of shell diameter, *Powelliphanta superba prouseorum* (Powell, 1946) from New Zealand, with a shell diameter of up to 90 mm is evidently the largest (Powell 1979)). South African rhytidids are obligate carnivores and the larger species of *Natalina* are well-known predators of other terrestrial molluscs. Details of prey detection and capture in *Natalina* were provided by Herbert (1991) and Herbert and Kilburn (2004). Prey detection is thought to involve chiefly the labial palps and inferior tentacles, but this is inferred from behavioural observations and there are no experimental data to confirm this. On contact with the prey, the predator extends the oral region slightly, exposing the inner lip area, the odontophore is then rapidly thrust forward, the anterior portion with enveloping radula emerging and extending some distance beyond the mouth. There is no evidence of a proboscis-like structure as reported in *Ouagapia* (Crosse, 1894) by Kondo (1943). The radula teeth are splayed outward as they pass over the anterior of the odontophore, gripping and tearing the flesh of the prey as the odontophore is then withdrawn.

Small molluscs (e.g., species of *Sheldonia* Ancey, 1888; Urocyclidae) may be consumed in one bite, the body being wrenched out of the shell, but larger-shelled prey is eaten more slowly, the predator repeatedly tearing off pieces of flesh as it penetrates
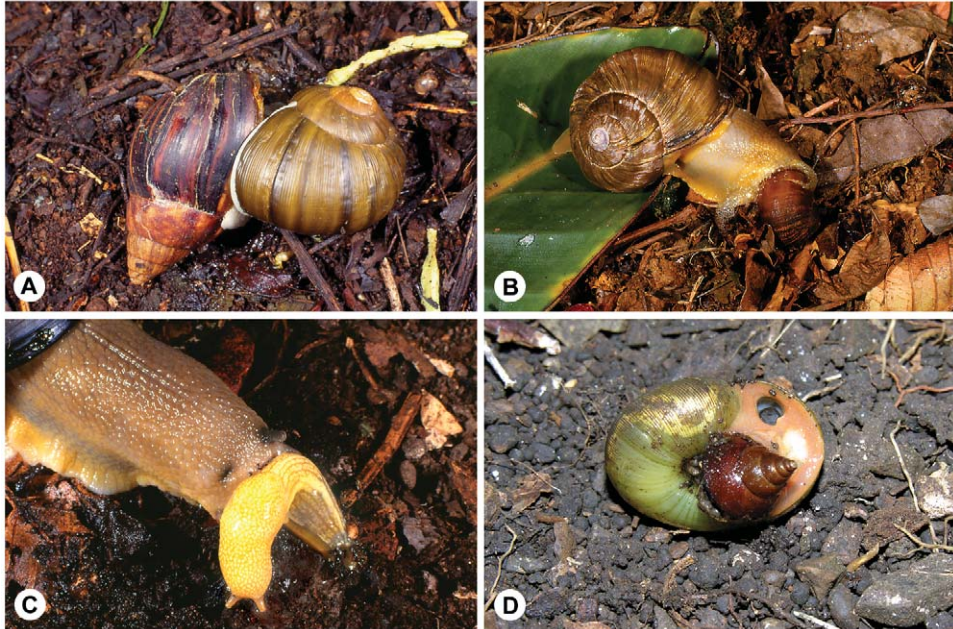

Fig. 3. Feeding in *Natalina*: (A–C) *N. cafra natalensis*, captive animals consuming: (A) *Achatina immaculata*, (B) *Cornu aspersum* and (C) *Elisolimax flavescens*; (D) *N. beyrichi* as found in leaf-litter, Mntafufu, E. Cape, with tail inserted in shell of *Gittenedouardia carinifera*, extracting calcium (NMSA W2970).

further into the victim's shell (Figs 3A, B). Slugs are eaten relatively rapidly in a series of bites during which the victim is drawn progressively into the mouth, often in pieces (Fig. 3C). Earthworms also constitute part of the diet of *Natalina* species and it has been speculated that a range of other soft-bodied invertebrates may also be consumed, but specific examples of such are wanting. The diet of species of *Afrorhytida* and *Capitina* is assumed to comprise largely of terrestrial molluscs, but there have been few field observations to verify this. However, *A. trimeni* has been found feeding on a species of *Chondrocyclus* Ancey, 1898 (Cyclophoridae). The above notwithstanding, since information for many species is completely lacking, arthropods cannot be excluded as prey items, as in the case of some species of the New Zealand genus *Wainuia* Powell, 1930, which feed primarily on leaf-litter amphipods (Efford 2000). A summary of the prey species documented to date for the species treated here is provided in Table 1. Further comparative information on the diet of carnivorous terrestrial molluscs can be found in the review by Barker and Efford (2004).

Carrion has also been cited as part of the diet, but there are no documented cases and early reports of *Natalina* species feeding on human corpses after Zulu tribal conflicts (Connolly 1912) have never been substantiated (Bruggen & Appleton 1977) despite being oft-repeated in the literature. We can, however, record that a specimen of *Afrorhytida knysnaensis* was collected trying to gain access to a dead mouse caught in a mammal trap (O. Bourquin, pers. comm.). Furthermore, since captive *Natalina cafra* will consume steak (Woodward 1895) and minced beef, it is quite reasonable to infer that wild individuals might scavenge on animal flesh when the opportunity arises. Captive animals have also been reported to feed on boiled potato (Gibbons 1880) and water-melon (Layard in Benson 1864), but there are no records of wild specimens feeding on vegetable matter.

Cannibalism is not infrequent, with adult animals attacking and feeding on smaller members of their own species. This somewhat unexpected behaviour merits further study, particularly with regard to its influence on courtship rituals and mating. When collecting rhytidids in the field, care needs to be taken to ensure that specimens are kept apart as they are particularly prone to attack each other when confined in the same container.

So as to maximise the nutritional benefit available in their snail prey, species of *Natalina* will also extract much of the calcium carbonate present in the shell. This they do by inserting the tip of the tail into the aperture of the empty prey shell (Fig. 3D), or wrapping it around the outside. By a process that is not fully understood, but which presumably involves acidic secretions from the pedal mucosa, the calcium carbonate of the prey shell is dissolved and absorbed by the predator to supplement its own calcium resources, leaving only the thin, tissue-like periostracal layer (Bruton *et al*. 1988; Appleton & Heeg 1999). Almost certainly this is a modification of an ability to dissolve calcium carbonate from rock, coral and other shells which is common in the Stylommatophora (Williams 1951; Frick 1965; Herbert & Kilburn 2004). Actively crawling animals have been seen carrying empty prey shells attached to the tail and Appleton and Heeg (1999) have suggested these are taken to 'larders' hidden in the vegetation for subsequent calcium extraction in safe surroundings. Old dead shells of large snails (e.g., species of *Cochlitoma* Férussac, 1821; Achatinidae) encountered fortuitously may be used for the same purpose (Herbert & Kilburn 2004). Similar use of prey snail shells has been reported by McLauchlan (1951) in the Australian genus *Austrorhytida* Smith, 1897 and by Barker and Efford

TABLE 1

Summary of information concerning the diet of southern African rhytidid snails belonging to the genera *Afrorhytida*, *Capitina* and *Natalina*.

Higher taxon	Prey item Genus / species	Predator	Reference
Mollusca (snails)			
Gastropoda	unspecified	*Capitina schaerfiae*	Layard in Benson 1864.
Cyclophoridae	*Chondrocyclus* sp.	*Afrorhytida trimeni*	herein
Achatinidae	*Achatina immaculata* Lamarck, 1822	*Natalina cafra natalensis*	herein
	Cochlitoma granulata (Krauss, 1848)	*Natalina cafra natalensis*	herein
	Cochlitoma vestita (Pfeiffer, 1855)	*Natalina wesseliana*	herein
	Metachatina kraussi (Pfeiffer, 1846)	*Natalina cafra natalensis*	Bruggen 1969: 14.
Subulinidae	unspecified	*Natalina wesseliana*	Bruggen & Appleton 1977: 33 (assumed).
Cerastidae	*Gittenedouardia carinifera* (Melvill & Ponsonby, 1897)	*Natalina beyrichi*	herein
Streptaxidae	*Ennea* [= *Gulella*] spp.	*Natalina cafra*	Gibbons 1880.
Urocyclidae	*Sheldonia* spp.	*Natalina cafra natalensis*	Herbert 1991.
Helicidae	*Cornu aspersum* (Müller, 1774)	*Natalina cafra cafra* and *N. cafra natalensis*	Woodward 1895, Bruton *et al.* 1988, Herbert 1991, Appleton & Heeg 1999.
	Helix pomatia Linnaeus, 1758	*Natalina cafra*	Woodward 1895.
Mollusca (slugs)			
Veronicellidae	*Laevicaulis* spp.	*Natalina cafra natalensis*	herein
Chlamydephoridae	*Chlamydephorus gibbonsi* Binney, 1879	*Natalina wesseliana*	herein (freshly ingested animal found in crop)
Urocyclidae	*Elisolimax flavescens* (Keferstein, 1866)	*Natalina cafra natalensis*	Herbert 1991.
Oligochaeta			
Microchaetidae	*Microchaetus papillatus* Benham, 1892	*Natalina cafra natalensis*	Herbert 1991.
	Proandricus sp.	*Natalina cafra eumacta*	herein (found in crop)
	Proandricus sp.	*Natalina quekettiana montistempli*	herein (found partially digested in crop)
	Microchaetus pondoanus Michaelsen, 1913	*Natalina beyrichi*	herein

(2004) in New Zealand genus *Rhytida*, who suggested it is a conserved ancient trait on account of its occurrence in widely separated regions and in phylogenetically disparate rhytidid lineages. As stated above, it is probably simply a minor modification of a calcium acquiring trait that is widespread in the Stylommatophora. It is also recorded in the Streptaxidae, another carnivorous family (Williams 1951; Kasigwa *et al*. 1983).

Predators

In contrast to the situation in New Zealand where the predators of the larger rhytidids have been relatively well documented (Powell 1930; Meads *et al*. 1984; Stringer & Montefiore 2000; Walker *et al*. 2008), almost nothing is known of the predators of southern African species. Terrestrial crabs, carabid, drilid and lampyrid beetles, and snail eating birds, such as coucals, francolins and guineafowl, are potential predators, as are the larger lizards (e.g., *Varanus* spp.) and a number of omnivorous mammals such as baboons, mongooses, genets, civets, otters, honey badgers, jackals and some rodents, as well as insectivores such as shrews and hedgehogs. However, there have been no documented cases of any of these animals preying on southern African rhytidids. In the forest habitats which many species favour, the bushpig (*Potamochoerus porcus* (L., 1758)) is likely to be a significant predator. This animal vigorously roots through the forest litter and consumes anything potentially edible. We have on a number of occasions found freshly crushed *Natalina* shells in the over-night foraging tracks left by bushpigs. In southern Africa, streptaxid snails are generally small (mostly *Gulella* spp.) and are unlikely to be significant predators of the larger rhytidids. In all probability they are more likely to fall prey to the rhytidids. Other significant causes of mortality may include anthropogenic factors such as trampling by livestock and fire (see conservation notes under species accounts).

Reproductive biology

Surprisingly little is known of the reproductive biology and behaviour of any of the larger southern African rhytidids. Herbert and Kilburn (2004) have documented the mating behaviour of *Natalina cafra* (subsp. *natalensis*). This is of relatively short duration, courtship and copulation being completed in less than one hour after initial contact. Both partners are active participants, one climbing onto the shell of the other and nuzzling its neck with its mouth while the partner arches its head and neck upward, moving it from side to side. These roles may then be reversed prior to a relatively brief copulation lasting less than 10 minutes. These remarks, however, were based on only two observed copulation events and further documentation is required. The shell-mounting behaviour is unusual for a low-spired species (Asami *et al*. 1998; Davison *et al*. 2005) and suggests unilateral mating rather the reciprocal mating in which case mating is normally face-to-face. In unilateral mating participants will have differing roles (donor−male and receiver−female), as was suggested for *Austrorhytida capillacea* (Férussac, 1832) by McLauchlan (1951). However, Herbert and Kilburn (2004) speculated that penetration was in fact reciprocal, and Jordaens *et al*. (2009) have shown that mating position is not in fact a reliable indicator for reciprocity of penis intromission and sperm exchange (nor is shell shape a reliable predictor of mating position). More detailed study of mating behaviour of these snails is clearly needed. There have been no recorded observations on subsequent egg-laying and hatching in southern African species, and there are thus no data on oviposition sites, clutch size and egg hatching

time. A little fragmentary information, however, is available concerning the eggs of some species.

In *Natalina cafra* the eggs (Fig. 15H) are large (10–16×8–12 mm) and when newly laid the outer egg casing is whitish and soft, comprising minute, closely packed crystals (?calcium carbonate) in a flexible matrix (which turns leathery in alcohol). In *N. quekettiana* the eggs are smaller (approximately 7.2×5.5 mm) (Fig. 35F) and are encased in a thin, brittle, off-white to yellowish white shell, also composed of minute, closely packed crystals. This apparent difference in the rigidity of the outer egg casing needs to be further investigated, since the eggs observed in *N. cafra* were freshly laid, while those of *N. quekettiana* were somewhat older. It is possible that the egg casing is flexible when newly laid, but hardens upon exposure to the air. Larval development within the egg evidently extends beyond the embryonic (protoconch) phase such that approximately 0.25 whorls of the teleoconch are laid down prior to hatching (observations based on Natal Museum specimens labelled as newly hatched juveniles). This explains the fact that the egg dimensions cited above are somewhat larger than the protoconch dimensions given in the respective species treatments below. A relatively strong growth-line, probably demarcating hatching, is evident in many shells (at approx. 0.25 whorls post-protoconch), as was noted also in *Paryphanta* by Stringer and Montefiore (2000). The eggs of *Afrorhytida* and *Capitina* are unknown.

Some aspects of the life cycle and reproduction of Australasian rhytidids have been discussed by McLauchlan (1951), Meads *et al.* (1984) and Stringer *et al.* (2002). Data on growth rates and longevity of southern African species is lacking, but Stringer *et al.* (2002) estimated a potential lifespan of at least 8.8 years for *Paryphanta busbyi watti* Powell, 1946, and McLauchlan (1951) postulated 8.5 years for species of *Austrorhytida* and *Strangesta* Iredale, 1933. These estimates are not unreasonable, but that of 40 years (based on growth scars considered to be annual rings) given by Meads *et al.* (1984) for the larger species of *Powelliphanta* O'Connor, 1945 seems improbable.

COMPARATIVE MORPHOLOGICAL OBSERVATIONS

Protoconch (Fig. 4)

The protoconch typically comprises approximately 1.25 whorls, its junction with the teleoconch is sometimes, but not always marked by a growth discontinuity or flaw. For the most part it is sculptured by close-set axial riblets, though these may be indistinct on the first whorl. In *Capitina* there may also be traces of spiral threads. Although some intra-specific variation in the diameter of the protoconch is evident, there is in general a positive correlation between protoconch size and the adult shell size for the respective species. In the larger *Natalina* species protoconch diameter is usually 7.0 mm or more, in the smaller members of the *Natalina quekettiana* complex 4.5–5.0 mm, in *Afrorhytida* 2.5–5.2 mm and in *Capitina* 4.0–7.0 mm. The relatively large size and distinct sculpture of the protoconch in these genera contrasts markedly with the smaller (diameter <2.0 mm) and essentially smooth, glossy, protoconch of the remaining southern African rhytidids (genus *Nata s.l.*, Fig. 4D).

From examination of newly hatched juveniles, it is evident that growth within the egg proceeds beyond the protoconch stage, such that approximately 0.25 teleoconch whorls are added prior to hatching (see *Reproductive biology* above). At this point as second growth flaw may be present, but in some specimens growth evidently proceeds
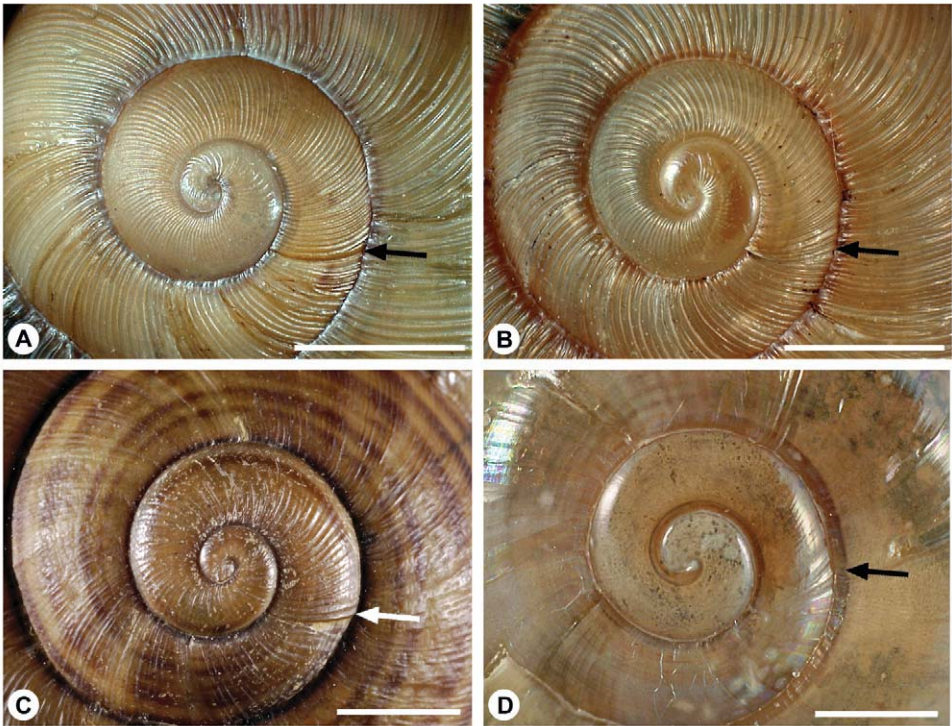
Fig. 4. Protoconchs of *Natalina*, *Afrorhytida*, *Capitina* and *Nata* (all NMSA): (A) *Natalina cafra cafra*
(W4225), scale bar = 5.0 mm; (B) *Afrorhytida trimeni* (V7904), scale bar = 2.5 mm; (C) *Capitina
schaerfiae* (W5672), scale bar = 2.5 mm; (D) *Nata* sp. n. (W6029), scale bar = 0.5 mm; arrows
mark protoconch/teleoconch junction.

smoothly, leaving no obvious growth discontinuity either at the end of the protoconch
or at hatching.

Head-foot (Figs 5, 35, 49, 55)

As is typical of the Rhytididae and carnivorous snails in general (Watson 1915), the
head-foot of *Afrorhytida*, *Capitina* and *Natalina* is notable for the length of the neck
region, particularly in *Natalina*, such that in the fully extended crawling animal the
shell is situated above the posterior half of the foot. Nonetheless, the tail is prominent
(unlike *Nata s.l.*) and usually acutely pointed, often extending well beyond the posterior
limit of the shell in *Natalina*. The length of the neck is primarily correlated with the
very long and muscular odontophore, but doubtlessly also enables the animal to
penetrate further into the shells of its snail prey. A pair of narrow, but distinct longitudinal
skin grooves runs dorsally along the mid-line of the neck. The foot is holopodous and
the tail possesses neither a caudal pore nor appendage. The sole is undivided, though it
may be more darkly pigmented laterally. The optic and inferior tentacles are long, the
former with a distinct, downwardly directed bulb at the tip, the eye lying dorsally, set
back from the tip. A pair of highly mobile, elongate-trigonal labial palps is present,
one each side of the mouth, beneath the inferior tentacle. These are particularly well
developed in the large *Natalina* species. Significantly, such palps are absent in species
of *Nata s.l.*, but are recorded in some Australian rhytidid genera (Smith 1979). Labial
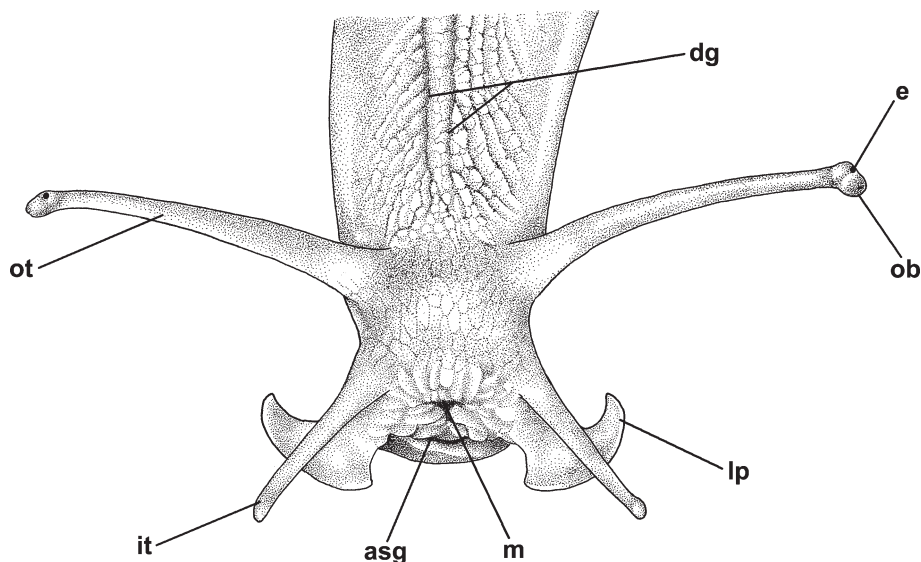
Fig. 5. *Natalina cafra cafra* (Férussac, 1821), anterior view of head showing sensory appendages. Abbreviations: asg – aperture of suprapedal gland, dg – dorsal skin grooves, e – eye, it – inferior tentacle, lp – labial palp, m – mouth, ob – optic bulb, ot – optic tentacle.

palps of very similar appearance also occur in other unrelated carnivorous groups (Streptaxidae and Oleacinidae) and are almost certainly analogues of similar function, but independent origin. The position of the genital pore is discussed below.

The colour of the head-foot and mantle edge of all species in all genera is evidently variable, sometimes considerably so. In most cases the dorsal portion of the neck is darker than the sides of the foot and there is often a paler longitudinal stripe extending posteriorly from the base of each optic tentacle. The mantle edge, pedal margin and the tip of the tail are frequently of an orange hue (occasionally yellow), sometimes vividly so. Similar bright orange-red pigmentation of the pedal margin and/or mantle edge is evident in some Australian species belonging to the genera *Strangesta* and *Victaphanta* (McLauchlan 1951; Smith 1969; and pers. observ.). The tentacles, particularly the optic ones are usually of a darker, somewhat greyish hue.

Due to intra-specific variability, head-foot colour seems to be of limited value for species discrimination and usually shows no obvious geographically consistent pattern within species. In most cases, data on body coloration is available for too few specimens to make meaningful assessments. This notwithstanding and even though samples sizes are small, in some cases individuals from certain localities do exhibit consistent and perhaps atypical body coloration, for example specimens of *Afrorhytida kraussi kraussi* from Grootvadersbosch are all orange or reddish, whereas elsewhere they are grey-brown to maroon-brown.

The underlying cause or causes of such colour variation are not clear. Whilst it may be genetically determined and thus of potential phylogenetic significance, it could also be related to diet or the mineral composition of the soil and thus unrelated to phylogeny, even when geographic patterns are evident. At present, too little information is available to meaningfully interpret this phenomenon. In the case of the Australian *Victaphanta*
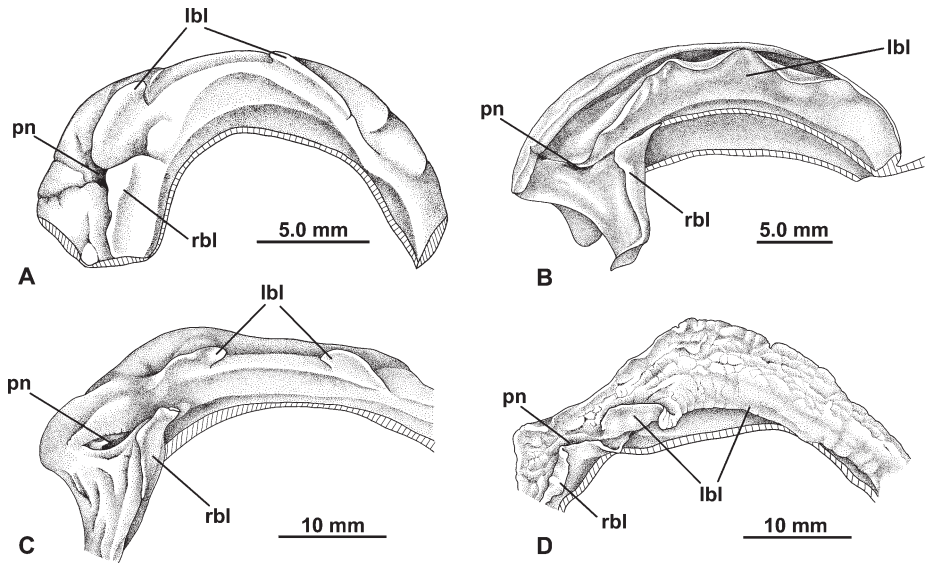
Fig. 6. Mantle edge anatomy of *Afrorhytida*, *Capitina* and *Natalina*, showing variation in left body lobe structure (all NMSA): (A) *Afrorhytida knysnaensis* (W5211); (B) *Capitina calcicola* sp. n. (W3201); (C) *Natalina* (*Natalina*) *cafra natalensis* subsp. n. (V8415); (D) *Natalina* (*Tongalina*) *wesseliana* (V7668). Abbreviations: lbl – left body lobe of mantle, pn – pneumostome, rbl – right body lobe of mantle.

atramentaria (Shuttleworth, 1852) and *V. compacta* (Cox & Hedley, 1912), Smith (1969) reported apparently consistent inter-specific differences in pigmentation of the mantle edge and pedal margin, but recent observations (Moussalli unpubl. data) indicate that there are additional population-related colour differences which complicate this picture.

Mantle edge (Fig. 6)

The edge of the mantle skirt is divided into left and right lobes, either side of the pneumostome. These encircle the base of the neck in the active animal. That on the right is relatively constant in appearance, but the form of the left lobe is highly variable. In *Capitina* it forms one continuous low flange around the neck (Fig. 6B), whereas as in *Afrorhytida* (Fig. 6A) and all but one *Natalina* species it is divided into two smaller lobes separated by a low ridge (Fig. 6C). The condition in *Natalina* (*Tongalina*) *wesseliana* (Fig. 6D) represents a third state in which the mantle edge as a whole is hypertrophied and the left lobe comprises a broad skirt in which the upper and lower portions are more or less confluent, separated only by a sinuous discontinuity. A fourth condition is present in *Nata s.l.*, resembling that in *Natalina*, but differing in that the lower left lobe has a narrow base and bears lateral flanges on both sides (Watson 1934).

Pulmonary anatomy (Fig. 7)

Sigmurethrous. The kidney is narrowly rectangular to elongate trigonal and lies to the right of the pericardium. It is usually somewhat longer than the pericardium, its anterior portion abutting the pulmonary vein, but it is not reflexed over the anterior pericardium as in *Nata* (Watson 1934). The primary ureter runs from the anterior extremity of the kidney (where the ureteric pore (nephropore) is located) to the extreme posterior corner of the pulmonary cavity. In *Natalina* and *Afrorhytida* it is relatively broad, but
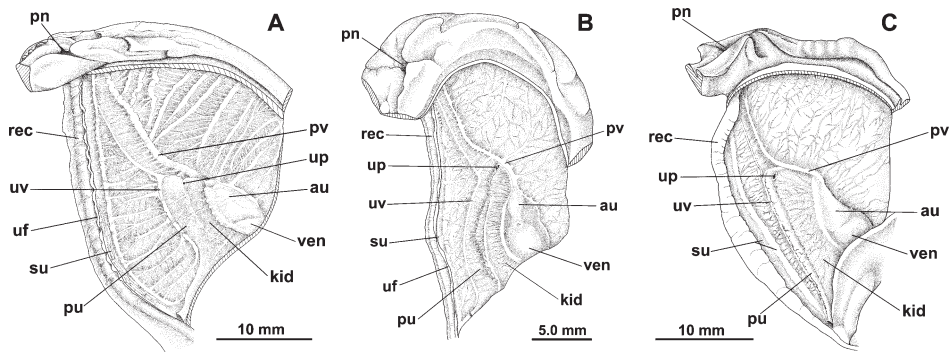
Fig. 7. Pulmonary anatomy of *Natalina*, *Afrorhytida* and *Capitina* (all NMSA): (A) *N. cafra cafra* (W4220); (B) *A. knysnaensis* (W5211); (C) *C. schaerfiae* (W5672). Abbreviations: au – auricle, kid – kidney, pn – pneumostome, pu – primary ureter, pv – pulmonary vein, rec – rectum, su – secondary ureter, uf – ureteric fold on rectum, up – ureteric pore, uv – ureteric vein, ven – ventricle.

narrower in *Capitina*. At its posterior limit the primary ureter discharges into the secondary ureter which, although open, runs as an almost completely enclosed channel beside the rectum, terminating beside the anus. In *Natalina* and *Afrorhytida* the rectum bears a longitudinal fold, the ureteric fold, which forms part of the wall of the secondary ureter.

The mantle lining the pulmonary cavity is heavily vascularised and the intermeshing blood vessels conspicuous, particularly so in the larger species of *Natalina*, in which the blood vessels stand out prominently relative to the intervening tissue. The pulmonary vein is the most conspicuous blood vessel, but there is an additional longitudinal vessel, the ureteric vein which runs to the right of the pulmonary vein and along the right margin of the primary ureter. At the anterior end of the primary ureter, a transverse vein connects this ureteric vein with the pulmonary vein. The ureteric vein drains oxygenated blood from the lung wall adjacent to the rectum and secondary ureter. In *Capitina* the blood vessels of the lung wall are darkly pigmented and the venation pattern is thus conspicuous. There is no evidence of a mantle gland posterior to the mantle collar as described by Smith (1970) in *Victaphanta* and Kondo (1943) in *Ouagapia*.

Radula (Fig. 8)

Reflecting a convergent trend evident in many families of carnivorous snails, rhytidids lack a jaw and possess a radula in which the number of teeth per transverse row is reduced when compared to the polyglossate radula typical of herbivorous Stylommatophora. At the same time the radula is longer, the tooth rows strongly V-shaped and the individual teeth frequently larger, each with a single, sharply pointed mesocone but with neither ectocones nor endocones (Watson 1915; Solem 1974; Barker & Efford 2004). In *Afrorhytida*, *Capitina* and *Natalina* the radula conforms to this general beloglossan pattern (Jungbluth *et al*. 1985), but there are significant modifications in terms of within-row variation in tooth size and the development of the base-plates, particularly in *Afrorhytida* and *Natalina*, resulting in marked and consistent differences between the genera, to which Watson (1934) has already drawn attention. A small rachidian tooth is present in all three genera (absent in most species of *Nata*).

In *Natalina* (Fig. 8A) the radula formula is 1+(5–9)+(10–30), with <3.5 rows/mm in adults. In *N. cafra* it attains a length of 58 mm, with up to 80 transverse rows. The number of lateral teeth is relatively low (frequently five, rarely up to 8 or 9 per half

row). The laterals increase rapidly in size, the outermost being a very large and robust tooth, twice or more the length of the innermost one, with a well-developed, quadrate base-plate. The distinction between the lateral and marginal series is pronounced. All marginal teeth are vestigial and there are no teeth of intermediary size adjacent to the largest (outermost) lateral. In this regard the *Natalina* radula resembles that of *Rhytida* and *Austrorhytida* species (Powell 1930; Smith 1987), except that marginal teeth are far more numerous in *Natalina*. In *N. wesseliana* and species belonging to the *N. cafra* complex, which are of a large size, the number of marginal teeth exceeds 20 in adults, but in the smaller members of the *N. quekettiana* complex there are generally fewer than 20. This difference is almost certainly a function of size, since juveniles of the *N. cafra* complex also have fewer marginal teeth than adults. The same does not apply to the lateral teeth, the number of which is generally greater in the smaller species of the *N. quekettiana* complex (6–9, except *N. reenenensis* which has five) than in the members of the *N. cafra* complex and *N. wesseliana* (usually five, rarely six, but eight in *N. cafra eumacta*). In terms of the number of lateral teeth, there is no difference evident between juveniles and adults.

In *Afrorhytida* (Fig. 8B) the radula formula is 1+(7–15)+(7–24), with 3.2–4.6 rows/ mm in adults. The lateral teeth are generally more numerous than in *Natalina* although there is considerable inter-specific variation in this regard. The increase in size of the laterals is small at first, becoming substantial toward the outer end of the series, the outermost 3 or 4 teeth having large, quadrate base-plates. The largest lateral tooth, frequently the penultimate one, is at least twice the length of the innermost one. Although the distinction between the lateral and marginal series is pronounced, the innermost 1 or 2 (more in *A. knysnaensis*) marginal teeth are of intermediate size and only the outermost ones are vestigial.

In comparison with *Natalina* and *Afrorhytida*, the radula of *Capitina* (Fig. 8C) is distinctive in that the teeth are smaller (5.0–6.6 rows/mm in adults) and the outward increase in size of the lateral teeth is more even, with no one tooth being obviously larger than the others. The transition between the lateral and marginal teeth is therefore not distinct and they cannot be considered distinct series. The formula is 1+(20–32). The increase in size of the teeth in the latero-marginal series is less marked than in *Natalina* and *Afrorhytida*, the largest tooth not attaining twice the length of the innermost one.
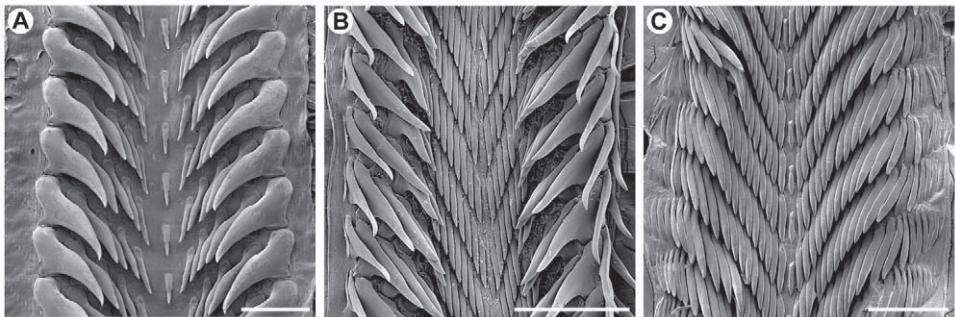

Fig. 8. Radulae of *Natalina*, *Afrorhytida* and *Capitina* (all NMSA): (A) *N. beyrichi* (Martens, 1890) (W0591), scale bar = 1.0 mm; (B) *A. kraussi* (Pfeiffer, 1846) (W3351), scale bar = 500 µm; (C) *C. calcicola* sp. n. (paratype, W3360/T2270), scale bar = 250 µm.
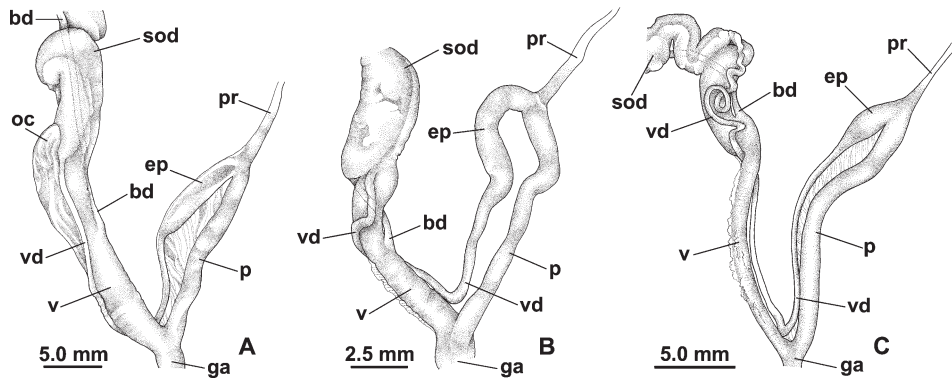
Fig. 9. Distal genitalia of *Natalina*, *Afrorhytida* and *Capitina* (all NMSA): (A) *N. cafra natalensis* subsp. n. (E7682), (B) *A. knysnaensis* (W4643), (C) *C. schaerfiae* (W5672). Abbreviations: bd – bursa copulatrix duct, ep – epiphallus, ga – genital atrium, oc – oviduct caecum, p – penis, pr – penial retractor muscle, sod – spermoviduct, v – vagina, vd – vas deferens.

Teeth 9–14 are the largest (but even these lack an obviously enlarged base-plate) after which there is a gradual decrease in size toward the edge of radula. Several Australasian taxa also possess a radula in which there is no obvious distinction between the lateral and marginal series. That of the limaciform genus *Schizoglossa* Hedley, 1892 from New Zealand (Powell 1930) is perhaps the most similar to *Capitina*.

Distal reproductive tract (Fig. 9)

Watson (1934) provided the first detailed, comparative discussion of the reproductive anatomy of southern African rhytidids and identified a number of distinctive character states. These were consistent with other morphological characters states (notably in the radula) and provided the basis for his revised supraspecific classification of the regional rhytidid fauna. In the case of *Natalina s.l.*, the subgroups he recognised have proven to be consistent with the lineages identified through molecular analyses (Moussalli *et al*. 2009).

The distal reproductive tract of *Afrorhytida*, *Capitina* and *Natalina* is relatively simple, lacking most of the specialised structures found in many Stylommatophora. However, any comparison of those structures present must always take into account differing states of specimen relaxation prior to preservation which can profoundly affect their size, shape and proportions. The genital pore is typically situated below and just posterior to the right optic tentacle, but in *Natalina wesseliana* it is displaced dorsally and posteriorly such that it lies dorsolaterally in the mid section of the neck. This contrasts markedly with the situation in *Nata* (and several Australasian genera) where the genital pore lies below the pneumostome. The genital atrium is simple and apically receives the openings of the penis base and vagina. The penis is generally long and slender and connects distally at a U-shaped bend to the epiphallus which lies more or less beside the penis. The internal wall of the penis is lined with papillae, these are extremely fine in *Natalina*, but somewhat coarser in *Afrorhytida* and *Capitina*. In *Natalina* and *Capitina* a small penis papilla is present at the apex of the penis where it joins the epiphallus, but this is absent in *Afrorhytida*. The penial retractor muscle is attached to the apex of the bend at the penis–epiphallus junction. The epiphallus is 0.5–0.75× the length of the penis in *Natalina* and *Afrorhytida*, but considerably shorter in *Capitina* (<0.25× length of penis).

It is lined internally by longitudinal folds and the wall is frequently thick and penetrated by microscopic diverticulae reflecting the presence of spines on the spermatophore. The vas deferens joins the epiphallus distally and continues to the base of the penis. In *Natalina* and *Capitina* the epiphallus and lower vas deferens are joined laterally to the penis by a web of connective tissue, whereas in *Afrorhytida* the epiphallus and vas deferens are free of the penis. At the base of the penis, the vas deferens turns sharply to run beside the vagina and free oviduct, ultimately fusing with the base of the prostatic portion of the spermoviduct. Usually the vas deferens is simple, but it may occasionally be somewhat convoluted, particularly near its origin from the spermoviduct (*Capitina*), although this appears to be a somewhat individually variable character. In *Capitina* and *Afrorhytida* the retractor muscle of the right optic tentacle passes between the penis complex and the vagina, whereas in *Natalina* the penis lies to the right of the tentacle retractor.

The vagina is moderate to long and gives rise to a long and slender bursa copulatrix duct. This runs closely applied to the spermoviduct in *Capitina* and *Afrorhytida*, but in *Natalina* in which the spermoviduct is highly convoluted, it runs axially within the folds of the latter. The bursa copulatrix itself is very delicate, ovate, pyriform or reniform in shape, and lies within the visceral mass, just posterior to the reno-pericardial complex, surrounded in loose connective tissue. Close to the origin of the bursa copulatrix duct, the vagina may also give rise to a blind-ending caecum which is fused to the lower portion of the free oviduct by connective tissue. This oviduct caecum is well developed in species of *Natalina* but small or absent in *Afrorhytida*. In *Capitina* an oviduct caecum is absent, but the basal portion of the free oviduct is enlarged.

The spermoviduct is long, superficially folded and convoluted in all three genera, particularly so in *Natalina*, a character state contrasting with that of *Nata* spp. in which the spermoviduct, though superficially folded, is not also convoluted. Little variation is evident in the upper parts of the reproductive tract. The albumen gland when mature (or active) is large and crescentic, the hermaphrodite duct highly convoluted and the ovotestis, comprising many elongate acini, is embedded in the apical whorl of the digestive gland.

From a functional perspective, the site of spermatophore receipt is the enlarged free oviduct in *Capitina* (Fig. 75), the oviduct caecum in *Natalina* (Figs 12, 51) or the upper vagina in *Afrorhytida* (Figs 62, 68). The fact that the vagina and penis are of more or less equal length suggests that during copulation the penis is inserted fully into the vagina for spermatophore delivery. The narrowness of the bursa copulatrix duct renders it probable that only sperm discharged from the spermatophore and destined for lysis pass to the bursa itself. This is in contrast to the situation in *Nata*, in which the vagina is extremely short and the base of the bursa duct broad, suggesting that in this genus the spermatophore (if indeed such is formed) is deposited into the basal portion of the bursa duct.

Spermatophores (Fig. 10)

Although some New Zealand rhytidids are thought not to produce spermatophores (e.g., *Powelliphanta* spp., Walker *et al*. 2008), and presumably also some other taxa which lack an epiphallus (e.g., *Ouagapia*, *Rhytida* (*Amborhytida*) and *Victaphanta* spp., cf. Kondo 1943; Smith 1970; Smith & Kershaw 1972; Climo 1974), species of

Afrorhytida, Capitina and *Natalina* all have a distinct epiphallus that produces a spermatophore in which sperm are transferred during copulation. The presence of a spermatophore in *Natalina cafra* was first recorded and its structure briefly described by Murdoch (1901), but he evidently confused the head and tail of the structure. These are rarely encountered, but we have been fortunate to find a spermatophore in at least one species in each of the three genera. In nearly all cases this was an allospermatophore, located in the female tract, and was in fresh condition, indicating recent mating. Spermatophore bearing specimens from the south-western Cape were collected in early to mid October (*Capitina calcicola* and *Afrorhytida kraussi* respectively), and from late November to early March in KwaZulu-Natal and Eastern Cape (*Natalina* and *Afrorhytida burseyae* sp. n.), suggesting a spring mating period in the winter rainfall region (where the summer is hot and dry) and a late spring to summer mating period in the summer rainfall region. Full details of spermatophore morphology are given under the generic descriptions below, but it is evident that there are marked, clade-specific differences.

In *Capitina* (Fig. 10A) the spermatophore is tadpole-shaped, with irregular longitudinal ridges on the head section, one side of which is distinctly concave. It is also short (length approx. 8.0 mm), corresponding with the short epiphallus. In *Afrorhytida* and *Natalina* (Figs 10B–F) the spermatophore is longer (up to 32 mm in *N. wesseliana*) more elongate and generally curved or sinuous. The proportions and ornamentation vary considerably between species and within genera, some examples bearing strong, but smooth longitudinal grooves and ridges, and others with antler-like or lobate, scale-like projections.

Although information concerning spermatophore morphology is currently incomplete, the available data and inferences from epiphallus structure suggest that it is consistent within genera and clades, and that spermatophores may be character-rich and thus a potential source of valuable data which may be both taxonomically and phylogenetically informative. Particular attention needs to be given to spermatophore structure in closely related subspecific lineages for which we currently have limited morphologically diagnostic data.

Fig. 10. Spermatophores of *Capitina*, *Afrorhytida* and *Natalina* (all NMSA): (A) *C. calcicola* sp. n. (paratype, W5670/T2265), length 8.2 mm; (B) *A. burseyae* sp. n. (paratype, W5231/T2260), length 10.5 mm; (C) *A. kraussi kraussi* (W5803), length 20 mm; (D) *N. cafra natalensis* subsp. n. (paratype, E7682/T2375), length 16.3 mm; (E) *N. quekettiana lucaris* subsp. n. (paratype, W3305/T2559), length 26.5 mm; (F) *N. wesseliana* (V7668), length 32 mm. The head of the spermatophore is uppermost in all cases and the lengths given are for the spermatophore as if straightened out.
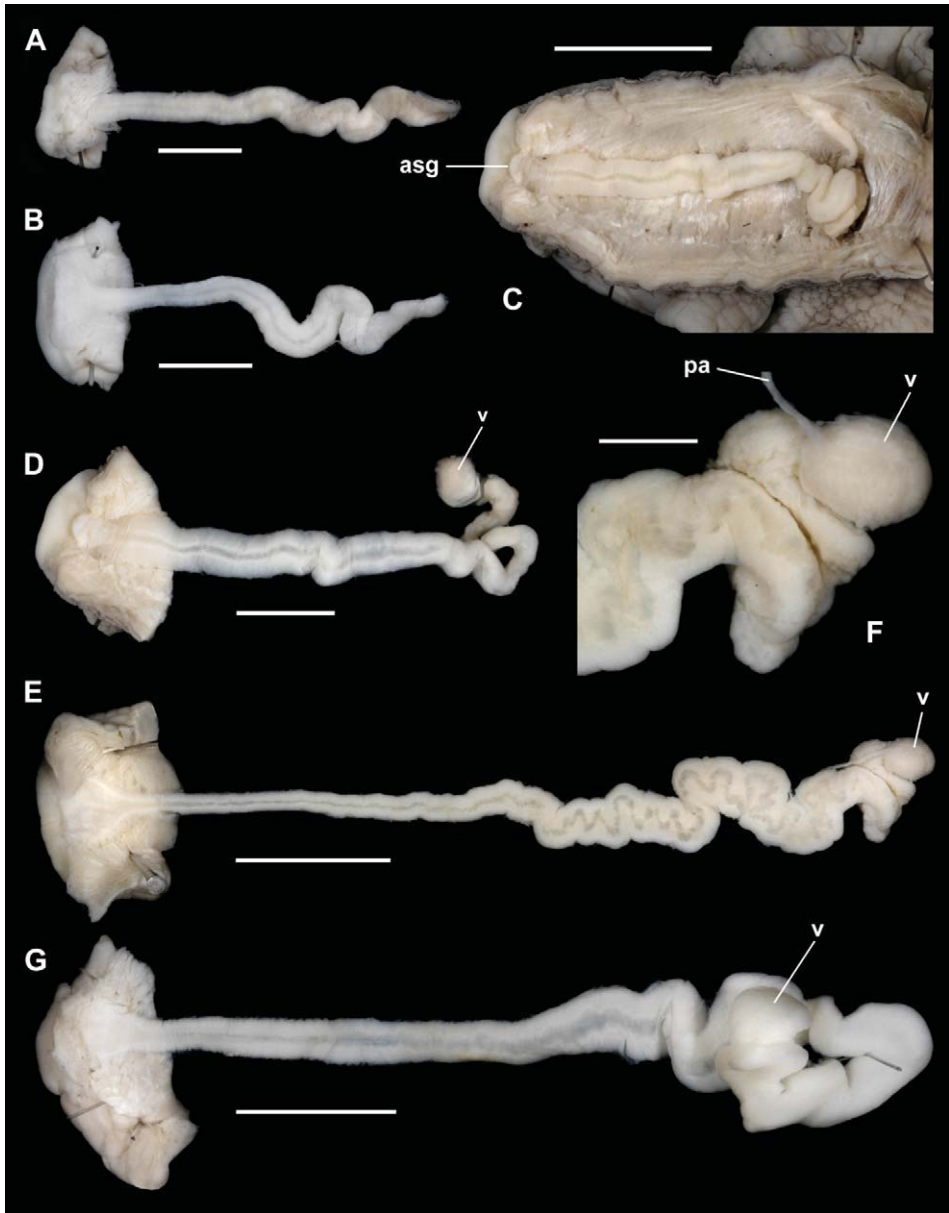
Fig. 11. Suprapedal glands of *Capitina*, *Afrorhytida* and *Natalina* (all NMSA): (A) *C. schaerfiae* (W5672), scale bar = 5.0 mm; (B) *A. knysnaensis* (W3351), scale bar = 5.0 mm; (C, D) *N. quekettiana lucaris* subsp. n. (W3310): (C) pedal cavity with suprapedal gland *in situ*, scale bar = 10 mm; (D) dissected gland, scale bar = 5.0 mm; (E, F) *N. wesseliana* (V7668): (E) entire gland, scale bar = 20 mm; (F) enlargement of distal end showing terminal vesicle, scale bar = 5.0 mm; (G) *N. cafra cafra* (W4220), scale bar = 10 mm. Abbreviations: asg – aperture of suprapedal gland, pa – pedal artery, v – vesicle at posterior end of suprapedal gland.

Suprapedal gland (Fig. 11)

The suprapedal gland of rhytidids is well developed and lies beneath the odontophore and ventral ganglia, on top of the pedal musculature, rather than within it as in many herbivorous forms (Watson 1915). It is loosely attached to the floor of the body cavity by scattered strands of connective tissue, and is overlain by a network of blood vessels and nerves supplying and innervating the foot. It terminates in a small pocket at the posterior end of the body cavity, where the pedal artery enters the musculature of the tail (Fig. 11C). The shape and size of the gland shows considerable individual variation, related to the degree to which the animal was contracted when preserved. This notwithstanding, some broad patterns are evident. In all cases, glandular tissue is present almost throughout the length of the central duct, in contrast to the condition in *Nata* in which the glandular tissue ends abruptly, some distance prior to the posterior end of the duct (Watson 1934).

In *Capitina* (Fig. 11A) the gland is sinuous, of more or less even width, tapering slightly at the posterior limit. That of *Afrorhytida* is essentially the same (Fig. 11B), though the anterior section is often somewhat more slender. In neither of these genera is the posterior part of the gland enlarged to form a sack-like vesicle, although there is evidence of some structural differentiation of the tissue at the gland tip. In the larger species of *Natalina* (*Natalina*) (Fig. 11G) the anterior half of the gland is straight and considerably thinner than the posterior half, which is usually folded and looped back on itself at least once, complexly so according to the figure provided by Hoffmann (1940). At the posterior limit, buried beside the pedal artery in the pocket within the pedal muscle is a thin walled terminal vesicle, held firmly in place by connective tissue. In smaller *Natalina* species (*N. quekettiana* complex), it is the anterior part of the gland that is broadest and it tapers progressively toward the posterior end, prior to a small but distinct terminal vesicle (Figs 11C, D). The gland attains its maximum size in *Natalina* (*Tongalina*) *wesseliana,* reaching a length of up to 90 mm in a well relaxed specimen (Figs 11E, F). It resembles that of the other large *Natalina* species except, probably as a result of the well extended head-foot, it is less extensively looped back on itself, revealing tight sinuosity in the central duct of the posterior half of the gland. A distinct terminal vesicle is again present (Fig. 11F).

Watson (1915) speculated that, since the suprapedal gland is frequently well developed in carnivorous snails and slugs, including unrelated families, it may function in feeding as well as in locomotion. Subsequently, Herbert (2000) has shown that mucus secretion, almost certainly from the suprapedal gland, is involved in the feeding behaviour of millipede-eating chlamydephorid slugs. The possibility that suprapedal gland mucus has toxic properties is clearly an interesting one and merits further study.

TAXONOMY

Superfamily Rhytidoidea Pilsbry, 1893

Family Rhytididae Pilsbry, 1893

Rhytididae Pilsbry, 1893 [February], in 1892–93: 135.
Paryphantinae Godwin-Austen, 1893 [October]: 8; Solem 1959: 147 (Paryphantidae).
Occirheneidae Iredale, 1939: 73.

Diagnosis: Shell globose to discoidal, minute to very large; occasionally reduced and shield-like; aperture lacking dentition; umbilicus open, except when shell is reduced

(*Schizoglossa*). Pulmonary anatomy sigmurethrous, primary ureter closed, secondary ureter generally open; distal genitalia lacking accessory structures, epiphallus often present, flagellum usually absent; foot lacking peripodial groove, sole undivided, caudal pore and appendage absent; suprapedal gland well developed, lying above pedal musculature; jaw absent, radula beloglossan; buccal mass elongate, large and muscular; head and neck elongate. Carnivorous.

Key to genera within *Natalina s. l.*

1   Axial riblets on apical surface weak, interacting with faint spiral lines to produce a microscopically malleated sculpture; colour pattern usually including dark brownish spiral bands; left body lobe of mantle an uninterrupted collar; radula with no clear distinction between lateral and marginal series, teeth progressively and smoothly increasing and then decreasing in size from middle to edge of radula .... **Capitina**

–   Shell sculpture on apical surface largely comprising axial riblets only; coloration uniform or with irregular axial bands in somewhat darker shades; left body lobe of mantle comprising two small lobes separated by a low ridge or two confluent hypertrophied lobes; outer lateral teeth of radula very large, marginals much smaller, with or without inner marginals of intermediate size 2

2   All marginal teeth vestigial; epiphallus and vas deferens joined to penis by a web of connective tissue; penis situated to right of optic retractor muscle; adult shell diameter frequently exceeding 40 mm; apertural lip of adult, even if slightly thickened, with membranous periostracal fringe .... **Natalina**

–   Inner marginal teeth (2 or more) of intermediate size; epiphallus and vas deferens not joined to penis by a web of connective tissue; penis situated to left of optic retractor muscle; adult shell diameter not exceeding 35 mm; apertural lip of adult commonly thickened, at least basally, lacking membranous periostracal fringe ....
.... **Afrorhytida**

Genus *Natalina* Pilsbry, 1893

Aerope: Albers in Martens 1860: 83 [as subgenus of *Helix* Linnaeus, 1758] *non* Leach in Desmarest, 1823 [Crustacea]; *non* White, 1847 [Crustacea]; *non* Thomson in Jeffreys, 1876 [Echinodermata].
Natalina: Pilsbry 1893 in 1892–93: 135. Type species: *Helix caffra* [*sic*] Férussac, 1821, by original designation.

Diagnosis: Shell moderate to very large (adult diameter up to 75.5 mm), thin and fragile, lenticular to globose, olive-green to brown, frequently with irregular darker axial bands, but lacking spiral colour pattern; apical surface sculptured with close-set axial riblets, usually lustreless, base smoother and more glossy; peristome interrupted in parietal region; outer lip thin with membranous periostracal fringe, sometimes slightly thickened basally; umbilicus open, width variable; protoconch of ±1.25 whorls, diameter >4.5 mm, with distinct, close-set, axial riblets more or less throughout. Outermost lateral teeth of radula huge, all marginal teeth vestigial (no teeth of intermediate size between lateral and marginal series). Labial palps well developed. Penis elongate and cylindrical, situated to right of retractor muscle of right optic tentacle; epiphallus well developed (50–75 % of penis length); epiphallus and lower vas deferens joined to penis by connective tissue web; vagina long; oviduct caecum present and well developed. Suprapedal gland long, distally convoluted and with a terminal vesicle.

Notes: As indicated in the Introduction, following our previous work (Moussalli *et al.* 2009), we employ the genus *Natalina* in a restricted sense, treating taxa formerly considered subgenera (viz. *Afrorhytida* and *Capitina*) as distinct genus-level entities. This is based on a evidence from a suite of consistently differing morphological characters and marked divergence in DNA sequence data. In addition, we propose a new subgenus for *Natalina wesseliana* which represents a distinct and basally divergent lineage within *Natalina*, and which exhibits several anatomical autapomorphies that set it apart from the remaining species.

Natalina is endemic to southern Africa, occurring to the south and east of the Great Escarpment and ranging from the Baviaanskloof, E. Cape to the Blyderivier area, Mpumalanga (24.56°S) and the mouth of the Limpopo R. valley in southern Mozambique (25.11°S).

Key to subgenera of *Natalina*

1 Last whorl of shell expanding rapidly; umbilicus small and largely concealed by reflected columella lip; genital pore situated high on neck, well posterior to right optic tentacle; skin of neck coarsely granular. North of Mfolozi R. only, below 700 m ....**Tongalina** subgen. n.
– Last whorl expanding regularly but not rapidly; umbilicus generally larger and more clearly visible; genital pore ventral to and just posterior to right optic tentacle; skin of neck relatively finely granular. Mostly south of Mfolozi R., but if north, then associated with Afrotemperate forest above 1000 m ....**Natalina** *s. s.*

Subgenus *Natalina* Pilsbry, 1893

Diagnosis: Skin texture finely to moderately granular; genital pore ventral and just posterior to right optic tentacle; left mantle lobe divided into two smaller lobes, separated by low ridge.

Radula: Long, up to 58 mm in length (*fide* Connolly 1939), with up to 80 broadly V-shaped transverse rows of teeth, 0.95–3.5 rows/mm in adult; formula 1+(5–9)+(10–30); rachidian small and sharply pointed, cusp and base-plate more or less of equal length; lateral teeth progressively increasing in size from first to last, innermost slender and more or less straight, outermost one very large, more than twice as long as innermost one, and with a quadrate, laterally indented base-plate and strong, curved, acutely pointed cusp; marginal teeth all vestigial, no teeth of intermediate size and boundary between lateral and marginal series thus abrupt.

External anatomy (Figs 5, 6C, 15A–G): Left body lobe of mantle divided into two relatively small lobes separated by a low ridge (Fig. 6C); skin texture finely to moderately granular; labial palps well developed; optic and inferior tentacles with a ventrally distended apical bulb; tail region of foot flattened and acutely pointed when animal actively crawling; genital pore ventral and just posterior to right optic tentacle.

Distal genitalia (Figs 9A, 12, 13): Penis long, of more or less uniform width, often somewhat sinuous *in situ*, its wall relatively thin; lumen lined throughout by finely micro-papillate epithelium, micro-papillae close-set and extremely numerous (Fig. 13A), sometimes aligned in indistinct longitudinal rows. Apex of penis with small papilla,

through which epiphallus lumen connects with penis lumen; size and shape of penis papilla variable, depending on preservation, its surface microscopically wrinkled rather than micro-papillate. Penial retractor muscle attached at apex of penis, where the latter curves backwards to join epiphallus. Epiphallus relatively long, 0.5–0.75 of penis length and reflexed to lie beside it; frequently with grey-black pigmentation within its wall; sometimes with a distinct bulla on outer side, immediately above insertion of vas deferens (Fig. 13B); lining of epiphallus lumen with distinct longitudinal ridges or folds (Figs 13A, C), but details variable, reflecting spermatophore morphology and discussed further in species treatments below. Vas deferens runs alongside penis base, vagina and free oviduct, sometimes sinuous in the latter region, before fusing with spermoviduct. A web of connective tissue joins lower vas deferens and epiphallus to penis; that between epiphallus and penis a double layer, connecting both sides of epiphallus to penis.

Genital atrium simple, cylindrical; lumen wall with longitudinal folds. Vagina moderately long (but relatively shorter than in *Capitina*) and slender; attached laterally to body wall by a well-developed series of muscle fibres; merges with free oviduct at point of origin of bursa copulatrix duct, at which point there arises a cylindrical oviduct caecum; caecum closely applied to base of free oviduct and fused to it by connective tissue;
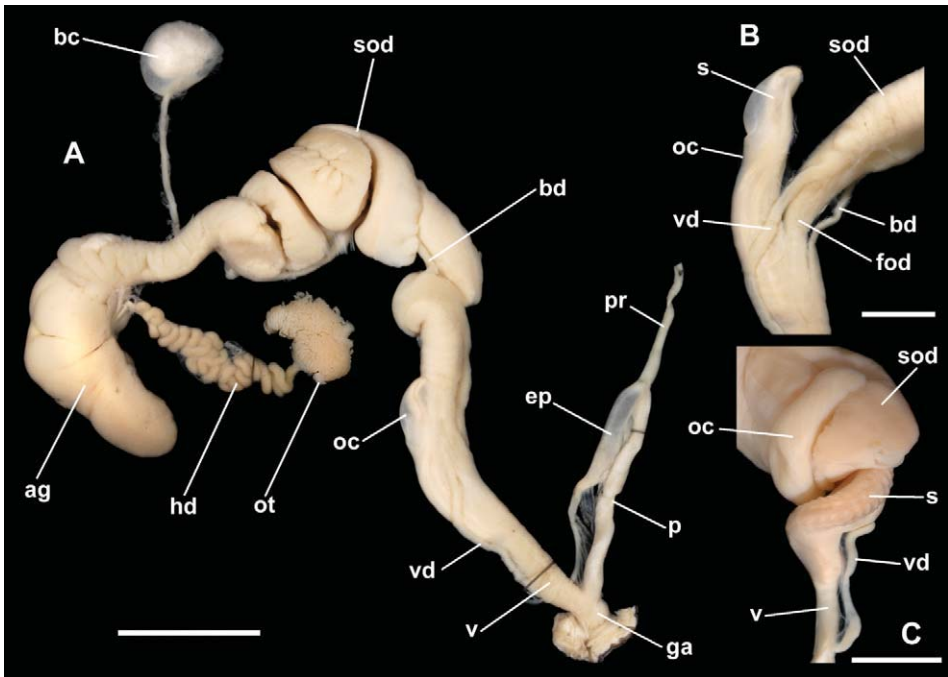

Fig. 12. *Natalina s. s.* genital system: (A, B) *N. cafra natalensis* subsp. n. (paratype, NMSA E7682/T2375): (A) entire reproductive tract, scale bar = 10 mm; (B) oviduct caecum (with spermatophore), teased away from free oviduct, scale bar = 5.0 mm; (C) *N. quekettiana lucaris* subsp. n. (paratype, NMSA W3305/T2559), oviduct caecum (with spermatophore) twisted around free oviduct and base of spermoviduct, scale bar = 5.0 mm. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bd – bursa copulatrix duct, ep – epiphallus, fod – free oviduct, ga – genital atrium, hd – hermaphrodite duct, oc – oviduct caecum, ot – ovotestis, p – penis, pr – penial retractor muscle, s – spermatophore, sod – spermoviduct, v – vagina, vd – vas deferens.

inner wall of vagina with smooth, slender longitudinal folds (Fig. 13D); similar but somewhat thicker folds line free oviduct and oviduct caecum. Bursa copulatrix duct long and very slender, attached to free oviduct by connective tissue and then running within convolutions of spermoviduct to bursa copulatrix situated posterior to pericardium; bursa very thin-walled, variable in shape, generally empty but occasionally
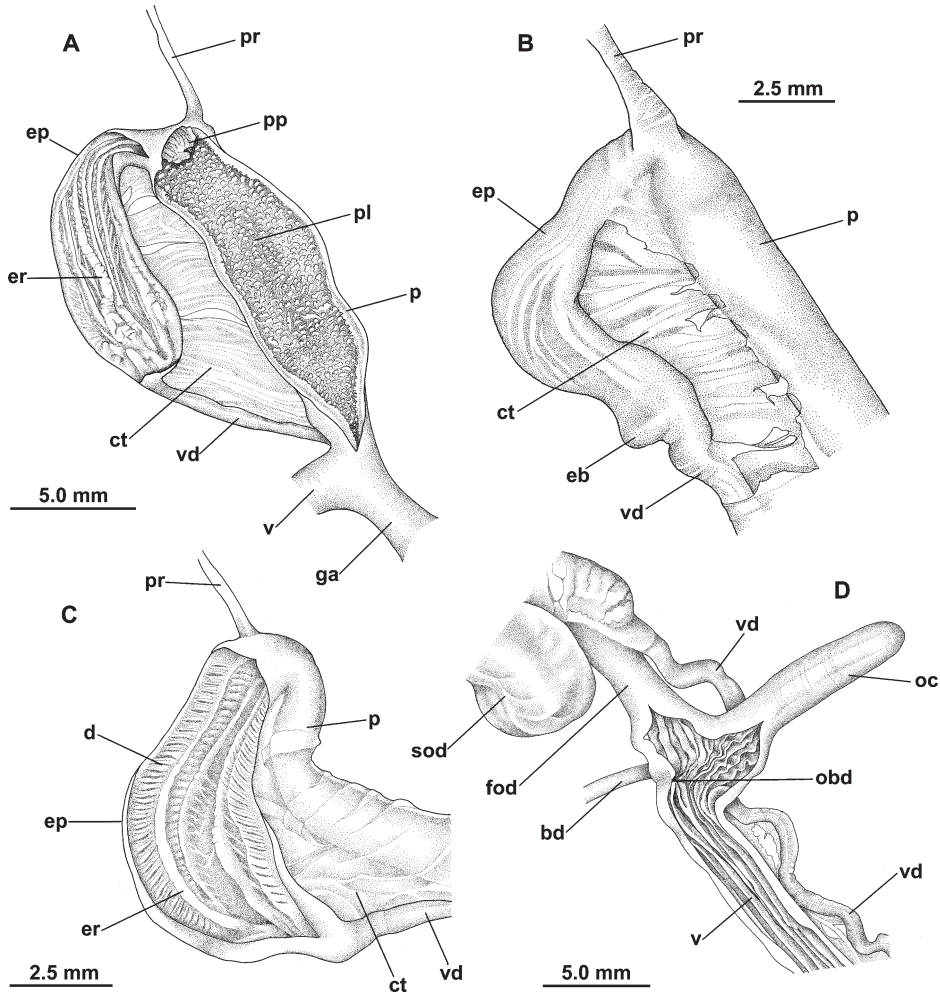

Fig. 13. Distal genitalia of *Natalina s.s.* (all NMSA): (A) *N. cafra natalensis* subsp. n. (1392), lower male tract with penis and epiphallus cut open to show internal structure; (B) *N. cafra cafra* (W4220), external view of epiphallus showing bulla at base of epiphallus, close to its junction with vas deferens; (C) *N. quekettiana quekettiana* (W6646), epiphallus opened longitudinally to show internal ridges and intervening diverticulae; (D) *N. c. natalensis* subsp. n. (1392), lower female tract showing oviduct caecum (caecum dissected away from free oviduct and spermoviduct base to which it is fused with connective tissue in life) and vagina which has been opened longitudinally to reveal internal folds. Abbreviations: bd – bursa copulatrix duct, ct – connective tissue web, d – slit-like diverticulae in epiphallus wall, eb – epiphallus bulla, ep – epiphallus, er – internal epiphallic ridge, fod – free oviduct, ga – genital atrium, obd – opening of bursa copulatrix duct, oc – oviduct caecum, p – penis, pl – penis lumen with micropapillate lining, pp – penis papilla, pr – penial retractor muscle, sod – spermoviduct, v – vagina, vd – vas deferens.

containing a whitish amorphous mass. Spermoviduct thrown into strong convolutions and with distinct oviducal and prostatic portions, the former with superficial folds; hermaphrodite duct highly convoluted; ovotestis comprising a loose assemblage of vermiform acini, embedded in apical whorl of digestive gland.

Spermatophores (Fig. 14): Allospermatophores are occasionally found, nearly always singly, in the female tract, mostly in specimens collected in late spring to mid summer. Autospermatophores in the epiphallus are far less frequently encountered.

Larger species of *Natalina s.s.* (Figs 14A–E): Spermatophores elongate (up to 26 mm in total length), whitish to pale apricot, of firm substance; gently or sharply curved, but generally little twisted. Anterior 1/2–2/3 tapers toward head, sculptured by 6–8 strong longitudinal ridges with well-developed intervening grooves; ridges become subdivided by secondary grooves as spermatophore width increases, creating intercalating second
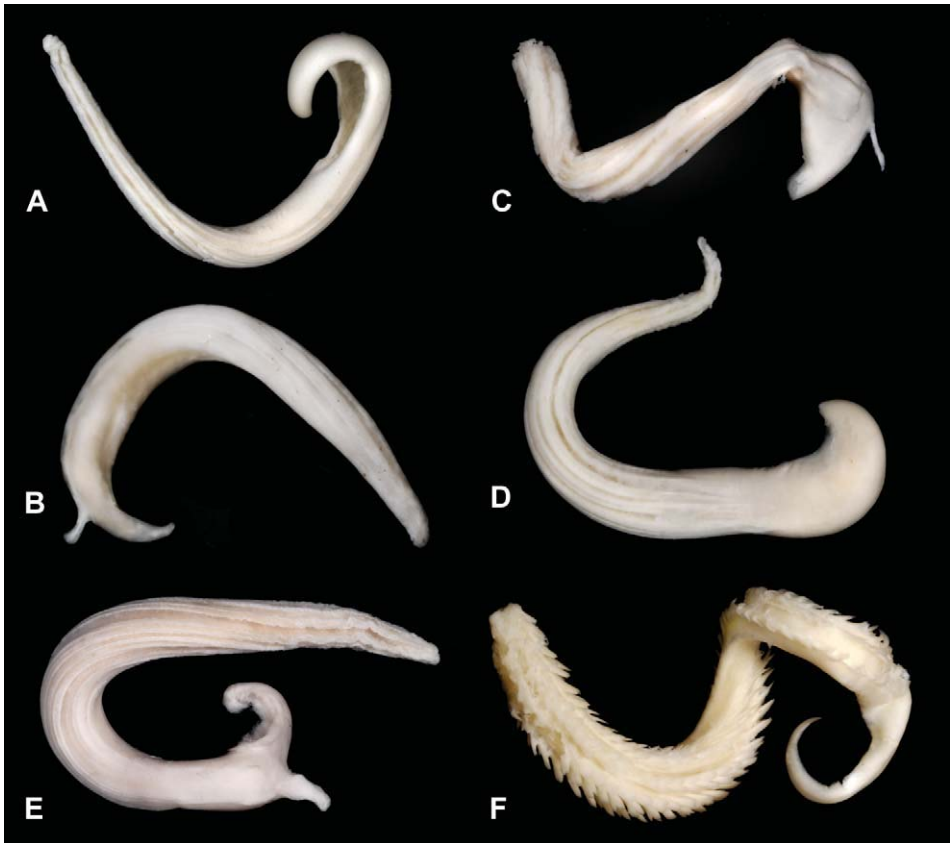

Fig. 14. *Natalina s. s.* spermatophores (all NMSA): (A) *N. cafra amathole* subsp. n. (W4193), length 21 mm; (B) *N. cafra natalensis* subsp. n. (W7136), length 18.3 mm; (C) *N. cafra eumacta* (W4055, Manubi Forest), distorted spermatophore with finger-like process on tail region, length 12 mm; (D) *N. c. eumacta* (W4160, Manubi Forest), well preserved spermatophore lacking finger-like process on tail region, length 18.5 mm; (E) *N. beyrichi* (W4123), length 25.8 mm; (F) *N. quekettiana lucaris* subsp. n. (paratype, W3305/T2559), length 26.5 mm. The lengths given are for the spermatophore as if straightened out.

order ridges; ridges smooth, lacking spines or scales; grooves and ridges usually obsolete on posterior third; tail region distinctly curved, inner side of curve split open to allow escape of sperm. A small, subterminal finger-like or thumb-like process may be present on outer side of spermatophore where the tail begins to curve round, the presence of this structure correlates with the presence of a bulla on the epiphallus.

Allospermatophores were located almost entirely within oviduct caecum (Fig. 12B) with tail region close to opening of free oviduct; recurved tip of tail usually projects into base of bursa copulatrix duct and thumb-like process extends into vagina. Functionally, these terminal processes probably serve to hold the spermatophore in the optimal position by slotting into place at the trifurcation of the vagina, free oviduct and bursa copulatrix duct, such that the subterminal vent of the spermatophore cups the base of the free oviduct (see *Natalina wesseliana*). Some variation in spermatophore form is evident between and within taxa, and is detailed in the species treatments below. However, since so few spermatophores are available for each taxon, it is not possible to assess whether small differences between subspecies are consistent and thus whether they represent reliable taxonomic characters.

Natalina quekettiana complex (Fig. 14F): Spermatophore known only from one specimen of *N. quekettiana lucaris* subsp. n. Spermatophore elongate and with strong spiral twist (straightened length 26.5 mm); pale apricot and of firm substance; anterior two thirds with deep longitudinal grooves on sides and outer (convex) surface, ridges between grooves bearing coarse, backwardly directed, scale-like spines; a broad, smooth band running along inner surface of spiral; spines well developed, with narrow base and flat, expanded blade with two or more lobes. Longitudinal ridges weakening posteriorly, finally becoming little more than rows of feeble spines and disappearing completely on the short, smooth, recurved tail; base of tail with a narrow vent. Spermatophore positioned with anterior half located in oviduct caecum (coated in coagulated white mucilage) and posterior half in upper vagina (Fig. 12C).

The morphology of the lining of the epiphallus lumen of other taxa in the *N. quekettiana* complex indicates that they too will have spermatophores with scale-like spines, suggesting that this is an autapomorphy for this smaller-shelled clade. Such relatively large, lobate spines are quite distinct from the small, antler-like spines observed in the *Afrorhytida* spermatophore.

Key to species of *Natalina s. s.*

1 Adult diameter exceeding 40 mm; radula with >20 marginal teeth per half row in adult; spermatophore lacking spines 2

– Adult diameter not attaining 40 mm; radula with <20 marginal teeth per half row in adult; spermatophore spinose (judged by internal morphology of epiphallus) .... **N. quekettiana** complex

2 Umbilicus wide, not covered to any appreciable degree by reflected columella lip; shell typically depressed (less so in Hluleka region) with low spire. Primarily coastal, from the Msikaba R. south to the Kei R. valley .... **N. beyrichi**

– Umbilicus relatively narrow and usually partly obscured by columella lip, though still clearly patent; shell proportions very variable, last whorl rarely conspicuously flattened and shell generally more globose. Widely distributed in KZN and E. Cape, but absent in north-eastern part of E. Cape .... **N. cafra**

Fig. 15. *Natalina s.s.*, living animals of larger species (all NMSA): (A) *N. beyrichi*, Hluleka (W2895), shell diameter 41.5 mm; (B) *N. cafra cafra*, Mountain Drive, Grahamstown (W5212), shell diameter 30.0 mm; (C) *N. cafra amathole* subsp. n., Hogsback (paratype, W6371/T2309), shell diameter 39.0 mm; (D) *N. cafra natalensis* subsp. n., Pietermaritzburg (specimen not collected), shell diameter approx. 58 mm; (E) *N. c. natalensis* subsp. n., Mtamvuna (paratype, W0308/T2370), shell diameter 40.3 mm; (F) *N. cafra eumacta*, Mazeppa Bay (W4044), shell diameter 40.4 mm; (G) *N. c. eumacta*, Dwesa (V7868), shell diameter 48.3 mm; (H) *N. c. eumacta*, egg, Manubi Forest (W4067), scale in millimetres.

Natalina cafra (Férussac, 1821)

The conspicuous disjunction in the distribution of *N. cafra* (Fig. 16) has remained an unexplained anomaly. Populations occur over a considerable extent in both KwaZulu-Natal and E. Cape, but there is a range hiatus of over 175 km in the north-eastern part of E. Cape (between Xora and Mtamvuna rivers), where no specimens have been recorded from either coastal or inland localities. Although this area cannot be described as well sampled, its malacofauna has been the focus of a number of recent surveys jointly undertaken by the Natal Museum and East London Museum. It is therefore likely that the lack of records from this region, particularly of a large and conspicuous animal such as this, reflects a genuine absence. A similar hiatus is evident in the distribution of the cerastid *Gittenedouardia meridionalis* (Pfeiffer, 1848) (Herbert & Kilburn 2004).

Molecular data has now shed further light on this issue, indicating that the KwaZulu-Natal population constitutes a distinct genetic lineage standing apart from the E. Cape population (Moussalli *et al.* 2009). Furthermore, the E. Cape population itself comprises three distinct lineages with strong geographic structure. Although these findings add to the complexity of the problem, they also illuminate some of the associated taxonomic uncertainties surrounding the use of the available names in identifying specimens.

In the light of this genetic data, it has been necessary to completely re-evaluate the taxonomy of *N. cafra*. Accordingly, we recognise each of the lineages identified genetically as separate subspecies. This decision is strongly supported by the fact that the lineages are geographically allopatric (Fig. 16), acknowledging that sampling of the Amathole lineage is limited. Nevertheless, in terms of shell characters and soft part anatomy there is little, and sometimes nothing which serves to reliably differentiate the subspecies morphologically. Variation in shell proportions and colour is considerable, while the anatomy of the distal reproductive tract is highly conservative. Some of the subspecies, however, show consistent (though not diagnostic) features in shell proportions which are discussed below. There also appear to be consistent differences in the number of lateral teeth per transverse row of the radula, but in some cases this data is based on a limited sample.

Connolly (1939) described globose, *cafra*-like specimens as a new species, *Natalina compacta*, but in practice it has in the past been difficult to apply this name with confidence due to intergrading variability in shell proportions. However, sequence data from a globose *Natalina* specimen from the type locality of *N. compacta* (and thus almost certainly representative of that taxon) indicates that it clusters, together with less elevated southern Eastern Cape specimens, in a well-supported *N. cafra cafra* clade (Moussalli *et al.* 2009). We thus consider *Natalina compacta* to be a synonym of *N. cafra cafra*.

A further complication emerging from the analysis of molecular data is the fact that *Natalina cafra* appears paraphyletic (Moussalli *et al.* 2009). *N. beyrichi*, itself comprising a well-supported clade showing little genetic diversity, nests with strong support within the *N. cafra* complex, as sister taxon to the E. Cape *N. cafra* lineage. *N. beyrichi*, however, is a morphologically distinctive taxon which overlaps in distribution with *N. cafra* between the Kei and Mbashe rivers, yet the two remain clearly separable in the overlap zone. We thus have a situation where the gene tree does not match the species tree. Funk and Omland (2003) have outlined a number of genetically legitimate reasons why gene trees may render species paraphyletic, and suggest that speciation by
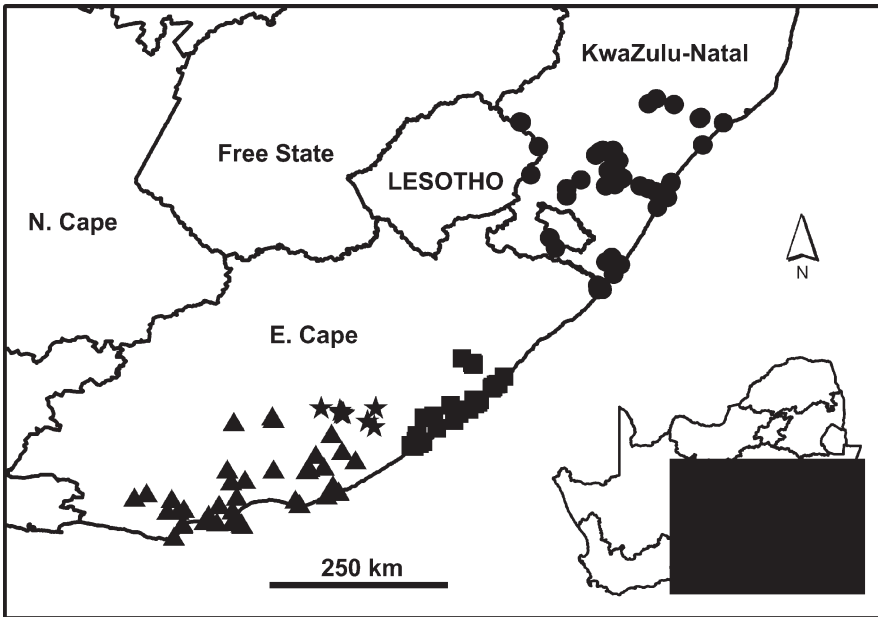
Fig. 16. Distribution of *Natalina cafra* subspecies: *N. c. cafra* (triangles), *N. c. amathole* subsp. n. (stars),
N. c. natalensis subsp. n. (circles), *N. c. eumacta* (squares).

peripheral isolation ('budding') may commonly result in the nesting of a geographically restricted daughter species within a more widely distributed parental species. Similarly, Avise and Robinson (2008) have drawn attention to gene tree *vs* species tree discordance due to the phenomenon of hemiplasy resulting from the sorting of ancestrally polymorphic lineages retained across successive nodes in a species tree. Given the absence of morphological differentiation between the E. Cape and KZN *N. cafra* lineages, and the fact that resolution at this level in our phylogenetic tree is largely provided only by mtDNA (Moussalli *et al*. 2009), we consider that the evidence currently available is insufficient to justify forcibly removing this paraphyly by recognising the KwaZulu-Natal lineage as a distinct species. Of course, this may ultimately need to be considered if additional morphological and molecular evidence is obtained.

Key to subspecies of *Natalina cafra*

1 KwaZulu-Natal only (Eshowe south to Mtamvuna R. valley) ....
   .... **N. cafra natalensis** subsp. n.
– Southern and south-eastern E. Cape only (Mbashe R. valley west to Baviaanskloof)
   2

2 Shell proportions very variable, spire generally rather low; aperture obliquely oval, generally wider than high; radula with five pairs of lateral teeth per transverse row. Coastal regions of southern E. Cape and inland to Albany district ....
   .... **N. cafra cafra**
– Last whorl of shell globose; spire prominent; aperture generally higher than wide; radula with 6–8 pairs of lateral teeth per transverse row 3

3 Radula with eight pairs of lateral teeth per transverse row. Coastal regions from Mbashe R. valley south to East London .... **N. cafra eumacta**
– Radula with six pairs of lateral teeth per transverse row. Amathole Mts only .... **N. cafra amathole** subsp. n.

Natalina cafra cafra (Férussac, 1821)

Figs 4A, 5, 7A, 11G, 13B, 15B, 16–20

Helix (*Helicophanta*) *cafra*: Férussac 1821 in 1821–22: 25 [or 29 depending on issue]; 1821 in 1819–32, pl. 9A, fig. 8; Beck 1837 in 1837–38: 46; Deshayes & Milne-Edwards 1838: 107; Deshayes 1851 in Férussac & Deshayes 1820–51: 198, pl. 9A, fig. 8 (as *Helix caffra* [*sic*]). Type loc.: 'La Cafrerie' [Delalande] = E. Cape. (Connolly cited the locality 'Uitenhage (*fide* Férussac)' but we have been unable to find reference to Uitenhage in any of Férussac's works. Deshayes (1851 in Férussac & Deshayes 1820–51) later gave the locality as 'la Cafrerie aux environs du cap de Bonne Espérance, et particulièrement vers la baie d'Algoa'.)

Helix caffra [*sic*]: Wood 1828: 40, pl. 7, fig. 36; Catlow & Reeve 1845: 120; Krauss 1848: 75 (in part); Pfeiffer 1848: 40; 1851 in 1850–53: 52, pl. 74, figs 1–3 (plate dated 1849); Reeve 1851 in 1851–54: sp. 179; Hanley 1856: 228, supplement, pl. 7, fig. 36; Morelet 1889: 19.

Paryphanta caffra [*sic*]: Adams & Adams 1855 in 1854–58: 226.

Aerope caffra [*sic*]: Mörch 1865: 395; Pfeiffer 1878 in 1878–81: 26; Tryon 1885: 131, pl. 25, fig. 13; Pilsbry 1890: 41, pl. 1, figs A–F.

Rhytida caffra [*sic*]: Gibbons 1880: 95–96.

Natalina caffra [*sic*]: Pilsbry 1893 in 1892–93: 135; Woodward 1895: 270–277; Melvill & Ponsonby 1898: 170; Sturany 1898: 30 (in part); Murdoch 1901: 171, pl. 17, fig. 11; Möllendorff 1903: 20, pl. 3, figs 4–7; Connolly 1912: 90; Hodgson 1989: 30.

Natalina cafra: Watson 1934: 157; Connolly 1939 (in part): 104; Hoffmann 1940: 87–96; Barnard 1951: 142, pl. xxi, fig. 6; Kilburn 1973: 10–11 (in part); Herbert 1991: 6–11 (in part); Bieler & Slapcinsky 2000: 38, fig. 26, map 25; Schileyko 2000: fig. 969.

Natalina compacta Connolly, 1939: 108, pl. 3, figs 1–3 [in part]; Hodgson 1989: figs 2, 3a (radula). Type loc.: Mountain Drive, Grahamstown, E. Cape [Farquhar]. **Syn. n.**

not *Natalina caffra* [*sic*]: Bruggen 1969: 57, nor *Natalina cafra*: Herbert & Kilburn 2004: 220 [= *Natalina cafra natalensis* subsp. n.], nor *Natalina cafra*: Bruggen 2004: 46 [= *Natalina quekettiana* complex].
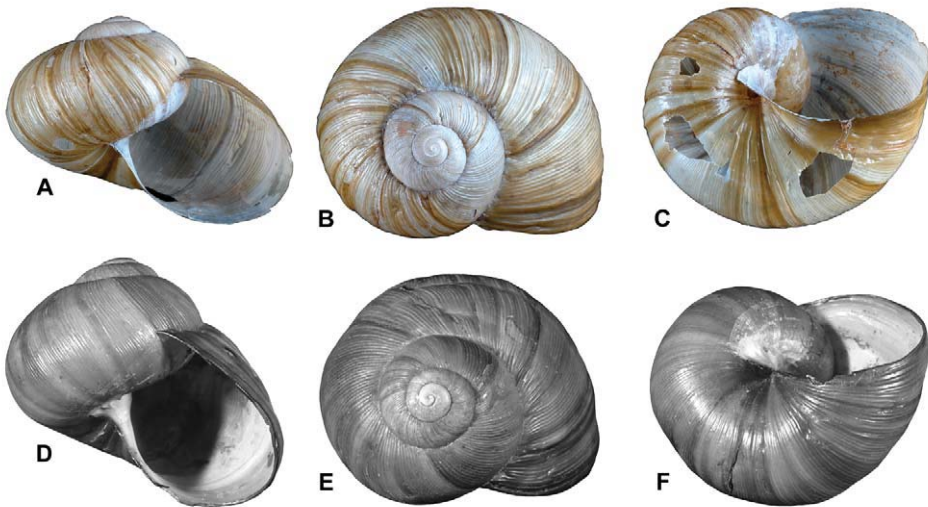

Fig. 17. *Natalina cafra cafra* (Férussac, 1821), type material: (A–C) figured syntype of *Helix cafra* Férussac, 1821, diameter 58.6 mm (MNHN 21050, photo courtesy of Barbara Buge); (D–F) holotype of *Natalina compacta* Connolly, 1939, diameter 50.4 mm (BMNH 1937.12.30.1305–6).
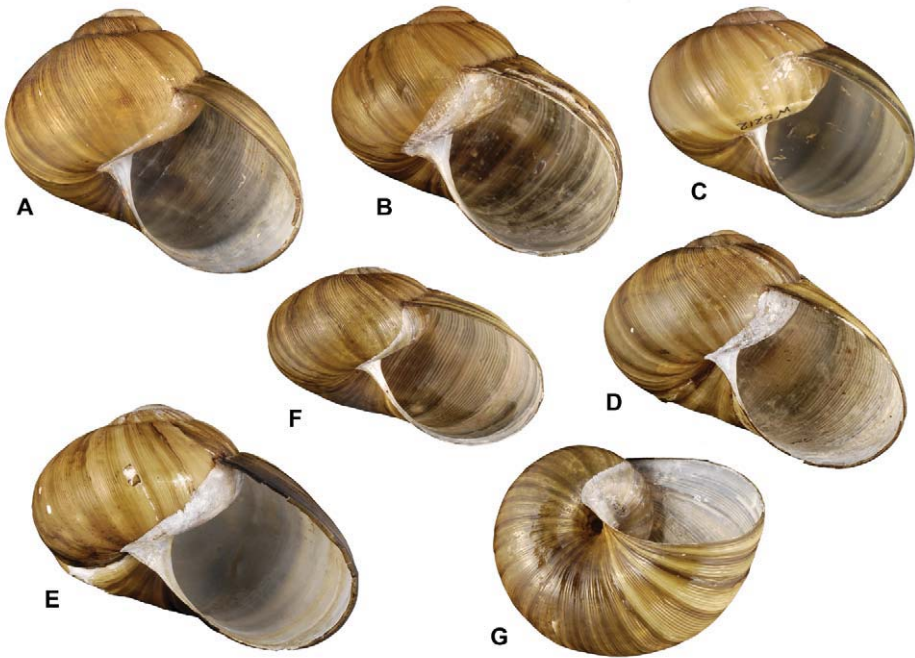
Fig. 18. *Natalina cafra cafra* (Férussac, 1821) (all NMSA): (A) Grahamstown (E7900), diameter 55.0 mm; (B) Grahamstown (V2473), diameter 53.5 mm; (C) Grahamstown, Mountain Drive (W5212), diameter 40.0 mm (animal grew to this larger size in captivity, cf. Fig. 15B); (D) Woody Cape Nat. Res. (W4631), diameter 54.0 mm (W4631); (E) Port Elizabeth (A446), diameter 60.4 mm; (F, G) Woody Cape Nat. Res. (W4631), depressed specimen, diameter 49.5 mm.

Etymology: From Latin *cafer*, orig. Arabic *kafir* (a non-believer).

Identification: Shell large to very large; proportions very variable, some specimens globose, others more depressed with a low spire and somewhat more rapidly expanding whorls; umbilicus open, width narrow to moderate, partially obscured by reflected columella lip. Cannot be reliably distinguished from other subspecies of *N. cafra* using shell characters alone. *N. beyrichi* differs in having a much wider, unobstructed umbilicus and is typically more depressed. Southern E. Cape.

Description (Figs 17, 18): Shell large to very large, thin and fragile; shell proportions very variable, some specimens globose (Fig. 18A, i.e. those named *N. compacta* by Connolly) others considerably more depressed (Fig. 18F); last whorl descending gently toward aperture in adult, but suture at outer lip generally remaining slightly above mid-whorl. Protoconch diameter typically 7–8 mm (Fig. 4A). Apical surface dull, sculptured by close-set axial riblets; riblets become weaker below periphery and evanesce toward umbilicus; umbilical margin sculptured by growth-lines rather than riblets; base generally more glossy, particularly around umbilical margin, but there is no clear line of disjunction between dull apical surface and base; growth flaws and repairs frequent and often distinct, particularly on last adult whorl; umbilical width moderate to rather narrow; umbilicus usually partially obscured by reflected columella lip; aperture drooping outward basally, its long axis somewhat oblique; outer lip very thin with a projecting periostracal fringe.

Periostracum greenish to olive-brown in fresh specimens, with frequent, unevenly spaced, radial bands in darker shades, particularly on last whorl; old specimens frequently faded and more yellowish. Underlying shell translucent white or almost transparent when fresh, with exterior colour and banding showing through.

Dimensions: Largest specimen, diameter 75.5 mm (*fide* Connolly 1939), but few specimens exceeding 65 mm in diameter; H:D of adults 0.60–0.94 (N=27).

Living animal (Figs 5, 15B): Head-foot grey or greyish brown to dark orange-brown; darker dorsally and usually but not always with a paler longitudinal stripe running backward from base of each optic tentacle; tentacles and labial palps darker grey-brown; skin texture finely granular; posterior portion of foot flat and trigonal, tip of tail rather acutely pointed; mantle edge frequently orange or orange-brown, even when the body is grey-brown; labial palps well developed.

Radula (Fig. 19). Formula 1+5+(20–30) (N=4); length up to 53 mm, with up to 57 transverse rows of teeth (but no radulae from very large specimens available). Pilsbry (1890) illustrated only 11 marginal teeth per half row of an adult specimen, but it seems probable that he failed to observe some of the minute outer teeth. The radula of a small juvenile (NMSA W3272, diameter 12.5 mm) was approximately 12 mm in length with 47 transverse rows and formula 1+5+10, suggesting that the number of marginals increases with growth, but the number of laterals does not (see also Connolly (1939: 106) for similar observations concerning a juvenile of *N. c. natalensis*).

Distal genitalia: Few mature specimens available. Epiphallus with a well-developed bulla on outer wall near its junction with vas deferens (Fig. 13B); lumen of epiphallus lined by 4 or 5 well-developed longitudinal ridges with weaker second and third order intermediaries; ridges microscopically transversely fimbriate, those on the inner wall (adjacent to penis) extending for entire length of epiphallus, those on outer wall ending at base of bulla, which itself has a hollow core.
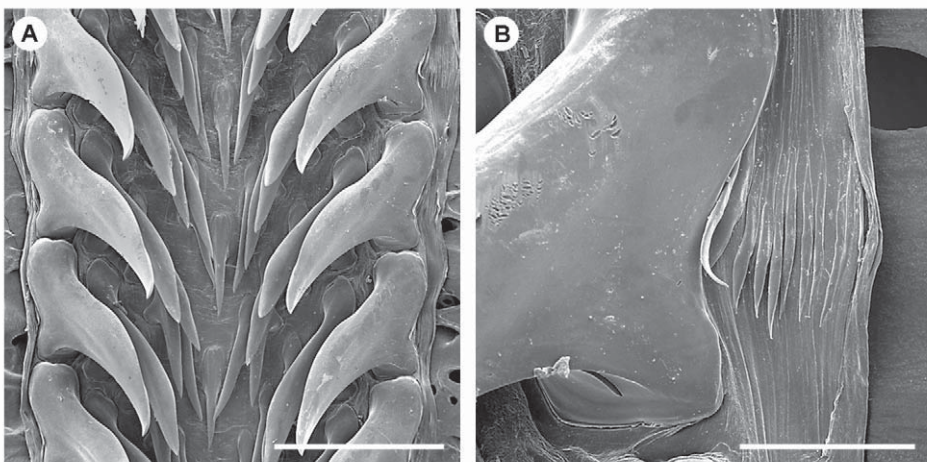
Spermatophore: Unknown.

Fig. 19. *Natalina cafra cafra* (Férussac, 1821), radula, Coerney (NMSA W4220): (A) rachidian and lateral teeth, scale bar = 1.0 mm; (B) vestigial marginal teeth, scale bar = 250 µm.

Type material: Two syntypes of *Helix cafra* Férussac, 1821 in MNHN (21050), one is the figured specimen, diameter 58.6 mm, height 43.0 mm (Figs 17A–C). Holotype and paratype of *Natalina compacta* Connolly, 1939 in BMNH (1937.12.30.1305–6), holotype (Figs 17D–F) diameter 50.4 mm, height 46 mm (51 mm and 43 mm *fide* Connolly, 1939); one possible paratype in Manchester Museum (EE.5691, Grahamstown, *fide* McGhie 2008).

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: <u>South-western E. Cape:</u> Baviaanskloof wilderness area, Kougaberge (33.67188°S:24.33008°E), 800–1000 m, grassland/fynbos, D. Clark, 1999 (V8525); Baviaanskloof Wilderness Area, vicinity of Berg Plaas (33.61522°S:24.48499°E), 886 m, montane sparse fynbos, grassland, A. Moussalli & D. Stuart-Fox, 15/iii/2005 (W3255); ~15 km S of Andrieskraal (33.83867°S:24.74515°E), 328 m, riverine thicket, in leaf-litter, A. Moussalli & D. Stuart-Fox, 14/iii/2005 (W4600); Elandsberge, opposite Cockscomb (33.68893°S:24.80056°E), 600 m, grassy fynbos, under rocks, station 08–051, D. Herbert, L. Davis & M. Cole, 21/ix/2008 (W6517); Hankey, Sarah Bartmann municipal grounds (33.83834°S:24.88594°E), 75 m, thicket, in leaf-litter and under fallen aloes, station 08–050, D. Herbert, L. Davis & M. Cole, 21/ix/2008 (W6525); Hankey area, Kleinrivier road (33.81429°S:24.95415°E), 255 m, thicket, in leaf-litter and under fallen aloes, station 08–053, D. Herbert, L. Davis & M. Cole, 21/ix/2008 (W6508); Cape St Francis, 7 Edward Rd (34.16777°S:24.83040°E), coastal garden (C. & B. Logie), D. Herbert, 09/x/2000 (V8581); Jeffreys Bay area, Kabeljous R. mouth (34.017°S:24.933°E), on land side of dune on east side of river mouth, C. Logie, 'Snailiens' project, 03/i/2001 (V8862); ditto (34.00253°S:24.94015°E), coastal succulent scrub, in leaf-litter, A. Moussalli & D. Stuart-Fox, 14/iii/2005 (W3272); ditto (34.00253°S:24.94015°E), coastal succulent scrub, in leaf-litter, A. Moussalli & D. Stuart-Fox, 16/xii/2005 (W4225); St Francis Bay, Van Staden's beach (33.96667°S:25.21670°E), C. Vernon, 18/x/1986 (ELM D10039); Port Elizabeth area, Island Forest Res. (33.98668°S:25.37151°E), low coastal forest, in leaf-litter, station 08–040, D. Herbert, L. Davis & M. Cole, 18/09/2008 (W6406); Uitenhage (33.76373°S:25.39764°E), valley thicket, in leaf-litter and under fallen aloes, A. Moussalli & D. Stuart-Fox, 22/xii/2005 (W4830, W5490); ditto, Vanes Estate (33.767°S:25.400°E), 'Snailiens' Project, pupils of Thomas Muir School, 2001 (V9034); Port Elizabeth, Redhouse (33.833°S:25.567°E), Mrs T.V. Paterson, 1980 (E7905); Port Elizabeth (33.917°S:25.600°E), F. Holland (E7895); ditto (33.917°S:25.600°E), F. Cruden, 1927 (A0446, W5984); ditto, Mrs J. Longstaff (BMNH Acc. No. 906); ditto, Walmer, leg. Staples, 15/xi/2006 (ELM D15211); ditto, Marine Drive (33.9973°S:25.6827°E), dune scrub, D. Herbert, 13/x/2000 (V8612); ditto, Cape Recife, nr gate to reserve (34.01325°S:25.69160°E), dune scrub, D. Herbert & G. Rossouw, 13/x/2000 (V8567). <u>South-central E. Cape:</u> Zuurberg (33.3167°S:25.5000°E) (A7050); Grassridge, PPC mining concession (33.66244°S:25.62116°E), bontveld, under fallen aloes and in grass clumps, station 08–042, D. Herbert, L. Davis & M. Cole, 19/ix/2008 (W6416); Coerney (33.44828°S:25.72420°E), 134, m, valley thicket, in leaf-litter, A. Moussalli & D. Stuart-Fox, 12/xii/2005 (W4220); Colchester area, WNW (33.680516°S:25.770376°E), sand/siltstones of Sundays River formation, M. Mostovski, 13/vii/2009 (W6927); Bedford, Maestroom Forest (32.64860°S:26.06833°E), M. Bursey, 15/i/2002 (ELM D13770, juvenile); Alicedale, Roodekrans (33.3167°S:26.0830°E) (E7904); Woody Cape Nat. Res. (33.69938°S:26.35977°E), 216 m, coastal indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 11/xii/2005 (W4631); ~12 km S of Alexandria (33.75207°S:26.41048°E), 167 m, coastal thicket, in leaf-litter, A. Moussalli & D. Stuart-Fox, 11/xii/2005 (W4739); Grahamstown, Mountain Drive (33.32784°S:26.49952°E), grassy fynbos on top of hill, under old dry eucalypt log, V. Ndibo, 10/iii/2007 (W5212); ditto (33.325°S:26.517°E) (E7863, E7902); Grahamstown (33.300°S:26.533°E), R.H. Ivy, 01/x/1910 (V2473); Grahamstown, Resolution, Fort Brown (33.133°S:26.617°E) (E7894, E7909); Kasouga (33.64759°S:26.75219°E), coastal dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 10/xii/2005 (W5472); ~13 km N of Double Drift Game Res. (32.86658°S:26.81436°E), valley thicket, under dead aloe, A. Moussalli & D. Stuart-Fox, 02/xii/2005 (W5164); Port Alfred (33.6°S:26.9°E) (E7892); Port Alfred (Kowie) (33.6°S:26.9°E) (E7892, V2456, ELM D10956); Port Alfred, east of Kowie R. (33.59194°S:26.90472°E), coastal forest, M. Bursey, 26/xi/2006 (ELM D15009); Alice area, Breakfast Vlei (33.0833°S:26.9500°E) (E7893); Peddie (33.200°S:27.117°E), Howard, x/1924 (A7053).

Additional literature records (material not seen): SOUTH AFRICA: *E. Cape*: Somerset East (32.717°S:25.583°E), Miss Bowker (Connolly 1912); Bedford (32.683°S:26.083°E) (Connolly 1912); Bathurst (33.517°S:26.833°E) (Connolly 1912).

Distribution (Fig. 20): Known only from the southern E. Cape, along the coast and in the mid and lower catchments of the Gamtoos, Sundays and Great Fish rivers; from the Baviaanskloof in the west to the Peddie area in the east, inland to the Grahamstown area and Great Fish River Conservancy; altitudinal range extending from the coast to approx. 1000 m. Records from the Somerset East and Bedford area require confirmation as they are either literature records or based on juvenile shells.

Habitat: Evidently tolerant of relatively dry environments and occurs in a wide variety of vegetation types in the south of the broader Albany Thicket biome, including coastal fynbos and strandveld, montane grassy fynbos, bontveld, thornveld, various types of thicket, coastal forest and suburban gardens; in leaf-litter beneath shrubs and bushes, buried under rocks and fallen aloes, or within dense grassy clumps and sheltering in rocky outcrops. Common, though generally at low densities, but locally relatively abundant in calcium-rich areas such as the limestone habitats at Grassridge, north of Port Elizabeth (Alexandria Formation).

Notes: Shell proportions vary considerably, but intergrade completely. Depressed specimens may resemble *N. beyrichi*, but in *N. c. cafra* such specimens have a more rapidly expanding last adult whorl and the umbilicus remains consistently narrower. Elevated specimens resemble the other E. Cape subspecies, *N. c. amathole* and *N. c. eumacta*, except that the umbilicus of such specimens of *N. c. cafra* is generally narrower.

When proposing the name *Natalina compacta*, Connolly (1939) distinguished his new taxon from *N. cafra* solely on the grounds of its more globose shape. Molecular data has shown that similarly globose shells from the type locality of *N. compacta* cluster together with less elevated specimens (Moussalli *et al.* 2009) typical of *N. c. cafra*. The relative proportions of the shell therefore do not appear to provide reliable taxonomic information. We thus consider *Natalina compacta* Connolly, 1939, to be a synonym of *N. c. cafra*.

Conservation: *Natalina c. cafra* is widespread and relatively common. Due to its catholic habitat requirements and tolerance of moderately dry environments, its area of occupancy is unlikely to be conspicuously fragmented. There is thus no evidence to suggest that the subspecies is threatened at present.
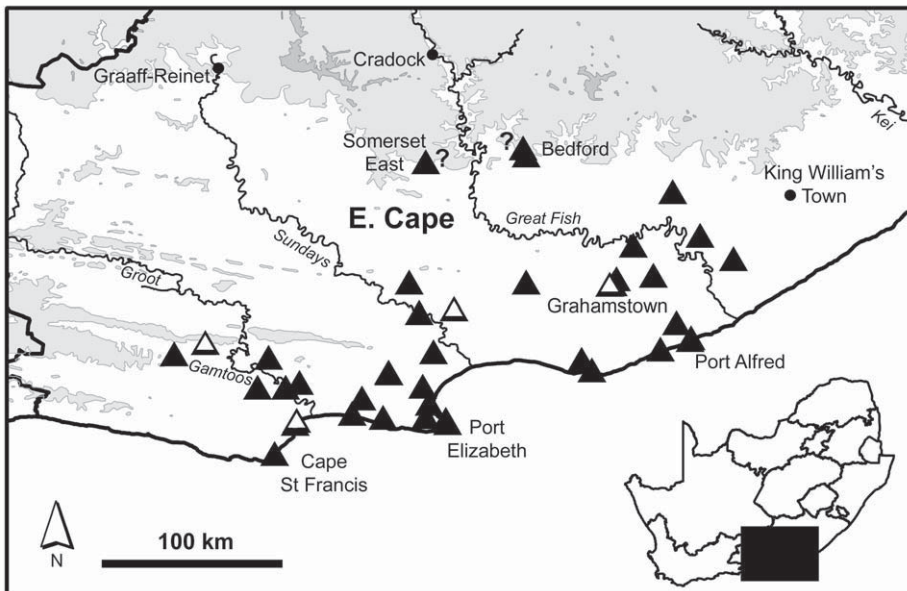

Fig. 20. Distribution of *Natalina cafra cafra* (Férussac, 1821). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

Natalina cafra amathole subsp. n.

Figs 14A, 15C, 16, 21–23

Natalina compacta Connolly, 1939: 108 [in part, but not holotype].

Etymology: A toponym reflecting the geographical distribution of the taxon in the Amathole Mts, E. Cape, South Africa.

Identification (Fig. 21): For general description see *Natalina c. cafra* above. Closely resembles the other subspecies of *N. cafra*, from which it cannot be reliably distinguished using shell characters alone. *N. c. amathole*, however, seems not to attain such a large size, and shows much less variation in shape than *N. c. cafra*, all specimens being consistently globose but still falling within the H:D range exhibited by the nominotypical subspecies. Umbilicus perhaps generally slightly broader than in *N. c. cafra*, but this is difficult to quantify, as there is no clear limit to the umbilical rim. Most similar to *N. c. eumacta*, particularly in terms of its globose proportions, relatively weak axial ribbing and the somewhat more broadly patent umbilicus. That subspecies, however, is more variable in periostracum colour (some individuals distinctly brown). Radula with six pairs of lateral teeth in each transverse row, compared to five in *N. c. cafra* and eight in *N. c. eumacta*.

Periostracum coloration similar to *N. cafra cafra*, usually of an olive-green or olive-brown hue when fresh, but evidently not as brown as some populations of *N. cafra eumacta*.

Dimensions: Holotype, diameter 40.5 mm; largest specimen (NMSA V8092, Katberg), diameter 50.4 mm; H:D of adults 0.78–0.90 (N=8).

Living animal (Fig. 15C): Limited data available. Head-foot fawn-brown to pale grey-brown with a diffuse pale stripe running backwards along neck from base of each optic tentacle; tentacles grey; pedal margin tinged yellow or orange.
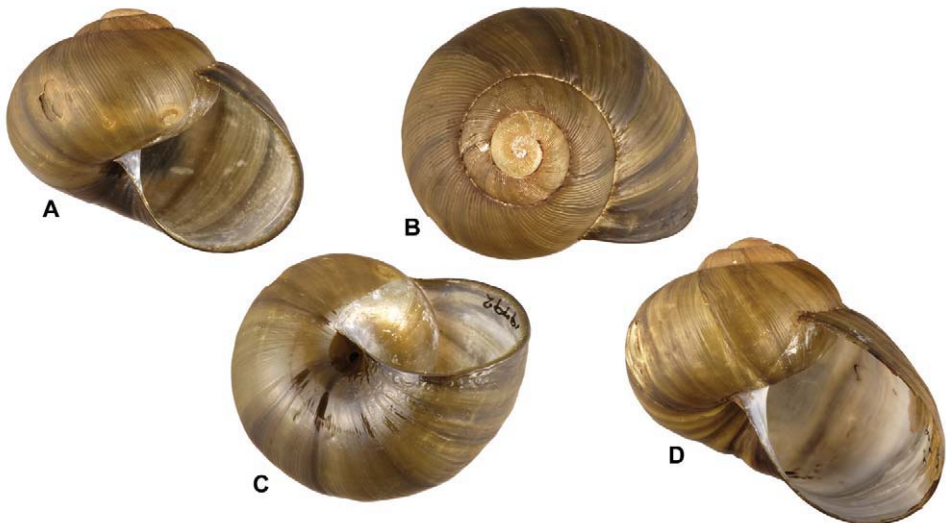

Fig. 21. *Natalina cafra amathole* subsp. n., Hogsback, E. Cape: (A–C) holotype (NMSA V9792/T2308), diameter 40.5 mm; (D) paratype (NMSA E7864/T2311), diameter 49.0 mm.
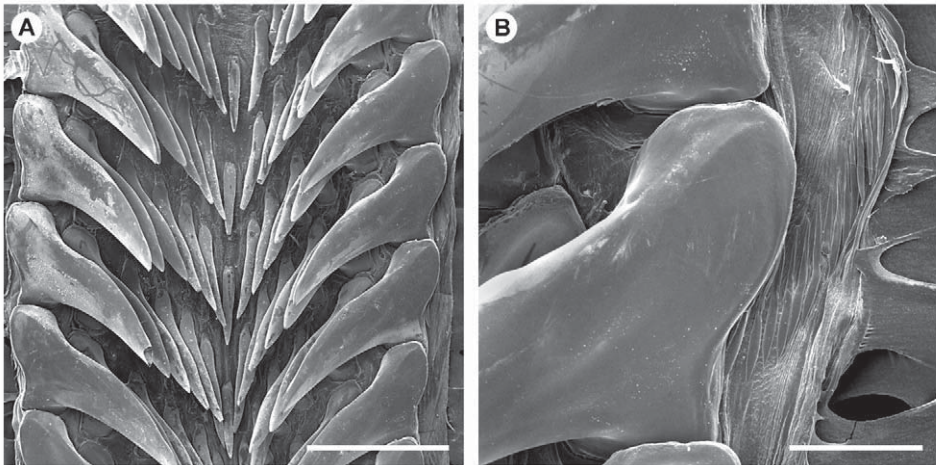
Fig. 22. *Natalina cafra amathole* subsp. n., radula, Hogsback (NMSA W4193/T2313): (A) rachidian and lateral teeth, scale bar = 1.0 mm; (B) vestigial marginal teeth, scale bar = 250 µm.

Radula (Fig. 22): Formula 1+6+~25 (N=3); length in adult 32–40 mm, with 50–60 rows of teeth. The radula is essentially the same as that of the nominotypical subspecies except that the lateral teeth in *N. c. amathole* consistently number six pairs per transverse row, compared to five in *N. c. cafra*. These figures, however, are based on a relatively small sample.

Distal genitalia: As in *Natalina c. cafra*, but no bulla evident on epiphallus.

Spermatophore (Fig. 14A): A well preserved allospermatophore has been found in one specimen, collected in early December (NMSA W4193). Spermatophore relatively slender, straightened length approx. 21 mm; anterior 2/3 tapering gently toward head, with 6–8 primary longitudinal ridges; ridges cease well before recurved tail and posterior third largely smooth. Very similar to that of *N. c. eumacta* and *N. beyrichi* but more slender and without a subterminal process at base of tail. The spermatophore of *N. c. natalensis* is proportionately broader and the longitudinal ridges continue almost to the tail tip.

Holotype (Figs 21A–C): SOUTH AFRICA: *E. Cape*: Hogsback, env. of Madonna & Child waterfall (32.60703°S:26.96268°E), 1075 m, indigenous forest, in leaf-litter, D. Herbert, M. Bursey & G. Redman, 25/i/2002 (NMSA V9792/T2308).

Paratypes: SOUTH AFRICA: *E. Cape*: same data as holotype (BMNH 20100123, 1 specimen; NMSA W6371/T2309, 7 specimens); Hogsback (32.600°S:26.933°E), J. Hewitt (NMSA E7864/T2311, 1 specimen); Hogsback (32.600°S:26.933°E), Dr Rattray, 1919 (NMSA V2012/T2312, 1 specimen); Hogsback (32.59766°S: 26.95865°E), indigenous forest, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Bursey, 1/xii/2005 (NMSA W4193/T2313, 1 specimen); Hogsback environs (32.58935°S:26.93563°E), indigenous forest, A. Moussalli & D. Stuart-Fox, 21/i/2005 (NMSA W4829/T2310, 1 specimen); Hogsback, Madonna and Child forest (32.5670°S:26.9167°E), M. Bursey, 25/i/2002 (ELM D13624, 1 specimen).

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Katberg, north of Fort Beaufort (32.533°S:26.683°E), V. Fitzsimons, 1947 (V8092); Hogsback, Madonna and Child forest (32.5670°S:26.9167°E), M. Bursey, 25/i/2002 (ELM D13624); Hogsback, env. of Madonna & Child waterfall (32.60703°S:26.96268°E), indigenous forest, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Bursey, 1/xii/2005 (W4196); Hogsback, Dr Rattray, i/1918 (NMSA V6840); Hogsback, J. Hewitt, xii/1933 (NMSA W6001); Mount Kempt (32.7000°S:27.2667°E), Bigalke, 15/vi/1986 (ELM D11299); Stutterheim, Kologha Forest (32.533°S:27.367°E), C. Vernon, 25/x/1992 (ELM D13139).

Additional literature records probably referable to this subspecies (material not seen): SOUTH AFRICA: *E. Cape*: Pirie Mountain (32.767°S:27.350°E), Godfrey (Connolly 1912).

Distribution (Fig. 23): A narrow-range E. Cape endemic, known only from the Amathole Mts; occurs at altitudes of 1100–1400 m.

Habitat: Little habitat data available, but appears primarily to inhabit southern mist-belt forest; in leaf-litter and under logs. Moderately common in forests in the Hogsback area.

Notes: This taxon is erected primarily on the basis of DNA data, which indicate that material of *Natalina cafra* from the Amathole region forms a distinct genetic lineage (Moussalli *et al*. 2009). At present, such information is only available for specimens from the Hogsback area and individuals from other localities in the Amathole mountains have been identified with this material only on the basis of similarity in shell form and the number of lateral teeth in the radula. Additional molecular sequence data will be needed before their identity can be confirmed.

Connolly (1939) identified this Hogsback material with his new taxon *Natalina compacta*, but DNA sequence data for topotypic *N. compacta* material show it to belong within the *N. c. cafra* lineage (see above).

Conservation: *Natalina c. amathole* is evidently a narrow-range taxon, but the precise extent of its distribution is uncertain and requires further study. From the limited data available it is clear that the indigenous forests of the Amathole Mountains, particularly in the Hogsback area, are likely to be important for the conservation of this taxon.
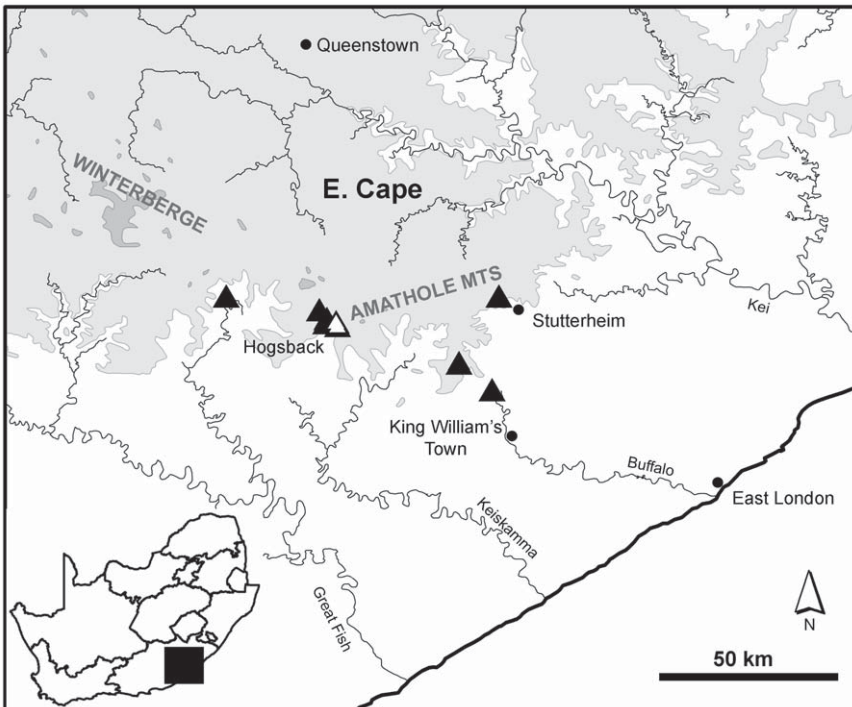

Fig. 23. Distribution of *Natalina cafra amathole* subsp. n. Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al*. 2009); contours at 1000 m and 1500 m.

Natalina cafra eumacta (Melvill & Ponsonby, 1892), **stat. rev.**

Figs 14C, D, 15F–H, 16, 24–26

Helix (*Aerope*) *eumacta*: Melvill & Ponsonby 1892: 237, pl. 13, fig. 4. Type loc.: originally cited as 'Natal', but label with type states 'Bashee River, Idutywa', E. Cape [Crawford].
Natalina eumacta: Pilsbry 1893 in 1892–93: 135; Melvill & Ponsonby 1898: 170; Sturany 1898: 31; Möllendorff 1903: 22, pl. 3, fig. 9; Connolly 1912: 93; 1939: 106.

Identification (Fig. 24): For general description see *N. c. cafra*. Much less variable in shape than *N. c. cafra*, all adult specimens being somewhat globose and more similar to *N. c. amathole*, particularly in terms of the relatively weak axial ribbing and the slightly more broadly patent umbilicus, but evidently attains a larger size than the Amathole subspecies and the periostracum is commonly brown rather than green, although some distinctly green individuals (Fig. 15F) may co-occur with brown ones (Fig. 15G). Characteristically, the radula has eight pairs of lateral teeth per transverse row.

Dimensions: Largest specimen (NMSA E2067, The Haven), diameter 56.4 mm; H:D of adults 0.70–0.86 (N=23).

Living animal (Figs 15F, G): Head-foot pale to dark grey-brown; dorsal part of neck usually darker; paler longitudinal neck stripes usually indistinct; pedal margin and mantle skirt commonly bright orange or orange-red.

Radula (Fig. 25): Formula 1+8+(20–30) (N=5); length in adult up to 43 mm, with 59–76 transverse rows of teeth. A juvenile specimen (NMSA W4627) with a radula of 15.5 mm in length similarly possessed eight lateral teeth per half row. Another specimen (NMSA W4005) had eight laterals on the left of the rachidian and nine on the right.

Distal genitalia: As in *Natalina c. cafra*. A small, but distinct bulla is present on the epiphallus in some populations (e.g., northern coastal localities at The Haven and Dwesa), but evidently not all.

Spermatophore (Figs 14C, D): Auto and allospermatophores have been found in specimens collected in late November and late February (NMSA W4044, W4055,
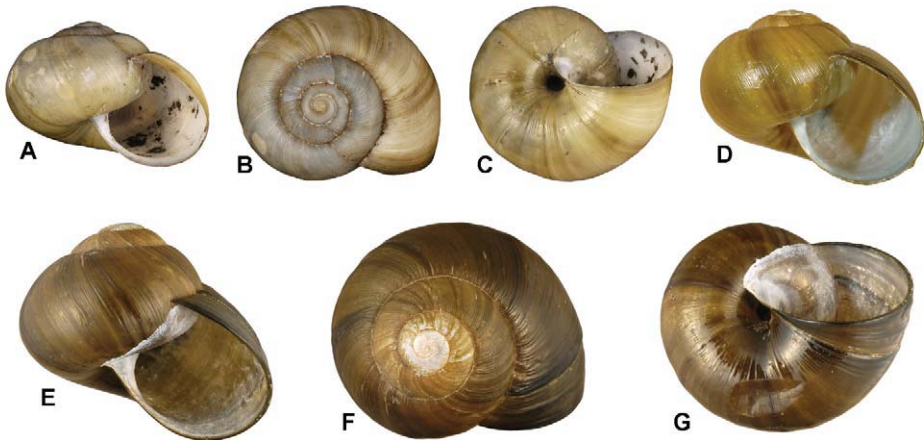

Fig. 24. *Natalina cafra eumacta* (Melvill & Ponsonby, 1892): (A–C) lectotype (juvenile) of *Helix* (*Aerope*) *eumacta* Melvill & Ponsonby, 1892 (BMNH 1905.1.26.2), diameter 30.3 mm; (D) juvenile, Holme Park farm, Komga District (NMSA W5990), diameter 36.6 mm; (E–G) adult, Dwesa Nat. Res. (NMSA V7868), diameter 51.8 mm.
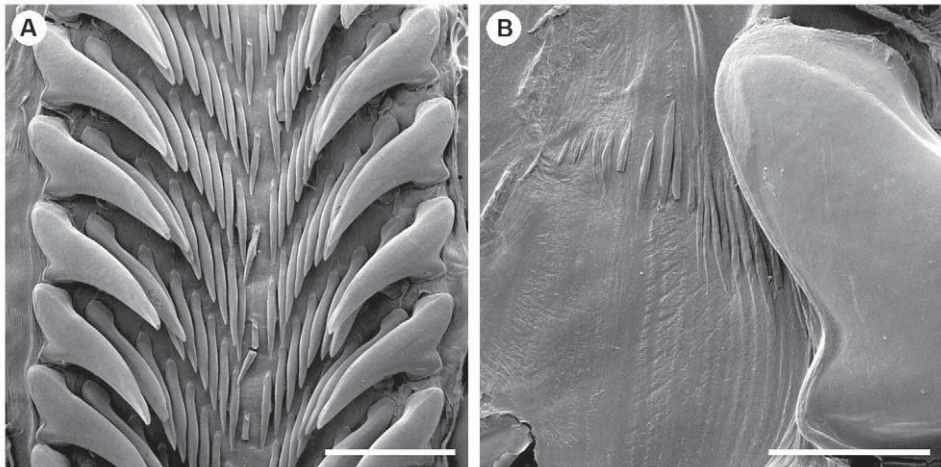
Fig. 25. *Natalina cafra eumacta* (Melvill & Ponsonby, 1892) radula, Dwesa Nat. Res. (NMSA V7868): (A) rachidian and lateral teeth, scale bar = 1.0 mm; (B) vestigial marginal teeth, scale bar = 250 µm.

W4160, W4161), suggesting that mating occurs throughout the summer months. Spermatophore closely resembles that of *N. c. amathole*, but is less slender, anterior two-thirds with 6–8 primary longitudinal ridges, posterior third smooth; straightened length up to 18.5 mm. In one allospermatophore, a small, slender, finger-like process was present in the mid-line on the outer side of recurved tail (Fig. 14C). It is not present in all cases and appears to be correlated with the presence of a bulla on the epiphallus. It is far less robust than the thumb-like process present in *N. beyrichi*. Spermatophores from other individuals from the same locality lacked this structure (Fig. 14D).

Type material: According to Melvill and Ponsonby (1892) there were two original specimens. One is present in the BMNH (1905.1.26.2) and is to be considered lectotype (designated Connolly 1912: 93), diameter 30.3 mm (immature) (Figs 24A–C). The present location of the second specimen is unknown.

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Mbashe R. valley, nr Bashee Bridge (N2) (31.92461°S:28.45113°E), 470 m, riverine thicket, in leaf-litter and under fallen aloes, A. Moussalli & D. Stuart-Fox, 23/xi/2005 (W4627, W5371); Collywobbles, overlooking vulture colony (31.9917°S:28.5917°E), 585 m, sparse valley thicket invaded with *Lantana*, in leaf-litter under aloes and bushes, D. Herbert & L. Davis, 20/ii/ 2006 (W4077/8); ditto (31.9833°S:28.5833°E), C. Vernon, 20/iv/1985 (ELM D11080), 29/iii/1991 (ELM D12585); Xora, Kumqolo Forest (32.1500°S: 28.9833°E), D.J. Hodgkinson, 12/viii/2003 (ELM W02620); between Nkanya and Bulungulu rivers (32.1500°S:28.9833°E), Wood, 15/vi/1939 (ELM D06209); The Haven Nat. Res., vicinity of camp ground (32.24435°S:28.90600°E), 15 m, coastal dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 16/xi/ 2005 (W4150); Mbashe R. mouth, nr The Haven, bush just above sand hills (32.250°S:28.883°E), *ex* Albany Mus. (E2067); Dwesa Nat. Res. (32.280°S:28.842°E), coastal forest, in leaf-litter, common, D. Herbert, 06/iii/2000 (V7868); ditto (32.304°S:28.828°E), coastal forest, in leaf-litter, D. Herbert, 05/iii/ 2000 (V7885); Qora Mouth, forest along north bank of estuary (32.4433°S:28.6750°E), coastal forest, in leaf-litter, D. Herbert & L. Davis, 21/ii/2006 (W4018); Manubi Forest (32.44321°S:28.59800°E), coastal forest, M. Bursey, 13/iv/2005 (W3015); ditto (32.44433°S:28.5983°E), coastal forest, in leaf-litter, D. Herbert & L. Davis, 22/ii/2006 (W4055, W4067); ditto, ~7 km west of Mazeppa Bay (32.45255°S: 28.60487°E), 190 m, coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 19/xi/2005 (W4160); Mazeppa Bay (32.47700°S:28.65409°E), 71 m, coastal dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 20/xi/2005 (W4161); ditto (32.48008°S:28.6431°E), dune forest, in leaf-litter, D. Herbert & L. Davis, 23/ii/2006 (W4044, crop contained anterior half of large earthworm); Mcelwana estuary, between Cebe and Mazeppa Bay (32.49741°S:28.61445°E), C. Vernon, 01/i/2005 (ELM D14989); Kentani (32.500°S: 28.332°E), wattle plantation (V7289); Nxaxo, second dune (32.56918°S:28.54153°E), coastal forest, M. Bursey, 14/iv/2005 (W3012); Qolora R. mouth, west bank, nr Trennery's Hotel (32.6167°S:28.4167°E), M. Bursey, 05/iv/2006 (ELM D14778); Mpetu, Ocean View farm (32.64806°S:28.09383°E), C. Vernon,
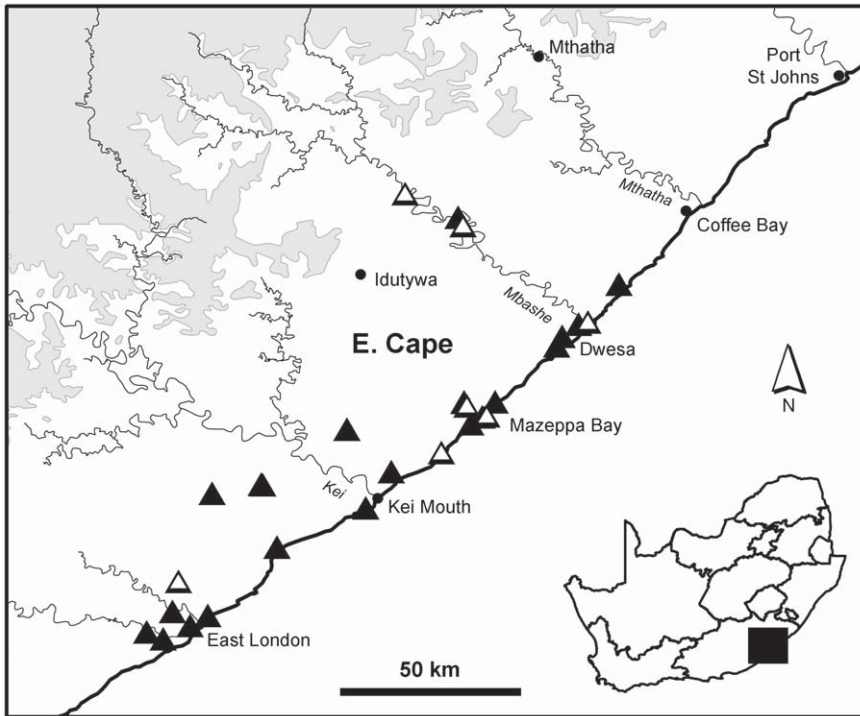
Fig. 26. Distribution of *Natalina cafra eumacta* (Melvill & Ponsonby, 1892). Triangles with a white
centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contour at
1000 m.

01/xii/1993 (ELM D13140); ditto (32.64898°S:28.09741°E), forest, in leaf-litter, D. Herbert, L. Davis &
M. Bursey, 03/iii/2007 (W5213, W5217); Komga District, Holme Park farm (32.670278°S:27.971945°E),
riverine forest, M. Bursey, 25/i/2008 (W5990); Morgan Bay, northern side of Inchara R. (32.70667°S:
28.35333°E), coastal bush, in leaf-litter, Herbert, Davis & Bursey, 03/iii/2007 (W5173); Viskop, east
bank of Cefane R. (32.804720°S:28.133055°E), M. Bursey, 20/xi/2006 (ELM W03061); Gonubie River
mouth, J.H. Power, (BMNH 1937.12.30.7147–48); East London, Thorn Park farm (32.89028°S:
25.88806°E), M. Bursey, 07/xi/1993 (ELM W02414); ditto, Nahoon R. valley (32.9650°S:27.8733°E),
Bigalke, 16/xii/1975 (ELM W00852); ditto, Bonza Bay (32.97472°S:27.96110°E), C. Vernon, 20/vii/
1986 (ELM D11288); ditto, Umtiza Nat. Res. (33.016°S:27.809°E), coastal forest, in leaf-litter, A. Moussalli
& D. Stuart-Fox, 26/xi/2005 (W5467); ditto, Sunnyridge (33.0333°S:27.8500°E), C. Quickelberge, 15/
xii/1973 (ELM D05167); ditto (33.0333°S:27.8500°E) (ELM D05988/9).

Distribution (Fig. 26): Endemic to the coastal region of the eastern E. Cape, extending
from the East London area to just north of the Mbashe River; primarily coastal, but ex-
tending inland along the Kei and Mbashe river valleys, to an altitude of approximately
600 m.

Habitat: Occurs in dune and coastal scarp forest as well as in drier, more open thicket
habitats in river valleys; in forest leaf-litter, under logs and fallen aloes, and buried
beneath bush clumps. Locally common in coastal scarp forest.

Notes: The most distinctive morphological feature of this subspecies is the greater
number of lateral teeth per row in the radula (8 pairs rather than 5 or 6 pairs). Efford
(2000) has documented similar non-overlapping subspecific variation in the number
of radula teeth per row in *Wainuia urnula* (Pfeiffer, 1855).

We associate this material with *Helix eumacta* Melvill & Ponsonby, 1892, with some hesitation. Survey work has revealed the presence of two distinct rhytidid species at its type locality, firstly the *Natalina cafra* material under discussion here, and secondly a species of *Afrorhytida* (*A. burseyae* sp. n.). The lectotype of *Helix eumacta*, however, is clearly not a species of *Afrorhytida*, having an protoconch diameter of approx. 7.0 mm, and it must therefore be considered a species of *Natalina*. Connolly (1939) noted that it much resembled a worn juvenile *N. cafra,* but mentioned minor differences in spire height and strength of sculpture. Compared with the *N. cafra* material under discussion, the lectotype of *H. eumacta* is both less globose and lower spired (H:D=0.70), sufficiently so to suggest that it may not be conspecific (compare Figs 24A and 24E, but ignore colour difference as the lectotype is over 100 years old and probably much faded). No further specimens resembling the lectotype have been found in the vicinity of the type locality; however, an immature specimen from the Komga area (Holme Park farm, NMSA W5990) is proportionately close to the lectotype and has a similar spire profile (Fig. 24D). This specimen, and all others examined from the vicinity of the type locality, have a radula with eight pairs of lateral teeth typical of this lineage. Consequently we have chosen to employ the name *eumacta* for the present subspecies and consider the lectotype to be a juvenile and unusually low-spired specimen.

Conservation: The distribution of *Natalina c. eumacta* is not extensive, spanning only a distance of approx. 150 km along the coast and extending only approx. 60 km inland. However, it has been recorded from more than 20 localities within its range and appears to be relatively common in coastal scarp forests, some of which fall within formally conserved areas (e.g., Dwesa Nat. Res.). There is at present, therefore, little to suggest that the species is threatened. Nonetheless, such forests, even those in nature reserves, are threatened by a number of factors including subsistence harvesting, invasive alien plants and trampling by cattle, and their efficacy as conservation refuges in the long term will depend much on political considerations. The possibility of future threat thus remains.

Natalina cafra natalensis subsp. n.

Figs 3A–C, 6C, 9A, 10D, 12A, B, 13A, D, 14B, 15D, E, 16, 27–29

Helix caffra [*sic*]: Krauss 1848: 75 (in part).
Natalina caffra [*sic*]: Sturany 1898: 30 (in part); Connolly 1912: 90 (in part); Bruggen 1969: 57.
Natalina cafra: Connolly 1939: 104, pl. 3, fig. 7, text-fig. 8 (in part); Kilburn 1973: 10–11 (in part); Herbert 1991: 6–11 (in part); Herbert & Kilburn 2004: 220.
not *Natalina cafra*: Bruggen 2004: 46 [= *N. quekettiana* complex].

Etymology: Name derived from its geographical occurrence, the province of KwaZulu-Natal.

Identification (Fig. 27): For general description see *Natalina c. cafra*. Closely resembles the nominotypical subspecies, from which it cannot be reliably distinguished using shell characters alone. Shell proportions and level of periphery variable, but H:D ratios fall entirely with the range of those of *N. c. cafra*. Generally less globose than *N. c. eumacta* and particularly *N. c. amathole*.

Dimensions: Holotype diameter 59.4 mm, height 49.2 mm; largest specimen (NMSA A7041, 'Natal'), diameter 75.0 mm, but few specimens exceeding 65 mm in diameter; H:D of adults 0.67–0.85 (N=27).

Living animal (Figs 15D, E): Head-foot pale fawn-brown to yellowish brown or orange-brown, occasionally grey; dorsal part of neck usually darker; neck region often with a paler longitudinal stripe running backward from base of each optic tentacle; pedal margin and mantle skirt usually yellowish, less often orange.

Radula (Fig. 28): See *Natalina c. cafra*, no morphological differences evident; formula 1+5+(20–30) (N=8, two in BMNH); length in adult up to 58 mm (*fide* Connolly 1939), perhaps more in very large individuals), with 50–60 transverse rows of teeth. Connolly (1939) reported a newly hatched juvenile from Pietermaritzburg as having a formula 1+5+12 (slide in BMNH).

Distal genitalia (Figs 12, 13A, D): As in *N. c. cafra*. In most specimens the epiphallus lacks a distinct bulla, but there is evidence of a slight swelling in some specimens. The longitudinal ridges lining the epiphallus lumen extend for almost its entire length.

Spermatophore (Fig. 14B): A fresh spermatophore was spontaneously produced by and isolated captive animal in September (NMSA W7136). In general form this closely resembled the spermatophores of *N. c. amathole* and *N. c. eumacta*; anterior 2/3 with 6–8 primary longitudinal ridges; posterior third smooth but retaining three indistinct
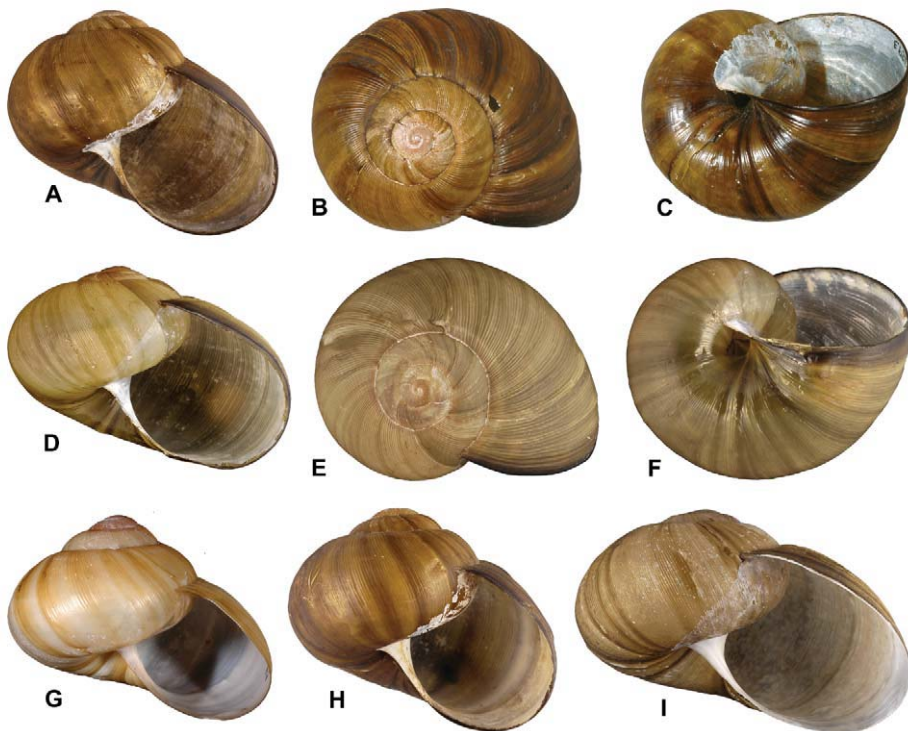

Fig. 27. *Natalina cafra natalensis* subsp. n.: (A–C) holotype (NMSA V3293/T2365), diameter 59.0 mm; (D–F) Durban Bluff, olive-green specimen (SAMC 36934), diameter 63.0 mm; (G) Karkloof, high spired specimen (faded) with periphery below mid-whorl (paratype, NMSA 2204/T2368), diameter 56.0 mm; (H) Prestbury, Pietermaritzburg, globose specimen (paratype, NMSA V2515/T2374), diameter 59.0 mm; (I) 'Natal', large, depressed specimen (NMSA A7041), diameter 75 mm.
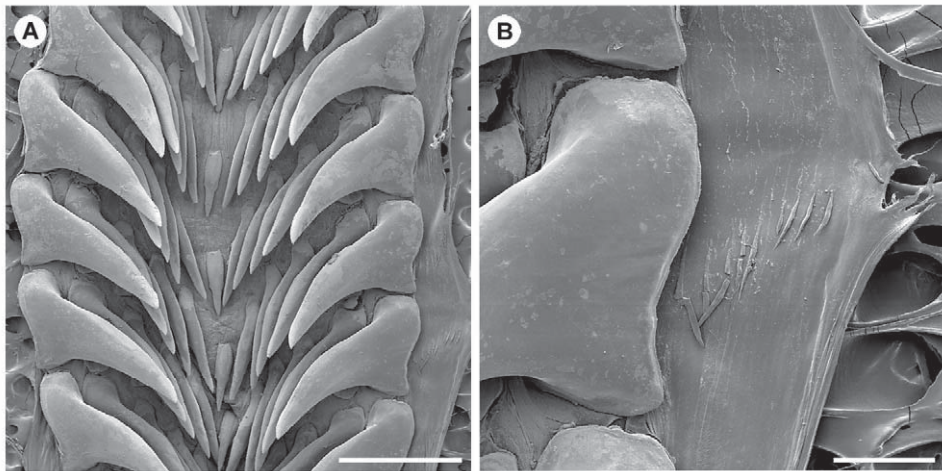
Fig. 28. *Natalina cafra natalensis* subsp. n., radula, Karkloof Forest (NMSA V8415): (A) rachidian and lateral teeth, scale bar = 1.0 mm; (B) vestigial marginal teeth, scale bar = 250 µm.

keels, two lateral and one dorsal; straightened length 18.3 mm. A small finger-like process was present at the base of the recurved tail region. This was stouter than that sometimes present on the *N. c. eumacta* spermatophore, but less well developed than that of *N. beyrichi*.

An allospermatophore (Fig. 10D) was found in a further specimen, collected in January (paratype, NMSA E7682/T2375). This was less strongly curved and had more well-developed longitudinal ridges, the strongest of which extended posteriorly, as three angular keels, almost to the tail tip; straightened length 16.3 mm. However, in this example a finger-like process was not evident on the tail region, suggesting that, as in *N. c. eumacta*, the presence of this structure is a variable feature.

Holotype (Figs 27A–C): SOUTH AFRICA: *KZN*: Ashburton, nr Pietermaritzburg (29.670°S:30.453°E), 670 m, in thornveld garden, R. Miller, ii/1996 (NMSA V3293/T2365).

Paratypes: SOUTH AFRICA: *KZN*: Same data as holotype (NMSA W6615/T2366, 1 specimen); Karkloof, Shafton Estate, De Magtenberg Forest (29.31795°S:30.19115°E), 1272 m, S. Miya, 13/xii/2006 (NMSA W5144/T2373, 1 specimen); Karkloof (approx. 29.30°S:30.23°E), A.J. Taynton, *ex* Burnup coll'n, pre 1930 (2204/T2368, 1 specimen); Pietermaritzburg, 30 Payn St (29.610°S:30.389°E), suburban garden, found dead in pond, D. Herbert, xii/2001 (ELM D16035 (ex NMSA V9637), 1 specimen); Pietermaritzburg, Scotts-ville (29.6230°S:30.3967°E), in garden, D. Herbert, ii/1989 (BMNH 20100124 [*ex* NMSA E7579/T2369], 1 specimen); Pietermaritzburg, Prestbury (29.615°S:30.337°E), in garden, P. Croeser, 1995 (NMSA V2515/T2374, 1 specimen); south of Tugela R. mouth (approx. 29.233°S:31.492°E), dune forest, A.C. & W.H. van Bruggen, 03/i/1964 (NMSA B0035/T2367, 1 specimen); Durban, Stella Bush (approx. 29.880°S:30.988°E), H. Bell-Marley, 11/xi/1930 (NMSA E7896/T2376, 1 specimen); Ngele Forest (30.533°S:29.633°E), 1300 m, mist-belt *Podocarpus* forest, S. Bourquin, 1995 (NMSA V2514/T2371, 1 specimen); Port Edward (approx. 31.055°S:30.225°E), J. Stannard, i/1987 (NMSA E7682/T2375, 1 specimen); Mtamvuna Gorge Nat. Res., Loerie Trail (31.0600°S:30.1717°E), riverine/scarp forest, in leaf-litter, D. Herbert, 27/xii/2002 (NMSA W0308/T2370, 1 specimen).

Additional material (all NMSA unless otherwise indicated): SOUTH AFRICA: *KZN*: <u>Thukela valley and southern Zululand:</u> Qudeni Forest (28.64882°S:30.90391°E), mist-belt forest, A. Moussalli & D. Stuart-Fox, 21/v/2003 (W4833); Mfongosi (28.713°S:30.805°E), W.E. Jones (3365); Nkandla Forest Res., Chibini area (28.7227°S:31.1282°E), 1200 m, mist-belt forest, under logs and in leaf-litter, D. Herbert, M. Bursey & T. Nangammbi, 20/x/2003 (W1167); Eshowe (28.885°S:31.468°E), 500 m, amongst garden debris, R. Miller, 01/iv/1996 (V2903); ditto, Dlinza Forest (28.89300°S:31.44833°E), scarp forest, in leaf-litter, D. Herbert, 24/x/1998 (V6663); ditto (28.8945°S:31.4555°E), scarp forest, D. Eckard, 03/ii/2000 (V8087); ditto (28.90°S:

31.45°E), 520 m, scarp forest, under log, D. Eckard, 29/ix/1997 (V5298); Mtunzini, Umlalazi Nat. Res. (28.95170°S:31.75083°E), dune forest, found dead in recent excavation, I.M. Porter, 16/v/1987, don. R.H. Taylor (E476); south of Tugela R. mouth (29.23000°S:31.48804°E), 11 m, coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 11/xi/2006 (W4699). <u>KZN Midlands:</u> Karkloof Nat. Res. (29.301°S:30.230°E), 1300 m, mist-belt *Podocarpus* forest, R. Kilburn, D. Herbert & L. Davis, 27/ii/1995 (V1948, V2021); Karkloof, Mbona Private Nat. Res., Holbeck (29.30087°S:30.35948°E), found dead in burnt grassland, died eating *Cochlitoma granulata*, D. Herbert & L. Davis, 01/vii/2006 (W5117); ditto (29.30087°S:30.35948°E), in burnt grassland, D. Herbert, viii/2004 (W2276); ditto (29.30339°S:30.36525°E), mist-belt *Podocarpus* forest, in leaf-litter, D. Herbert, 24/x/2004 (W2405); ditto, lower forest (29.30406°S:30.36077°E), mist-belt *Podocarpus* forest, D. Herbert, L. Davis, A. Moussalli & D. Stuart-Fox, 23/v/2005 (W3152); Karkloof, Rockwood farm (29.3083°S:30.2250°E), O. Bourquin, 02/viii/1981 (B5288); ditto, Leopard's Bush (29.315°S:30.250°], *ca* 1350m, mist-belt *Podocarpus* forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 09/xii/1998 (V8415); ditto (29.317°S:30.258°E), mist-belt *Podocarpus* forest, in leaf-litter, inside dead *Cochlitoma* shell, D. Herbert, 09/i/1997 (V5322); ditto, Shafton Estate, De Magtenberg Forest (29.31795°S:30.19115°E), 1272 m, S. Miya, 13/xii/2006 (W5145); Curry's Post (29.362°S:30.142°E) (A7045); Albert Falls (29.430°S:30.428), (2205); Hilton (29.555°S:30.297°E), (A7048); Pietermaritzburg, Ferncliffe Nat. Res. (29.565°S:30.345°E), mist-belt *Podocarpus* forest, A. Moussalli, D. Stuart-Fox, D. Herbert & L. Davis, 1/iv/2005 (W4828); ditto, Town Bush Valley (29.56648°S:30.33917°E), suburban garden, A. Moussalli & D. Stuart-Fox, 24/ii/2006 (W4832); ditto, below World's View (29.580°S:30.333°E), grassy hillside with scattered trees, in litter beneath *Erythrina latissima*, D. Herbert & L. Davis, 13/xi/2005, (W3658); ditto (29.615°S:30.337°E), garden (with new laid eggs), 28/ii/1989 (W5049); ditto, Alexandra Road (29.617°S:30.383°E), W.G. Rump, v/1932 (1392); ditto, 17 Oribi Rd (29.628°S:30.383°E), suburban garden, D. Herbert, xii/1984 (V6368); ditto, Blackburrow's Ridge, newly hatched, C.F.W. Hime, 05/ix/1926 (3724); Pietermaritzburg area, Mkondeni (29.6512°S:30.4810°E), 727m, bushland, M. Hamer, 29/x/2007 (W5853); ditto, Mkondeni (29.65180°S:30.43847°E), 715 m, bushland, M. Hamer, 29/10/2007 (W5847); ditto, Bisley Valley Nat. Res. (29.65767°S:30.39159°E), open woodland, under rotting log, G. Redman, 01/iii/2003 (W0549); ditto, Ashburton, Kingthorpe farm (29.67915°S: 30.49849°E), 750–800 m, savannah grassland, M. Hamer *et al.*, 12/xi/2008; Boston area, on Impendle road (29.67150°S:29.95662°E), 1540 m, natural grassland, C. Grant, 20/xi/2006 (W4877); Thornville (29.733°S: 30.383°E) (A7049); Baynesfield, nr Maybole farm (29.750°: 30.267°E), mist-belt *Podocarpus* forest, O. Bourquin, xi/1964 (V6544); Bulwer area, 3 km to north (29.78160°S:29.77577°E), highly disturbed montane *Podocarpus* forest beside stream, crawling at night, A. Moussalli, 06/xii/2003 (W1417); Bulwer (29.877°S: 29.775°E), Dr. E. Warren (V4253); Nkawini Mt, Riverbank farm (29.88601°S:30.08859°E), 1030 m, *Protea* savannah burnt during winter, many forbs, half-buried in soil under *Protea*, A. Armstrong *et al.*, 8/x/2008 (W6593). <u>Central KZN coast and hinterland:</u> Hawaan Forest (29.7050°S:31.0917°E), coastal lowland forest, in leaf-litter, D. Herbert & L. Davis, 04/xii/1995 (V2117); Hawaan Forest(29.71 17°S:31.0883°E), 60 m, coastal lowland forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 12/x/1998 (V8106); Drummond (29.748°S: 30.700°E), W. G. Rump, 19/xii/1932 (B0037); Gillitts (29.783°S:30.800°E), R.S. Benton, 01/x/1963 (B0036); Durban, Burman Bush (29.817°S:31.017°E), coastal lowland forest, O. Bourquin, 25/x/1962 (3945, B0034); Pinetown (29.820°S:30.892°E), L. Trotter (2206); Durban, 49 Waller Crescent, Roseglen (29.82445°S: 31.00190°E), suburban garden, C. Uys, 6/iii/2006 (W5025); Durban, Pigeon Valley Nat. Res. (29.86403°S: 30.98506°E), coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 18/v/2005 (W4362); Durban, Pigeon Valley Park (29.880°S:30.967°E), 90 m, coastal lowland forest, in leaf-litter, Herbert, Kilburn & Davis, 31/iii/ 1995 (V2363); Durban, Stella Bush (29.880°S:30.988°E), H. Bell-Marley, 11/xi/1930 (B0038, W1385); Durban, Stellawood, F.G. Cawston (BMNH 37.12.30.1303); Durban, Bellair (29.892°S:30.953°E), indigenousbush, N. Gardiner (2141); Durban Bluff (29.895°S:31.047°E), Falcon coll'n (A9124); Umbogintwini (30.0167°S: 30.9170°E), Marley, 03/v/1919 (E7899); Port Natal [= Durban] (BMNH 57.1.16.7, G.C. Cato; 57.3.6.41, Sir W. Jardine Bt). <u>Drakensberg:</u> Cathedral Peak area, Fern Forest (Oqalweni Forest) (28.94329°S:29.18580°E), montane *Podocarpus* forest, in leaf-litter, D. Herbert (Earthwatch), 19/iii/2006 (W5483); Cathedral Peak area (28.945°S:29.205°E), 1900 m, below fire look-out tower, at edge of in open grassland, O. Bourquin, 14/i/1977 (V7109); Giant's Castle, Bannerman's Pass (29.2533°S:29.4200°E), 2350 m, alpine grassland, D.T. Rowe-Rowe, 26/ii/1976 (A7052); Cobham, Sani Pass (29.60800°S:29.32417°E), 2040 m, shrubland, D. Alletson, 25/iv/1996 (V3285). <u>Southern KZN:</u> Franklin area, Hebron farm (30.40327°S:29.56253°E), 1650 m, garden, J. Scott, vii/2008; Oribi Gorge Nat. Res., Hoopoe Falls trail (30.70765°S:30.26992°E), scarp forest, in leaf-litter, D. Herbert, 06/x/2001 (V9434); Port Shepstone (30.742°S:30.453°E) (A7043);Mar gate (30.863°S: 30.367°E), W.G. Rump, 1929 (B0090); Mtamvuna Gorge Nat. Res., western heights (31.000°S:30.167°E), in wetland area, R. Markham, 19/viii/1997 (V5271).

Rejected records: A record of *Natalina cafra* from Mbabane, Swaziland (Bruggen 2004) was based on a specimen belonging to the *N. quekettiana* complex (see below, Fig. 35A). Similarly, Connolly's record of the species from 'between Lydenburg and Delagoa' (Connolly 1939) probably refers either to the *N. quekettiana* complex or to *N. wesseliana*, but no material from this region is present in either NMSA or BMNH.

Distribution (Fig. 29): Endemic to KwaZulu-Natal, but widely distributed in central and southern regions, from the Eshowe–Qudeni area south to the border between KwaZulu-Natal and E. Cape (Mtamvuna R.); altitudinal range extensive, from the coast to 2350 m in the central Drakensberg.

Habitat: Occurs in a wide variety of habitats, ranging from indigenous forest (coastal to montane) to thornveld, valley bushveld and mist-belt and subalpine grassland; has also adapted well to suburban gardens; in leaf-litter and under logs or beneath shrubs and grass clumps, essentially in almost any sheltering microhabitat. Relatively common, particularly in the KZN Midlands, but population densities are generally low.

Notes: We have been unable to identify any morphological characters, either conchological or anatomical, which serve to distinguish this subspecies from the nominotypical one. It is clear, however, that specimens of *N. cafra* from KwaZulu-Natal constitute a monophyletic lineage which is genetically distinct from those occurring in E. Cape (Moussalli *et al*. 2009). In addition, there is a clear geographical gap in the north-eastern E. Cape separating the KwaZulu-Natal *N. cafra* populations from those in the E. Cape. At the coast this gap is filled by *N. beyrichi*, but evidently remains vacant at inland localities.

It is difficult to discern any clear geography-related pattern in the variability in shell proportions of *N. c. natalensis*, but specimens from Durban and the KwaZulu-Natal north coast tend to be less elevated (H:D<0.76). Juveniles may be confused with the
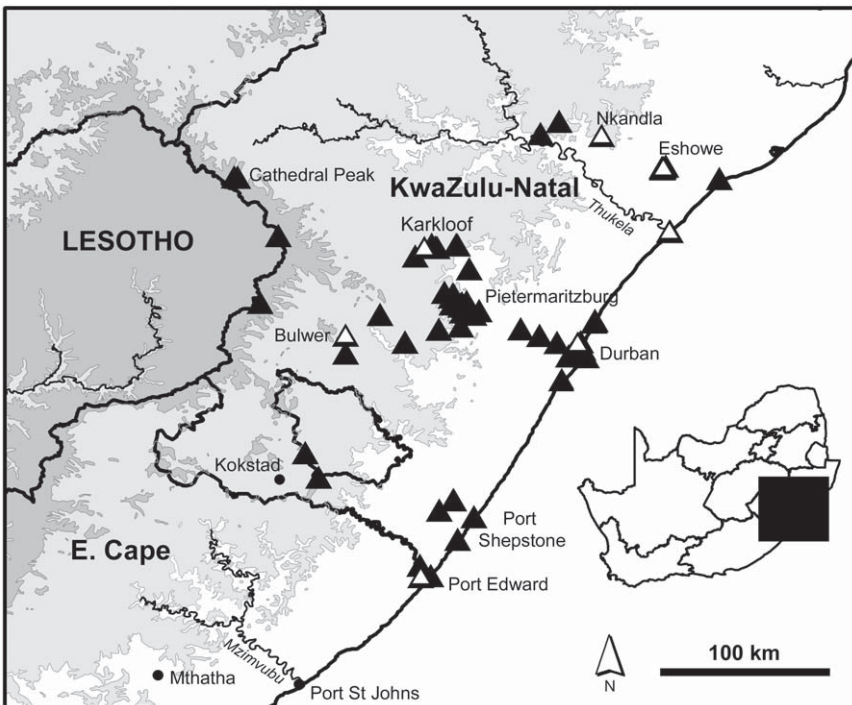

Fig. 29. Distribution of *Natalina cafra natalensis* subsp. n. Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al*. 2009); contours at 1000 m and 1500 m.

smaller Afromontane *Natalina* species, but the latter have a distinctly smaller protoconch (diameter 4.5–6.0 mm compared to 7.0–8.0 mm).

Conservation: Like the nominotypical subspecies, *N. c. natalensis* is widespread and common, and of catholic habitat requirements. Its distribution is not conspicuously fragmented (acknowledging sampling gaps) and it is evidently able to adapt to some extent to suburban habitats and thus to survive as a synanthrope. At present there is no evidence to suggest that the subspecies is threatened.

Natalina beyrichi (Martens, 1890)

Figs 3D, 8A, 14E, 15A, 30–32

Aerope beyrichi: Martens 1890: 85; 1894: 1; 1897: 35, pl. 6, figs 1–3. Type loc.: Pondoland [C. Beyrich].
Natalina beyrichi: Melvill & Ponsonby 1898: 170; Sturany 1898: 30; Möllendorff 1903: 21, pl. 4, figs 1–3; Connolly 1912: 90; 1939: 106, pl. 4, figs 1–3; Herbert & Kilburn 2004: 222.

Etymology: Named for Conrad Beyrich (dates not known), a German engineer. In 1888 he travelled through Pondoland (north-eastern E. Cape) with fellow German, Frans Ewald Bachmann, visiting localities from the Mtamvuna River south to Port St Johns.

Identification: A relatively easily identified species on account of its depressed shape, comparatively strongly sculptured base, wide umbilicus and coastal distribution in the
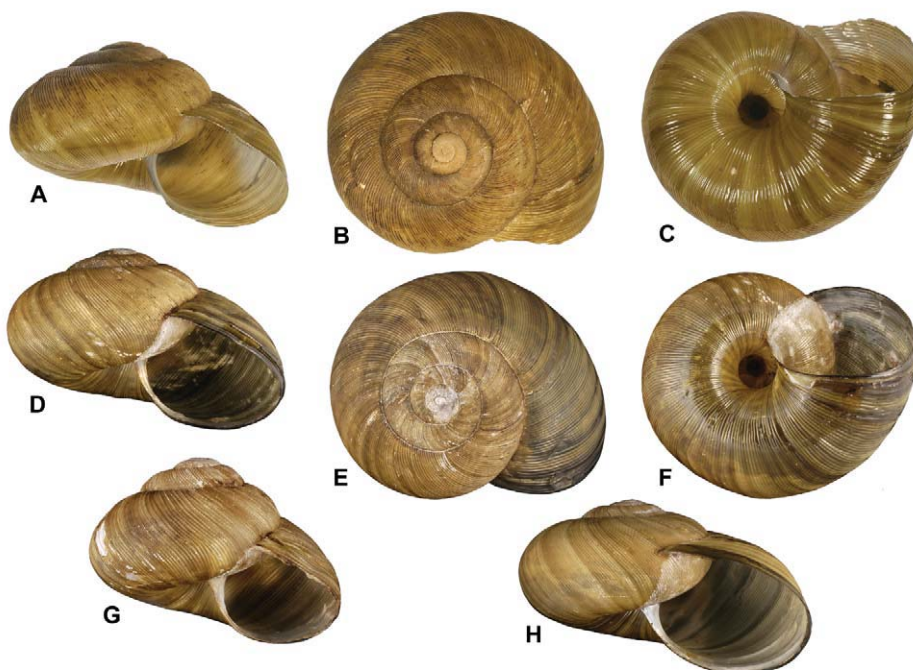

Fig. 30. *Natalina beyrichi* (Martens, 1890): (A–C) lectotype of *Aerope beyrichi* Martens, 1890 (here designated) (MNHU 42394), diameter 59 mm, height 38 mm (photographs courtesy of Thomas von Rintelin and Lothar Maitas); (D–F) Mbotyi (NMSA W0591), diameter 54.7 mm; (G) elevated specimen, Hluleka (NMSA W3023), diameter 41.0 mm; (H) depressed specimen, Port St Johns (NMSA E7862), diameter 57.5 mm.

north-eastern E. Cape; a range which overlaps only with that of *N. cafra eumacta* which is taller, more globose and has a narrower, partially obscured umbilicus.

Description (Fig. 30): Shell large and relatively depressed, thin and fragile; periphery at or below mid-whorl; suture somewhat above mid-whorl, but descending to a variable degree prior to aperture at maturity. Protoconch diameter typically 7–8 mm, but its limit difficult to determine in many specimens. Apical surface sculptured by close-set axial riblets which remain obvious on base; junction between dull upper surface and more shiny base forming a relatively distinct line at the periphery; umbilicus wide, not obscured at all by columella lip when viewed basally; long axis of aperture more or less horizontal or only slightly oblique; outer lip not thickened.

Periostracum olive-green to olive-brown with frequent radial bands in darker shades, particularly on last whorl.

Dimensions: Largest specimen (NMSA W5414, Port St Johns), diameter 63.1 mm; H:D of adults 0.57–0.74 (N=28).

Living animal (Fig. 15A): Head-foot grey to greyish brown or brown, dorsal neck region and optic tentacles somewhat darker, generally lacking pale longitudinal stripes extending backward from optic tentacles; sides of foot paler, particularly beneath shell; pedal margin tinged with orange, tail sometimes brightly so; mantle edge bright orange.

Radula (Fig. 31): Formula 1+5+~22 (N=2); length in adult 34–38 mm, with 44–56 transverse rows of teeth.

Distal genitalia: Epiphallus with a well-developed bulla near its junction with vas deferens; internally this has a hollow central core continuous with the epiphallus lumen, its junction with the latter being bounded by a raised circular flange.

Spermatophore (Fig. 14E): Well preserved allospermatophores have been found in two specimens, collected in early November (NMSA W4123, W4125). Straightened length 18–26 mm. In general form these resemble those of *N. cafra* subspp. and were strongly
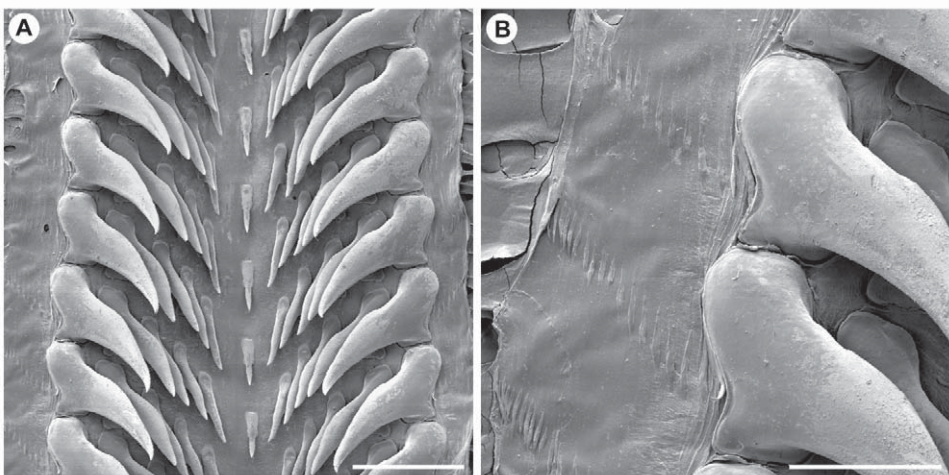

Fig. 31. *Natalina beyrichi* (Martens, 1890), radula, Mbotyi (NMSA W0591): (A) entire width of radula, scale bar = 1.0 mm; (B) vestigial marginal teeth, scale bar = 0.5 mm.

curved *in situ* in the oviduct caecum. Notably, they differ in having a well-developed thumb-like projection on the outer side, at the base of the recurved tail region. This is more substantial than the similar projection sometimes seen in the spermatophores of *N. c. eumacta* and *N. c. natalensis*. It is clearly formed in the epiphallus bulla.

Type material: Nine syntypes in Berlin Museum (MNHU: 42394). We designate the specimen figured by Martens (1897) and re-illustrated here (Figs 30A–C) to be the lectotype, diameter 59.5 mm, height 38.0 mm (Martens gave the dimensions as diameter 62 mm, height 40 mm, but this may refer to the largest specimen rather than the one figured). Connolly's mention of the 'type in Zool. Mus. Berlin' (Connolly 1912) does not constitute a lectotype designation since he did not specify any one specimen in particular.

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Mkambati Nat. Res., 'Super Bowl' forest at junction of Msikaba and KwaDlambu rivers (31.2955°S:29.9292°E), indigenous forest, in leaf-litter, M. Bursey, 05/iii/2001 (V9220 body only, shell in ELM D13333); ditto (31.2955°S:29.9292°E), indigenous forest, in leaf-litter beneath *Trichilia dregeana* Sonder, D. Herbert, 05/iii/2001 (V8916); Mbotyi, various sites beside road through upper section of forested scarp (Ntsubane Forest) (31.4298°S:29.7261°E), coastal forest, in leaf-litter, D. Herbert, 03/iii/2003 (W0591); Mbotyi Forest (31.43107°S:29.72656°E), *ca* 300 m, indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 3/xi/2005 (W4123); Magwa Falls, Egossa Forest (31.4333°S:29.6333°E), *ca* 500 m, R. Botha, 08/vii/2006 (ELM W02995); Port St Johns area, east bank of Mzimvubu R., 26 km upstream of mouth (31.509722°S: 29.448883°E), M. Bursey, 24/i/2006 (ELM D14771); Mntafufu, north side of river (31.5559°S:29.6261°E), coastal forest, in leaf-litter, one individual found eating *Gittenedouardia carinifera* (Melvill & Ponsonby, 1897), D. Herbert, L. Davis & M. Bursey, 23/iv/2005 (W1831, W2969, W2970, W3025); ditto, south side of river (31.55021°S:29.61777°E), coastal scarp forest, amongst talus and leaf-litter at base of road cutting, D. Herbert & M. Bursey, 29/iv/2004 (W1823); Port St Johns, east bank, 1 km from river mouth (31.60833°S: 29.55000°E), R. Botha, 06/vii/2006 (ELM W03000); ditto, Isinuka sulphur springs and travertine deposit (31.60953°S:29.47989°E), woodland/forest, in leaf-litter, D. Herbert, 04/iii/2003 (W0538); ditto, southern side of Mt. Thesiger (31.61185°S:29.50202°E), scarp forest, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 23/iv/2005 (W3029); ditto, north of Mzimvubu R. (31.61519°S:29.54526°E), indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 08/xi/2005 (W5414); Port St Johns (not further localised) (A7044, A7130, V2013, E7862, BMNH 1937.12.30.1304); ditto, Second Beach (31.64819°S:29.51746°E), 100 m, coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 05/xi/2005 (W4125, W5413); ditto, Silaka Nat. Res. (31.64903°S:29.50339°E), M. Bursey, 05/iii/2003 (ELM D13835); Nothintsila, *ca* 20 km NW of Hluleka Nat. Res. (31.74733°S:29.20008°E), 395 m, indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 14/xi/2005 (W4734); Mpande (31.74738°S:29.37078°E), coastal forest north of river mouth, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 21/iv/2005 (W2849, W2870, W2872, W2873); Hluleka Nat. Res. (31.8203°S:29.30303°E), coastal forest, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 20/iv/2005 (W3023, W2895, W2896); ditto (31.82333°S:29.30550°E), coastal forest, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 20/iv/2005 (W3047); Xora R. mouth area, Kwaqana Forest (32.13833°S:28.98750°E), M. Bursey, 15/ix/2005 (ELM D14544); Xora River mouth (32.150°S:28.983°E), washed into mangroves, V. van der Walt, 1997 (V5311); Xora, east bank of Xora river (32.15167°S:28.99222°E), M. Bursey, 26/viii/2001 (ELM D13345); ditto, Kumqolo Forest (32.15888°S:28.98481°E), M. Bursey, 12/vii/2003 (ELM D13686); ditto, Kumqolo Forest, small patch of coastal forest on west bank of river (32.159°S:28.985°E), in leaf-litter, M. Bursey, 14/ix/2005 (W5395); The Haven Nat. Res., vicinity of camp ground (32.24435°S:28.90600°E), 15 m, coastal dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 16/xi/2005 (W4149); Dwesa Nat. Res. (32.280°S:28.842°E), coastal forest, in leaf-litter, D. Herbert, 06/iii/2000 (V7869); Qora, east bank of river (32.433°S:28.667°E), M. Bursey, 21/ii/2006 (ELM D14798); Mpetu area, Tyityaba, Belladonna farm (32.56833°S:28.12500°E), 340 m, C. Vernon, 26/vii/1986 (ELM D10040).

Distribution (Fig. 32): A restricted-range E. Cape endemic, known only from the coastal hinterland between Mkambati Nature Reserve and the Kei River valley (Mpetu area). Its distribution seldom reaches far inland (maximum recorded distance from coast ±30 km) and extends along the coast for ±230 km; occurs from sea-level to 500 m.

Habitat: Primarily associated with scarp forests in the Transkei Coastal Belt, but extending also into forest patches within the Eastern Valley Bushveld; in leaf-litter and under logs; locally common.

Notes: *Natalina beyrichi* is unlikely to be confused with any other species on account of its depressed, widely umbilicate shell and coastal distribution in the north-eastern

E. Cape. There is some variation in shell height, with specimens from the Hluleka area often having a more elevated spire and in addition a slightly coarser sculpture (Fig. 30G). However, specimens of intermediate height are known and all possess the wide, open umbilicus typical of the species. In analyses of molecular data, elevated specimens cluster together with more typical specimens. Not surprisingly, given its restricted coastal distribution, genetic diversity within *N. beyrichi* is limited (Moussalli *et al.* 2009). The coastal forest habitats favoured by the species would have been largely continuous prior to the impact of humans, facilitating gene flow and preventing the differentiation of local subpopulations. In the south of its range, the distribution of *N. beyrichi* overlaps with that of *N. cafra eumacta*, but that taxon is markedly more globose. The zone of sympatry extends for approximately 70 km, between the Kei and Mbashe rivers, but the two taxa have been found to co-occur at few localities. Where they are syntopic, they remain easily separable with no evidence of intergrading.

Individuals have been collected consuming molluscan prey (e.g., *Gittenedouardia* spp., Cerastidae), but microchaetid earthworms (*Microchaetus pondoanus* Michaelsen, 1913) are often abundant in the coastal forests of Transkei (Plisko 2003, and pers. observ.) and these may also be important diet items. Captive animals have readily consumed such prey.

Conservation: *Natalina beyrichi* is a characteristic element of the coastal forests of the Transkei region and is currently listed as Critically Endangered [CR B1+2c] (IUCN
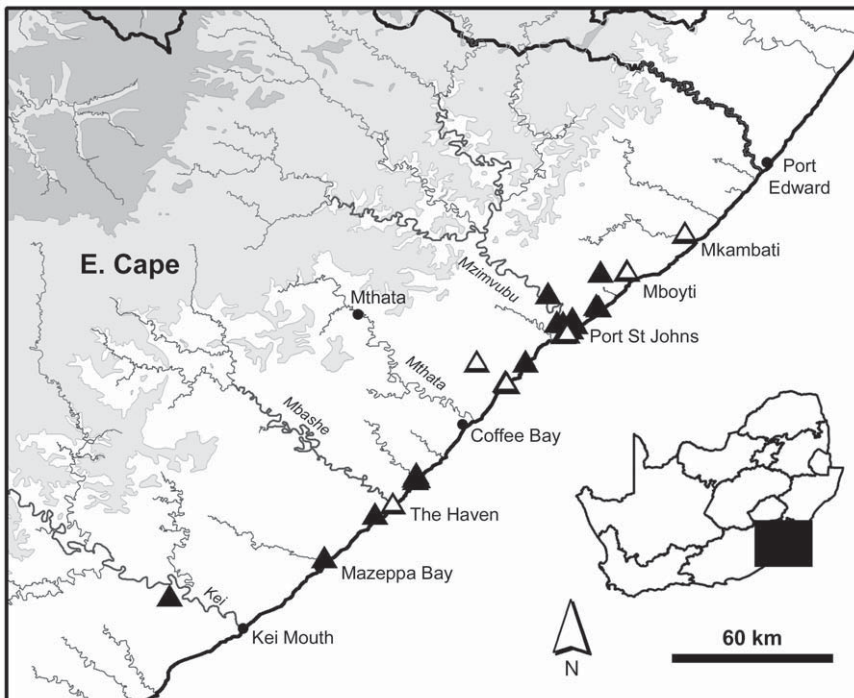

Fig. 32. Distribution of *Natalina beyrichi* (Martens, 1890). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

2010). This is due to its restricted distribution and the threats to coastal forest habitats in much of its range. Such threats are on-going and include mining, subsistence harvesting, invasive plants and trampling by cattle. However, despite its limited range, the species may be locally relatively common. It is protected in conserved areas such as Mkambati, Hluleka and Dwesa nature reserves, but the first and last of these are at or near the ends of its range. Populations in the Mbotyi to Port St Johns area, where it is currently most common, are not protected.

Natalina quekettiana complex

In addition to the large and conspicuous *Natalina s.s.* species discussed thus far, are three further species described from KwaZulu-Natal. These are all of smaller size and appear to be rare. In two cases they are known solely from the original samples, and only *N. quekettiana* has been collected again subsequent to its original description. However, on-going field work has brought to light additional small-shelled, but clearly adult *Natalina* specimens from a number of other localities in KwaZulu-Natal (Fig. 33). These are similar to the described taxa, but not clearly conspecific with any one of them. We have attempted to clarify this matter through analysis of DNA sequence data, but have been hindered in this by being unable to obtain fresh topotypic material of two of the described species (*N. inhluzana* and *N. reenenensis*), despite targeted attempts. We have, however, been able to obtain sequence data from topotypic material of *N. quekettiana* and a number of the indeterminate specimens from other localities.

From analyses of these data (Moussalli *et al.* 2009), it is clear that the small-shelled specimens collectively comprise a monophyletic lineage within *Natalina*, which we term the *N. quekettiana* complex. This is sister to the clade comprising *N. cafra* and *N. beyrichi* (Fig. 1). In terms of shell morphology, radula dentition, body coloration and genetic make up, this complex exhibits considerable internal diversity, although, with the exception of the epiphallus, the genital anatomy is the same. The spermatophore is known for only one subspecies, but this differs greatly from that of the larger *Natalina s.s.* species and *Natalina* (*Tongalina*) in bearing well-developed, lobate, scale-like spines. This differing spermatophore morphology is reflected in the internal structure of the epiphallus and, since this is similar in all members of the complex for which preserved material is available, it is likely that the presence of scale-like spines on the spermatophore will prove to be an autapomorphic trait for this clade as a whole (the spines on the *Afrorhytida* spermatophore are of a very different form).

The molecular data identified four allopatric subclades (Fig. 1), one comprising material from central and south-western Zululand, a second from the mist-belt regions of the KwaZulu-Natal Midlands, and two others from the central KwaZulu-Natal Drakensberg. The first two are sister taxa and can be differentiated from each other morphologically in terms of size and radula dentition. As a pair they comprise a mid-altitude radiation (600–1500 m). The two other subclades, from higher altitude forests in the foothills of the central Drakensberg (1350–1650 m), however, show no obvious or consistent differences in shell form (which is confusingly variable in the few specimens available) or radula dentition. Yet despite this and their geographical proximity, they are evidently not closely related, the one being sister to the mid-altitude subclade and the other representing a deeply divergent lineage arising at the base of the *N. quekettiana* clade.
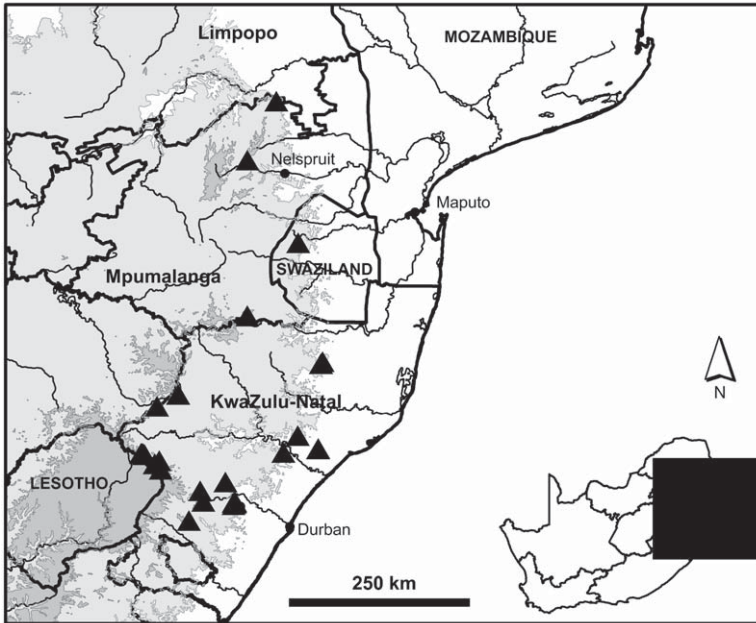
Fig. 33. Distribution of *Natalina quekettiana* complex; contours at 1000 m and 1500 m.

Neither appear to be referable to the similarly high altitude taxon *N. reenenensis* on account of differences in radula dentition.

This situation is clearly complicated and in need of further investigation, but for the present, we chose to treat this material as a single complex. However, in order to recognise the lineages identified through analyses of molecular data (in some cases supported by morphology), we propose to treat these as subspecies within a broadly interpreted *Natalina quekettiana*, the earliest available species-group name within the complex. We maintain *Natalina reenenensis* as a distinct species simply because we have no data upon which to base a change in its status. It is unique within the *N. quekettiana* complex in having only five pairs of lateral teeth per transverse row of the radula. We also have no new data concerning *N. inhluzana*, and treat this as a separate
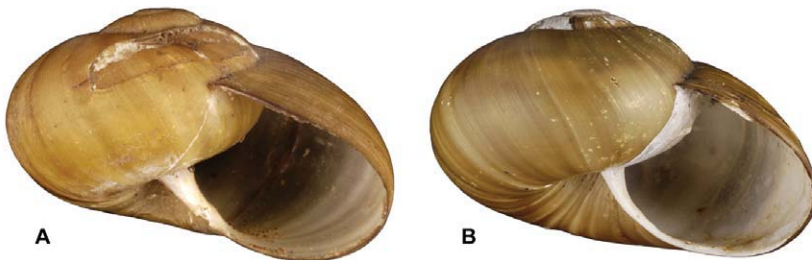
Fig. 34. *Natalina quekettiana* complex, unidentified material from the north-eastern escarpment: (A) Mbabane, Swaziland, diameter 28.0 mm (RMNH.MOL.109689); (B) Buffelskloof Nat. Res., Mpumalanga, diameter 30.1 mm (NMSA W6104).

entity too, but we strongly suspect that it is a synonym of *N. quekettiana quekettiana* (see below).

In addition to the above, are further small-shelled specimens (Fig. 34) from escarpment-edge habitats in Mpumalanga and Swaziland (locality details given below). These are shell-only samples and while we can be moderately confident that they belong to the *N. quekettiana* complex, we cannot reliably assign them to any of the taxa discussed below. They do, however, indicate that this complex ranges beyond KwaZulu-Natal along the north-eastern Drakensberg escarpment.
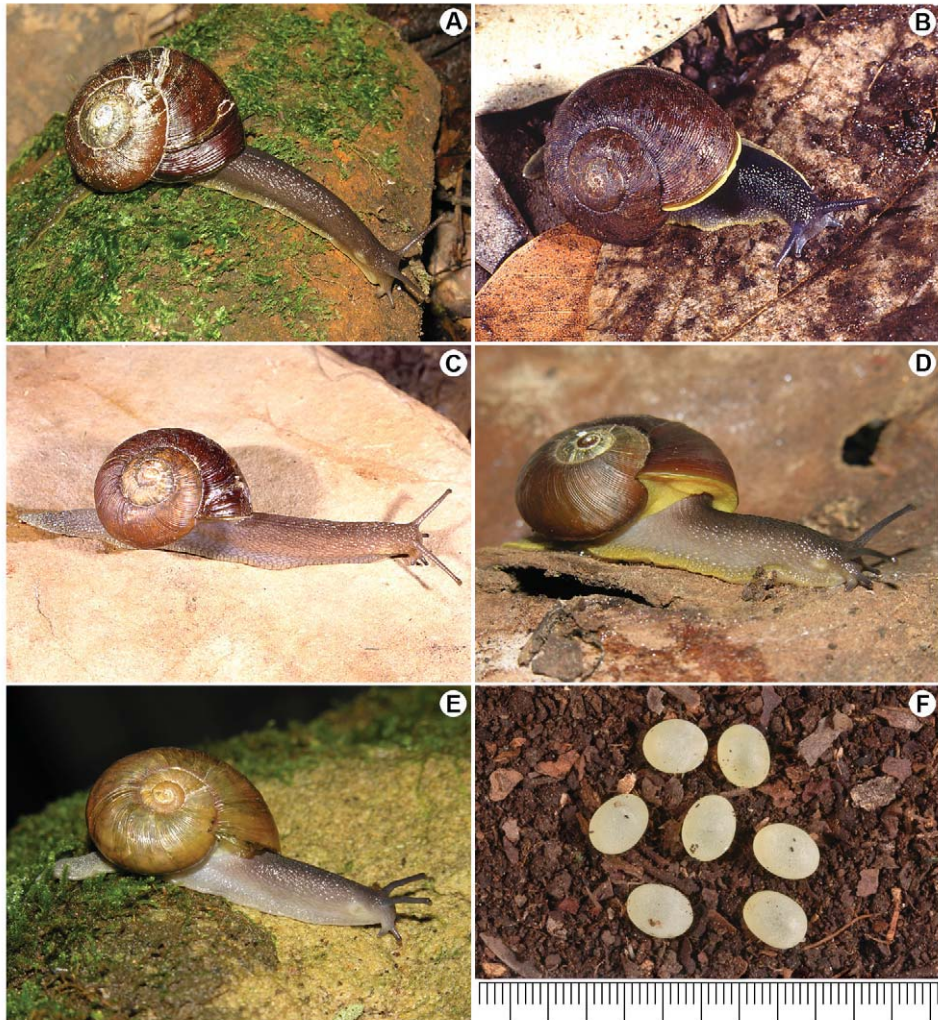
Fig. 35. *Natalina quekettiana* complex, living animals and eggs (all NMSA): (A) *N. q. quekettiana*, Ferncliffe, Pietermaritzburg (W6646), shell diameter 31.3 mm; (B) *N. q. lucaris* subsp. n., Ngome Forest (paratype, V2249/T2563), shell diameter 29.4 mm; (C) *N. q. dracomontana* subsp. n., Injasuthi (holotype, V7992/T2451), shell diameter 27.2 mm; (D) *N. q. dracomontana* subsp. n., Monk's Cowl area (paratype, W4101/T2452), shell diameter 26.4 mm; (E) *N. q. montistempli* subsp. n., Oqalweni, Cathedral Peak (holotype, W4084/T2422), shell diameter 23.9 mm; (F) *N. q. quekettiana*, eggs (W6646), scale in millimetres.

As a whole, the *N. quekettiana* complex is evidently confined to wet forest habitats, primarily Afrotemperate (montane) and mist-belt forests, but extends also into lower altitude scarp forest in southern Zululand (Fig. 33). Given this habitat specialisation, the distribution of the taxon is likely to be highly fragmented with many populations and perhaps species restricted to isolated forest islands within the rainforest archipelago. This patchy pattern is concordant with the considerable genetic diversity mentioned above, even between geographically proximate populations, for example those in central KwaZulu-Natal Drakensberg (Cathedral Peak *vs* Injasuthi–Monk's Cowl). It is thought that this derives from sequential isolation events associated with Plio-Pleistocene glacial cycles (see biogeographic summary).

Unidentified material belonging to the *Natalina quekettiana* complex: SOUTH AFRICA: *Mpumalanga*: Mariepskop Forest (24.56683°S:30.86232°E), 1520 m, mist-belt forest, J. Horn, 28/ii/2005 (NMSA W4720); nr Pienaar's R., between Pretoria and Lydenburg, 'Transvaal' (BMNH 78.1.30.3); Lydenburg area, 25 km south, Buffelskloof Nat. Res. (25.3°S:30.5°E), 1500 m, indigenous forest, in leaf-litter, D. Plowes (NMSA W6104); Wakkerstroom, 40 km ENE of, Paardeplaats Forest (27.23683°S:30.50250°E), 1472 m, indigenous forest, in leaf-litter, J. Horn & M. Lotter, 06/xi/2006 (NMSA W5569). SWAZILAND: Mbabane (26.330°S:31.133°E), >1250 m, L.D. Brongersma, 17/x/1938 (cited Bruggen (2004: 46) as *Natalina cafra*; RMNH.MOL.109689).

Key to taxa in *Natalina quekettiana* complex

1   Adult shell diameter >35 mm; radula with 6 pairs of lateral teeth per transverse row. Mist-belt and scarp forests of central and south-western Zululand and Kranskop area .... **N. q. lucaris** subsp. n.

–   Adult shell diameter <35 mm. Mist-belt forests of KZN Midlands and montane forest of Drakensberg escarpment 2

2   Occurring in mist-belt forests of KZN Midlands .... **N. q. quekettiana / N. inhluzana**

–   Occurring in montane forest of Drakensberg escarpment 3

3   Radula with 7–8 pairs of lateral teeth per transverse row. Central KZN Drakensberg 4

–   Radula with 5 pairs of lateral teeth per transverse row. Along escarpment edge in north-western KZN .... **N. reenenensis**

4   Shell of living animal with dark brown apical surface and greenish base. Injasuthi–Cathkin Peak area .... **N. q. dracomontana** subsp. n.

–   Shell of living animal relatively pale, more or less uniform greenish brown. Cathedral Peak area .... **N. q. montistempli** subsp. n.

Note: In view of the fact that the separation of the subspecies *N. q. dracomontana* and *N. q. montistempli* is based primarily on molecular data, and the fact that few living specimens have been collected, the morphological characters given in the key are at best tentative. The distributions given for all taxa within this complex should also be considered provisional.

Natalina quekettiana quekettiana (Melvill & Ponsonby, 1893)

Figs 13C, 35A, F, 36–38

Helix (Macrocyclis) quekettiana: Melvill & Ponsonby, 1893: 103, pl. 3, fig. 1; Moss 1894: 24, pl. 1, fig. 4 (radula). Type loc.: Town Bush, Pietermaritzburg [Quekett].
Macrocyclis quekettiana: Sturany 1898: 33.

Rhytida (*Afrorhytida*) *queckettiana* [*sic*]: Möllendorff 1903: 63, pl. 11, fig. 4.
Natalina quekettiana: Melvill & Ponsonby 1898: 170; Connolly 1912: 96; 1939: 107; Watson 1915: 168, 185; 1934: 158, pl. 19, fig. 5; Peile 1932: 103, fig. 2 [deformed radula tooth]; Herbert & Kilburn 2004: 223.
?*Helix* (*Dorcasia*) *inhluzana* Melvill & Ponsonby, 1894: 91, pl. 1, fig. 4. Type loc.: Inhluzan(i) Mountain [Nhlosane], Dargle, KwaZulu-Natal [Mrs Shaw]. See below.

Etymology: Named for Frederick Quekett (1849–1913), first curator of the Natal Society Museum's collections (1886–95) (the precursor of the NMSA) and subsequently curator of the Durban Natural History Museum (1895–1909).

Identification: Very similar to the montane *N. q. dracomontana* and *N. q. montistempli*, and at this stage cannot be reliably separated from them morphologically, given that the extent of intra-taxon variation in the latter two taxa is poorly known. May perhaps differ conchologically in that the last whorl is more strongly descendant prior to the aperture, the umbilicus a little wider and the base somewhat smoother in *N. q. quekettiana*. In addition, the shell periphery often lies below mid-whorl. Frequently resembles *N. q. lucaris* in shell and body colour, but is smaller and has more numerous la-
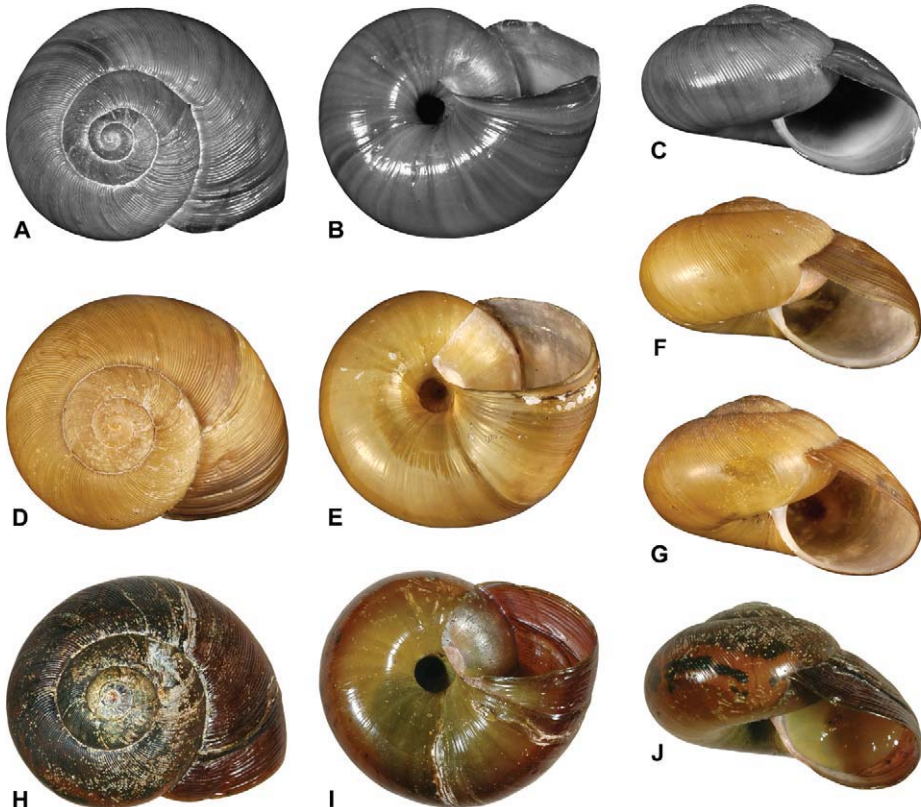
Fig. 36. *Natalina quekettiana quekettiana* (Melvill & Ponsonby, 1893): (A–C) holotype of *Helix* (*Macrocyclis*) *quekettiana* Melvill & Ponsonby, 1893 (BMNH 1905.1.26.1), diameter 30.0 mm; (D–F) faded specimen, Pietermaritzburg (NMSA A7057), diameter 30.2 mm; (G) elevated specimen, subadult, Pietermaritzburg (NMSA V6543), diameter 27.7 mm; (H–J) living specimen showing dark chestnut brown apex and greenish yellow base, Ferncliffe Nat. Res., Pietermaritzburg (NMSA W6646), diameter 31.3 mm.

teral teeth in the radula (8–9 pairs per row compared to 6). *N. reenenensis* also has fewer lateral teeth (5 pairs per row) and is generally paler and greener, though the shells available are all old.

Description (Fig. 36): Shell generally lenticular, but height of spire somewhat variable; adult shell comprising up to 4.75 whorls, the last usually noticeably descending prior to aperture in adult specimens; whorls rounded, periphery usually slightly below mid-whorl, suture a little above mid-whorl; base glossy, apical surface less so. Protoconch 4.5–5.0 mm in diameter, with distinct axial riblets throughout. Apical surface of teleo-conch sculptured by close-set axial riblets, these becoming much weaker at periphery and scarcely evident at all on base except around and within umbilicus; base also with traces of spiral striation in some specimens; aperture suboval, somewhat obliquely des-cending outwards; outer lip of adult frequently thickened basally, but sometimes also retaining a membranous periostracal fringe; adapical portion of outer lip often flattened; upper part of columella lip reflected; umbilicus of moderate width, not obscured to any appreciable degree by reflected columella lip.

Periostracum of living specimens dark chestnut-brown on apical surface (Figs 36H–J), extending a little below periphery to outer region of base, contrasting with lighter yellowish green umbilical and peri-umbilical region; empty shells paler, fading to yellowish brown or light olive-green in older museum material (Figs 36D–G).

Dimensions: Largest specimen (NMSA W6646, Ferncliffe Nat. Res.), diameter 31.3 mm; H:D of adults 0.58–0.68 (N=13).

Living animal (Fig. 35A): Head-foot dark grey-brown to grey-black, lacking paler longitudinal stripes on neck; tentacles similarly dark; skin texture finely granular; posterior portion of foot flat and elongate, tip of tail rather acutely pointed; pedal margin paler, frequently tinged with yellow; skin around genital pore also pale; mantle edge greyish yellow; lung wall variously mottled with dots and anastomosing blotches of black pigmentation, sometimes heavily so; labial palps present.

Radula (Fig. 37): Formula 1+(8–9)+(10–17) (N=7, one in BMNH); length up to 29 mm, with 68–80 broadly V-shaped transverse rows of teeth (see also Moss 1894). The number of marginal teeth in all members of the *N. quekettiana* complex is lower than in the larger species of *Natalina s.s.* (<20 *vs* >20 per half row in adults), although this is probably a function of their smaller size, since juveniles of the larger species have proportionately fewer marginal teeth.

Distal genitalia (Fig. 13C): Epiphallus lumen lined by 3 or 4 longitudinal ridges; interval on inner wall (adjacent to penis) smooth, relatively broad and thin-walled; wall of outer part of epiphallus thicker and the remaining intervals between ridges with numerous, close-set, transverse, slit-like pockets representing openings of diverticulae in thickened epiphallus wall; these strongest in mid to anterior part of epiphallus, but less well defined in posterior third and absent near junction with vas deferens; no epiphallus bulla evident.

Spermatophore: Unknown, but structure of epiphallus wall indicates that, as in *N. quekettiana lucaris*, it will have a smooth underside and well-developed scale-like spines in the mid to anterior region, on its convex outer surface.

Type material: Three specimens were mentioned in the original description, one in BMNH (1905.1.26.1) was designated lectotype by Connolly (1912: 96), diameter 30.0 mm, height 18.0 mm (Figs 36A–C). The location of the other two specimens is unknown.
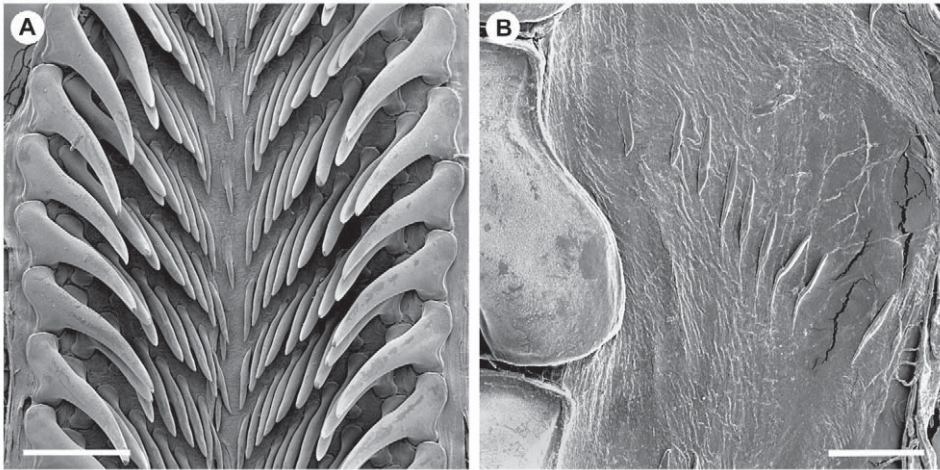
Fig. 37. *Natalina quekettiana quekettiana* (Melvill & Ponsonby, 1893), radula (NMSA V6543): (A) rachidian and lateral teeth, scale bar = 0.5 mm; (B) vestigial marginal teeth, scale bar = 100 μm.

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: *KZN*: Pietermaritzburg, Ferncliffe Nat. Res. (29.565°S:30.345°E), mist-belt *Podocarpus* forest, in leaf-litter, A. Moussalli, D. Stuart-Fox, D. Herbert & L. Davis, 1/iv/2005 (W4262); ditto (29.54848°S:30.34481°E), mist-belt *Podocarpus* forest, in leaf-litter accumulations amongst rocks beside path (common), D. Herbert & L. Davis, 16/xii/2008 (W6646); ditto (29.555°S:30.333°E), mist-belt *Podocarpus* forest, R. Kilburn, D. Herbert & L. Davis, 12/viii/1994 (V782); Pietermaritzburg, Town Bush (29.565°S:30.345°E), A.C. van Bruggen, 09/i/1962 (W3675); ditto (29.565°S:30.345°E), mist-belt *Podocarpus* forest, D. Herbert, xi/1984 (V2149); ditto (29.565°S:30.345°E), H.C. Burnup & H.A. Wager, 29/viii/1908 (A7055); ditto (29.565°S:30.345°E), (A7054, A7058); Pietermaritzburg, S. slopes of Hogsback Mountain (29.55°S:30.35°E), 975–1036 m, beneath rock, C. Griswold & P. Croeser, 20/xi/1984 (V6543); Pietermaritzburg, mist-belt *Podocarpus* forest, among dead leaves, R. Kilburn & B. Lamoral, 6/x/1969 (V2147); Pietermaritzburg, Boschkop [locality not known], 16/xii/1921 (A7062); Pietermaritzburg, Hilton Road (29.583°S:30.330°E) (A7059); Pietermaritzburg (A7057, 1490); Pietermaritzburg and Hilton, H. Burnup (BMNH 1937.12.30.1328–29); Bulwer area, 3 km to north (29.78160°S:29.77577°E), ~1500 m, highly disturbed montane *Podocarpus* forest beside stream, in leaf-litter, A. Moussalli, 06/xii/2003 (W1490).

Distribution (Fig. 38): Traditionally considered to be endemic to the escarpment northwest of Pietermaritzburg, but a juvenile, identified on the basis of DNA, has recently been collected in the Bulwer area, suggesting a wider distribution in the central KwaZulu-Natal Midlands (cf. *N. inhluzana*); occurs at altitudes of 1000–1500 m.

Habitat: Known only from southern mist-belt forest; in leaf-litter and under logs; very local and generally scarce except in Ferncliffe Nature Reserve, Pietermaritzburg where it is patchily common.

Notes: Connolly (1939) described the shell of *Natalina quekettiana* as being 'golden brown above and greenish yellow beneath', but whilst this is true of empty shells, particularly older museum specimens, it does not describe the shell coloration of living animals, in which the apical surface is substantially darker brown. In terms of its rather distinctly bicoloured shell, dark head-foot colour, and yellowish mantle and pedal margin, topotypic *N. q. quekettiana* resembles *N. q. lucaris*. That subspecies, however, attains a larger size and its radula has only six pairs of lateral teeth per transverse row. In terms of its size, *N. q. quekettiana* is more similar to the montane taxa in the *N. quekettiana* complex, but differs from these in that the shell periphery generally lies below mid-
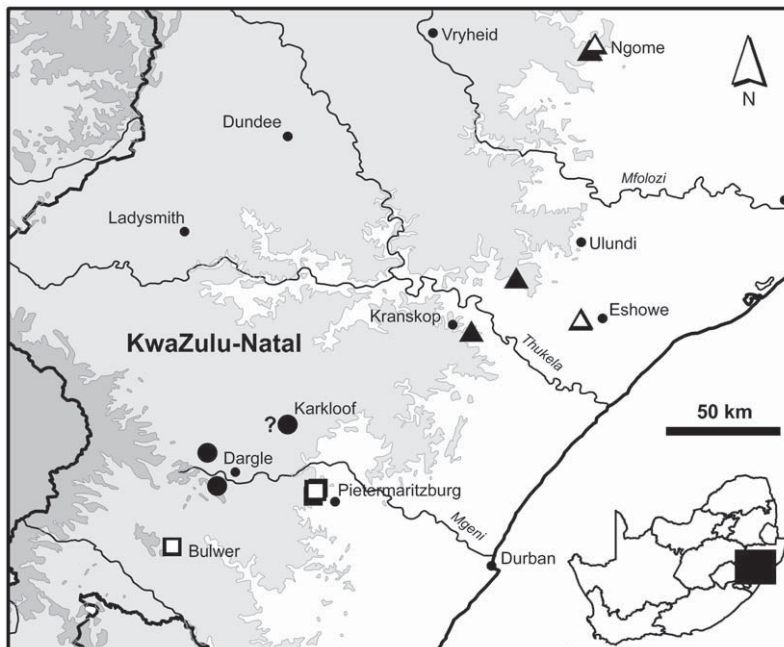
Fig. 38. Distribution of *Natalina quekettiana quekettiana* (Melvill & Ponsonby, 1893) (squares), *N. q. lucaris* subsp. n. (triangles) and *Natalina inhluzana* (Melvill & Ponsonby, 1894) (circles). Symbols with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

whorl, the last whorl is more strongly descendant prior to the aperture, the umbilicus a little wider and the base somewhat smoother. However, given that the montane taxa are all known from relatively few specimens and even fewer adult individuals, the reliability of these characters as species discriminators is not proven. As discussed above, the evidence for these taxa being distinct derives primarily from molecular data. *N. reenenensis*, for which we have no molecular data, is typically greener, but information on the colour of fresh or living shells is wanting. Its radula possesses only five pairs of lateral teeth per transverse row. We believe that *N. inhluzana* (Melvill & Ponsonby, 1894) will prove to be a synonym of *N. q. quekettiana* (see below).

Conservation: *Natalina q. quekettiana* was previously thought to occur only in the Pietermaritzburg area, but the data now available indicates that its distribution is more extensive, particularly if *N. inhluzana* (see below) is indeed a synonym. Nonetheless, given that the indigenous forests of the KwaZulu-Natal Midlands are some of the malacologically most well-known habitats in South Africa, the number of records for both *N. q. quekettiana* and *N. inhluzana* is surprisingly small. Despite targeted sampling, very few shells and only one living example have been found in recent years outside the Pietermaritzburg area. Notable is the absence of recent records from forests in the Karkloof region, the most extensive mist-belt forest complex in the KwaZulu-Natal Midlands. At present, the only locality at which the species can be described as common (albeit patchily so) is the Ferncliffe Nature Reserve, north-west of Pietermaritzburg. Whether this is due to a favourable edaphic characteristic of this locality (?doleritic

soils) is not known, but it is clear that this municipal reserve should be considered the most important site for the conservation of this snail. As such it should be afforded a high conservation status.

Natalina quekettiana lucaris subsp. n.

Figs 10E, 11C, D, 12C, 14F, 35B, 38–40

Etymology: From Latin *lucus* (a sacred grove or forest); in reference to the many traditionally sacred sites within the forests of central and southern Zululand, in particular Ngome and Nkandla Forests.

Identification (Fig. 39): For general description see *N. q. quekettiana* above. Attains a larger size than any of the other taxa in the *N. quekettiana* complex (adult diameter >35 mm); spire frequently also more elevated and periphery close to mid-whorl; axial riblets usually remaining distinct on base, but not always so; radula with six pairs of lateral teeth per transverse row.

As in *N. q. quekettiana*, fresh specimens have a darker brown apical surface and frequently a distinctly greenish base, but the contrast fades to a less intense yellowish brown and olive-green with time.

Dimensions: Holotype: diameter 38.4 mm, height 27.1 mm; largest specimen (W1114/T2562, Nkandla Forest), diameter 43.0 mm; H:D of adults 0.58–0.71 (N=11).

Living animal (Fig. 35B): Head-foot dark grey-black dorsally, sides of foot paler; neck region lacking paler, dorsolateral, longitudinal stripes; tentacles dark grey-black; margin of foot fringed with yellow or orange-yellow, mantle edge bright sulphur-yellow to orange; lung wall usually heavily mottled with dots and anastomosing blotches of black pigmentation.
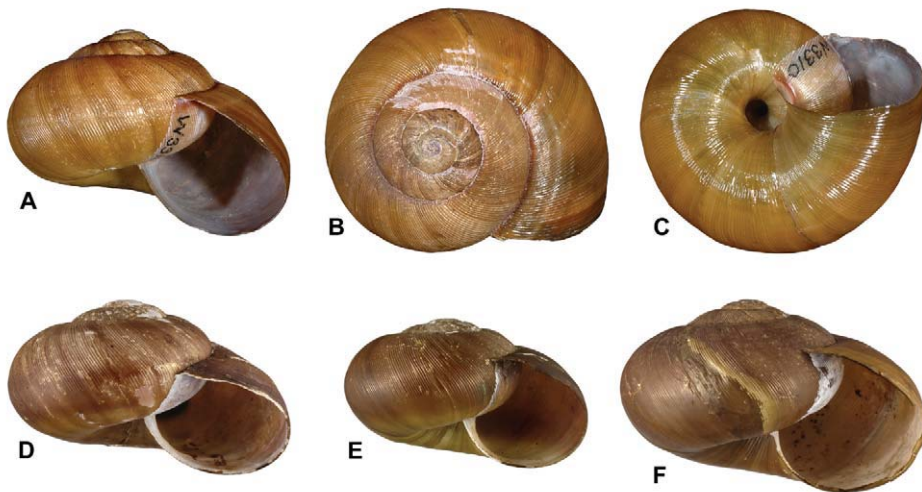

Fig. 39. *Natalina quekettiana lucaris* subsp. n. (all NMSA): (A–C) holotype (W3310/T2557), diameter 38.4 mm; (D) paratype, Ngome Forest (W3305/T2559), diameter 37.5 mm; (E) subadult paratype, Ngome Forest (W3305/T2559), diameter 34.9 mm; (F) largest paratype, Nkandla Forest (W1114/T2562), diameter 43.0 mm.
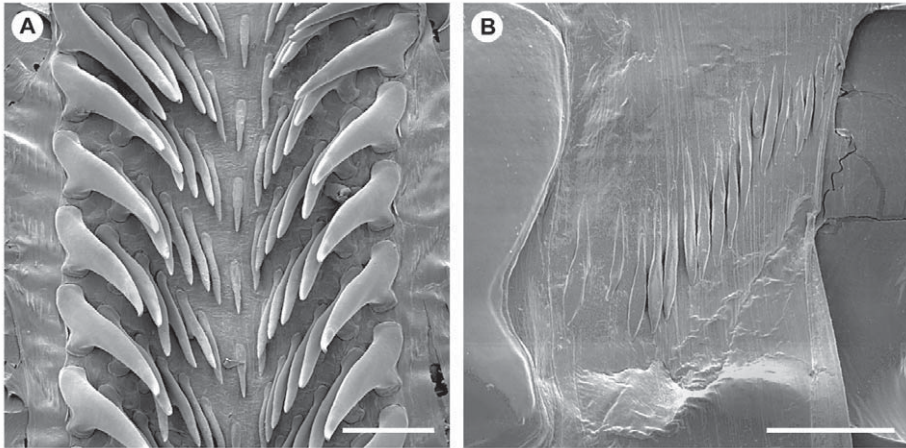
Fig. 40. *Natalina quekettiana lucaris* subsp. n., radula (paratype, NMSA W3305/T2559): (A) rachidian and lateral teeth, scale bar = 0.5 mm; (B) vestigial marginal teeth, scale bar = 100 µm.

Radula (Fig. 40): Like that of *Natalina q. quekettiana*, but with fewer transverse rows and only six lateral teeth per half row; formula 1+6+(17–20) (N=6, one in BMNH, Piele coll.); length up to 34 mm, with 49–66 broadly V-shaped transverse rows of teeth.

Distal genitalia: As for *Natalina q. quekettiana*.

Spermatophore (Figs 12C, 14F): Described and illustrated above in discussion of generic characters.

Holotype (Figs 39A–C): SOUTH AFRICA: *KZN*: Entumeni Nat. Res., (28.88836°S:31.38007°E), 620 m, scarp forest, under log, A. Moussalli & D. Stuart-Fox, 24/xii/2003 (NMSA W3310/T2557).

Paratypes: SOUTH AFRICA: *KZN*: Ngome Forest (27.827°S:31.415°E), 1200 m, mist-belt *Podocarpus* forest, dead under log near camp site, D. Herbert, 19/i/1995 (NMSA V657/T2560, 1 specimen); Ngome Forest, Ntendeka wilderness area (27.80177°S:31.43765°E), 1100 m, mist-belt forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 08/i/2004 (BMNH 20100125, 1 specimen; NMSA W3128/T2566, 3 specimens; W3305/T2559, 5 specimens; W3306/T2564, 2 juvenile specimens); Ngome Forest (27.8281°S:31.4190°E), 1110 m, mist-belt section of forest, mostly under logs, D. Herbert, 14/xii/1995 (NMSA V2249/T2563, 6 specimens); Nkandla Forest Res., Chibini area (28.7227°S:31.1282°E), 1200 m, mist-belt forest, under logs and in leaf-litter, D. Herbert, M. Bursey & T. Nangammbi, 20/x/2003 (NMSA W1114/T2562, 2 specimens); same data as holotype (NMSA W6854/T2558, 1 specimen; W3317/T2565, 2 juvenile specimens); Entumeni Nat. Res. (28.883°S:31.383°E), 700 m, scarp forest, in leaf-litter, O. Bourquin, vii/1981 (NMSA B5290/T2561, 1 specimen); Entumeni Nat. Res. (28.88583°S:31.37944°E), 663 m, scarp forest, in leaf-litter at base of large tree between forestry office and picnic site, M. & K. Cole, 13/i/2010 (ELM D16217/T027, 1 specimen); Kranskop, Zimbaba Bush (28.9328°S:30.9510°E), 1100 m, 1922 (NMSA A7060/T2568, 1 juvenile specimen; A7061/T2567, 2 juvenile specimens; A7135/T2569, 1 specimen).

Distribution (Fig. 38): Known primarily from the interior of Zululand (Ngome, Nkandla and Entumeni forests), but extending across the Thukela River valley to the Kranskop area; occurs at altitudes of 600–1200 m.

Habitat: Restricted to Afrotemperate and scarp forest; in leaf-litter and under logs; evidently scarce.

Notes: Molecular data indicate this subspecies to be the sister taxon of the nominotypical subspecies (Moussalli *et al.* 2009), which it resembles in terms of the bicoloured shell pattern in living specimens and the very dark head-foot coloration. It differs in attaining

a considerably larger size and in having only six lateral teeth per half row in the radula, compared to 8 or 9 in *N. q. quekettiana*.

Some variation in coloration, possibly geographical, is evident. Specimens from Ngome Forest have a distinctly bicoloured shell with a dark brown apical surface, whereas in those from Entumeni Forest the shell is less strongly bicoloured, with a chestnut to tan apical surface, and the mantle edge and pedal margin are orangish rather than bright yellow.

Conservation: The known extent of occurrence of *N. q. lucaris* is approx. 2500 km^2, but within this range its distribution is limited to islands of mist-belt and scarp forest. The forests from which it has been recorded include some of the largest such habitats remaining in KwaZulu-Natal (>2750 ha), and it is likely also to occur in Qudeni Forest, another large but very poorly sampled forest. These forests are in some cases formally protected, but the level of protection is variable and its efficacy is not guaranteed. Owing to their remote location in underdeveloped areas, the forests are subject to on-going anthropogenic pressure in the form of subsistence harvesting of forest products, grazing and trampling by livestock, and peripheral encroachment by small-scale agriculture.

Natalina quekettiana dracomontana subsp. n.

Figs 35C, D, 41–43

Etymology: From Latin *draco* (a dragon) and *mons* (a mountain); in reference to the Drakensberg.

Identification (Fig. 41): For general description see *Natalina q. quekettiana* above. The limited material available indicates this subspecies to vary considerably in shell
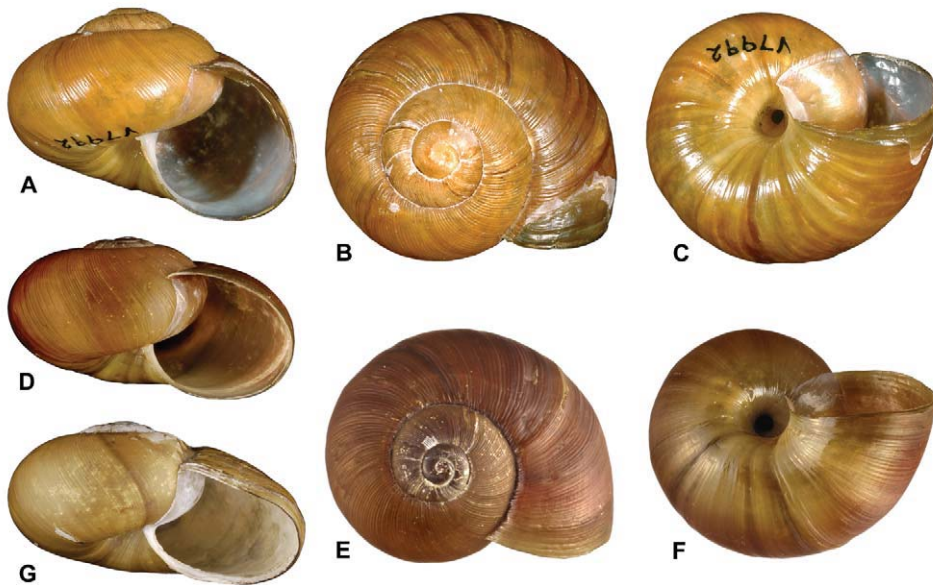

Fig. 41. *Natalina quekettiana dracomontana* subsp. n. (all NMSA): (A–C) holotype, diameter 27.2 mm (V7992/T2451); (D–F) paratype (subadult), recently live-collected, Monk's Cowl, diameter 26.4 mm (W4101/T2452); (G) depressed specimen, collected as empty shell, Monk's Cowl, diameter 30.2 mm (W4093/T2453).

proportions and colour, but there appear to be no clear-cut morphological characters that serve to reliably distinguish it from other subspecies within the *N. quekettiana* complex, except *N. q. lucaris* and *N. reenenesis* which have fewer pairs of lateral teeth per transverse row in the radula (but see also observations on epiphallus).

Dimensions: Holotype: diameter 27.2 mm, height 19.5 mm; largest specimen (NMSA W4093/T2453, Monks Cowl), diameter 30.2 mm; H:D including some slightly subadult specimens 0.55–0.72 (N=5) (0.55 in single available adult).

Living animal (information available for only two animals) (Figs 35C, D): Dorsal region of head-foot dark grey-brown to charcoal-grey, lacking paler longitudinal stripes on neck; tentacles of similar colour; sides of foot paler; mantle edge pale buff-brown or yellow, if yellow then pedal margin also yellow (Fig. 35D); lung wall without large black blotches, pigmentation mostly fine and tracking blood vessels, particularly to right of pulmonary vein.

Radula (Fig. 42): Formula 1+(7–8)+(12–19) (N=2); length up to 28.5 mm, with up to 70 V-shaped rows of teeth.

Distal genitalia: Epiphallus like that of *N. q. quekettiana*, but in both of the two mature specimens available there was a small bulla on the outer side of the epiphallus, just above its junction with the vas deferens. Internally the bulla possessed a short diverticulum of the main epiphallus lumen, suggesting that the spermatophore may possess a thumb-like or finger-like process on the tail region (cf. *N. beyrichi* and *N. cafra eumacta*).

Spermatophore: Unknown, but epiphallus structure suggests that as in other subspecies of *N. quekettiana*, the anterior two-thirds will bear well-developed scale-like spines. The possibility of an additional process on the tail (see previous paragraph), however, is something not so far evident in other subspecies within this complex.

Holotype (Figs 41A–C): SOUTH AFRICA: *KZN*: Injasuthi, central Drakensberg, (29.1417°S:29.4250°E), 1600 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 8/xii/1998 (NMSA V7992/T2451).

Paratypes: SOUTH AFRICA: *KZN*: Monk's Cowl area, forest below Sterkspruit Falls (29.03762°S: 29.40632°E), altitude 1350 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, Earthwatch, 15/iii/2006 (NMSA W4093/T2453, 2 specimens); ditto, forest below Sterkspruit Falls (29.03414°S:29.40685°E), 1420 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, Earthwatch, 15/iii/2006 (NMSA W4101/
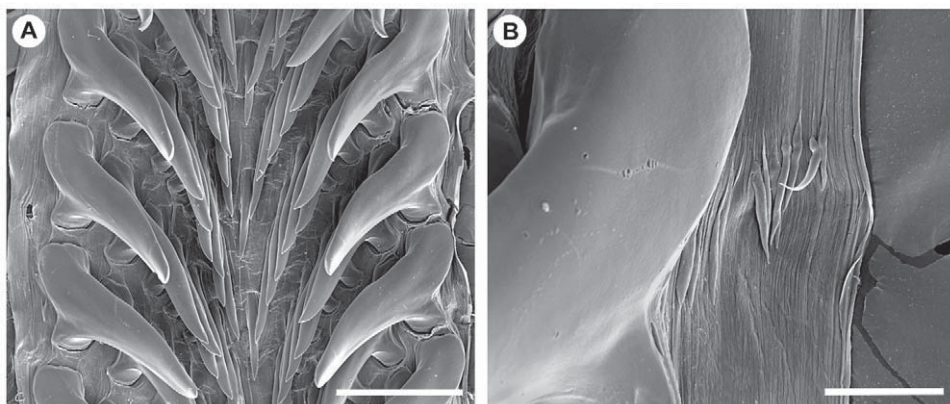

Fig. 42. *Natalina quekettiana dracomontana* subsp. n., radula, holotype (NMSA V7992/T2451): (A) rachidian and lateral teeth, scale bar = 0.5 mm; (B) vestigial marginal teeth, scale bar = 100 μm.

T2452, 1 specimen); Cathkin Peak area (29.037°S:29.388°E), Falcon coll'n (NMSA A7056/T2454, 3 specimens).

Other material examined: SOUTH AFRICA: *KZN*: Monk's Cowl area (29.03707°S:29.38753°E), 1650 m, indigenous forest, in leaf-litter, M. Hamer *et al.*, 09/iv/2006 (NMSA W5097).

Distribution (Fig. 43): Confirmed records only from the Mdedelelo [Cathkin Peak] and Injasuthi areas in the central KwaZulu-Natal Drakensberg; occurs at altitudes of 1350–1650 m.

Habitat: Afrotemperate forest, in leaf-litter; evidently rare.

Notes: We describe this as a new taxon primarily on the grounds of molecular data (Moussalli *et al.* 2009) which indicate it to represent a distinct lineage that is sister to the clade comprising *N. q. quekettiana* and *N. q. lucaris*. It shares with these taxa the distinctive bicoloured shell (living and fresh shells only), and in some individuals, the yellow mantle edge and pedal margin. Nearly all the material available is subadult and the aperture thus perhaps less oblique (more circular) than it would be at adulthood. In addition, there is also an indication of a difference in epiphallus structure, namely the presence of an epiphallus bulla, but this observation is based on only two specimens. Given that this character appears variable in *N. c. eumacta* and *N. c. natalensis*, its taxonomic significance must be interpreted with caution.

Conservation: The distribution of *N. q. dracomontana* is evidently somewhat greater than that of *N. q. montistempli*, but the available records suggest that its range is nonetheless very limited. It occurs in a formally conserved region (the uKhahlamba Drakensberg
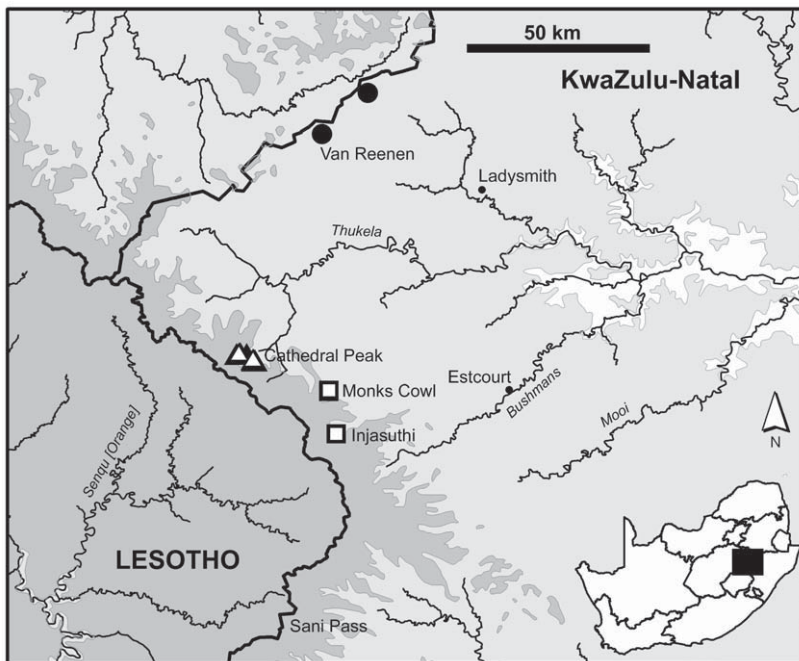

Fig. 43. Distribution of *Natalina quekettiana dracomontana* subsp. n. (squares), *N. q. montistempli* subsp. n. (triangles) and *N. reenenensis* Connolly, 1939 (circles). Symbols with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

World Heritage Site), where disturbance is low and thus its habitat is afforded a high degree of protection. On-going management practices, however, need to ensure that the integrity of forest patches within the broader mosaic of Drakensberg ecosystems is maintained. Uncontrolled fires in the neighbouring grasslands are likely to represent the most significant threat.

Natalina quekettiana montistempli subsp. n.

Figs 35E, 43–45

Etymology: From Latin *mons* (a mountain) and *templum* (a temple); with reference to Cathedral Peak.

Identification (Fig. 44): For general description see *Natalina q. quekettiana* above. Although limited material is available it is evident that the shell of the living animal is paler and more uniformly coloured than in any of the other subspecies discussed above. The distinctive bicoloured pattern present in fresh, live-collected shells of the other subspecies is not evident in *N. q. montistempli*, in which the apical and basal surfaces are more or less the same colour even in fresh, live-collected shells (Figs 44A–C). In terms of the pale shell colour it resembles *N. reenenensis*, but in that taxon the radula has only five lateral teeth per half row, compared to eight in *N. q. montistempli* (acknowledging that for both taxa details of radula dentition are known for very few specimens).

Dimensions: Holotype (largest specimen), diameter 28.0 mm, height 14.4 mm; H:D of adults 0.51–0.62 (N=9).

Living animal (information available for only one animal) (Fig. 35E): Dorsal region of head-foot dark grey, lacking paler longitudinal stripes on neck; tentacles somewhat darker; sides of foot progressively paler toward pedal margin, the latter not distinctively coloured, whitish beneath shell; mantle edge very pale, almost white; lung wall with some rather diffuse black pigmentation, particularly associated with blood vessels, but not heavily blotched.

Radula (Fig. 45): Formula 1+8+(14–18) (N=4); length up to 20.4 mm, with up to 71 broadly V-shaped rows of teeth.

Distal genitalia: Epiphallus structure typical of *N. quekettiana*; a bulla is not evident.
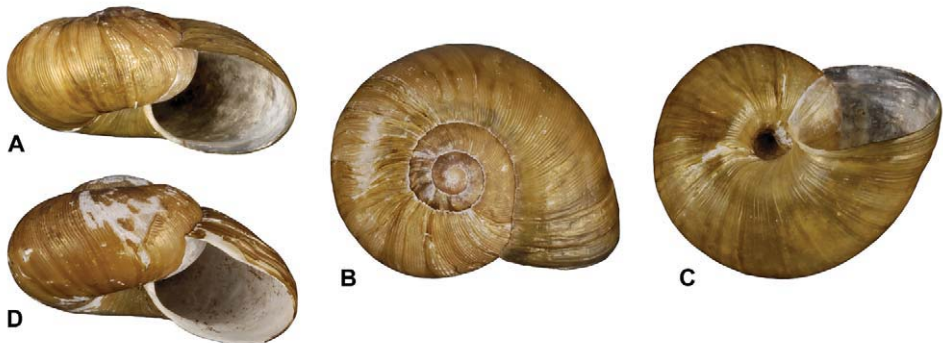

Fig. 44. *Natalina quekettiana montistempli* subsp. n.: (A–C) holotype, diameter 28.0 mm (NMSA W4084/T2422); (D) paratype from type locality, diameter 27.8 mm (NMSA W6653/T2428).
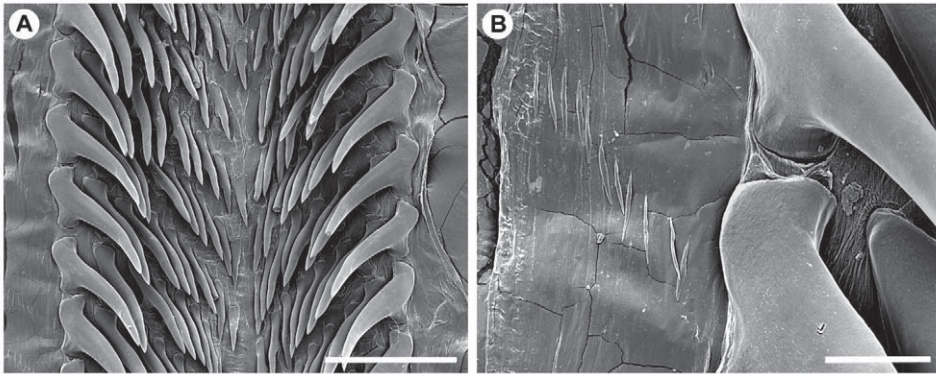
Fig. 45. *Natalina quekettiana montistempli* subsp. n., radula (holotype NMSA W4084/T2422): (A) rachidian and lateral teeth, scale bar = 0.5 mm; (B) vestigial marginal teeth, scale bar = 100 µm.

Spermatophore: Unknown. Epiphallus structure suggests that the anterior two-thirds will bear well-developed scale-like spines.

Holotype (Figs 44A–C): SOUTH AFRICA: *KZN*: Fern Forest (Oqalweni Forest), Cathedral Peak area, (28.94329°S:29.18580°E), 1531 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, Earthwatch, 19/iii/2006 (NMSA W4084/T2422).

Paratypes: SOUTH AFRICA: *KZN*: same data as holotype (NMSA W6653/T2428, 4 adults and 3 juveniles; W5095/T2449, 1 specimen); Cathedral Peak area, Oqalweni Forest (28.94265°S:29.18941°E), 1552 m, indigenous forest, in leaf-litter, M. Hamer *et al.*, 19/iii/2006 (NMSA W5093/T2448, 1 specimen); ditto, Oqalweni Forest (28.9422°S:29.1814°E), 1600 m, montane *Podocarpus* forest, in leaf-litter, A.C. & W.H. van Bruggen, 05/iv/1962 (NMSA B0044/T2447, 1 specimen); ditto, Rainbow Gorge (28.95813°S: 29.22070°E), 1550 m, montane *Podocarpus* forest, in leaf-litter, C. Uys, 06/i/2005 (NMSA W2605/T2446, 1 specimen; W4596/T2430, 4 specimens); ditto, Rainbow Gorge (28.96051°S:29.22455°E), 1518 m, indigenous forest, in leaf-litter, M. Hamer *et al.*, 12/iii/2006 (NMSA W5091/T2445, 2 specimens, crop contents included partially digested earthworms, *Proandricus* sp); ditto, Rainbow Gorge (28.96012°S: 29.22520°E), 1600 m, montane *Podocarpus* forest, in leaf-litter, C. Uys, 05/i/2005 (NMSA W2591/T2444, 1 specimen); ditto, Ndumeni Forest (28.961°S:29.222°E), 1550 m, under logs and rocks, C. Griswold, 22/ii/1984 (NMSA V7745/T2432, 1 specimen); ditto, Ndumeni Forest (28.961°S:29.224°E), 1550 m, under stone at foot of krantzes, A.C. & W.H. van Bruggen, 03/iv/1962 (NMSA V5205/T2431, 1 specimen); Cathedral Peak area, 1540 m, montane *Podocarpus* forest, R. Kilburn, 21/i/1984 (NMSA V2148/T2429, 1 specimen).

Distribution (Fig. 43): Known only from the Cathedral Peak area in the KZN Drakensberg; occurs at altitudes of 1500–1600 m.

Habitat: Afrotemperate forest, in leaf-litter.

Notes: As with *Natalina q. dracomontana*, we describe this material as a new taxon largely on account of molecular data (Moussalli *et al.* 2009) which indicate it to comprise a deeply divergent lineage within the *N. quekettiana* complex. However, although few adult specimens are available, there is also some evidence that the shell coloration is also distinctive.

This occurrence of a distinctive lineage of land snail in the Cathedral Peak area is mirrored by two achatinid species *Cochlitoma montistempli* (Bruggen, 1965) and *C. omissa* (Bruggen, 1965). It strongly suggests that this region of the Drakensberg has been subject to historical environmental conditions that have resulted in the long-term isolation and independent evolution of a distinctive and perhaps now relictual fauna of narrow-range endemics. Similar narrow-range endemism is found in the chameleon fauna of the Drakensberg (Tolley & Burger 2007) (see also biogeographic summary below).

Conservation: On account of its very limited distribution (known extent of occurrence is less than 3.0 km^2) *Natalina q. montistempli* is clearly a taxon of conservation concern. It occurs in a formally protected region (the uKhahlamba Drakensberg World Heritage Site) where disturbance is limited, but it is evident that the forests of the Cathedral Peak area harbour a fauna of particular interest and that they should be managed so as to keep disturbance to a minimum. Burning practices in the surrounding grasslands need to be particularly carefully managed.

Natalina inhluzana (Melvill & Ponsonby, 1894)

Figs 38, 46

Helix (*Dorcasia*) *inhluzana*: Melvill & Ponsonby 1894: 91, pl. 1, fig. 4. Type loc.: Inhluzan(i) Mountain
      [Nhlosane], Dargle, KwaZulu-Natal [Mrs Shaw].
Dorcasia inhluzana: Melvill & Ponsonby 1895: 165, pl. 12, fig. 6; Sturany 1898: 50.
Rhytida (*Afrorhytida*) *inhluziana* [*sic*]: Möllendorff 1903: 64, pl. 11, fig. 7.
Rhytida inhluzana: Melvill & Ponsonby 1907: 99.
Natalina inhluzana: Connolly 1912: 94; 1939: 109; Watson 1934: 158; Herbert & Kilburn 2004: 223.

Etymology: Named after Inhluzan(i) Mountain [Nhlosane], Dargle, KwaZulu-Natal, South Africa.

Identification: Very similar to *Natalina q. quekettiana*, differs only in being smaller (but has fewer whorls, 4.0–4.5 compared to 4.5–5.0) and in having slightly weaker axial sculpture on the apical surface. Largest specimen (lectotype), diameter 23.0 mm; H:D of adults 0.61–0.64 (N=4).

Radula and soft parts: Unknown.

Type material: Two specimens were mentioned in the original description, one in BMNH (1911.8.8.2) was designated lectotype by Connolly (1912: 94), diameter 23.0 mm, height 15.0 mm (Fig. 46). The paralectotype is in NMSA (2853/T592), diameter 22.4 mm, height 13.9 mm.

Additional material examined: SOUTH AFRICA: *KZN*: Inhluzana [Nhlosane] Mtn (29.55°S:29.93°E) (NMSA A7063, A7064, juveniles); Fort Nottingham, Tony Ker trail (29.41106°S:29.91512°E), 1575 m, mist-belt *Podocarpus* forest, D. Herbert & L. Davis, station 08–064, 18/xii/2008 (NMSA W6640); Karkloof, H. Burnup Coll'n (NMSA B0022).

Distribution (Fig. 38): Known only from the Nhlosane–Fort Nottingham region in the KwaZulu-Natal Midlands, and perhaps also the Karkloof area.

Habitat: Not specifically stated in original description or on specimen labels, but presumably mist-belt forest.

Notes: It seems probable that *N. inhluzana* is a synonym of *N. quekettiana quekettiana*. Although the type specimens of *N. inhluzana* have weaker axial sculpture than is typical

Fig. 46. *Natalina inhluzana* (Melvill & Ponsonby, 1894), lectotype of *Helix* (*Dorcasia*) *inhluzana* Melvill & Ponsonby, 1894 (BMNH 1911.8.8.2), diameter 23.0 mm.

of *N. q. quekettiana* from Pietermaritzburg, in other respects they very much resemble subadult specimens of the latter with 4.0–4.5 rather than 4.5–5.0 whorls. It is puzzling that neither Melvill and Ponsonby (1984) nor Connolly (1939) offered any comparison between *N. inhluzan*a and *N. quekettiana*, particularly considering the relative proximity of their type localities (approx. 40 km apart). Fresh material and DNA sequence data are needed before a more conclusive assessment of the validity of this taxon can be made. However, despite repeated attempts to obtain living material from the type locality, none has been found. The remaining forest habitats on the Nhlosane Mountain and its southerly spur are now of very limited extent and considerably degraded as a result of alien plant invasion, trampling by cattle and subsistence harvesting of forest products. It is likely that the species is now extinct at the type locality, but attempts to find it in more well-preserved and more extensive forest fragments in the broader Dargle–Nottingham Road area are on-going.

Somewhat worn shells closely resembling the holotype are present in the Natal Museum, with the locality given simply as 'Karkloof'. Although the Karkloof area is extensive and the locality data thus imprecise, it suggests that the species may occur more widely in this part of the central KwaZulu-Natal Midlands. Likewise, molecular data from an otherwise indeterminate juvenile from Bulwer (Moussalli *et al.* 2009) revealed it to be close to *N. quekettiana* from the type locality (see above), suggesting that this too is more widely distributed in the central KwaZulu-Natal Midlands than was previously thought. The possibility that there is a single species, varying somewhat in size and strength of sculpture, occurring in the mist-belt and lower altitude montane *Podocarpus* forests of the central KwaZulu-Natal Midlands seems likely.

Conservation: If genuinely a distinct species, *Natalina inhluzana* would undoubtedly qualify for ranking as a threatened species. However, since there is insufficient data on the taxonomic validity of the species, an evaluation of its threat status cannot be made at present (but see comments concerning *N. q. quekettiana* above).

Natalina reenenensis Connolly, 1939

Figs 43, 47

Natalina reenenensis: Connolly 1939: 108, pl. 2, figs 5–8. Type loc.: Van Reenen, KwaZulu-Natal [Burnup]; Herbert & Kilburn 2004: 223.

Etymology: Named after the type locality, Van Reenen, KwaZulu-Natal, South Africa.

Identification: Closely resembles subspecies within the *Natalina quekettiana* complex; attains a slightly larger size than all except *N. q. lucaris*; typically has a relatively low profile (H:D<0.60), a more narrowly entering umbilicus and the radula has fewer lateral teeth per transverse row (five pairs).

Description (Fig. 47): Shell lenticular, spire generally low; adult shell comprising up to 4.5 whorls, the last descending slightly prior to aperture in adults; periphery evenly rounded, at or near mid-whorl; suture above mid-whorl; apical surface microscopically sculptured by extremely fine spiral lineation, producing lustreless, silky sheen which continues on to base, only becoming glossy near umbilicus. Protoconch/teleoconch junction generally ill-defined; protoconch ±5.0 mm in diameter, apical portion initially almost smooth, becoming plicate at suture and thereafter with distinct, close-set, axial riblets extending from suture to suture. Axial riblets continue on teleoconch but become

more uneven on last half whorl; riblets weaken at periphery, the base generally sculptured only by growth-lines and traces of spiral striae; riblets re-appear in umbilicus; aperture suboval, slightly obliquely descending outwards; outer lip of adult a little thickened, particularly where columella and basal lips merge, but sometimes throughout in gerontic specimens, thin and with membranous periostracal fringe in subadults; upper part of columella lip weakly reflected; umbilicus of moderate width, but narrowing relatively quickly internally, not obscured by reflected columella lip.

Periostracum of museum specimens straw-yellow to light olive-green with darker axial bands in a slightly deeper shade; base not appreciably paler than apical surface. One fresher, but damaged shell recently collected near type locality with a distinctly browner coloration.

Dimensions: Largest specimen (NMSA W4689), diameter 32.4 mm; H:D of adults 0.53–0.59 (N=11).

Living animal: No data available.

Radula: Like that of *N. quekettiana*, but with fewer lateral teeth; formula 1+5+?16 (radula slide prepared by A.J. Peile in NMSA); length 22.3 mm, with 69 broadly V-shaped rows of teeth. Another radula slide in BMNH (Gwatkin) has the same formula.

Type material: Holotype in BMNH (1937.12.30.1307–8) [2 specimens, holotype undamaged and with red dot], diameter 30.3 mm (31 mm *fide* Connolly 1939), height 17.5 mm (Figs 47A–C); paratypes in NMSA, same data as holotype, dated iii/1918 (V2010/T1356, 8 specimens; V2009/T1355, 3 specimens).

Additional material examined: SOUTH AFRICA: *KZN*: De Beers farm, approx. 15 km NE of Van Reenen (28.30403°S:29.50240°E), 1841 m, afrotemperate forest, dead in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Cunningham, 10/ix/2006 (NMSA W4689).

Distribution (Fig. 43): Known only from the Drakensberg escarpment in the Van Reenen area, north-western KwaZulu-Natal.

Habitat: No details recorded with original specimens, but presumably found in Afrotemperate forest, *ca* 1500–1800 m; evidently scarce.
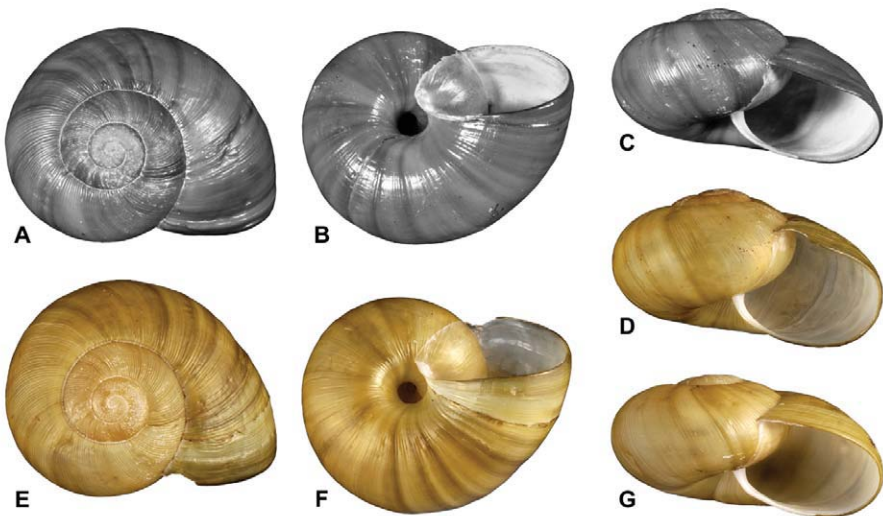

Fig. 47. *Natalina reenenensis* Connolly, 1939: (A–C) holotype (BMNH 1937.12.30.1307–8), diameter 30.3 mm; (D–F) paratype (NMSA V2010/T1356), diameter 30.5 mm; (G) paratype, depressed specimen (NMSA V2010/T1356), diameter 29.3 mm.

Notes: In the original description, Connolly (1939) compared this species with *Natalina kraussi* (now in *Afrorhytida*) noting that it was larger and of a much greener colour. Surprisingly, he did not compare his new taxon with *N. quekettiana*, with which it is much more similar. In reality the material available, even though old and thus faded, is not noticeably greener than some specimens of *N. quekettiana* of a similar age. The fading of shells which may be rich chestnut-brown when alive to a paler olive-green with advancing time seems a general phenomenon in these snails. Even though Connolly's original description mentioned the green colour, an old label in paratype lot NMSAV2009/T1355 states 'live, Mar. 1918'. The shells were thus already around 20 years old when Connolly drew up the description. The green colour must thus be viewed with caution, for it is neither distinctive of dead shells of the species, nor is it likely to reflect shell colour in the living animal. A badly broken but recently collected shell was of a much browner hue.

Natalina reenenensis almost certainly belongs within the *N. quekettiana* clade, but DNA sequence data are needed to confirm this. Although little material is available, the species seems to differ in having a relatively narrow, slightly eccentric umbilicus and the lustreless sheen of the apical surface extends well below the periphery, and only the peri-umbilical region is glossy. In *Natalina q. quekettiana* the periphery is often less evenly rounded and displaced slightly towards the base, the spire usually taller (H:D 0.58–0.68 compared with <0.60), and the umbilicus is noticeably wider. *Natalina q. montistempli* is perhaps the most similar taxon, but like all the other subspecies of *N. quekettiana*, it has more than five pairs of lateral teeth per transverse row. More definitive comment on this species must await the collection of additional living specimens.

Distribution data suggest the existence of a genuine hiatus between the populations of *N. reenenensis* and those of the geographically closest subspecies in the *N. quekettiana* complex, *N. q. montistempli*. Despite extensive sampling in the intervening forests of the Royal Natal National Park (Bruggen, Hamer, Herbert and Moussalli), no *Natalina* specimens have been found there.

Conservation: *Natalina reenenensis* is evidently both rare and of limited distribution. Only one damaged shell has been found since the original description. The original sample collected by Henry Burnup evidently contained over a dozen live-taken specimens, suggesting that the species was common, but this was perhaps a very local phenomenon. With a known distribution including only two localities and covering only a 15 km length of the escarpment edge in north-western KwaZulu-Natal, the species would certainly qualify for listing as a threatened species. The extent of its habitat has declined historically and its quality remains threatened, particularly by veld fires encroaching from the neighbouring grasslands. However, this region of the Drakensberg escarpment is not well-sampled and a more meaningful assessment of the conservation status of *N. reenenensis* must await further survey work.

Subgenus **Tongalina** subgen. n.

Type species: *Helix cafra wesseliana* Kobelt, 1876.

Etymology: With reference to Tongaland, the territory historically encompassing southern Mozambique and northern KwaZulu-Natal.

Diagnosis: Skin texture in neck region coarse; genital pore situated high on neck and well posterior to right optic tentacle; left body lobe of mantle hypertrophied, divided into two lobes, but these confluent, separated only by a sinuous discontinuity.

Notes: *Natalina* (*Tongalina*) is monotypic, the only known species being *N. wesseliana*. In terms of shell morphology it is very close to the larger species of *Natalina s.s.* and indeed *N. wesseliana* was initially described merely as a variety of *N. cafra*. Several character states of the soft parts (see diagnosis), however, differ markedly from those found in *Natalina s.s.* indicating not only that it is a distinct species, but that it represents a highly divergent lineage of its own. This is supported by molecular data which place it as a basally divergent taxon within *Natalina*.

   Natalina (*Tongalina*) *wesseliana* occurs at low altitudes (<700 m) in north-eastern KwaZulu-Natal and southern Mozambique. The distributional data available to date indicate that its range does not overlap with any other species of *Natalina*.

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Natalina (*Tongalina*) *wesseliana* (Kobelt, 1876)

Figs 6D, 10F, 11E, F, 48–52

</div>

Helix cafra var. *wesseliana*: Kobelt 1876: 149, pl. 5, fig. 1; Pfeiffer 1877: 558. Type loc.: not originally specified, but given as 'South Africa (*fide* Kobelt)' by Connolly (1939); label with holotype states 'Natal'.
Aerope caffra [*sic*] var. *wesselliana* [*sic*]: Tryon 1885: 131, pl. 25, fig. 14.
Natalina caffra [*sic*] var. *wesseliana*: Melvill & Ponsonby 1898: 170; Sturany 1898: 30; Möllendorff 1903: 21, pl. 3, fig. 8; Connolly 1912: 91.
Natalina wesseliana: Connolly 1925: 122; 1939: 107; Bruggen 1969: 58; Herbert & Kilburn 2004: 221.
Natalina (*Natalina*) *wesseliana*: Bruggen & Appleton 1977: 32.

Etymology: Perhaps named in honour of Marthinus Wessel Pretorius (1819–1901), president of the Transvaal Republic and the Orange Free State.
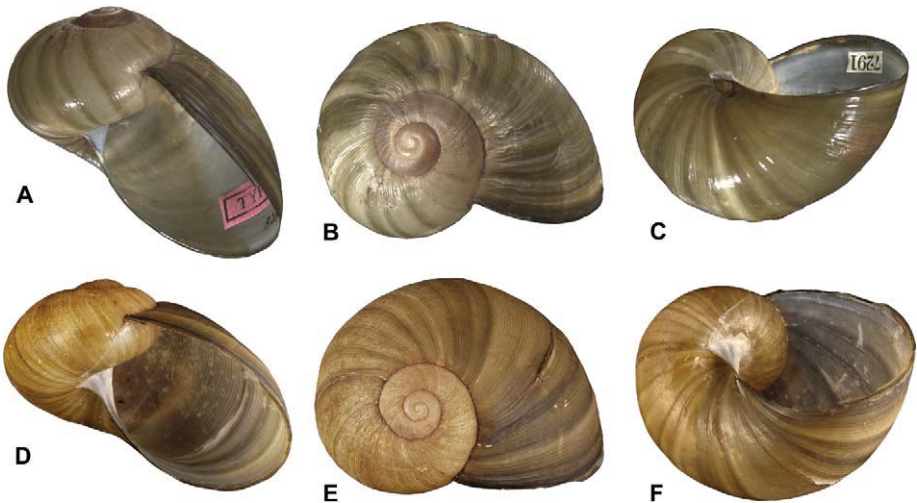

Fig. 48. *Natalina* (*Tongalina*) *wesseliana* (Kobelt, 1876): (A–C) holotype of *Helix cafra* var. *wesseliana* Kobelt, 1876 (SMFD 8287), diameter 46.0 mm (images courtesy of Ronald Janssen and Eike Neubert); (D–F) Bhanga Neck, Kosi Bay (NMSA D9888), diameter 57.2 mm.
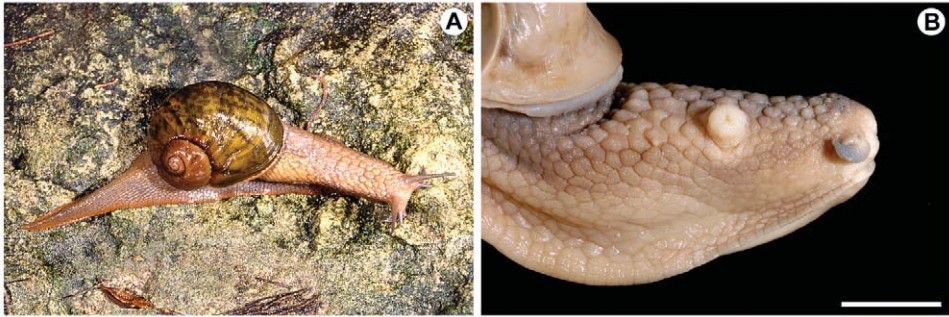
Fig. 49. *Natalina* (*Tongalina*) *wesseliana* (Kobelt, 1876): (A) living specimen, Cape Vidal (specimen not collected), extended length approx. 230 mm; (B) preserved specimen showing dorsal position of genital pore with penis partially everted (NMSA W5719), scale bar = 20 mm.

Identification: Shell characterised by its narrow umbilicus which is largely obscured by the reflected columella, and the rapidly expanding, somewhat auriform shell. May possibly be confused with *N. cafra natalensis* especially when juvenile, but the coarse skin texture of the neck of *N. wesseliana* and the position of its genital pore are distinctive, as is its northern, low altitude distribution.

Description (Fig. 48): Shell large to very large, thin and fragile; last adult whorl expanding rapidly and suture descending slightly towards aperture; sculptured by close-set axial riblets which sometimes extend on to base; protoconch diameter 7.0–8.5 mm, the axial riblets generally finer and more close set than in *Natalina s.s.*; umbilicus narrow, for the most part obscured by reflected columella lip; aperture ovate, large and drooping obliquely downwards (long axis of aperture strongly oblique); outer lip thin, membranous periostracal fringe well developed.

Periostracum olive-green to olive-brown with occasional darker radial bands, particularly just behind outer lip.

Dimensions: Largest specimen (NMSA 2118, 'Zululand'), diameter 69.0 mm. H:D of adults 0.70–0.88 (N=9).

Living animal (Fig. 49A): Head-foot brownish, tinged with orange at pedal margin; mantle edge hypertrophied, the left body lobe comprising two contiguous lobes separated by a sinuous discontinuity (Fig. 6D), orange; skin of neck region very coarsely textured with roundly conical projections, each often with a small pit in the centre; posterior region of foot extensive, flattened and pointed; genital pore situated high on neck, well posterior to right optic tentacle (Fig. 49B); lung wall variably marked with black pigmentation, usually with some diffuse spiral bands.

Radula (Fig. 50): Like that of *Natalina s.s.* species; formula 1+5+>20 (N=2); length up to 46 mm (but almost certainly longer in large specimens), with 56–60 broadly V-shaped transverse rows of teeth.

Distal genitalia: Essentially the same as in *Natalina s.s.* species, except for the position of the genital pore. The penis and epiphallus are strongly sinuous *in situ* and the papillation of wall of penis lumen has a zig-zag longitudinal orientation. Interior of epiphallus with 6–7 well-developed longitudinal ridges with finer second and third order intermediary ridges. A small bulla is evident on the epiphallus, close to its junction with the vas deferens.
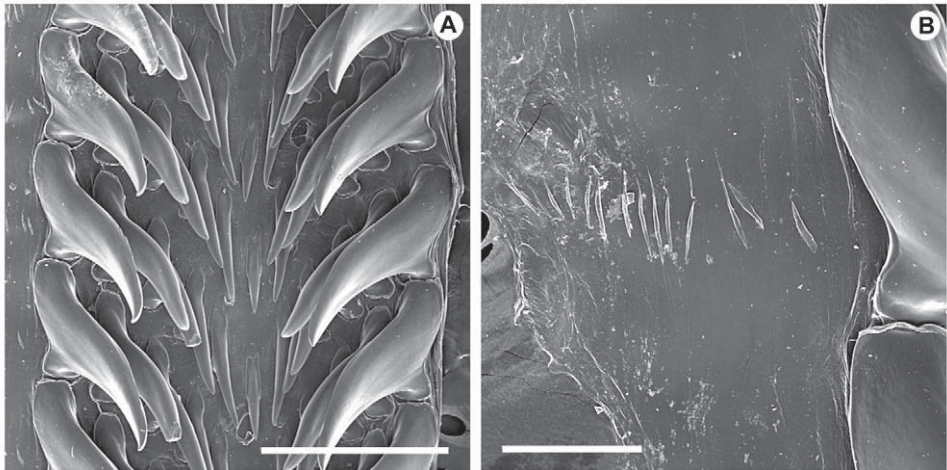
Fig. 50. *Natalina* (*Tongalina*) *wesseliana* (Kobelt, 1876), radula (NMSA V7668): (A) rachidian and lateral
teeth, scale bar = 1.0 mm; (B) vestigial marginal teeth, scale bar = 250 µm.

Spermatophore (Fig. 51): Well preserved allospermatophores from the oviduct caecum
of two specimens have been examined (NMSA V7668, W5719) collected in late
November and late December respectively. These resemble the spermatophores of the
larger *Natalina s. s.* species in bearing keel-like longitudinal ridges and lacking spines.
One spermatophore was particularly long (straightened length approx. 32 mm) and
slender (Fig. 51B), with a pronounced spiral twist; the other one similar but somewhat
less slender and not strongly twisted, though still distinctly curved. Spermatophore of
more or less uniform width for most of its length, tapering at both ends; 4 or 5 major
longitudinal ridges anteriorly, increasing to 6 or 7 in mid region, with occasional weaker
intermediaries; crests of major ridges themselves usually appearing bifid. Near sperma-
tophore head, inner surface of spiral bears a deep groove, which becomes progressively
broader and more shallow toward mid region, ending at subterminal vent. In one spe-
cimen, posterior portion of spermatophore asymmetrically T-shaped and obliquely
twisted relative to main shaft of spermatophore (Fig. 51C); vent situated at T-junction
and extending into arms, one of which comprises the strongly recurved tip of the tail
and the other a shorter, less strongly recurved thumb-like process. This posterior sperma-
tophore morphology also evident in the other example, but thumb-like process only
weakly developed.

In situ, the spermatophore head lay pressed against the extreme end of the oviduct
caecum and the posterior portion was situated such that the recurved tail extended into
the base of bursa copulatrix duct and the thumb-like process into the vagina. In this
position the vent lay immediately beneath the end of the free oviduct, and it seems
likely that the function of these posterior processes is to anchor the spermatophore in
place, once it is in the correct position.

Unusually, in specimen NMSA W5719 the caecum was distended and sack-like and
contained two spermatophores, one relatively fresh (situated as described above) and
the other partially degraded. In a third specimen (NMSA V7668) the caecum contained
three more extensively degraded spermatophores, each compacted into an oval mass.
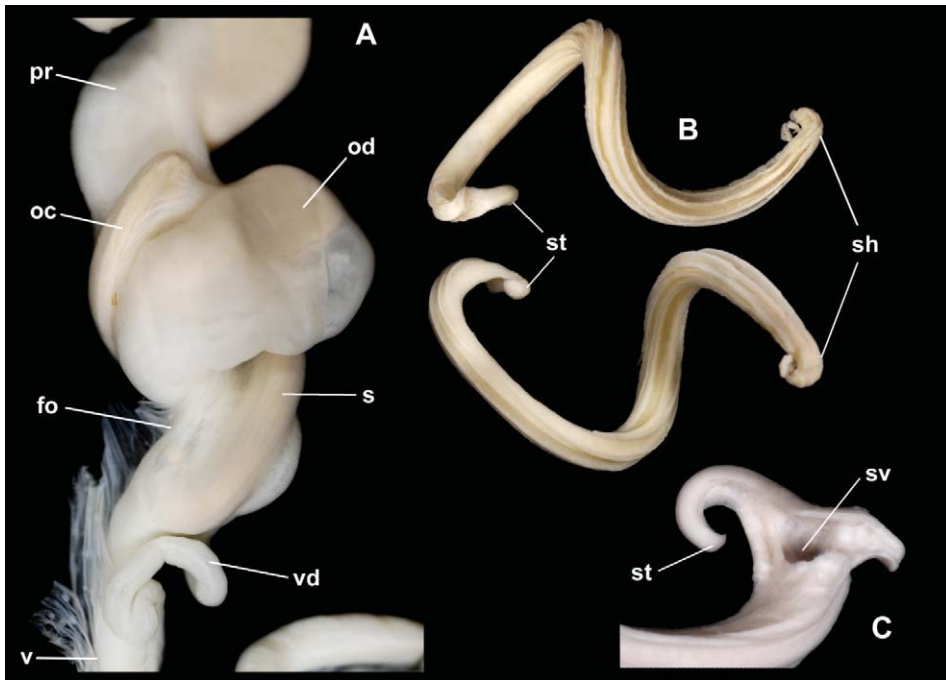
Fig. 51. *Natalina* (*Tongalina*) *wesseliana* (Kobelt, 1876), oviduct caecum and spermatophore (all NMSA): (A) spermatophore *in situ* in oviduct caecum (V7668); (B) two views of extracted spermatophore, straightened length 32 mm (V7668); (C) tail region of spermatophore (W5719). Abbreviations: fo – free oviduct, od – oviduct, oc – oviduct caecum, pr – prostate gland, s – spermatophore inside oviduct caecum, sh – spermatophore head, st – spermatophore tail, sv – spermatophore vent, v – vagina, vd – vas deferens.

Type material: Holotype of *Helix cafra* var. *wesseliana* Kobelt, 1876 (Figs 48A–C) in Senckenberg Museum (SMFD 8287), Natal, coll. Kobelt, *ex* Maltzan, 1878, diameter 46.0 mm, height 40.5 mm (*fide* Ronald Janssen).

Additional material examined (all NMSA unless otherwise indicated): MOZAMBIQUE: Praia do Xai-Xai camping grounds (25.11324°S:33.74019°E), 24 m, dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 27/xii/2006 (L7364); Maputo area, environs of Lagoa Ricatla [Rikatla] (25.767°S:32.617°E), H. Junod (BMNH 1937.12.30.1330–31); Ponta do Ouro (26.833°S:32.892°E), dune forest, in leaf-litter, M. Evans, x/2006 (L7491). SOUTH AFRICA: *KZN*: Kosi Bay (26.958°S:32.833°E), F. Toppin, 1906 (B0020); ditto (SAMC A34748); Kosi Bay (26.86922°S:32.88258°E), coastal dune forest, transect E, Symes, Lovell & Combrink, 21/x/2003 (W1430); Bhanga Neck (27.005°S:32.863°E), O. Bourquin, i/1965 (B0077); Bhanga Neck, behind visitors quarters (27.005°S:32.863°E), coastal dune thicket, R. Fregona, 12/vii/1987 (D9888); Lebombo Mts, Hlatikulu Nat. Res. (27.32466°S:31.98981°E), 647 m, scarp forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 29/xii/2007 (W5719); ditto (27.32622°S:31.99813°E), scarp forest, A. Moussalli & D. Stuart-Fox, 19/v/2003 (W4831); Mkhuze Game Res. [station MAxC], *Acacia xanthophloea* grove beside Msunduzi River (27.74705°S:32.28982°E), dead amongst plant debris around tree trunks [perhaps flood borne], Earthwatch Team 5, 23/xi/2003 (W1326); Makowe (27.967°S:32.117°E), J. Crosly (1489); Hluhluwe Game Res. (28.075°S:32.055°E), 400 m, scarp forest, in leaf-litter, Herbert, Seddon & Tattersfield, 30/xi/1998 (V7668); ditto, (28.077°S:32.045°E), 460 m, scarp forest, in leaf-litter, Herbert, Seddon & Tattersfield, 29/xi/1998 (V7684); ditto, Hilltops Camp walk (28.0830°S:32.0417°E), 400 m, scarp forest, D. Herbert, 01/vii/1996 (V3820); ditto, in forest between research station and perimeter fence (28.097°S:32.067°E), 460 m, scarp forest, in leaf-litter, D. Herbert, 15/i/1995 (V0573); St Lucia system: False Bay Park (27.95852°S: 32.35919°E), sand forest, in leaf-litter and under logs, Earthwatch Team 9, 15/i/2005 (W3060); ditto (27.96460°S:32.37869°E), closed woodland/forest on fossiliferous sediments beside lake, in leaf-litter and under logs, Earthwatch Team 8, 05/xi/2004 (W2447); ditto (27.969750°S:32.372615°E), sand forest, under dead log in leaf-litter, A. Armstrong *et al.*, 06/iii/2001 (V9188); ditto, Mpophomeni Trail (27.975°S:32.358°E),

30 m, woodland thicket and sand forest, D. Herbert, 03/i/1996 (V2166); Cape Vidal, Bhangazi Hill (28.123°S:32.555°E), 60–80 m, dune forest, in leaf-litter, specimen found eating *Cochlitoma vestita*, Herbert, Seddon & Tattersfield, 27/xi/1998 (V7976, V7980); ditto (28.130°S:32.547°E), 60–80 m, dune forest, in leaf-litter, Herbert, Seddon & Tattersfield, 27/xi/1998 (V7943); Eastern Shores forest walk (28.23°S:32.49°E), coastal lowland forest, under log, D. Herbert, 19/x/1997 (V5381). SWAZILAND: Ingwavuma Road (27.083°S:31.967°E), 275–370 m, A.C. & W.H. van Bruggen, 01/xi/1964 (B0096).

Observation records: SOUTH AFRICA: *KZN*: Sodwana Bay, forest beside Lake Mgobezeleni (27.53833°S: 32.66670°E), coastal forest, D. Herbert, 07/ii/2004; Cape Vidal, NPB camp site (28.13°S:32.55°E), ±20 m, dune forest and *Casuarina* mosaic, found crawling on track after rain, D. Herbert, 18/x/1997.

Additional literature records (material not seen): MOZAMBIQUE: Marracuene [Vila Luiza] (25.7369°S: 32.6764°E), P.H. Boshoff (Bruggen 1967: 28, specimen damaged, identification tentative, Bruggen *in lit*. v/2008). SOUTH AFRICA: *KZN*: Lake Sibaya environs (27.400°S:32.733°E), Appleton (Bruggen & Appleton 1977).

Distribution (Fig. 52): Central Zululand (Hluhluwe and Cape Vidal) north to the Limpopo R. in southern Mozambique (Xai-Xai), mostly near the coast. To date not recorded further inland than Hluhluwe Game Reserve and the Lebombo Mountains on the Maputaland−Swaziland border, reaching 650 m above sea level, but there are uncon-firmed records of large *Natalina* specimens from Mpumalanga (Nelspruit) which may belong to this species (Sirgel pers. comm.).

Habitat: Recorded from dune, coastal lowland and scarp forest, but may also occur in other well-wooded habitats; in leaf-litter and under logs; locally common. All localities lie within either the Indian Ocean Coastal Belt or the Lowveld Savannah bioregions of Mucina and Rutherford (2006).

Notes: The somewhat auriform and narrowly umbilicate shell of *Natalina wesseliana* is distinctive. It is currently known only to the north of the Mfolozi R. and is the only
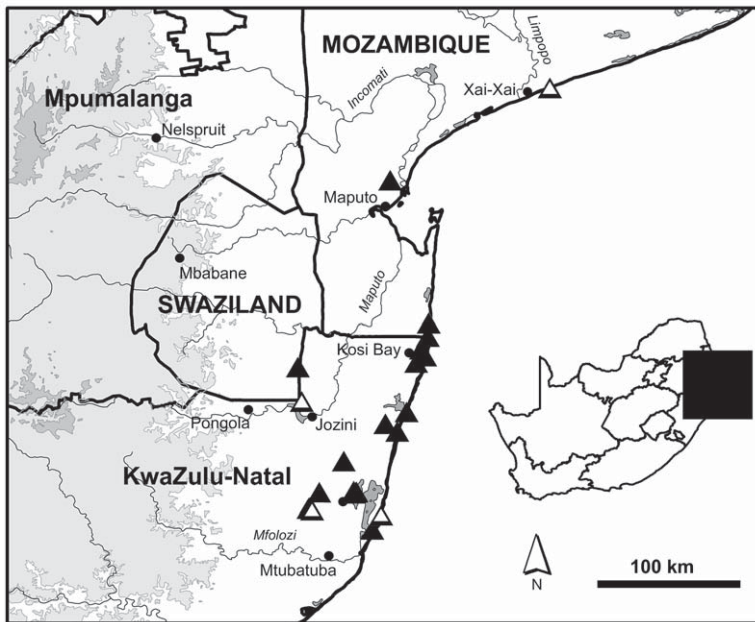

Fig. 52. Distribution of *Natalina* (*Tongalina*) *wesseliana* (Kobelt, 1876). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

Natalina species so far know from altitudes of less than 1000 m lying north of this river. The living animal is spectacular and the very coarse texture of the skin in the neck region is conspicuous. When actively crawling the animal is reluctant to retreat into its shell. It has been found feeding on *Cochlitoma vestita* (Pfeiffer, 1855) (Achatinidae) and a large individual was found with a specimen of the carnivorous slug *Chlamydephorus gibbonsi* Binney, 1879 (Chlamydephoridae) in its crop. The latter was cut into three almost completely detached fragments, which, given the considerable thickness and rigidity of the skin of chlamydephorid slugs, attests to the efficacy of the radula of large *Natalina* species.

Conservation: Listed as Vulnerable [B1+2bc] (IUCN 2010) on account of its limited distribution and the on-going threats to coastal forest habitats in south-east Africa. Fortunately, many of the South African localities at which it is known to occur are situated in formally protected areas, namely the iSimangaliso Wetland Park (World Heritage Site, formerly Greater St Lucia Wetland Park) and Hluhluwe Game Res., where it is not uncommon in dune and scarp forest habitats. However, north of Maputo in Mozambique, much of the indigenous vegetation in the coastal hinterland has been lost and only isolated fragments remain.

Genus *Afrorhytida* Möllendorff, 1903

Afrorhytida: Möllendorff 1903: 61. Type species: *Helix knysnaensis* Pfeiffer, 1846, by original designation.
Hyperrhytida Watson, 1934: 156. Type species: *Helix (Aerope) trimeni* Melvill & Ponsonby, 1892, by original designation.

Diagnosis: Shell of moderate size (adult diameter up to 31 mm), lenticular to globose, more or less uniformly yellowish or greenish brown, or brown, lacking spiral colour pattern; apical surface sculptured with close-set axial riblets, base smoother and more glossy; outer lip slightly thickened and without periostracal fringe; peristome interrupted in parietal region; umbilicus open, width narrow to moderate; protoconch of approx. 1.25 whorls, sculptured by axial riblets (sometimes weak), diameter 2.5–5.0 mm. Radula possessing rachidian tooth; outer lateral teeth conspicuously larger than marginal teeth; inner marginal teeth small but not vestigial. Labial palps present, but relatively small; left body lobe of mantle divided into two lobes, separated by a low ridge. Penis elongate and cylindrical, situated to left of retractor muscle of right optic tentacle; epiphallus well developed (approx. 50–75 % of penis length); epiphallus and lower vas deferens not joined to penis by connective tissue web; vagina long; oviduct caecum absent or little more than a small lateral pouch. Distal part of suprapedal gland sinuous but not convoluted, lacking a swollen terminal vesicle.

Radula (Figs 58, 64, 67, 71): Length up to 22.5 mm, with up to 85 V-shaped transverse rows of teeth, 3.2–4.5 rows per/mm in adult; formula varies considerably with species (Table 2); rachidian present, but small; inner lateral teeth slender and acuminate, increasing slightly in size; outer 2 or 3 laterals considerably larger, each with a stout quadrate base-plate and curved, sharply pointed cusp; marginal teeth either rapidly or gradually decreasing in size and becoming vestigial at radula margin, but always with 1 or 2 of intermediate size adjacent to outermost lateral tooth, more in *A. knysnaensis*.

The boundary between the lateral and marginal series is easy to determine in *Afrorhytida knysnaensis* where the largest tooth (the outermost lateral) has a stout, quadrate base-plate and is followed by a much smaller (0.5–0.66× length of largest

TABLE 2. *Afrorhytida* species, inter-specific variation in radula formula.

Species	Radula formula
Afrorhytida knysnaensis	1 + (7–10) + (>17)
Afrorhytida kraussi	1 + (11–15) + (11–16)
Afrorhytida burseyae	1 + (12–14) + (7–9)
Afrorhytida trimeni	1 + (13–14) + (6–9)

tooth) and far less robust tooth with a reduced base-plate (the innermost marginal). In the remaining species, however, the distinction is less clear and the largest tooth is followed by one which is only slightly smaller (0.75–0.9× length of largest tooth) and which retains a robust cusp and well-developed, quadrate base-plate. In this case, though it is not the largest tooth, we have included this latter tooth in the lateral series. For these species therefore, it is the penultimate lateral tooth that is the largest.

In *A. trimeni* and *A. burseyae* sp. n. the number of marginal teeth is usually less than 10 and there are more laterals than marginals. In *A. knysnaensis* and *A. kraussi* there are more than 10 marginals and they equal or outnumber the laterals.

External anatomy (Figs 6A, 55): Left body lobe of mantle divided into two relatively small lobes separated by a low ridge (Fig. 6A); skin texture moderately granular; neck region usually with a paler longitudinal line extending backward from the base of each optic tentacle, often bordered laterally by a darker line; labial palps present but relatively small; optic and inferior tentacles with a ventrally distended apical bulb; tail region of foot short; genital pore ventral and just posterior to right optic tentacle.
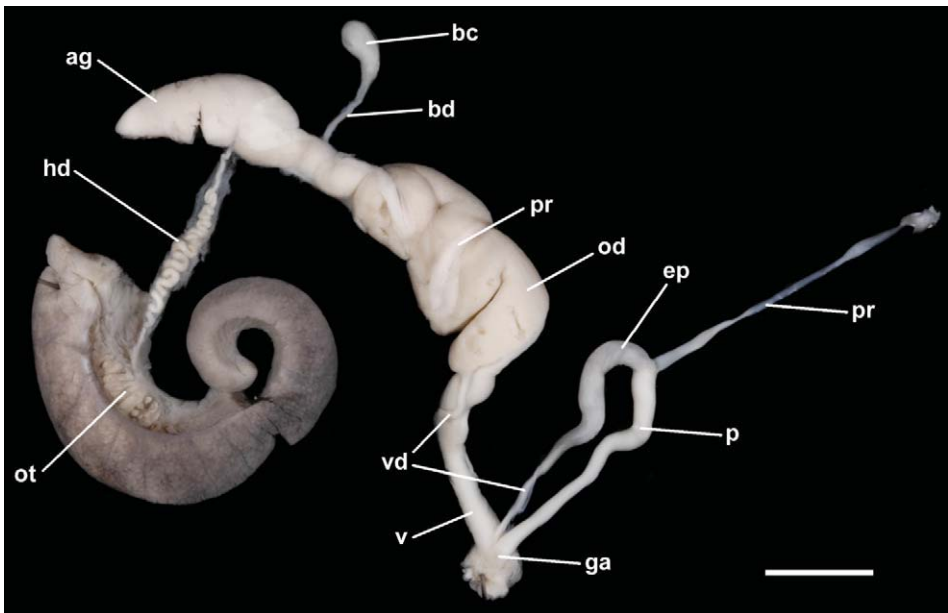

Fig. 53. *Afrorhytida knysnaensis* (Pfeiffer, 1846), reproductive tract (NMSA W4643), scale bar = 5.0 mm. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bd – bursa copulatrix duct, ep – epiphallus, ga – genital atrium, hd – hermaphrodite duct, od – oviduct, ot – ovotestis, p – penis, pr – prostate gland, pr – penial retractor muscle, v – vagina, vd – vas deferens.

Distal genitalia (Figs 9B, 53, 54): Penis long, elongate-cylindrical, usually tapering slightly toward its base, often somewhat sinuous *in situ*, but not strongly so; penis length and thickness of its wall variable and dependent on relaxation state during pre-servation; internal lumen lined by papillate epithelium (Fig. 54A), papillae coarser than those of *Natalina* and less tightly packed, somewhat angular and irregularly positioned, but alignment generally longitudinal rather than transverse, particularly in basal
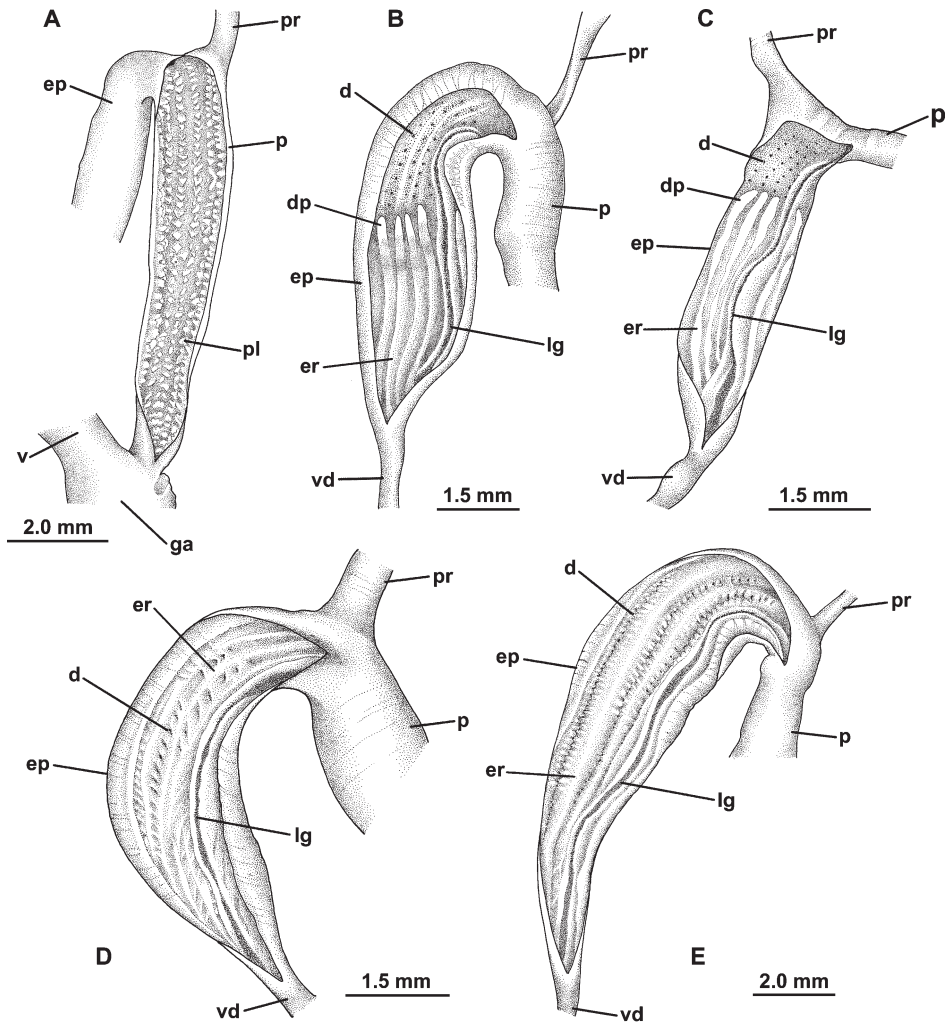
Fig. 54. Penis and epiphallus of *Afrorhytida* species, cut open longitudinally to show internal structure (all NMSA): (A) *A. knysnaensis*, penis (W4248, Cradock); (B) *A. knysnaensis*, epiphallus (W4643, Somerset East); (C) *A. trimeni*, epiphallus (W4206, Kap R.); (D) *A. burseyae* sp. n., epiphallus (paratype, W5231/T2260); (E) *A. kraussi kraussi*, epiphallus (V6578, Wilderness). Abbreviations: d – diverticulae in epiphallus wall, dp – digit-like pilaster at end of ridge, ep – epiphallus, er – internal epiphallic ridge, ga – genital atrium, lg – longitudinal groove between well-developed folds on inner side of epiphallus, p – penis, pl – penis lumen with papillate lining, pr – penial retractor muscle, v – vagina, vd – vas deferens.

region. Apex of penis evidently lacking a distinct papilla, its lumen communicating directly with epiphallus lumen; epiphallus joins penis at U-shaped bend, to which penial retractor muscle is attached. Epiphallus well developed, 0.50–0.75 of penis length, tapering toward its junction with vas deferens, reflexed to lie beside penis, but not joined to it by connective tissue web. Internal morphology of epiphallus exhibiting considerable inter-specific variation (Figs 54B–E), mirroring morphology of spermatophore. In all species its inner wall (facing penis) bears two well-developed longitudinal folds which extend for the full length of the organ, between which is a narrow groove; remaining wall of lumen bears a series of longitudinal ridges of varying strength and length, with microscopic pits in their intervals, in a pattern which appears to vary with species. Pits generally occur where epiphallus wall is thickest and represent the openings of minute diverticulae in which the spermatophore spines are moulded; their arrangement thus determines the pattern of spines on spermatophore; diverticulae usually visible externally as diffuse white specks in epiphallus wall. Vas deferens runs alongside penis base, vagina and free oviduct, sometimes sinuous in the latter region, before it fuses with spermoviduct. It is closely applied to the vagina and oviduct and held in place by connective tissue, but its lower region is free of the penis base.

Vagina of moderate length (relatively shorter than in *Capitina* and *Natalina*) generally of more or less even width, but basally swollen in *Afrorhytida kraussi*, attached laterally to body wall by a series of well-developed muscle fibres; vagina merges with free oviduct at point of origin of bursa copulatrix duct or just above this; an oviduct caecum is lacking or present merely as a short pouch-like vestibule into which the free oviduct opens, just above the origin of the bursa copulatrix duct (in *Afrorhytida knysnaensis* and *Afrorhytida trimeni*); inner wall of vagina with longitudinal folds in 2–3 orders of magnitude; similar but somewhat thicker folds lining free oviduct. Bursa copulatrix duct long and slender, attached to free oviduct by connective tissue and then running beside convoluted spermoviduct (not within its convolutions) to bursa itself, situated posterior to pericardium and kidney; bursa elongate-ovate to pyriform, very thin-walled. Spermoviduct with distinct oviducal and prostatic portions, the former with superficial folds.

Spermatophores (Figs 10, 62, 68): Allospermatophores have been found in the female tract of *Afrorhytida burseyae* sp. n. and *A. kraussi* and are discussed in detail under the respective species treatments. These differ considerably in shape, size and ornamentation, suggesting that spermatophore morphology is species specific and may ultimately provide useful supplementary morphological characters to test the validity of the species as currently delimited. However, at present very few spermatophores have been encountered and those of *A. knysnaensis* and *A. trimeni* are unknown. The spermatophores of *Capitina* and *Natalina* are of a very different form and are compared in the introductory section.

Notes: *Afrorhytida* has traditionally been considered a subgenus of *Natalina* (Connolly 1939). However, the morphology of the radula, distal reproductive tract and spermatophores show that *Afrorhytida* exhibits several character states quite distinct from those present in the *Natalina* radiation. In addition, molecular data indicate that *Afrorhytida* represents highly divergent monophyletic lineage worthy of recognition as a separate genus (Moussalli *et al.* 2009).

Characteristic features of the reproductive tract that separate *Afrorhytida* from *Natalina* are the fact that the penis lies to the left of the retractor muscle of the right optic tentacle (to its right in *Natalina*), the epiphallus and lower vas deferens in *Afrorhytida* are not connected to the penis by a web of connective tissue, and a distinct oviduct caecum is absent, at most there is a small swelling just above the origin of the bursa copulatrix duct. In terms of the radula, whereas the transition between the lateral and marginal series is abrupt in *Natalina*, there being no teeth of intermediate size, in *Afrorhytida* there is always at least one tooth of intermediate size outside the largest lateral.

Afrorhytida comprises a group of medium-sized rhytidids endemic to the Cape region. They occur in a wide range of habitats from coastal fynbos and scrub, to montane fynbos, various types of thicket, Afrotemperate forest and even Nama Karoo. Shell proportions appear to vary considerably within species and to overlap between species, such that species identification based on shell characters alone is frustratingly difficult. We have been able to define species boundaries only through the use of a combination of shell and radula characters, and molecular data. The above notwithstanding, we are confident in our correlation of the species thus identified with the nominal taxa described to date, even though the latter were based on shell characters alone.

Watson (1934) proposed the taxon *Hyperrhytida* as a section within *Afrorhytida*, defined largely by radula characters (inner laterals with laterally flanged cusps), and included in it *A. trimeni* and *A. arguta*. As shown below these two names in fact refer to a single species and therefore the characters which Watson used to define *Hyperrhytida* are species-level characters. Although the low number of marginal teeth (<10) in both *A. trimeni* and *A. burseyae* sp. n. may represent a synapomorphy providing some support for the existence of an *Afrorhytida* lineage distinct from *Afrorhytida s. s.*, molecular data do not support a sister group relationship between these two taxa.

Key to species of *Afrorhytida*

1 Radula with lateral teeth outnumbering marginals. South-eastern and eastern E. Cape 2

– Radula with marginal and lateral teeth of more or less equal number, or marginal teeth outnumbering laterals. W. Cape and western and central E. Cape 3

2 Shell sculptured with axial ribs which remain strong on last whorl; H:D of adult <0.7; shell colour predominantly brown in fresh specimens. Primarily in forest .... **A. trimeni**

– Axial ribs conspicuous on spire whorls, but noticeably weaker or obsolete on last whorl; H:D of adult >0.7; colour distinctly yellowish or greenish brown. Thicket and more open habitats .... **A. burseyae** sp. n.

3 Shell lenticular to subglobose, yellowish brown to greenish brown, interior without pinkish lilac sheen; marginal teeth of radula relatively gradually decreasing in size, only the outermost ones vestigial. Catchments of the Sundays and Great Fish rivers and neighbouring coastal areas ....**A. knysnaensis**

– Shell lenticular, generally brownish when fresh, interior of fresh shells with a pale pinkish lilac sheen; marginal teeth of radula rapidly decreasing in size, with only 1 or 2 teeth of intermediate size. W. Cape and south-western E. Cape .... **A. kraussi**
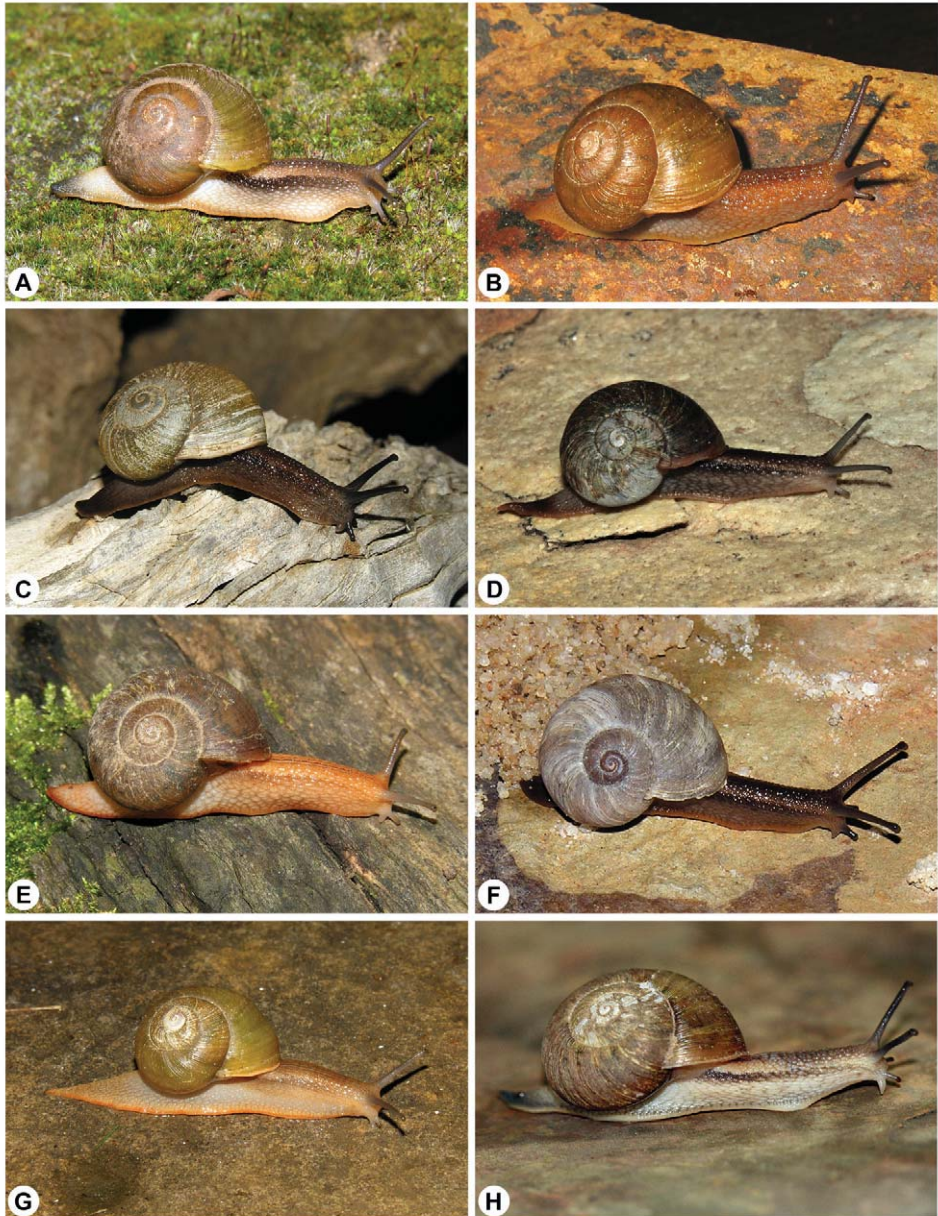
Fig. 55. *Afrorhytida* species, living animals (all NMSA): (A) *A. knysnaensis*, Fort Beaufort (W5211), shell diameter 19.0 mm; (B) *A. knysnaensis*, Cradock (W4248), shell diameter 22.0 mm; (C) *A. knysnaensis*, Kompasberg, Nieu Bethesda (W6097), shell diameter 20.4 mm; (D) *A. kraussi kraussi*, Featherbed Nat. Res., Knysna (W4671), shell diameter 16.8 mm; (E) *A. k. kraussi*, Grootvadersbosch (W5803), shell diameter 23.8 mm; (F) *A. kraussi oraria* subsp. n., De Hoop Nat. Res. (paratype, W3292/T2363), shell diameter 13.4 mm; (G) *A. burseyae* sp. n., Wedgeley farm, Kei River Valley (paratype, W5229/T2258), shell diameter 19.3 mm; (H) *A. trimeni*, Kap River (W4206), shell diameter 24.5 mm.

Afrorhytida knysnaensis (Pfeiffer, 1846)

Figs 6A, 7B, 9B, 11B, 53, 54A, B, 55A–C, 56–60

Helix knysnaensis: Pfeiffer 1846a (dated 1845): 131; 1846b: 439; 1848: 84; 1853 in 1853–60: 343, N° 858,
      pl. 133, figs 5, 6; Philippi 1847: (37) 85, pl. 7, fig. 5; Krauss 1848: 76; Reeve 1852 in 1851–54:
      sp. 403. Type loc.: 'Knysna, Cape of Good Hope' [Cuming coll'n] – erroneous and here emended
      to Fort Beaufort, E. Cape, South Africa.
Helix (Pella) knysnaensis: Pfeiffer 1879 in 1878–81: 102; Tryon 1887: 106, pl. 20, fig. 75.
Aerope knysnaensis: Pilsbry 1889: 277, pl. 9, figs A–G, J.
Natalina knysnaensis: Pilsbry 1893 in 1892–93: 135; 1908 in 1907–08: xi, pl. 52, fig. 4 (lung) [not 1 as
      stated]; Melvill & Ponsonby 1898: 170; Sturany 1898: 31; Connolly 1912: 94; 1939: 111 [not
      text-fig. 9 = *Afrorhytida kraussi*].
Natalina coerneyensis Melvill & Ponsonby, 1894: 91, pl. 1, fig. 2; 1898: 170; Moss 1894: 25, pl. 2, fig. 2;
      Sturany 1898: 31; Connolly 1912: 92; 1939: 112. Type loc.: Coerney, north of Port Elizabeth, E.
      Cape. **Syn. n.**
Rhytida (Afrorhytida) knysnaensis: Möllendorff 1903: 61, pl. 11, figs 1, 2.
Rhytida (Afrorhytida) coerneyensis: Möllendorff 1903: 64, pl. 11, fig. 8.
Natalina insignis Melvill & Ponsonby, 1907: 98, pl. 6, fig. 9; Connolly 1912: 94; 1939: 113. Type loc.: Tea-
      fontein farm, between Riebeek East and Grahamstown, E. Cape [Dr Schönland, *per* Farquhar].
      Syn. n.
Natalina (Afrorhytida) knysnaensis: Schileyko 2000: fig. 970.

Etymology: Named after the purported, but evidently erroneous, type locality, Knysna,
W. Cape, South Africa.

Identification: A variable species in terms of shell proportions and body coloration.
Elevated, subglobose specimens closely resemble *Afrorhytida burseyae* sp. n., but attain
a slightly larger size and have a somewhat wider umbilicus. Depressed specimens may
closely resemble *A. kraussi kraussi* and *A. trimeni,* but in both of these the shell is of a
richer brown hue when fresh and lacks a yellowish or greenish tint. *A. kraussi kraussi*
also has a pinkish lilac blush inside the aperture of fresh shells and *A. trimeni* has axial
sculpture which remains strong on the last adult whorl. The most distinctive features
of *A. knysnaensis* concern its radula which differs from that of all other *Afrorhytida*
species in that the outermost lateral tooth rather than the penultimate one is the largest.
Furthermore, it generally has fewer lateral teeth (<10 per half row) and more numerous
marginal teeth (>16 per half row), such that the lateral:marginal ratio is 0.50 or less
(compared to 1.0 or more in the other species). The outward reduction in size of the
marginal teeth is also noticeably more gradual. Juvenile specimens of *Natalina cafra
cafra* may co-occur with *A. knysnaensis* and be of similar size, but these have a much
larger protoconch, less deeply penetrating umbilicus and fewer whorls for their size.

Description (Figs 56, 57): Shell proportions very variable, ranging from subglobose
(H:D=0.75–0.86, Figs 57A–E) to lenticular (H:D=0.55–0.65, Figs 57J–L); adult shell
comprising 4–5 whorls, the last usually descending somewhat prior to aperture, some-
times conspicuously so; base glossy, apical surface less so, but still retaining some
lustre when fresh. Protoconch 3.7–5.2 mm in diameter, apical portion more or less
smooth, axial riblets developing only toward end of final whorl and protoconch relatively
weakly sculptured compared to other species; protoconch/teleoconch junction usually
poorly defined. Apical surface of teleoconch sculptured by close-set axial riblets, these
becoming weaker and less well defined toward end of last adult whorl and on base;
base also with traces of spiral liration; aperture subcircular to roundly-ovate and some-
what obliquely descending; outer lip slightly thickened and occasionally weakly
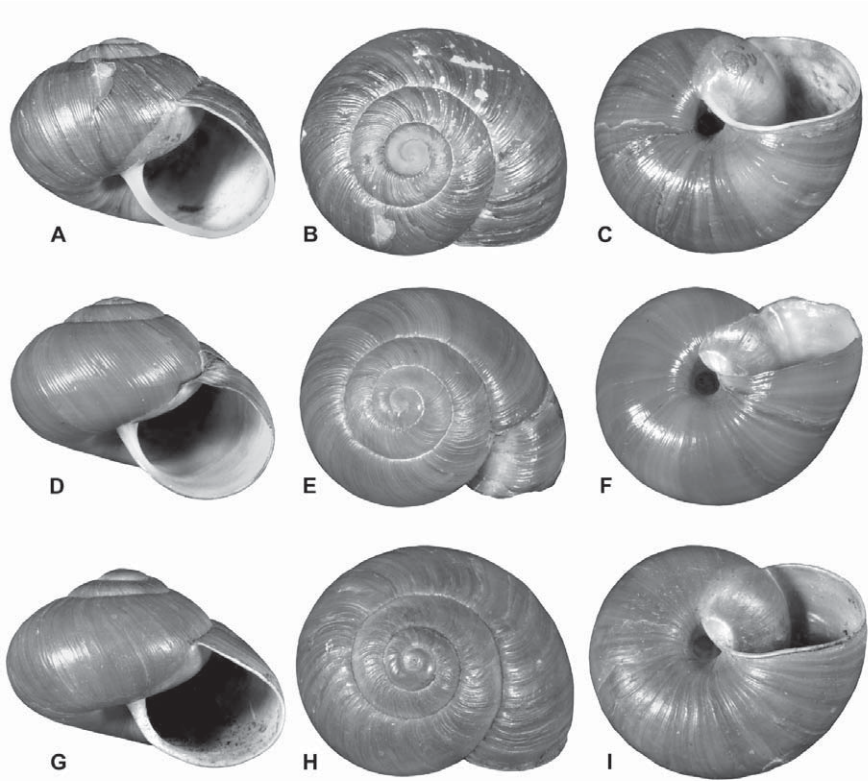reflected in adult specimens, sometimes weakly thickened internally in senescent indivi-

Fig. 56. *Afrorhytida knysnaensis* (Pfeiffer, 184), type material: (A–C) lectotype of *Helix knysnaensis* Pfeiffer, 1846 (designated Connolly 1912: 94) (BMNH 20080612), diameter 24.2 mm; (D–F) holotype of *Natalina coerneyensis* Melvill & Ponsonby, 1894 (BMNH 1911.8.8.4), diameter 22.5 mm; (G–I) holotype of *Natalina insignis* Melvill & Ponsonby, 1907 (BMNH 1902.6.26.12), diameter 29.4 mm.

duals; upper part of outer lip frequently somewhat flattened in depressed specimens; umbilicus of moderate but variable width, wider in depressed specimens than in subglobose ones in which it is partially obscured by reflected upper portion of columella lip.

Periostracum of fresh specimens usually a shade of yellowish brown with a slight greenish tinge; for the most part relatively uniform, but sometimes with faint axial variation in intensity. Underlying shell and interior of aperture milky-white (no trace of pinkish or lilac hue, cf. *Afrorythida kraussi*); apical periostracum frequently eroded, even in living specimens.

Dimensions: Largest specimen (BMNH 1563, Grahamstown), diameter 31.0 mm, height 21.1 mm, but few specimens exceeding diameter 25 mm and height 19 mm. H:D of adults 0.55–0.86 (N=42).

Living animal (Figs 55A–C): Coloration very variable, ranging from more or less uniformly pale apricot-orange to dark maroon-black; other specimens more contrastingly coloured with sides of foot pale flesh and dorsal neck region darker grey-black with a paler, dorsolateral, longitudinal stripe on each side extending backward from optic
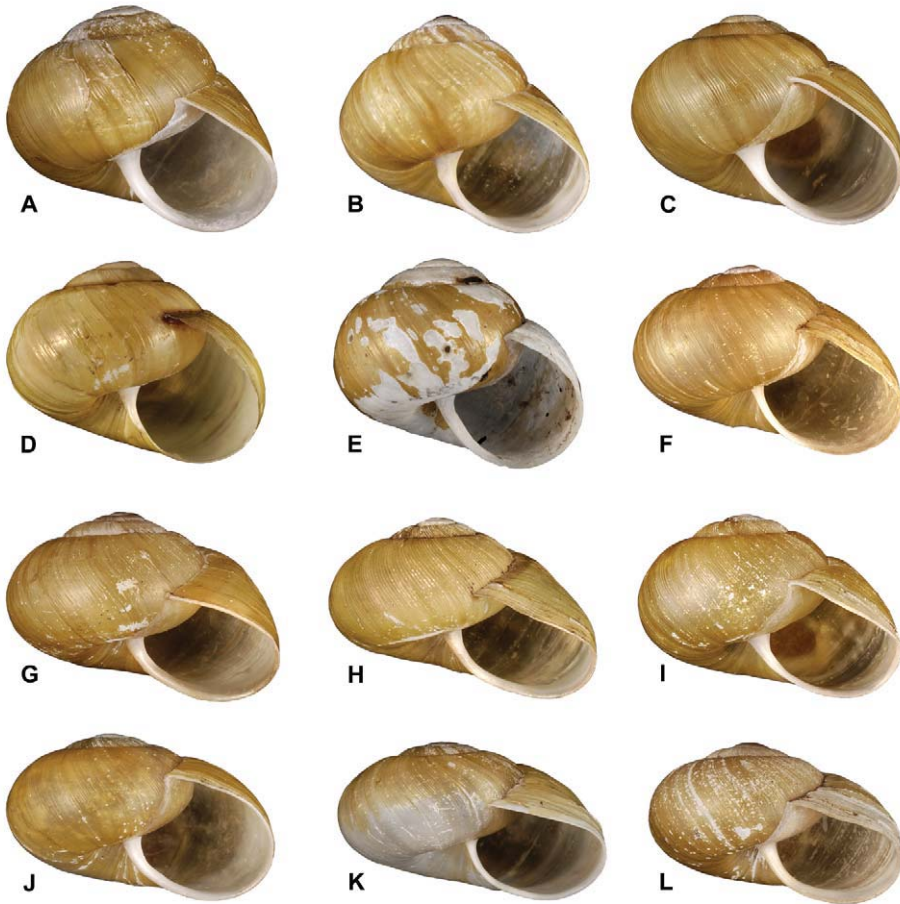
Fig. 57. *Afrorhytida knysnaensis* (Pfeiffer, 1846) (all NMSA): (A) Fort Beaufort (W5211), diameter 25.6 mm; (B) Port Elizabeth (1498), diameter 19.3 mm; (C) Fort Beaufort (V7729), diameter 23.9 mm; (D) Bedford (B0015), diameter 23.4 mm; (E) Port Alfred (W1395), diameter 24.2 mm; (F) Koedoeskop, SE of Somerset East (V6774), diameter 23.3 mm; (G) Jansenville (W6060), diameter 23.5 mm; (H) Graaff-Reinet (W6093), diameter 19.6 mm; (I) Cradock (W4248), diameter 21.8 mm; J. Somerset East (V6845), diameter 21.2 mm; (K) Cradock (1496), diameter 22.4 mm; (L) Kompasberg, Nieu Bethesda (W6097), diameter 20.4 mm. (A–E) globose specimens, (F–I) intermediate specimens, (J–L) lenticular specimens.

tentacle; tentacles usually darker grey, particularly the optic ones; pedal margin occasionally, but rather rarely, more brightly coloured; tip of tail also often somewhat more intensely pigmented; mantle edge coloration similar to body colour; pigmentation of lung wall variable, usually limited and seldom heavy.

Radula (Fig. 58): Formula 1+(7–10)[1] +(17–24) (N=8); length up to 19 mm, with 60–80 V-shaped rows of teeth, 3.6–4.4 rows/mm in adult; lateral and marginal series clearly differentiated. Rachidian short, its cusp and base-plate more or less equal in length;

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[1] Pilsbry (1889) illustrated a radula with 12 lateral teeth under the name *Aerope knysnaensis*, but the geographical origin of the specimen was not stated (see notes below).
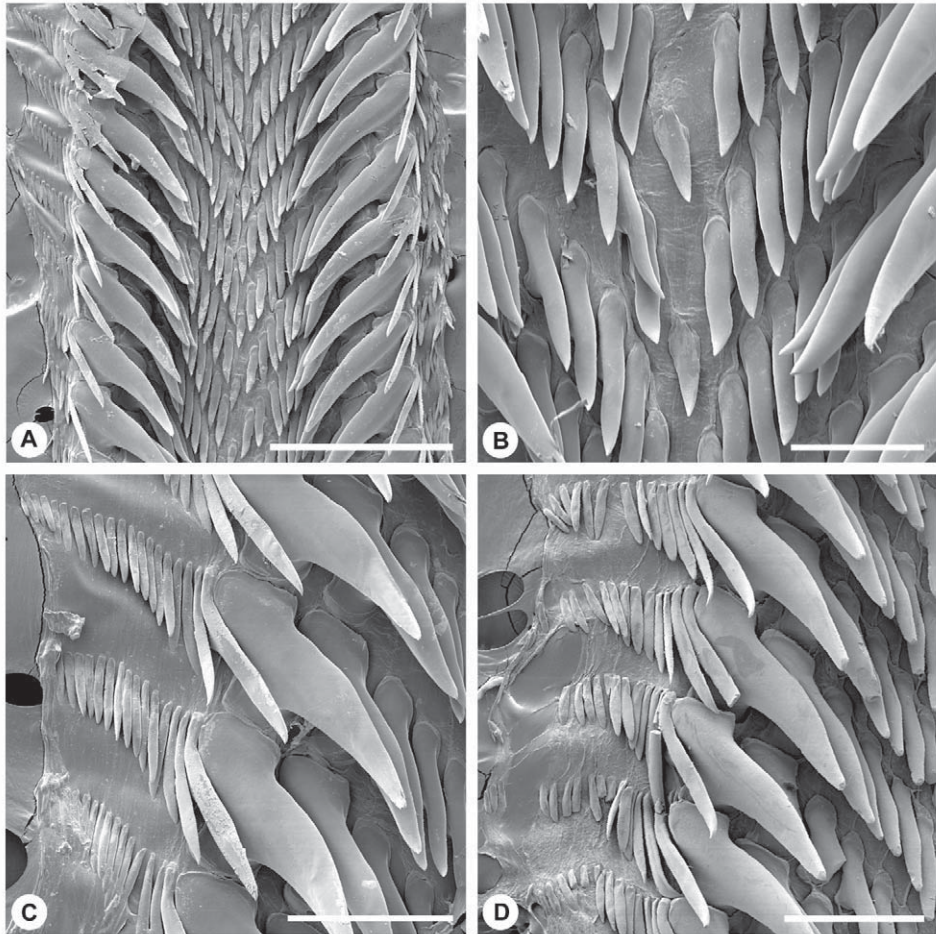
Fig. 58. *Afrorhytida knysnaensis* (Pfeiffer, 1846), radula: (A–C) Fort Beaufort (NMSA W5211): (A) entire width of radula, scale bar = 0.5 mm; (B) rachidian and inner lateral teeth, scale bar = 150 µm; (C) outer lateral and marginal teeth, scale bar = 250 µm; (D) Cradock (NMSA W4248), outer lateral and marginal teeth, scale bar = 250 µm.

inner lateral teeth more or less parallel-sided, tapering to a point at tip, increasing slightly in size from first to fifth or sixth; outer 2 or 3 laterals considerably larger, with a strong quadrate base-plate and well-developed curved cusp (length of cusp variable between individuals, frequently relatively stout); outer lateral tooth the largest. Marginal teeth slender and more delicate with a much reduced base-plate, innermost one 0.50–0.66 length of outer lateral, remainder decreasing gradually in size, in decreasing increments, toward radula margin, only those at the extreme edge truly vestigial.

Distal genitalia (Figs 9B, 53, 54A, B): See generic description. Epiphallus 75 % or more of penis length, but variable in proportions and curvature, sometimes with distinct greyish pigmentation; distal half broader, progressively narrowing toward vas deferens; mid region of lumen with a transverse ring of four to five short, swollen, longitudinally orientated, white, digit-like pilasters, each narrowly attached to lumen wall; smooth,

low ridges extend from these toward vas deferens, often greyish in colour; lumen wall anterior to pilasters with indistinct ridges between each of which lies a longitudinal row of punctations marking the openings of minute diverticulae in lumen wall, these extending to penial end of epiphallus and visible as striae in cut wall. Papillae lining penis lumen loosely arranged in longitudinal rows.

No spermatophores have been found, but the morphology of the epiphallus suggests that the tail region of the spermatophore may bear weak, longitudinal ridges and the anterior half will possess four to five rows of spinose projections.

Type material (Fig. 56): Lectotype of *Helix knysnaensis* Pfeiffer, 1846 in BMNH (20080612) (designated Connolly 1912: 94), diameter 24.2 mm (Figs 56A–C), plus two paralectotypes (20080613). Holotype of *Natalina coerneyensis* Melvill & Ponsonby, 1894 in BMNH (1911.8.8.4), diameter 22.5 mm (23.3 mm *fide* Connolly 1939) (Figs 56D–F). Holotype of *Natalina insignis* Melvill & Ponsonby, 1907 in BMNH (1902.6.26.12) [Dr Schönland], diameter 29.4 mm (Figs 56G, H).

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: North-western E. Cape (west of Great Fish R.): Nieu Bethesda area, Kompasberg slopes (31.79092°S:24.55475°E), 1600 m, water course krantz in rocky grassland, beneath bushes and grass clumps, Herbert, Davis & Cole, 15/iii/2008, (W6097); Cradock (32.16220°S:25.60580°E), 921 m, succulent karoo, at the base of *Acacia*, M. Cunningham, viii/2003 (W4248); Cradock (32.183°S:25.617°E) (B0028, V5276, V6635, BMNH 1937.12.30.1376–7); Cradock (32.183°S:25.617°E), ix/1897 (E7914); Cradock (32.183°S: 25.617°E), amongst loose boulders (1496); Graaff-Reinet (32.25°S:24.55°E) (W1374); Graaff-Reinet, Camdeboo Nat. Park, Valley of Desolation view site (32.26585°S:24.49203°E), 1350 m, in deep shaded gully between dolerite cliffs, D. Herbert, L. Davis & M. Cole, 14/iii/2008 (W6093); Mountain Zebra Nat. Park (32.24683°S:25.43352°E), 1450 m, rocky outcrop on hilltop ridge, amongst rocks and under small bushes, Herbert, Davis & Cole, 17/iii/2008 (W6118); Witmoss, N of Cookhouse (32.533°S:25.733°E), A. Reeve, *ex* J. Farquhar (B0046, BMNH 1937.12.30.1378–9); Somerset East, Glen Avon Nat. Res. (32.67436°S: 25.64463°E), 978 m, valley thicket/indigenous forest, A. Moussalli & D. Stuart-Fox, 24/xii/2005 (W4847); ditto, 'Craigie Burn' (32.6850°S:25.6783°E) (B0025); ditto, Bosberg (32.70°S:25.55°E) (3054, B0030, V6845); ditto, slopes of Bosberg (32.70257°S:25.57605°E), indigenous woodland, in leaf-litter, D. Herbert, M. Bursey & G. Redman, 22/i/2002 (V9790); ditto, Bosberg Nat. Res. (32.70734°S:25.55959°E), 777 m, indigenous forest, under rocks, A. Moussalli & D. Stuart-Fox, 24/xii/2005 (W4643); ditto, vicinity of camping grounds (32.70734°S:25.55959°E), 771 m, indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 16/iii/2005 (W4846); Somerset East (32.717°S:25.583°E), *ex* Mrs Howard and Dr Becker (B0027, B0026, V6841); Jansenville, Meerlust Suid farm (32.87148°S:24.64085°E), rocky area with dense aloes and bush clumps, under dead aloes, D. Herbert, L. Davis & M. Cole, 12/iii/2008 (W6068); ditto (32.86520°S:24.67360], 450 m, rocky N facing hillside with aloes, noors and bush clumps, under dead aloes, D. Herbert, L. Davis & M. Cole, 11/iii/2008 (W6053); ditto, Fontein Camp (32.85977°S: 24.63966°E), 450 m, rocky area with aloes, noors and bush clumps, under dead aloes, D. Herbert, L. Davis & M. Cole, 11/iii/2008 (W6060); Jansenville, Alwynsfontein farm (32.87949°S:24.60543°E), 500 m, valley floor with aloes, noors and bush clumps, under dead aloes, D. Herbert, L. Davis & M. Cole, 11/ iii/2008 (W6067); Koedoeskop farm SE of Somerset East (32.9753°S:25.1717°E), 498 m, on stony ridge, specimen found trying to reach dead mouse in mammal trap, O. Bourquin, 06/xi/1998 (V6774). Southern E. Cape (south of Great Fish R.): Port Elizabeth (33.917°S:25.600°E), F. Cruden, ii/1922 (1498, E7903); ditto, A.J. Peile (NMH 2242); ditto, MacAndrew coll'n, 05/i/1909 (BMNH un-numbered); Addo area, 6 km SW (33.593664°S:25.648581°E), 30 m, aloes and other succulents, leg. B. Muller & M. Mostovski, 12/vii/2009 (W6930); Coerney (holotype of *Natalina coerneyensis*) (33.4500°S:25.7333°E) (BMNH 1911.8.8.4); Grahamstown, Teafontein farm (holotype of *Natalina insignis*) (33.23300°S:26.25417°E), Dr Schönland via J. Farquhar (BMNH 1902.6.26.12); Grahamstown, 'St J. M.', 31/iii/1909 (BMNH MacAndrew coll'n 1563); Port Alfred (33.6°S:26.9°E) (W1395). Central E. Cape (north-east of Great Fish R.): Baviaans Valley between Bedford and Tarkastad, Wapadskloof, Huntley Glen farm (32.40945°S: 26.11472°E), under fallen stems of *Aloe ferox* and under stones, M. Bursey, 31/xii/2006 (W5255); Bedford (32.683°S:26.083°E), J. Farquhar (B0015); Alice (32.783°S:26.833°E) (V6839); Alice area, Breakfast Vlei (33.0833°S:26.9500°E) (BMNH un-numbered); Fort Beaufort (32.783°S:26.633°E), J.S. Taylor, x/ 1945 (V7729); Fort Beaufort, agricultural college farm (32.80544°S:26.63381°E), valley thicket with aloes and euphorbs, in leaf-litter under fallen aloes, D. Herbert, L. Davis & M. Bursey, 07/iii/2007 (W5211); ~13 km N of Double Drift Game Res. (32.86658°S:26.81436°E), 573 m, valley thicket, under dead aloes, A. Moussalli & D. Stuart-Fox, 2/xii/2005 (W4749, W5164).

Additional literature records (Connolly 1939; material not seen): SOUTH AFRICA: *E. Cape*: Enon, north of Port Elizabeth (33.40°S:25.55°E), Hartwig; Sandflats Station [nr Paterson] (33.43°S:26.95°E), J. Crawford.

Distribution (Fig. 59): Endemic to E. Cape; occurs in the catchments of the Sundays and Great Fish rivers, from low altitudes near the coast to 1600 m in the Sneeuberge. The original type locality (Knysna) is evidently erroneous (see notes below for emendation).

Habitat: Found largely in the Albany Thicket biome (Mucina & Rutherford 2006), and in isolated mist-belt forest patches within this, but also extending into the south-eastern Nama Karoo. Evidently catholic in its habitat requirements, but favouring patches of relatively dense vegetation. These, however, vary greatly in plant composition from forest to mixed woody thicket, spekboom thicket (*Portulacaria afra* Jacq.), *Aloe – Euphorbia* dominated scrub and, at higher altitudes, shrubby rock outcrops in more open Karoo escarpment grassland. Lives buried in leaf-litter beneath shrubs and bush clumps, under logs and fallen aloes, and amongst rocks; evidently not rare, but population densities generally low.

Notes: The material here treated as *Afrorhytida knysnaensis* exhibits considerable variation in shell proportions (Fig. 57). This notwithstanding, the sculpture and coloration of the teleoconch is relatively consistent, as is the weak axial sculpture on the protoconch and the morphology of the radula, in which the outermost lateral tooth is the largest and there are many marginal teeth of intermediate size. The material thus identified forms a well-supported monophyletic clade in analyses of molecular data (Moussalli *et al.* 2009), corroborating the morphological evidence. There is, however, considerable genetic diversity within this clade (Fig. 1), indeed the highest level exhibited of the all the
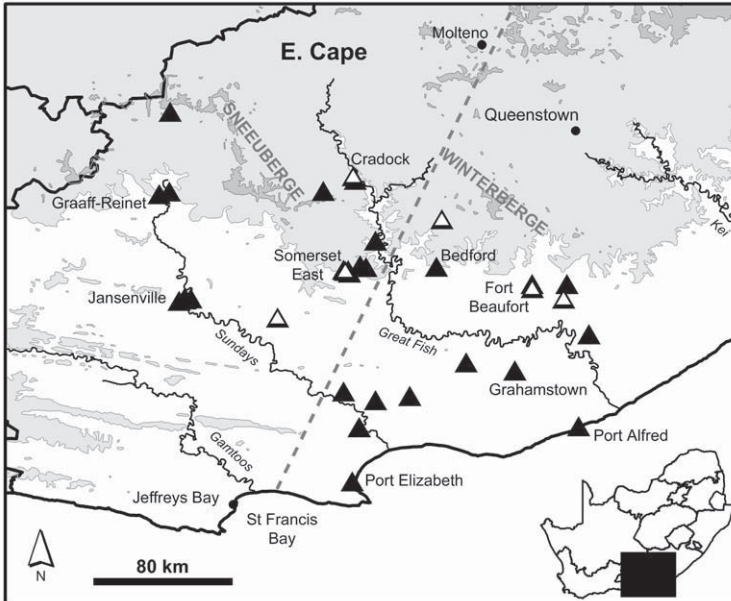
Fig. 59. Distribution of *Afrorhytida knysnaensis* (Pfeiffer, 1846). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m. The dashed line between St Francis Bay and Molteno corresponds to the similar line drawn in Fig. 60, separating populations with more lenticular shells (north-west) from those with subglobose shells (south-east).

species examined here (e.g., mean uncorrected P-distances of 0.49 for the protein coding mitochondrial gene COI). Thus, there exists the possibility that this taxon constitutes more than one cryptic species.

H:D measurements indicate a north-west to south-east trend in shell proportions, with shells from the north-west being consistently less globose than those from the south-east (Fig. 60). The dotted line in this figure, separating subglobose and lenticular populations, when redrawn on the distribution map to separate the same individuals (Fig. 59), runs approximately south-west to north-east (St Francis Bay to Molteno), dividing the relatively elevated, subglobose south-eastern specimens from the more depressed, lenticular north-western individuals. Additionally, within the south-eastern region, shells from the Port Elizabeth area are noticeably smaller (adult diameter approx. 20 mm). There is, however, no clear disjunction evident within this north-west *vs* south-east trend in shell proportions (Fig. 60). The line has been positioned for illustrative purposes, and in reality the variation is evidently more clinal than categorical. Some specimens are thus of intermediate proportions, but this notwithstanding, the trend is clear.

Somewhat similar geographic structuring is evident in DNA sequence data (Moussalli *et al.* 2009), with analyses of such data identifying strongly supported clades from the Somerset East-Cradock area and from the eastern part of the Fish River valley (Fort Beaufort and Greater Fish River Conservancy). However, individuals from other localities do not cluster in a N−W to S−E pattern consistent with this. At present sequence data are available for too few specimens to determine the degree of concordance between phylogeographic structure and the geographic variation evident in shell proportions. Alternatively variation in shell proportions may not be genetically correlated, but may instead be determined by N−W to S−E variation in environmental parameters such as temperature and/or rainfall.
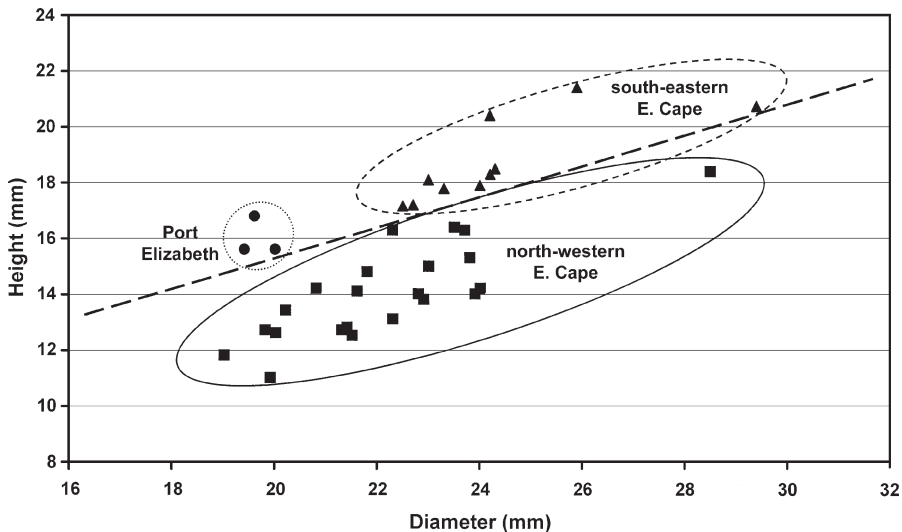

Fig. 60. *Afrorhytida knysnaensis* (Pfeiffer, 1846), plot of height/diameter measurements, showing differing shell proportions in different populations. The diagonal dashed line corresponds to the line drawn between St Francis Bay and Molteno in the distribution map (Fig. 59).

The small, subglobose individuals from the Port Elizabeth area are currently known from shells alone, there is thus no anatomical or molecular data to confirm that we are correct in referring them to *A. knysnaensis*. In addition to being small and relatively globose, they have a more elevated spire and a more acute apex (Fig. 57B). In this respect it is noteworthy that Pilsbry (1889) illustrated a radula under the name *Aerope knysnaensis* (locality unspecified) with 12 lateral teeth per half row. This figure is higher than any of the material examined herein, but an old radula slide in the Natal Museum labelled '*Natalina knysnaensis*, Port Elizabeth' (not associated with a shell) likewise has 12 lateral teeth per half row. Since Pilsbry's material (sent by J. Ponsonby) may well have originated in the Port Elizabeth area, there is a possibility that this conchologically divergent population may in addition possess a somewhat distinct radula and perhaps represent a separate and undescribed species. Attempts to collect additional material in the Port Elizabeth area, so that this possibility could be explored further, have been unsuccessful.

The locality given in the original description is evidently erroneous, as is commonly the case with material from the Hugh Cuming collection (Dance 1986). Knysna lies some 200 km west of the westernmost known records for this species. In accordance with recommendation 76A.2 of the Code (ICZN 1999), we here emend the type locality to be Fort Beaufort. Specimens closely resembling the type series have been found recently in the vicinity of this town. The fort was constructed as a military frontier defence in 1822 and became established as a town in 1837. It is thus possible that material from this locality could have come into the possession of early 19th century British collectors such as Cuming, well before its description in 1846.

Synonymy: Connolly (1939) maintained '*Natalina*' *knysnaensis* and '*N.*' *coerneyensis* as distinct species, but stated that he would have placed *coerneyensis* 'without hesitation in the synonymy of *knysnaensis*', were it not for differences in the radula. His assessment of the radula of '*N.*' *knysnaensis* was based on a radula slide identified under that name in the Gwatkin collection (present in BMNH) with the locality "Cape". This he compared with another radula slide in the same collection identified as '*N.*' *coerneyensis* and the figure of the radula of '*N.*' *coerneyensis* (from Coerney) published by Moss (1894). Re-evaluation of Connolly's illustration of the '*N.*' *knysnaensis* radula (Connolly 1939, text-fig. 9) and the slide still present in the BMNH, in the light of the data now available, indicates it was from an incorrectly identified specimen. The outer lateral teeth are relatively slender and the largest is clearly the penultimate one rather than the outermost one. This combined with the relatively large number of marginal teeth (16 per half row) indicates that the radula was in all probability from a specimen of *A. kraussi*. Since subglobose specimens typical of *A. knysnaensis* have a radula indistinguishable from that of topotypic specimens of '*N.*' *coerneyensis*, we conclude that *Natalina coerneyensis* Melvill & Ponsonby, 1894 is a junior synonym of *A. knysnaensis*. Although the type material of *A. knysnaensis* is incorrectly localised, it is clearly subglobose and H:D ratios indicate that both names are likely to apply to the south-eastern population discussed above.

Natalina insignis Melvill & Ponsonby, 1907 is anatomically unknown. Attempts to find living material at the type locality were unsuccessful. Although large, the holotype falls within the range of variability exhibited by *A. knysnaensis* and a specimen of very similar shape (NMSA V6774 from Koedoeskop farm, SE of Somerset East (Fig. 57F),

ca 120 km west of the type locality of *N. insignis*) has a radula typical of *A. knysnaensis* and groups within this clade in molecular analyses (Moussalli *et al.* 2009). We therefore consider this name to be a further synonym of *A. knysnaensis*. In terms of the H:D ratio these specimens are of somewhat intermediate shell proportions.

Afrorhytida kraussi (Pfeiffer, 1846)

Moussalli *et al.* (2009) have shown that *Afrorhytida* material occurring in the mountains of the southern Cape Fold Belt (Langeberge to Port Elizabeth) and adjacent coastal regions constitutes a monophyletic lineage which was identified as the *A. kraussi* complex. From a morphological perspective this complex includes two clearly distinct forms. Firstly, a form with an essentially brown shell, representing typical *A. kraussi*, which is widespread and occurs in a variety of habitats from southern Afrotemperate forest to montane sandstone fynbos, and secondly a smaller form with a thicker, paler shell which is evidently confined to coastal habitats in the De Hoop region. Since this latter form is clearly and consistently diagnosable we describe it as a new taxon, choosing for the present to rank it as a subspecies within a broadly interpreted *A. kraussi*, primarily on account of the molecular data which shows it to cluster within this complex.

As a whole, the *A. kraussi* complex has high genetic diversity (mean uncorrected P-distances of 0.44 for the protein coding mitochondrial gene COI; refer to Fig. 1) and exhibits strong west-east phylogeographic structure (Moussalli *et al.* 2009). This structure is more consistent with the predominantly west-east distribution of the material, than it is with the habitat of origin (i.e. forest *vs* fynbos). However, other than for the De Hoop material, we have been unable to identify any clear morphological characters which could serve to discriminate between the constituent subclades, and which might thus justify further specific or subspecific division. This notwithstanding, there is some evidence that the genetically divergent lineage occurring in isolated Afrotemperate forest patches at the western limit of the range (i.e. Grootvadersbosch and Tradoupas) exhibits a discernable trend toward larger size and frequently has a distinct reddish head-foot coloration (see below). In contrast, morphologically similar and geographically proximate specimens from sandstone fynbos in the mountains inland of Mossel Bay are widely disjunct genetically, yet there is no obvious physical feature in this area which stands out a potential biogeographic barrier. Given apparently anomalous patterns such as this, and the paraphyly resulting from the nesting of the morphologically distinct De Hoop lineage within the typical *A. kraussi* clade, it is evident that resolution of taxonomic uncertainties and phylogenetic relationships within the *A. kraussi* complex must await more detailed study of material more broadly representative the distribution of the species, particularly with respect to DNA sequence data.

Afrorhytida kraussi kraussi (Pfeiffer, 1846)
Figs 10C, 54E, 55D, E, 61–63, 64A–D, 65D

Helix kraussi: Pfeiffer 1846*c*: 70; 1848: 197; Krauss 1848: 77, pl. 4, fig. 24; Reeve 1854 in 1851–54: sp. 1391. Type loc.: '*Outeniqua prom. bon. spei.* (Krauss.)', later given as '*In sylvis Outeniqua, provinc. George*' by Krauss (1848).
Helix sturmiana Pfeiffer, 1853*a*: 253; 1853*b*: 150; 1854: 142; 1854 in 1853–60: 397, Nº 944, pl. 144, figs 3, 4; Reeve 1853 in 1851–54: sp. 1132; Pilsbry 1890 in 1890–91: pl. 36, figs 28, 29. Type loc.: originally unknown (Cuming Coll'n), later given as Delagoa Bay [southern Mozambique], but without justification (Pfeiffer 1878 in 1878–81: 62 as *Macrocyclis*).

Macrocyclis sturmiana: Pfeiffer 1878 in 1878–81: 62.
Helix (*Acusta*) *kraussi*: Tryon 1888: 50, pl. 10, fig. 30.
Dorcasia kraussi: Pfeiffer 1879 in 1878–81: 187; Sturany 1898: 50; Pilsbry 1895 in 1893–95: 173.
Phasis sturmiana: Sturany 1898: 41; Pilsbry 1893 in 1893–95: 37.
Helix (*Ampelita*) *sturmiana*: Pfeiffer 1879 in 1878–81: 184.
Rhytida kraussi: Melvill & Ponsonby 1898: 170 (= *sturmiana*).
Rhytida (*Afrorhytida*) *kraussi*: Möllendorff 1903: 63, pl. 11, figs 5, 6.
Natalina kraussi: Connolly 1912: 94; 1925: 122; 1939: 112, pl. 3, figs 8–10.
Natalina liliacea Preston, 1912: 17; Connolly 1912: 95; 1939: 114. Type loc.: 'Knysna Forest, Cape Colony'
    [Cox]. **Syn. n.**
Natalina knysnaensis: Connolly 1939: text-fig. 9 (radula).
Natalina (*Afrorhytida*) *kraussi*: Bruggen 1970: 468.
Not *Rhytida kraussi*: Moss 1894: 25, pl. 1 fig. 3; nor *Rhytida Kraussii* [*sic*]: Cooke 1895: 232 [= *Nata
    vernicosa* (Krauss, 1848)].

Etymology: Named for Christian Ferdinand Friedrich Krauss (1812–91), the early German explorer-naturalist and later director of the natural history museum in Stuttgart, who wrote the first scientific work devoted to southern African molluscs (Krauss 1848).

Identification (Fig. 61): The shell of *Afrorhytida k. kraussi* is considerably less globose than that of *A. burseyae* sp. n. and typical (south-eastern) specimens of *A. knysnaensis*. In shell proportions and colour it most closely resembles *A. trimeni*, but in the present species the last adult whorl is generally less deep and has less distinct axial ribs. Additionally, in *A. trimeni* the radula has distinctively shaped inner lateral teeth and fewer marginal teeth (see below). The more lenticular shells of north-western specimens of *A. knysnaensis* are generally of a paler, somewhat yellowish or greenish hue and the radula of that species has more strongly developed inner marginal teeth and the outer lateral tooth rather than the penultimate one is the largest. In fresh specimens of *A. k. kraussi* the pinkish lilac sheen of the interior is also diagnostic.

Description: Shell generally lenticular, but proportions somewhat variable; adult shell comprising 4.0–4.5 whorls, the last frequently descending somewhat prior to aperture in adult specimens; base glossy, apical surface less so. Protoconch 4.5–5.0 mm in diameter, with distinct, relatively coarse axial riblets more or less throughout. Apical surface of teleoconch sculptured by close-set axial riblets, these becoming weaker and less well defined toward end of last adult whorl and on base; base also with traces of spiral liration; aperture subcircular to roundly ovate and somewhat obliquely descending; outer lip thin but not membranous (in adult), its basal portion and columella lip slightly thickened; upper part of columella lip weakly reflected; umbilicus relatively wide and not obscured to any appreciable degree by reflected columella lip.

Periostracum of fresh adult specimens usually predominantly brown, without a yellowish or greenish tinge, but young specimens sometimes paler and somewhat greenish; all specimens tending to fade and eventually becoming slightly yellowish; coloration generally uniform, but occasionally with slight axial variation in intensity. Underlying shell whitish, interior of aperture with a pale, but distinct pinkish lilac wash.

Dimensions: Largest specimen (NMSA W4748, Marloth Nat. Res.), diameter 28.4 mm, height 18.4 mm, but some specimens appear to be adult at diameter 21 mm; H:D of adults 0.48–0.67 (N=39).

Living animal (Figs 55D, E): Few specimens have been examined or photographed alive, but the coloration of the living animal is evidently variable. Head-foot of specimens from both forest and fynbos habitats in the Knysna–Tsitsikamma area (typical) generally
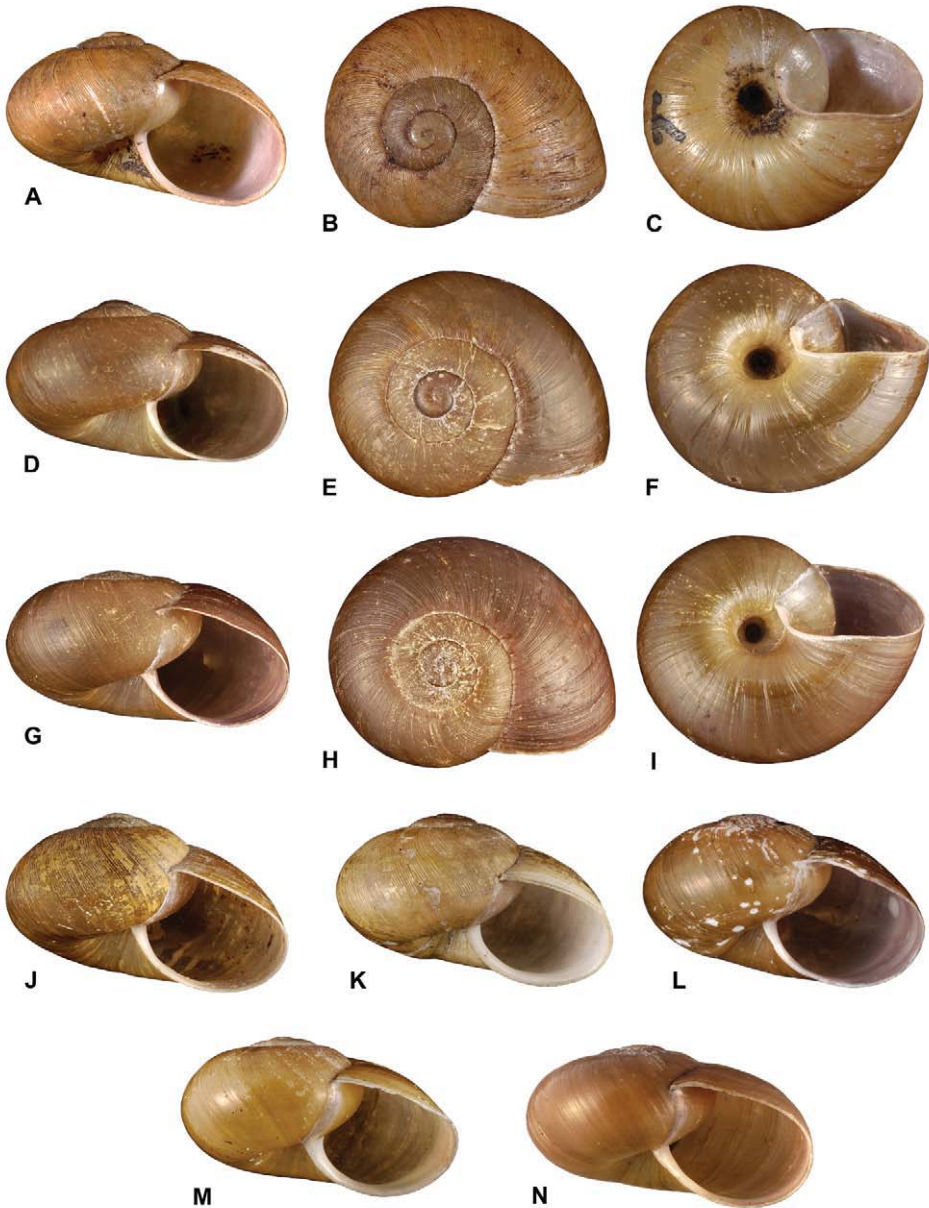
Fig. 61. *Afrorhytida kraussi kraussi* (Pfeiffer, 1846): (A–C) holotype of *Natalina liliacea* Preston, 1912, Knysna Forest (ISNB MT/525059), diameter 20 mm; (D–F) Diepwalle, Knysna Forest (NMSA W4845), diameter 21.7 mm; (G–I) Grootvadersbosch (NMSA W5803), diameter 25.9 mm; (J) Wilderness area (NMSA V6580), diameter 24.1 mm; (K) holotype of *Helix sturmiana* Pfeiffer, 1853 (BMNH 20080064), diameter 20.8 mm; (L) Formosa Peak Trail, Tsitsikammaberge (NMSA W3212), diameter 24.0 mm; (M) Cloetespas, Herbertsdale area (NMSA W3207), diameter 23.7 mm; (N) Engelseberg summit, Outeniekwaberge (NMSA W3211), diameter 22.8 mm.

shades of dark brown (Fig. 55D), usually darkest in neck region and tail, but with a conspicuous pale, dorsolateral, longitudinal stripe on each side of neck, extending backward from optic tentacle; sides of foot paler; optic tentacles dark grey-brown; pedal margin may be tinged with orange; mantle edge mostly dirty yellowish cream; lung wall usually heavily marked with black. Specimens from Grootvadersbosch (Fig. 55E), however, though similarly patterned, are primarily of an orange to reddish hue, frequently brightly so along the dorsal neck and pedal margin.

Radula (Figs 64A–D): Formula 1+(11–15)+(11–16) (N=5); length up to 22.5 mm, with 70–85 V-shaped rows of teeth, 3.2–4.3 rows/mm in adult. Rachidian cusp somewhat longer than its base-plate. Inner lateral teeth more or less parallel-sided, apically acuminate and differing little in size; outermost 3 or 4 lateral teeth considerably larger, with a stout elongate-quadrate base-plate and long, slender, gently curved, sharply pointed cusp; penultimate lateral larger than outermost one; precise shape and curvature of outer laterals somewhat variable between individuals. Innermost marginal tooth relatively large (0.50–0.75 length of outer lateral), the second and subsequent marginals very much smaller and essentially vestigial.

Distal genitalia (Fig. 54E): See generic description. Epiphallus 75 % or more of penis length, broadest near penis, tapering slowly toward vas deferens and merging smoothly therewith; occasionally with distinct greyish pigmentation; inner side of lumen wall (that adjacent to penis) with two strong folds with an intervening groove running entire length of epiphallus; remaining lumen wall with 2 or 3 low longitudinal ridges in thickened portion nearer to penis, with a row of minute punctations (sometimes paired) in their intervals, these extending to penial end of epiphallus; punctations represent openings of slender diverticulae in epiphallus wall which are visible as striae in cut wall; lumen wall nearer to vas deferens smooth or with shallow ridges, but no punctations.

Spermatophore (Figs 10C, 62): A single allospermatophore was found in a specimen from Grootvadersbosch (collected in mid October). It was situated in the upper vagina and free oviduct; the anterior half occupying almost the entire length of the free oviduct and the posterior half extending well down into the upper vagina, the opening of the bursa copulatrix duct more or less level with the middle of the spermatophore. Spermatophore itself S-shaped and twisted, approx. 20 mm in total length (straightened); anterior third slender and spinose; posterior two-thirds smooth, comprising a somewhat broader mid-piece, tapering to an acuminate tail. Anterior region somewhat quadrate in cross section, the angles on the convex surface set with a row of close-set, antler-like projections, each comprising a narrow stalk which divides into a branched array of 5–8 sharp spines; these spinose ridges continue posteriorly to start of mid-piece, diminishing and disappearing soon thereafter; a third row of similar projections present on one side of head region, but this terminating abruptly, some distance prior to the other rows; concave surface of anterior half smooth, with angular margins, broadening on mid-piece. No obvious vent present in tail region, but concave wall of mid-piece evidently thin and perhaps representing rupture site for sperm release.

Type material: Holotype of *Helix kraussi* Pfeiffer, 1846 in Stuttgart Museum, now lost (cf. Herbert & Warén 1999), but illustrated by Connolly (1939: pl. iii, figs 8–10), diameter 20.7 mm [considerably smaller than the measurements given by Pfeiffer (1846*c*) and Krauss (1848). Holotype of *Helix sturmiana* Pfeiffer, 1853 in BMNH (20080064), diameter 20.8 mm (Fig. 61K). Holotype of *Natalina liliacea* Preston, 1912 in ISNB MT/525059 (Dautzenberg Coll'n), diameter 20 mm, height 12.3 mm (the height of 16.5 mm given by

Preston is clearly an error) (Figs 61A–C); paratype in BMNH (1911.8.22.59), diameter 20.2 mm, height 12.65 mm (20.5 mm and 13.8 mm *fide* Connolly 1939).

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: <u>Langeberge</u>: Marloth Nat. Res. (33.98975°S:20.45439°E), Afrotemperate forest, A. Moussalli & D. Stuart-Fox, 23/ii/2005 (W4748); Swellendam area, Langeberge Mts, northern side (33.967°S:20.483°E), 1250 m, in collapsed mole-hill, V. Millard, i/2001 (V8788); Tradoupas, approx. 10 km S of Barrydale (33.97660°S:20.70311°E), 353 m, riparian indigenous forest/ fynbos, A. Moussalli, 26/viii/2006 (W4678); Grootvadersbosch Nat. Res. (33.99595°S:20.81288°E), 402 m, Afrotemperate forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 22/ii/2005 (W3350); Grootvadersbosch Nat. Res. (33.99595°S:20.81288°E), 402 m, Afrotemperate forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 22/ii/2005 (W3351); Grootvadersbosch (33.983°S:20.830°E) (W889); Grootvadersbosch Nat. Res. (33.98197°S:20.83363°E), Afrotemperate forest, in leaf-litter under logs, D. Herbert & L. Davis, 13/x/2007 (W5803); Langeberge, Lemoens Hoek Mts (Grootberg] (33.917°S: 20.867°E), K.H. Barnard (SAMC A7244). <u>Outeniekwaberge and Swartberge</u>: Herbertsdale area, Cloetesberg, Cloetespas (33.92083°S:21.76028°E), 375 m, dry fynbos, under rocks, M. Cunningham, 5/viii/2003 (W3207); Herbertsdale area (34.04594°S:21.88528°E), 360 m, K. Tolley, 28/xi/2005 (W4099); Attakwasberge (33.82580°S:21.9250°E), 560 m, montane fynbos, under rocks, M. Cunningham, viii/2003 (W4780); Swartberg Pass, between Prince Albert and Oudtshoorn (33.35°S:22.05°E), K.H. Barnard (BMNH 1937. 12.30.1380); Engelseberg summit (33.86940°S:22.13420°E), 1500 m, montane fynbos, under rocks, M. Cunningham, viii/2003 (W3211); Montague Pass, north of George (33.89142°S:22.42912°E), 620 m, montane fynbos, under rocks, A. Moussalli & D Stuart-Fox, 11/iii/2005 (W4849); Prince Albert, Meiringspoortberg (33.4167°S:22.5500°E), 1850–2000 m, K.H. Barnard (NMH 1937.12.30.1344). <u>Coastal southern Cape (Wilderness–Tsitsikamma–St Francis Bay)</u>: Wilderness area (33.983°S:22.583°E), indigenous forest, J.S. Taylor, 1964/5 (V5196, V6578, V6579, V6580); Wilderness, Kaaimansrivier (33.983°S:22.583°E), J.S. Taylor, 21/xi/1964 (V5198); Wilderness, Touwsrivier (33.983°S:22.583°E), J.S. Taylor, 19/ix/1964 (V5197); Wilderness Nat. Park, Touwsrivier (33.98348°S:22.60949°E), indigenous forest, deep in leaf-litter, A. Moussalli & D. Stuart-Fox, 13/iii/2005 (W4784); Sedgefield (34.0333°S:22.7833°E), C. Vernon, 15/iii/
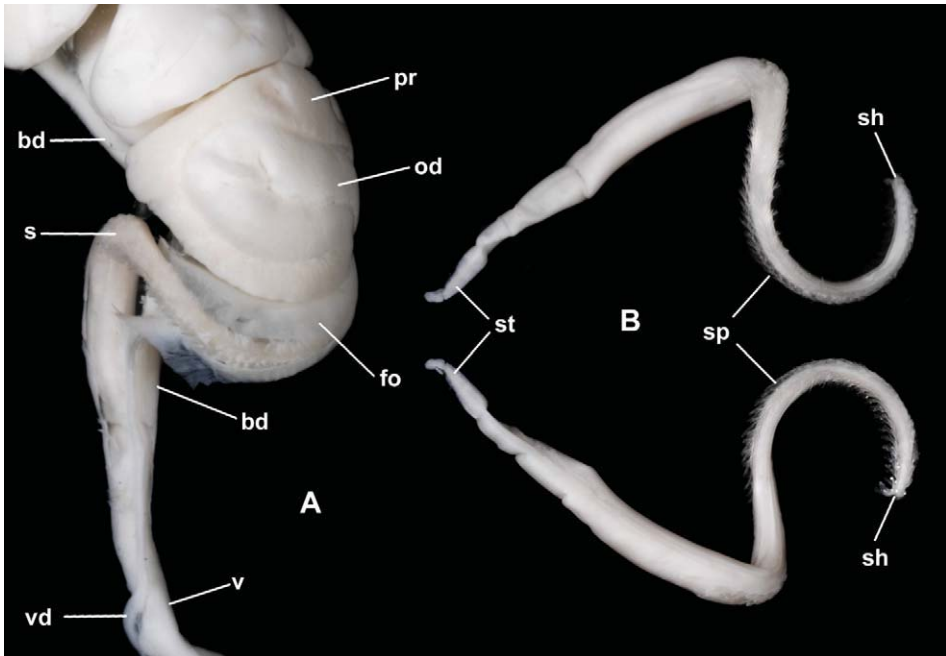

Fig. 62. *Afrorhytida kraussi kraussi* (Pfeiffer, 1846) spermatophore (NMSA W5803): (A) *in situ* in upper portion of vagina and free oviduct (wall opened); (B) extracted spermatophore, total length 20 mm (straightened). Abbreviations: bd – bursa copulatrix duct, fo – free oviduct, od – oviduct, pr – prostate, s – spermatophore, sh – head of spermatophore, sp – spines on anterior region of spermatophore, st – tail of spermatophore, v – vagina, vd – vas deferens.

1985 (ELM D11079); 4 km west of Keurhoek (33.95191°S:22.91220°E), indigenous forest, A. Moussalli &
D. Stuart-Fox, 12/iii/2005 (W4747); Knysna Forest (holotype *Natalina liliacea*) (34.033°S:23.033°E) (ISNB/
MT/525059); ditto, MacAndrew coll'n, *ex* Preston, 19/vi/1911 (BMNH 1563); Knysna, Featherbed Nat.
Res. (34.08040°S:23.06361°E), indigenous forest, in leaf-litter, A. Moussalli, 22/viii/2006 (W4671); Knysna,
Diepwalle region, vicinity of King Edward VIII tree (33.95656°S:23.15256°E), 423 m, indigenous forest,
in deep leaf-litter, A. Moussalli & D. Stuart-Fox, 12/iii/2005 (W4845); Knysna area, Harkerville Nat. Res.,
Kranshoek Trail (34.08713°S:23.22577°E), 29 m, Afrotemperate forest, under rock, A. Moussalli, 21/viii/
2006 (W4667); Nature's Valley, Salt River area (33.983°S:23.533°E), indigenous forest, D. Herbert, 19/ix/
2003 (W1178); Tsitsikamma Mountain, Formosa Peak Trail (33.86390°S: 23.70190°E), fynbos, under rocks,
M. Cunningham, 05/iii/2003 (W3212); Baviaanskloof wilderness area, Kougaberge (33.67492°S:
24.20997°E), fynbos, under stones, D. Herbert, 10/x/2000 (V8621); Van Staden's River (*ca* 33.75°S:25.20°E),
1891 (V7799); Lady's Slipper Nat. Res., Van Stadensberg, (33.89091°S:25.26659°E), montane fynbos,
amongst rocky outcrop after fire, A. Moussalli & D. Stuart-Fox, xii/2005 (W6176); ditto (33.88941°S:
25.27019°E), 560 m, Kouga grassy sandstone fynbos with abundant *Watsonia*, in pockets of fine dark soil
on rock outcrops, D. Herbert, L. Davis & M. Cole, 08–057, 22/ix/2008 (W6426).

Additional literature records (material not seen): Langeberge, Zuurbrak Peak (33.85°S:20.65°E), 1400 m
(Connolly 1939); Swartberg Pass, Platberg (33.317°S:22.030°E), *ca* 1550 m, under stones, 5–6/i/1951
(Bruggen 1970); Outeniqua, George District, Krauss (Connolly 1939); Outeniqua Mts, Robinson Pass
(33.8830°S:22.0167°E), 615 m, under stones, 7/i/1951 (Bruggen 1970); Montagu Pass, Doorn River
(33.883°S:22.430°E), Haughton (Connolly 1939); Knysna (34.033°S:23.033°E), Power (Connolly 1939);
Plettenberg Bay, Keurbooms River bush (34.017°S:23.417°E), Barnard (Connolly 1939, as *N. liliacea*);
Kromme River (? Kromrivier, Kareedouberge, 33.99°S:24.30°E), Moran (Connolly 1939).

Rejected literature records: Grahamstown (33.300°S:26.533°E), Miss Glanville, *fide* Layard (Connolly 1939);
Great Fish Point area, Tharfield farm (33.5500°S:27.0167°E), Miss Bowker (Connolly 1939).

Distribution (Fig. 63): Endemic to the south-central regions of the Cape, from the western
Langeberge in the west, eastwards to Van Stadensberg in the St Francis Bay area, from
the coastal hinterland through the Outeniekwaberge and reaching the Groot Swartberge
inland of the Little Karoo; from low altitudes near the coast to 2000 m in the Groot
Swartberge. Literature records from further east (Grahamstown and Great Fish Point)
are almost certainly incorrect, despite being recorded by Connolly (1939). More probably
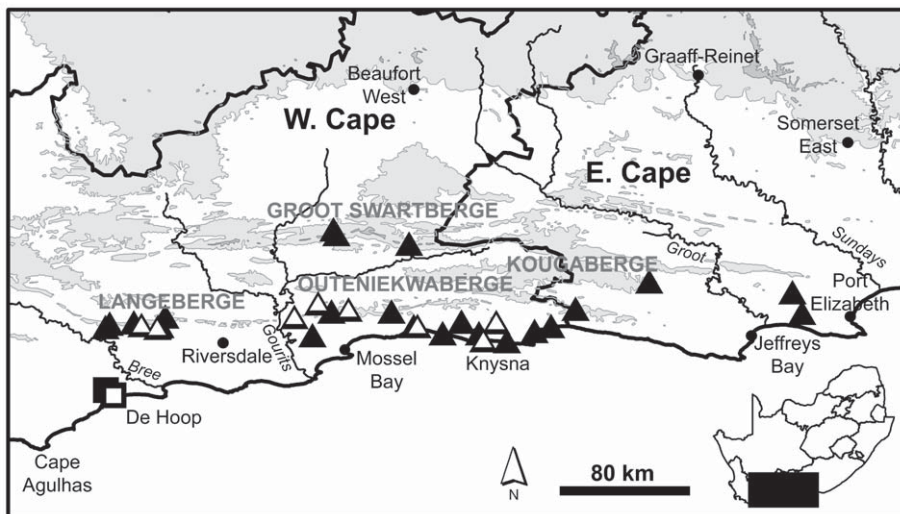they refer to specimens of *Afrorhytida knysnaensis* or *A. trimeni*. For most of its range,

Fig. 63. Distribution of *Afrorhytida kraussi* (Pfeiffer, 1846): *A. k. kraussi* (triangles), *A. k. oraria* subsp. n.
(squares). Symbols with a white centre indicate localities for specimens used in DNA analyses
(Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

A. kraussi is the only *Afrorhytida* present, but there is possible sympatry with both *A. knysnaensis* and *A. trimeni* in the greater Port Elizabeth area.

Habitat: Evidently occurs at low density in a wide variety of habitats from southern Afrotemperate forest to sandstone fynbos at higher altitudes in the mountains of the Cape Fold Belt; in leaf-litter and under logs in forest habitats, and under rocks, amongst clumps of vegetation and in pockets of soil on rock outcrops in fynbos habitats.

Notes: Shells vary considerably in shape, size and umbilical width. Those from fynbos habitats at higher altitudes tend to be smaller, whilst those from isolated forests in the west (e.g., Grootvadersbosch) tend to be largest. The latter also have conspicuously more red pigmentation on the head-foot and furthermore appear to constitute a genetically distinct lineage (Moussalli *et al.* 2009). Similarly, Tolley and Burger (2007) have also shown that the Grootvadersbosch population of the dwarf chameleon *Bradypodion damaranum* (Boulenger, 1887) is genetically distinct from the remaining population in the Outeniekwa–Tsitsikamma region. The Grootvadersbosch forest is also home to two narrowly endemic subulinid land snails, *Euonyma barnardi* Connolly, 1929 and *E. decipiens* Connolly, 1929.

Synonymy: Melvill and Ponsonby (1898) and Connolly (1912, 1939) treated *Helix sturmiana* Pfeiffer, 1853 as a synonym of the present species. The holotype originated from the Cuming collection and was of unknown provenance, but Pfeiffer later cited Delagoa Bay (environs of Maputo, Mozambique), though without explanation (Pfeiffer 1878 in 1878–81). Since no *Afrorhytida* species are known from north of E. Cape, this is without doubt erroneous. The holotype is almost identical in shape to specimens of *A. kraussi* from the Wilderness area (compare Figs 61J and 61K) and it is quite possible that early collectors could have obtained material from this region. We concur with prior authors in treating *Helix sturmiana* Pfeiffer, 1853 as a synonym of *A. kraussi*.

Connolly (1939) correctly noted that *Natalina liliacea* Preston, 1912 was less globose than [typical] specimens of *Afrorhytida knysnaensis*, but it is puzzling that he did not compare it with *A. kraussi*, particularly given that the localities he cited for *N. liliacea* overlap extensively with those he gave for *A. kraussi*. We consider that the pinkish lilac blush typically seen in the aperture of *N. liliacea* (and from which the name derives) is a character likewise present in fresh specimens of *A. kraussi kraussi*. Although Pfeiffer (1846*c*) did not mention this in his original description of *Helix kraussi*, when discussing the species Krauss himself stated 'Die Mündung selbst ist be dem kleinen und wohlerhalten Exemplar blass violett' ['The aperture itself of the small and well preserved specimen is pale violet'] (Krauss 1848: 77). Connolly indicated that the shell of *N. liliacea* was 'prone to assume a distinct lilac hue in rather weather-worn condition' indicating that he misinterpreted the origin of the species name which relates to a feature of fresh rather than weather-worn shells. Since we can find no characters by which these two nominal taxa can be distinguished, we place *Natalina liliacea* Preston, 1912 in synonymy with *Afrorhytida kraussi kraussi*. The type localities (Knysna and the George district respectively) are not far distant (<60 km apart), and a forested habitat is specifically mentioned for both.

Conservation: *Afrorhytida kraussi kraussi* occurs over an extensive area of the southern Cape (E–=W distance approx. 450 km) and is known to occur in a number of formally protected areas. These include both low altitude forest habitats as well as montane
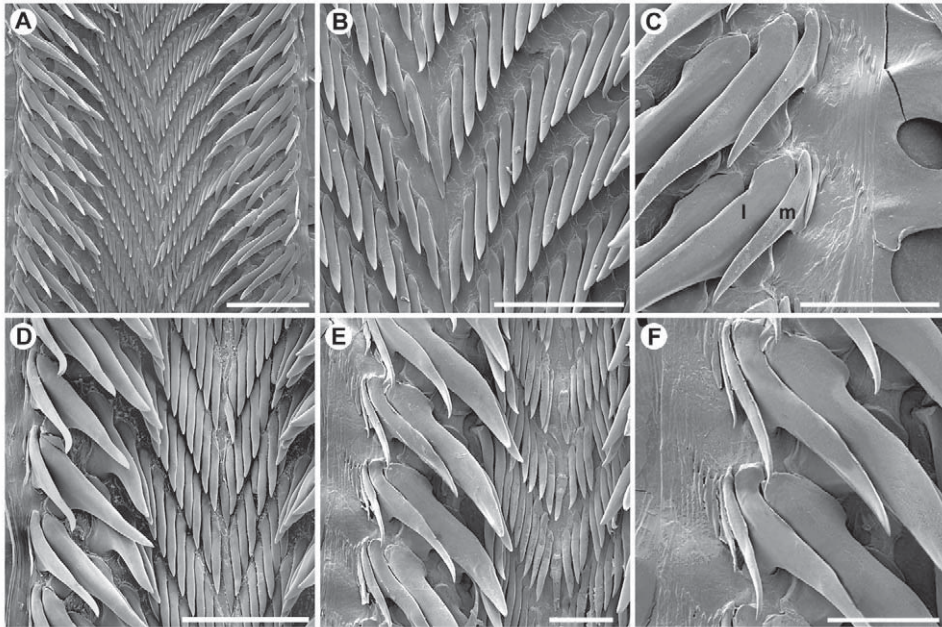
Fig. 64. *Afrorhytida kraussi* (Pfeiffer, 1846), radula (all NMSA): (A–D) *A. k. kraussi*: (A–C) Diepwalle,
Knysna (W4845): (A) entire width of radula, scale bar = 0.5 mm; (B) rachidian and inner laterals,
scale bar = 250 µm; (C) outer lateral base-plates and marginals, scale bar = 200 µm (l – outer
lateral; m – inner marginal); (D) Grootvadersbosch (W3351), half-row, scale bar = 0.5 mm; (E,
F) *A. k. oraria* subsp. n., De Hoop (paratype, W3292/T2363); (E) half-row, scale bar = 100 µm;
(F) outer lateral base-plates and marginals, scale bar = 100 µm.

sandstone fynbos. This notwithstanding, fynbos habitats in much of the central Cape
Fold Belt are subject to aggressive invasion by alien plants (pine and hakea) which
threatens large-scale habitat transformation and degradation (Cowling *et al.* 2009). The
potentially distinct western lineage appears to be restricted to isolated forest patches of
limited extent and is likely to meet the criteria for red-listing on account of its narrow
range, should this eventually be shown to be a distinct taxon.

Afrorhytida kraussi oraria subsp. n.

Figs 55F, 63, 64E, F, 65A–C

Etymology: From *orarius* (Latin), of the coast; referring to its association with coastal
fynbos and dune strandveld habitats.

Identification (Fig. 65): For general description see *Afrorhytida k. kraussi* above. Shell
shape and sculpture resembling *A. k. kraussi*, but with distinctive coloration (see below);
protoconch smaller (diameter 2.5–3.0 mm) and shell thicker. Does not appear to attain
as large a size as the nominotypical subspecies (diameter of largest specimens 23.1 and
28.4 respectively), but adult size evidently varies considerably in the latter.

Periostracum very thin, pale buff, not evident in most specimens; underlying shell
mostly whitish with apical region frequently darker, pinkish purple to maroon; last
adult whorl often with occasional, irregular, purplish or maroon-brown axial bands,
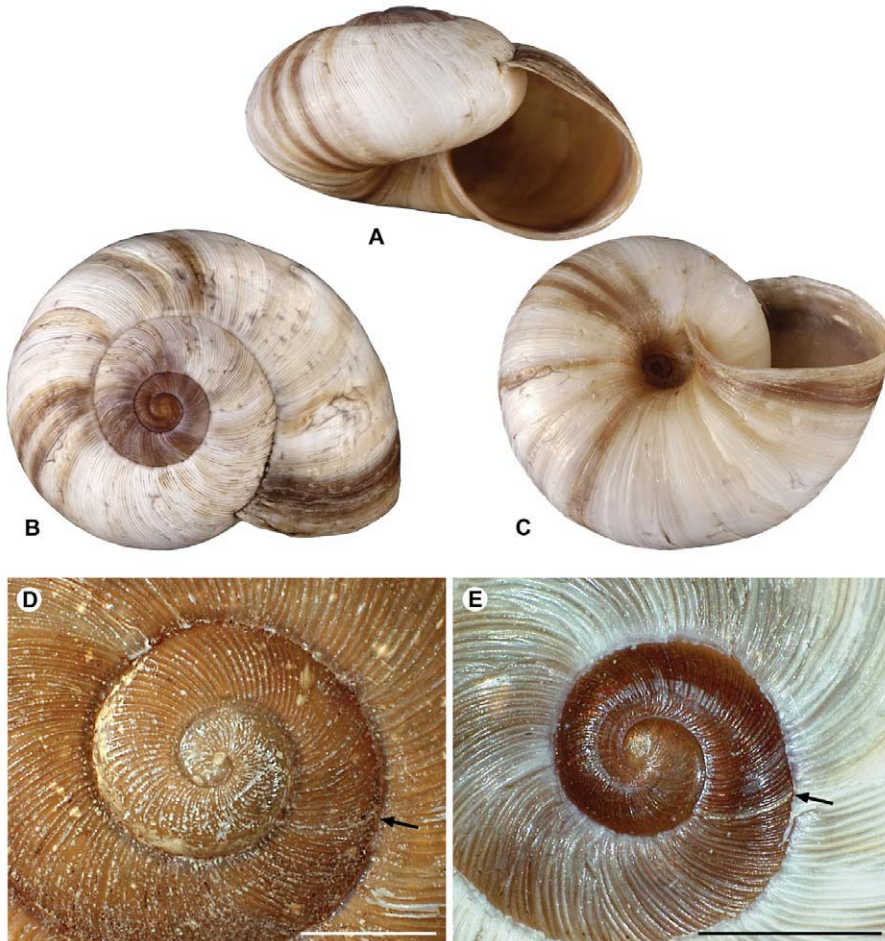
Fig. 65. *Afrorhytida kraussi* (Pfeiffer, 1846) (all NMSA): (A–C) *A. k. oraria* subsp. n., holotype (fresh specimen, V6780/T2361), De Hoop Nat. Res., diameter 22.3 mm; (D) *A. k. kraussi*, protoconch, Wilderness (V6578); (E) *A. k. oraria* subsp. n., protoconch, De Hoop Nat. Res. (paratype, W3292/T2363). Scale bars = 2.0 mm; arrows mark protoconch/teleoconch junction.

particularly behind outer lip of adult. Shell also sparsely pock-marked with small, dark flecks, these often associated with small growth imperfections; interior of aperture buffish in fresh specimens, the darker subterminal band, if present, visible through shell.

Dimensions: Holotype, diameter 22.3 mm, height 13.3 mm; largest specimen (NMSA W3297), diameter 23.1 mm, height 13.3 mm; H:D of adults 0.56–0.64 (N=12).

Living animal (data available for only one specimen) (Fig. 55F): Head-foot coloration similar to that of typical *A. k. kraussi*, but somewhat darker maroon-brown, very dark dorsally; pedal margin tinged with orange; mantle edge similarly maroon-brown; lung wall with some irregular dark pigmentation, mostly tracking underlying blood vessels.

Radula (Figs 64E–F): As in *A. k. kraussi*.

Distal genitalia: All live-taken material immature.

Holotype (Figs 65A–C): SOUTH AFRICA: *W. Cape*: De Hoop Nat. Res. (34.450°S:20.383°E), 60 m, W. Sirgel, don. i/1999 (NMSA V6780/T2361).

Paratypes: SOUTH AFRICA: *W. Cape*: De Hoop Nat. Res. (34.47512°S:20.51969°E), coastal dune scrub, in leaf-litter, A. Moussalli & D. Stuart-Fox, 24/ii/2005 (NMSA W3292/T2363, 1 juvenile specimen; W3297/T2362, 8 adult specimens, 2 juveniles; ELM D15857, 1 specimen); De Hoop Nat. Res., around Koppie Alleen (34.4667°S:20.5167°E), ground-dwelling in strandveld, A. Wood, 22/viii/1994 (NMSA W5776/T2364, 2 specimens).

Distribution (Fig. 63): A narrow-range endemic; known only from the De Hoop Nature Reserve, W. Cape, South Africa, at altitudes of <100 m.

Habitat: Recorded only from De Hoop limestone fynbos and Overberg dune strandveld (cf. Mucina & Rutherford 2006); in sandy soil beneath forbs, shrubs and bushes.

Notes: The considerable degree to which *Afrorhytida k. oraria* differs in shell characters from the nominotypical subspecies would traditionally result in it being considered a distinct species. However, in the analysis of molecular data undertaken by Moussalli *et al.* (2009), this De Hoop material clustered within the broader assemblage of material considered to represent the *A. kraussi* complex. Its radula too is indistinguishable from that of members of this complex. Although this assemblage exhibits considerable genetic diversity and may ultimately be shown to be an aggregate of sibling taxa, with the exception of specimens from De Hoop, we have been unable to identify any consistent spatially or genetically correlated patterns in the morphological variation evident. However, since this De Hoop material is clearly conchologically distinct, we consider it merits nomenclatural recognition as a diagnosable entity, ranked for the present as a subspecies. We are aware, however, that some of the conchological characters of this coastal lineage may relate to environmental conditions, particularly edaphic characters (calcium-rich soils) and this is a topic requiring further study.

Conservation: *Afrorhytida k. oraria* is evidently a taxon of restricted range, but it occurs in a surprisingly poorly sampled area and additional survey work is needed in order to obtain a clearer picture of its distribution. Although currently known only from De Hoop Nature Reserve, the coastal limestone habitat, which it evidently favours, extends considerably beyond the confines of this reserve in the broader Bredasdorp–Stilbaai area. The taxon may thus have a somewhat less restricted distribution than the available data indicate. A meaningful assessment of its threat status must await further information, but this notwithstanding, potential threats are evident, particularly habitat transformation due to the invasion of exotic *Acacia* species.

Afrorhytida burseyae sp. n.
Figs 10B, 54D, 55G, 66–69

Etymology: Named for Mary Bursey (now Cole), malacologist at the East London Museum who has collected much valuable land snail material and helped enormously with field logistics.

Identification: Shell very similar to that of elevated specimens of *A. knysnaensis*, but with a somewhat narrower umbilicus. Differs consistently from that species in having more lateral teeth and fewer marginal teeth in the radula (Table 2), and comprises a distinct genetic lineage within *Afrorhytida*. Evidently restricted to the region encompassing the catchments of Kei and Mbashe rivers, whereas *A. knysnaensis* occurs further to the west, in the catchments of the Sundays and Great Fish rivers.
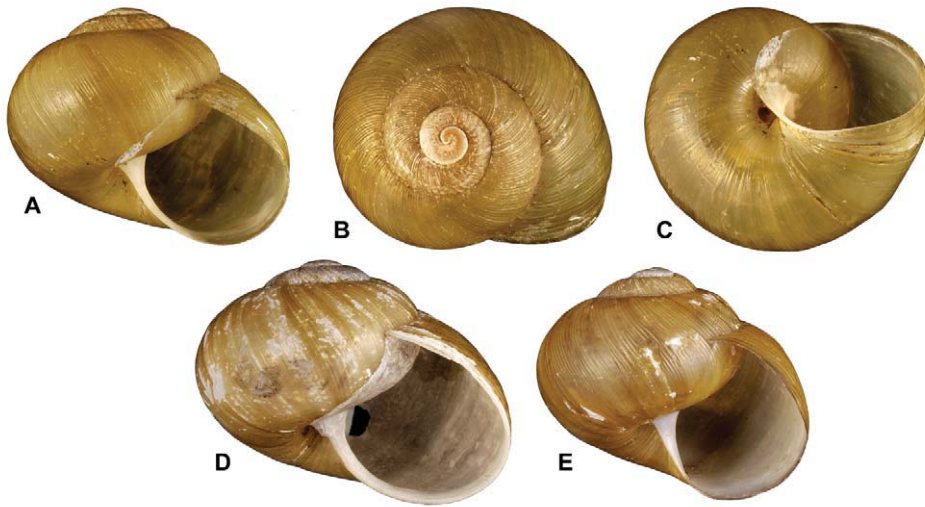
Fig. 66. *Afrorhytida burseyae* sp. n.: (A–C) holotype (NMSA W5228/T2257), diameter 21.1mm; (D) Engcobo, paratype (SAMC 11289), diameter 23.8 mm; (E) Kei Pass, paratype (NMSA W5484/T2347), diameter 21.8 mm.

Description (Fig. 66): Shell subglobose, somewhat turbiniform; comprising up to 4.5 whorls, last adult whorl descending prior to aperture, but sometimes only weakly so; base glossy, apical surface less so, but still retaining some lustre when fresh. Protoconch 4.4–5.0 mm in diameter; apical portion more or less smooth, axial riblets developing during first whorl, initially weak, but strengthening toward end of whorl; protoconch/teleoconch junction usually poorly defined. Apical surface of teleoconch sculptured by close-set axial riblets, these becoming weaker and less well defined toward end of last adult whorl and on base; traces of weak, close-set, spiral liration between axial riblets, particularly on base; aperture subcircular to roundly-ovate; outer lip slightly thickened basally though scarcely so elsewhere (but most specimens slightly subadult and lip rather thin throughout); upper part of outer lip not flattened; umbilicus narrow, its margin rather steeply curving, partially obscured by reflected upper portion of columella lip in adults.

Fresh specimens more or less uniformly yellow-ochre to olive-green; little difference between apical and basal surfaces; occasional very slightly darker radial bands may be present.

Dimensions: Holotype, diameter 21.1 mm, height 17.5 mm; largest specimen (NMSA V6634, 'Pondoland'), diameter 26.4 mm; H:D of adults 0.74–0.87 (N=16).

Living animal (Fig. 55G): Head-foot pale apricot-orange to pale grey-brown; neck region somewhat darker brown, sometimes with a paler, dorsolateral, longitudinal stripe on each side extending backwards from optic tentacle; tentacles darker grey; sides of foot generally pale, often with a narrow orange band at pedal margin; mantle edge greyish white to apricot-orange; lung wall with limited black pigmentation.

Radula (Fig. 67): Formula 1+(12–14)+(7–9) (N=4); length up to 15.4 mm, with 60–70 V-shaped rows of teeth, 4.3–4.6 rows/mm in adult. Rachidian cusp somewhat longer
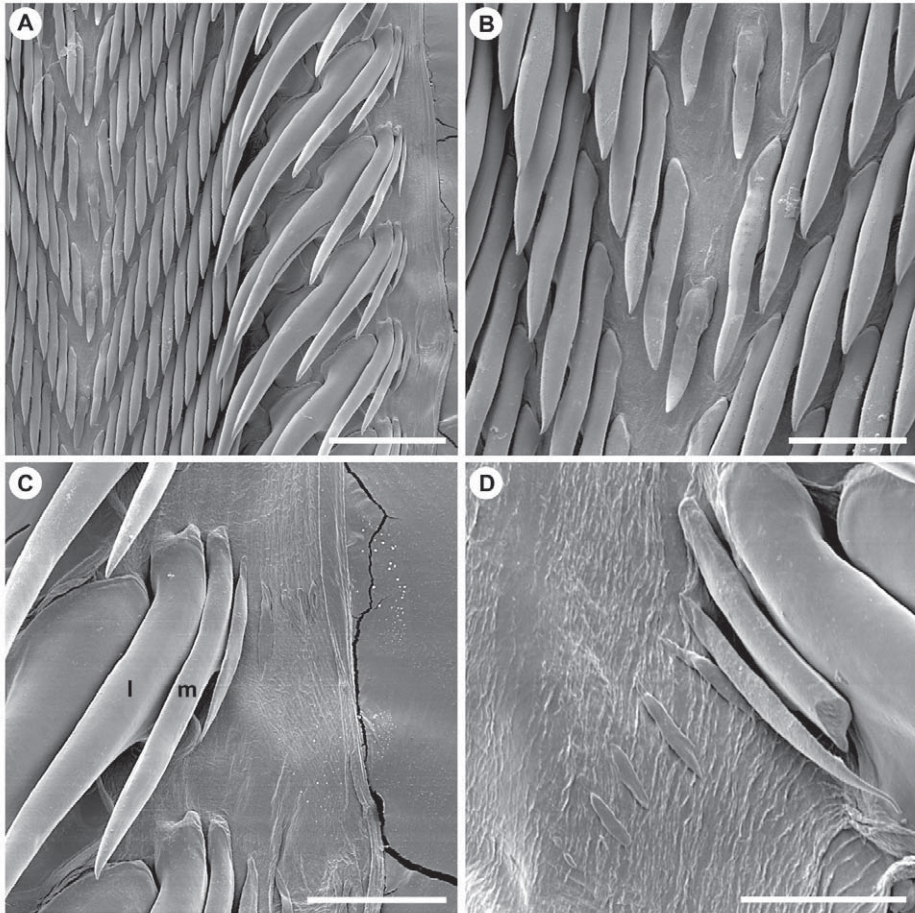
Fig. 67. *Afrorhytida burseyae* sp. n., radula (holotype, NMSA W5228/T2257): (A) half width of radula, scale bar = 250 µm; (B) rachidian and inner lateral teeth, scale bar = 100 µm; (C) lateromarginal transition zone, scale bar = 100 µm (l – outer lateral; m – inner marginal); (D) marginal teeth [7], scale bar = 50 µm.

than its base-plate. Inner lateral teeth (1–10) differing little in size, long and slender, more or less parallel-sided, apically acuminate with the tip sometimes slightly curved outward; outermost 3 or 4 lateral teeth increasing rapidly in size and developing stout quadrate base-plate, with relatively slender, gently curved, sharply pointed cusp; penultimate lateral is the largest. Innermost marginal tooth relatively large (approx. 0.66 length of outer lateral), second marginal retaining distinct cusp but subsequent marginals vestigial.

Distal genitalia: Epiphallus approx. 75 % length of penis; thick-walled for most of its length and frequently strongly curved; lumen wall with low, indistinct ridges between which are numerous, close-set, transverse pockets, representing openings of diverticulae in epiphallus wall (Fig. 54D); these concentrated in middle two-thirds corresponding with spinose mid-piece of spermatophore; sparse toward vas deferens and junction with penis.
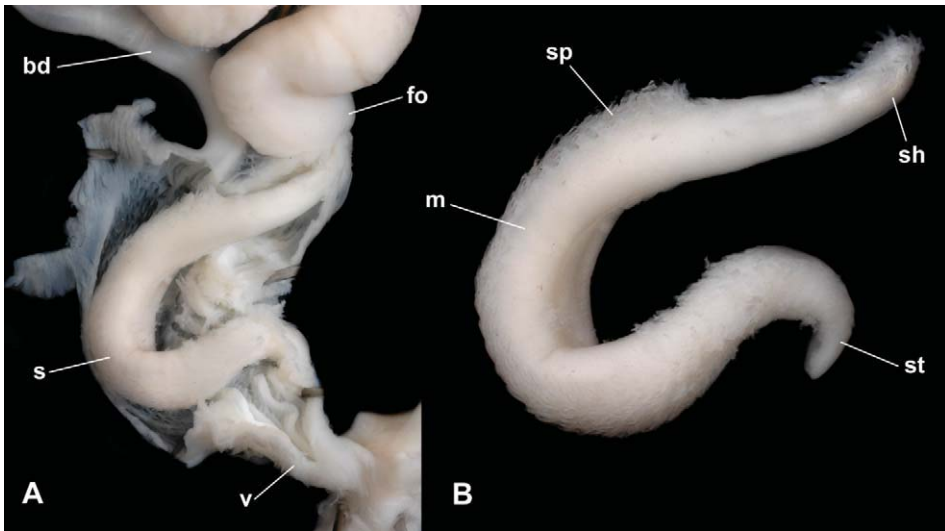
Fig. 68. *Afrorhytida burseyae* sp. n., spermatophore (paratype, NMSA W5231/T2260): (A) *in situ* in dissected upper portion of vagina and lower free oviduct, (B) extracted spermatophore, total length 10.5 mm. Abbreviations: bd – bursa copulatrix duct, fo – free oviduct, m – mid-piece of spermatophore, s – spermatophore, sh – spermatophore head, sp – spines on outer surface of mid-piece, st – spermatophore tail, v – vagina.

Spermatophore (Fig. 68): Well preserved allospermatophores have been found in the female tract of two specimens collected in early March, one per specimen. Spermatophore white to pale pink, U-shaped and of firm texture, evidently variable in size (about 6.5 mm and 10.5 mm in total length); comprising three distinct regions, a bluntly acuminate head, a broader, U-shaped mid-piece and a short, recurved tail. Inner surface of bend with a deep, longitudinal depression or groove, but otherwise spermatophore lacking strong longitudinal grooves/ridges; outer surface of mid-piece bearing numerous, small, close-set, forwardly directed, spine-like projections pressed flat against its surface; spines compound (finely branched apically); tail and head piece with few spines. No obvious vent present in the tail region, but spermatophore contents visible in inner groove of mid-piece in one specimen.

Spermatophores situated in upper part of vagina, in one specimen the head extended into base of free oviduct, in the other it extended into base of bursa copulatrix duct. Anterior half of mid-piece level with origin of bursa copulatrix duct and end of free oviduct, tail extending backward into lower, longitudinally ridged portion of vagina.

Surprisingly the spines on the mid-piece are directed toward the head region, an orientation which might impede rather than facilitate the passage of the spermatophore within the vagina, suggesting that it is deposited in this position by the penis of the partner during copulation. Even so, this orientation would seem to hinder its release from the epiphallus into the penis. The spines, however, appear less rigid than in other species suggesting a degree of flexibility. They may serve an anchoring function, holding the spermatophore in place once deposited.

Holotype (Figs 66A–C): SOUTH AFRICA: *E. Cape*: Wedgeley farm, Kei R. valley, NNE of Stutterheim, (32.28986°S:27.54674°E), 845 m, grassy bushveld, crawling at night on grass and stones beside farmhouse after rain, D. Herbert & L. Davis, 4/iii/2007 (NMSA W5228/T2257).

Paratypes: SOUTH AFRICA: *E. Cape*: same data as holotype (ELM D15855, 1 specimen; BMNH 20100126, 1 specimen; NMSA W5229/T2258, 3 specimens; NMSA W5230/T2259, 1 specimen; NMSA W5231/T2260, 1 specimen); Engcobo (31.66°S:28.00°E), *ca* 975 m (SAMC A11289, 1 specimen); Cathcart (32.29241°S: 27.13567°E), 1210 m, montane grassland/bushveld, small juvenile on grass blade, A. Moussalli, D. Stuart-Fox & M. Bursey, 30/xi/2005 (NMSA W4844/T2261, 1 specimen, juvenile); Sterkstroom, Koos Ras Nat. Res. (31.54935°S:26.57283°E), 1440 m, rocky outcrop with trees and shrubs, buried under grass clump, Herbert, Davis, Cole & Fearon, 09–005, 29/iii/2009 (NMSA W6712/T2489, 2 specimens, subadult); Mbashe River valley nr N2 bridge (31.92461°S:28.45113°E), 465 m, riverine thicket, in leaf-litter and under fallen aloes, A. Moussalli & D. Stuart-Fox, 23/xi/2005 (NMSA W5372/T2349, 3 specimens); Kei Pass (32.49364°S: 27.99175°E), 270 m, valley thicket, under rocks, A. Moussalli & D. Stuart-Fox, 23/xi/2005 (NMSA W5484/ T2347, 1 specimen); Gonubie R., Slippery Drift (32.80055°S:27.85583°E), *ca* 200 m, Jansen, 28/xii/2002 (ELM D13766, 1 specimen); East London area, 20 km inland, nr Nahoon Dam, Elizweni resort (32.915297°S: 27.818867°E), 140 m, thicket on north facing slope above Nahoon R., in leaf-litter, M. Bursey, 18/i/2007 (NMSA W5252/T2346, 2 specimens); ditto, Elizweni resort, on west bank of Nahoon R., M. Bursey, 18/iv/ 2006 (ELM D14971, 5 specimens); Berlin area, Mncotsho, Buffalo R. valley (32.917°S:27.583°E), *ca* 360 m, grassland with scattered bushes near beacon, M. Cole & C. Vernon, 06/xi/2007 (NMSA W6004/T2348, 3 specimens).

Other material examined: SOUTH AFRICA: *E. Cape*: Bailey, *ca* 1300 m, Miss Hickey (NMSA B0097); Ugie, *ca* 1300 m, Miss L. Britten, i/1923 (NMSA E7906); 'Pondoland', Mrs A. Filmer (NMSA V6842, V6634).

Distribution (Fig. 69): Endemic to E. Cape; recorded primarily from inland localities in the Great Kei River catchment and eastwards to the Mbashe and Mzimvubu catchments, but recorded also from smaller coastal drainage systems in the East London area (Buffalo, Nahoon and Gonubie rivers); occurs at altitudes of 140–1440 m.

Habitat: Evidently favours somewhat open habitats rather than forest; recorded from a range of vegetation types including grassy bushveld, montane shrubland and various types of thicket; hiding under fallen aloes and in grass clumps between rocks.
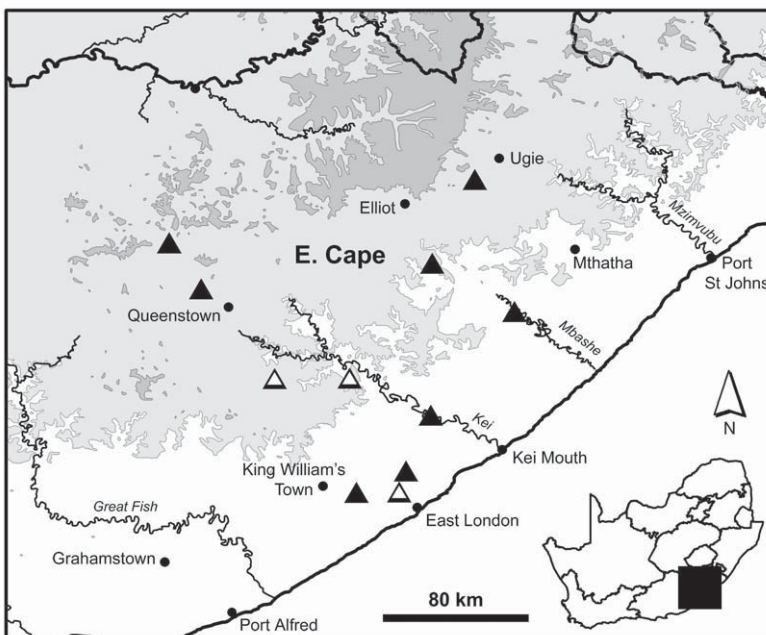

Fig. 69. Distribution of *Afrorhytida burseyae* sp. n. Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009); contours at 1000 m and 1500 m.

Notes: This species was initially thought to represent *Natalina eumacta* (Melvill & Ponsonby, 1892). However, examination of the holotype of that species BMNH (1905.1.26.2, Figs 24A–C) shows it to be considerably larger (diameter 30.3 mm) than any specimens of the present species. In addition it is not as globose, has a larger proto-conch and lacks any thickening of the aperture lip. We consider that *N. eumacta* represents the eastern coastal subspecies of *Natalina cafra* (see above).

The shell of *Afrorhytida burseyae* closely resembles that of elevated specimens of *A. knysnaensis* such as occur in the Greater Fish River Conservancy, and indeed it cannot be reliably distinguished from such specimens on shell features alone. Although few specimens have been observed alive, the head-foot colour of *A. burseyae* also resembles that of some specimens of the variably coloured *A. knysnaensis* and, given this variability in the latter species, body colour also seems unlikely to prove useful for species discrimination. However, the radula of *A. burseyae* differs markedly and con-sistently from that of *A. knysnaensis* in having many fewer marginal teeth and in the penultimate rather than the outmost lateral being largest. In these features it resembles *A. trimeni* from which it differs conchologically in having a considerably more globose, yellowish green rather than brown shell, with weaker axial sculpture and a much narrower umbilicus. Molecular data confirms that *A. burseyae* constitutes a distinct lineage within the *Afrorhytida* radiation, though its relationships to the other species are not resolved (Moussalli *et al.* 2009). Its radula morphology suggests that it is perhaps most closely related to *A. trimeni*, whereas its epiphallus morphology is closer to that of *A. kraussi* (Fig. 54).

Conservation: Although few specimens of *Afrorhytida burseyae* are available, it occurs in a very poorly sampled area and it may not be scarce where conditions are favourable. Its known extent of occurrence is considerable (approx. 15,000 km^2) and given that it favours open habitats, its area of occupancy is not likely to be particularly limited or fragmented. Thus despite being a newly discovered taxon, it seems unlikely that *A. burseyae* is threatened at present. In the long term, however, the continued transformation of natural habitats, associated with agricultural expansion, represents a potential threat, particularly so since the distribution of *A. burseyae* currently includes very few, if any, formally conserved areas.

Afrorhytida trimeni (Melvill & Ponsonby, 1892)

Figs 4B, 54C, 55H, 70–72

Helix (*Aerope*) *trimeni*: Melvill & Ponsonby 1892: 237, pl. 13, fig. 1. Type loc.: given as 'S. Africa', but label states 'Cape Colony' [Trimen].
Natalina tremeni [*sic*]: Pilsbry 1893 in 1892–93: 135.
Natalina trimeni: Pace 1895: 232; Melvill & Ponsonby 1898: 170; Sturany 1898: 31; Connolly 1912: 97; 1939: 114; Barnard 1951: 142, pl. xxi, fig. 7.
Rhytida (*Afrorhytida*) *trimeni*: Möllendorff 1903: 62, pl. 11, fig. 3.
Natalina arguta Melvill & Ponsonby, 1907: 98, pl. 6, fig. 8; Connolly 1912: 90; 1939: 115; Watson 1934: 156, pl. 19, fig. 10 [radula]. Type loc.: East London, E. Cape [Burnup]. **Syn. n.**

Etymology: Named for Roland Trimen (1840–1916), an entomologist and curator at the South African Museum (1872–95), who sent the original specimens to Melvill and Ponsonby.

Identification: The shell of *Afrorhytida trimeni* is characterised by its brownish rather than greenish colour and the fact that the axial sculpture remains distinct even on the

last adult whorl. *A. kraussi kraussi* has a similarly brown shell, but the whorls are less deep and the upper part of its outer lip is usually distinctly flattened; its radula also has more marginal teeth and lacks lateral flanges on the inner laterals. In terms of its radula *A. trimeni* is most similar to *A. burseyae* in that there are relatively few marginals (<10), but in the latter the innermost laterals lack lateral flanges and distinctly uncinate tips. Its shell is also considerably more globose and of a more yellowish green hue. *A. knysnaensis* is likewise generally more globose (except those from the north-west of its range) and more yellowish, and its radula has many more marginal teeth of intermediate size.

Description (Fig. 70): Shell globose-lenticular, spire height generally low but rather variable; comprising up to 4.75 whorls, last adult whorl descending slightly prior to aperture; apical surface lustreless, base more glossy. Protoconch diameter 3.5–4.1 mm, initially somewhat smooth, but with distinct axial riblets developing along adapical suture during first whorl, these extending to abapical suture on second whorl (Fig. 4B); protoconch/teleoconch junction usually poorly defined. Apical surface of teleoconch
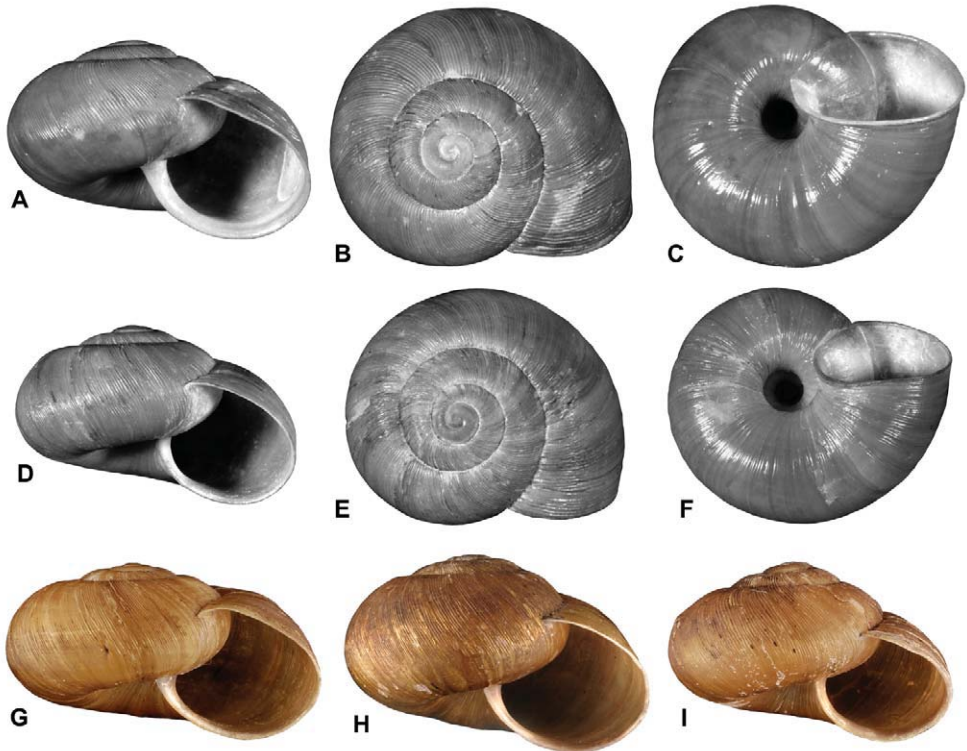
Fig. 70. *Afrorhytida trimeni* (Melvill & Ponsonby, 1892): (A–C) lectotype of *Helix* (*Aerope*) *trimeni* Melvill & Ponsonby, 1892 (BMNH 1911.8.8.3), diameter 23.8 mm; (D–F) holotype of *Natalina arguta* Melvill & Ponsonby, 1907 (BMNH 1911.8.8.6), diameter 20.5 mm; (G) low-spired specimen, Hamburg (NMSA W5254), diameter 25.5 mm; (H) deep-whorled specimen, Kap River Nat. Res. (NMSA W4206), diameter 23.9 mm; (I) high-spired specimen, Umtiza Nat. Res. (NMSA W4182), diameter 20.5 mm.

sculptured throughout by close-set axial riblets, these not becoming noticeably weaker on last adult whorl; riblets weaker below periphery and on base, but becoming stronger again around and into umbilicus; base with traces of weak, close-set, spiral lirae; aperture roundly-ovate; outer lip weakly, but distinctly thickened in adult, white; upper part of outer lip not or only minimally flattened; umbilicus deep and relatively wide, scarcely, if at all obscured by upper part of columella lip.

Fresh specimens more or less uniformly mid brown; little difference between apical and basal surfaces except that the former is dull and the latter glossy; some specimens with faint traces of slightly darker radial banding. Brown colour fading after death and becoming more yellowish brown; old specimens frequently yellow-ochre.

Dimensions: Largest specimen (NMSA W5254, Hamburg), diameter 25.5 mm; H:D of adults 0.56–0.70 (N=18).
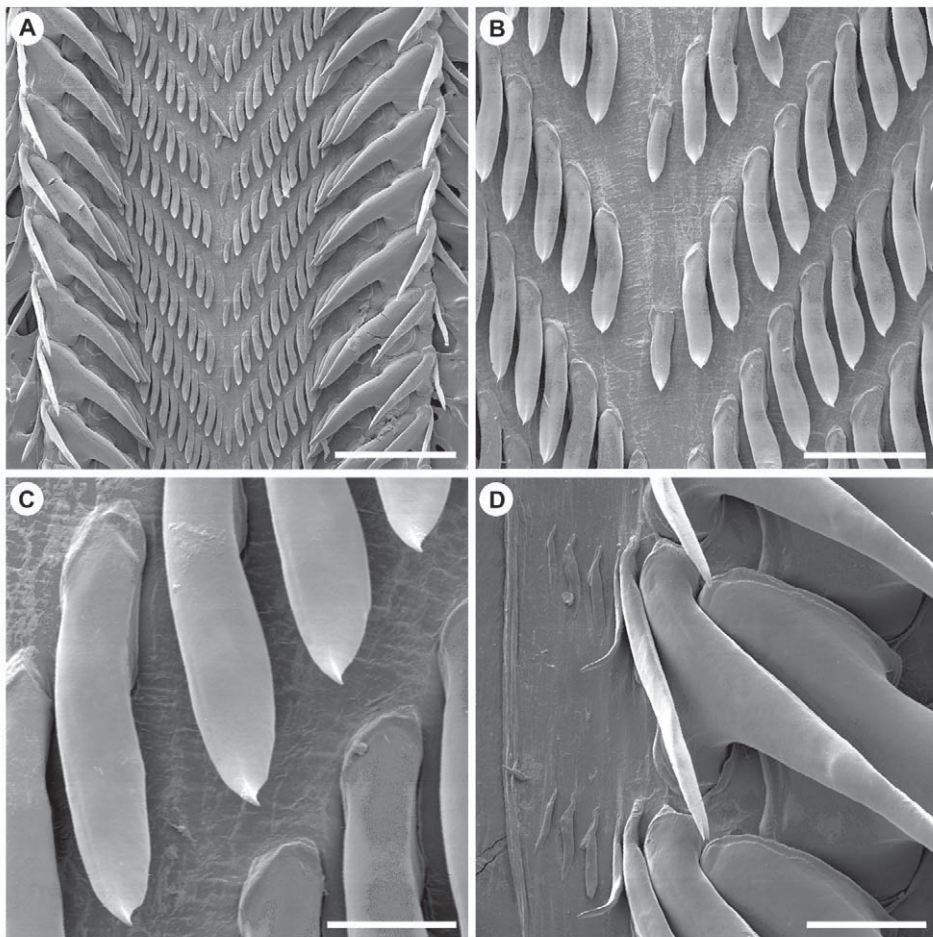
Fig. 71. *Afrorhytida trimeni* (Melvill & Ponsonby, 1892), radula: (A–C) Kap River Nat. Res. (NMSA W4206): (A) entire width of radula, scale bar = 0.5 mm; (B) rachidian and inner lateral teeth, scale bar = 150 µm; (C) inner lateral teeth, scale bar = 50 µm; (D) Umtiza, Nat. Res., East London (NMSA W5253), outer lateral base-plates and marginal teeth, scale bar = 100 µm.

Living animal (Fig. 55H): Information available from photographs of only two specimens. Head-foot grey-brown dorsally, with a paler longitudinal stripe extending backward from each optic tentacle, bordered ventrally by a conspicuous dark, grey-black line, boldest beneath shell; paler dorsal areas slightly tinged with apricot; sides of foot pale greyish white with darker skin grooves, slightly darker just above pedal margin; pedal margin itself whitish, slightly tinged with apricot; tentacles darker grey or grey-brown; mantle edge pale greyish white; lung wall often extensively marked with fine, anastomosing black blotches, not obviously following pattern of lung venation.

Radula (Fig. 71): Formula 1+(13–14)+(6–9) (N=4); length up to 19.5 mm, with 56–76, broadly V-shaped, transverse rows of teeth, 3.9–4.4 rows/mm in adult. Rachidian about two-thirds length of innermost lateral; cusp broadly acuminate, slightly longer than its base-plate. Inner lateral teeth (1–10), relatively short and broad, increasing only slightly in size, their cusps with a lateral flange on outer margin and a bluntly rounded apex bearing a small but distinct uncinate tip (Fig. 71C); outermost 3 or 4 lateral teeth increasing rapidly in size and developing a stout quadrate base-plate, with a strong, gently curved, sharply pointed cusp; penultimate lateral is the largest. Innermost marginal considerably smaller than outer lateral, with a much reduced base-plate, but retaining a distinct cusp; remaining laterals progressively smaller, the fourth and subsequent vestigial.

Distal genitalia: See generic description. Wall of penis lumen coarsely papillate; epiphallus approx. 0.75 length of penis; its internal structure (Fig. 54C) similar to that of *A. knysnaensis* in possessing longitudinal ridges with digit-like tips, except that there are only four such ridges additional to the pair of folds running along the inner wall, and the ridges are longer than in *A. knysnaensis*, extending forwards for approx. 0.75 of epiphallus length from its junction with vas deferens. Anterior to this the lumen wall is smoother, but bears indistinct longitudinal rows of pits running forward from the intervals between the swollen tips of the longitudinal ridges.

Spermatophore: No spermatophores have been found, but the internal morphology of the epiphallus suggests that the mid region and tail will be largely smooth, perhaps only with weak longitudinal furrows, but the anterior portion will bear approx. five rows of small spines on its outer, convex surface.

Type material: Lectotype of *Helix* (*Aerope*) *trimeni* Melvill & Ponsonby, 1892 (designated Connolly 1912: 97) (= figured syntype) in BMNH (1911.8.8.3), diameter 23.8 mm (24.2 mm *fide* Connolly 1939) (Figs 70A–C). Three paralectotypes in NMW 1955.158.736. Holotype of *Natalina arguta* Melvill & Ponsonby, 1907 in BMNH (1911.8.8.6), diameter 20.5 mm (Figs 70D–F); one paratype in NMSA (1495/T593).

Additional material examined (all NMSA unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Grahamstown, C.J. Swierstra, vi/1925 (V5278); ditto, *ex* Farquhar Coll'n (BMNH 1937.12.30.1345); ditto, bottom of Fernkloof, 475 m, under stones, i/1912 (E7908); Kap River Nat. Res. (33.48541°S: 27.08474°E), 65 m, indigenous forest, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Bursey, 9/xii/2005 (W4206); Port Alfred area, nr Kleinemonde, Tharfield farm. Miss E. L Barber (W5986); Begha R., Peddie District, J. Hewitt, xii/1935 (V6849); Hamburg, Keiskamma R. mouth (33.27555°S: 27.48639°E), 3 m, riverine forest on east bank near river mouth, in leaf-litter, M. Bursey, 14/ii/2007 (W5254, ELM W03187); East London, H. Burnup Coll'n (B0032); ditto, Umtiza Nat. Res. (33.016°S:27.809°E), 160 m, coastal forest, in leaf-litter, eating *Chondrocyclus* sp., D. Herbert & M. Bursey, 4/iii/2000 (V7904); ditto (33.016°S: 27.809°E), coastal indigenous forest, under log, A. Moussalli & D. Stuart-Fox, 26/xi/2005 (W4182, W5466); ditto, (33.01444°S:27.80806°E), forest, in leaf-litter, R. Botha, 07/ii/2007, don. M. Bursey (W5253, ELM W03208).

Additional literature records (material not seen): SOUTH AFRICA: *E. Cape*: Coega (Pace 1895); Port Alfred (*fide* Crawford, Connolly 1939).

Distribution (Fig. 72): Endemic to E. Cape Province. Recorded from the Grahamstown–
Port Alfred region east to East London, with one additional literature record from Coega,
near Port Elizabeth (Pace 1895); from sea level to approx. 500 m in the Grahamstown
area.

Records from the Somerset East–Cradock area given by Connolly (1912) were almost
certainly based on misidentified *A. knysnaensis* material (see also Schileyko 2000, fig.
971). He later omitted these records (Connolly 1939), suggesting that he had become
aware of this error. An old radula slide in the NMSA labelled '*Natalina trimeni*, Cradock',
clearly represents the radula of a specimen of *A. knysnaensis*.

Habitat: The limited habitat data available suggests that *A. trimeni* is primarily an in-
habitant of indigenous forest; in leaf-litter and under logs.

Notes: Analysis of molecular sequence data (Moussalli *et al.* 2009) indicates that material
from East London, previously known under the name *Natalina arguta* Melvill & Pon-
sonby, 1907 shows little genetic divergence from *Afrorhytida trimeni*. Likewise there
are no discernable differences in the radula. The reported differences in shell characters,
namely more distinct axial sculpture on the base, wider umbilicus and smaller size in *A.
arguta* (Connolly 1939), appear to be consistent in the limited material available, but
such differences could easily be accommodated within the variation of a single species.
The colour difference mentioned by Melvill and Ponsonby (1907), namely olivaceous
(*trimeni*) *vs* rufous-brown (*arguta*), is not apparent in the specimens available. The
disparity in size appears to be the most striking difference between the two populations.
Two evidently mature shells from East London (Umtiza Nat. Res.), each comprising *ca*
4.75 whorls, measure 19.7 mm and 20.3 mm in diameter, compared to 25.5 mm for a
shell from Hamburg also comprising *ca* 4.75 whorls. The largest shell available from
the East London area is 22.0 mm in diameter (ELM D15190), whereas many mature
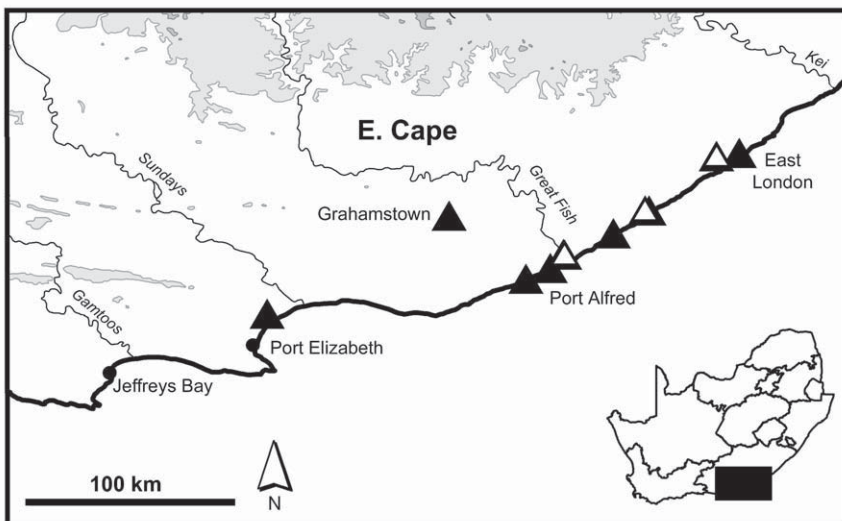
Fig. 72. Distribution of *Afrorhytida trimeni* (Melvill & Ponsonby, 1892). Triangles with a white centre
indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009). Contours at 1000
and 1500 m.

shells from other regions are larger than this. However, given that the East London material is genetically very close to that from other regions (Moussalli *et al.* 2009 and Fig. 1 herein), it may be that the size difference relates to undetermined ecological factors. While acknowledging that this is an issue which needs further investigation, we consider it unlikely that the two nominal taxa represent specifically distinct entities and place the name *Natalina arguta* in synonymy with *A. trimeni*. The most that could be justified would be to recognise the junior name as an eastern subspecies of smaller size, but we refrain from doing this on account of the limited material available, much of which is juvenile or subadult.

Conservation: The distribution of *Afrorhytida trimeni* is somewhat limited, but not highly restricted. Its range spans 230 km in the coastal region and extends up to 40 km inland, but given that it appears to favour forest habitats, its distribution within this range is likely to be fragmented. There are relatively few formally protected conservation areas within this area, but populations are known from both Umtiza and Kap River provincial nature reserves. The preservation of southern coastal forest and southern mist-belt forest habitat within the broader Albany Thicket biome (Mucina & Rutherford 2006) would appear to be important for the conservation of this species.

Genus *Capitina* Watson, 1934

Capitina: Watson 1934: 153. Type species: *Helix schärfiae* [= *schaerfiae*] Pfeiffer, 1861, by original designation.

Diagnosis: Shell of moderate size (adult diameter up to 34 mm), discoidal to globose-lenticular, usually with distinct spiral colour pattern; sculptured by anastomosing axial riblets producing a somewhat pitted or wrinkled sculpture; outer lip slightly thickened and without periostracal fringe; peristome interrupted in parietal region; umbilicus open, width moderate; protoconch of 1.25–1.5 whorls, with close-set axial riblets (Fig. 4C) and often with traces of spiral sculpture, diameter 4.0–7.0 mm. Radula possessing rachidian tooth; no clear distinction between lateral and marginal series and no one tooth noticeably larger than the others. Mantle lobe to left of pneumostome undivided. Penis very long, situated to left of retractor muscle of right optic tentacle; epiphallus short (<25 % of penis length); epiphallus and lower vas deferens connected to penis by connective tissue web; vagina very long; oviduct caecum absent. Distal part of suprapedal gland sinuous but not convoluted, lacking a swollen terminal vesicle.

External anatomy (Fig. 76): Left body lobe of mantle undivided, forming a continuous skirt over neck region (Fig. 6B); skin texture finely to moderately granular; labial palps present but not large; optic and inferior tentacles with a ventrally distended apical bulb; tail region of foot relatively short; genital pore ventral and just posterior to right optic tentacle; lung venation strongly delineated by black pigmentation.

Radula (Fig. 73): Formula 1+(20–32); length up to 15.5 mm, with up to 84 V-shaped transverse rows of teeth, 5.0–6.6 rows/mm in adult; no clear distinction between lateral and marginal series. Rachidian present, with a relatively short, broad cusp, one quarter to one third length of base-plate; remaining teeth (laterals and marginals), elongate and slender, progressively (slowly) increasing in size, those in middle of lateromarginal series largest, then decreasing in size somewhat more rapidly toward edge of radula, the outermost tooth being minute; inner teeth claw-like, with a relatively short, weakly
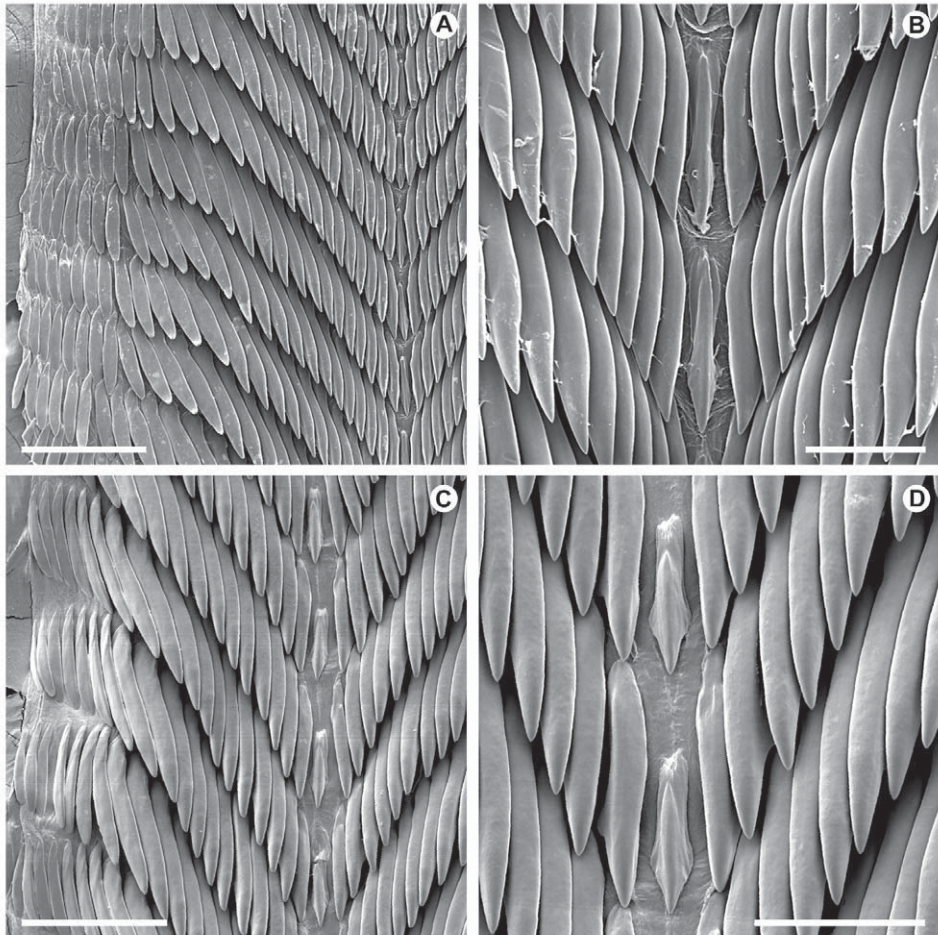
Fig. 73. *Capitina* species, radula: (A, B) *Capitina schaerfiae* (Pfeiffer, 1861), Oubos (NMSA W5672), scale
bars = 300 μm and 100 μm; (C, D) *Capitina calcicola* sp. n., Cape Agulhas (paratype, NMSA
W3360/T2270), scale bars = 200 μm and 100 μm.

curved, broadly acuminate cusp; larger teeth in middle of lateromarginal series with a
flatter, more elongate cusp, but lacking an enlarged quadrate base-plate; those peripheral
to this becoming spathulate, with a rounded tip and anteriorly acuminate base-plate.

Distal genitalia (Figs 9C, 74, 75): Penis very long and slender, often sinuously folded *in
situ*; its wall muscular, particularly towards base; internal lumen lined by papillate
epithelium (Fig. 75A), papillae close-set and relatively coarse, somewhat larger toward
penis base. Apex of penis with small, rounded penis papilla, through which epiphallus
lumen connects with penis lumen (Fig. 75A); penis papilla itself covered with micro-
papillae similar to those lining the penis lumen. Epiphallus short, <25 % of penis length;
joins penis at U-shaped bend where penial retractor muscle inserts; interior with longitu-
dinal ridges lining outer wall, lying opposite a broad, rugose, tongue-shaped pilaster on
inner wall (adjacent to penis) (Fig. 75B). Vas deferens runs alongside penis, vagina and
free oviduct, broader and thrown into a series of bends in the latter region, before it fuses

with spermoviduct. A web of connective tissue joins lower vas deferens and epiphallus to penis.

Vagina very long and slender with muscular wall; attached laterally to body wall by a well-developed series of muscle fibres; merges with free oviduct at origin of bursa copulatrix duct; interior wall of vagina with weakly crenulate, longitudinal ridges. Free oviduct expanded and thick-walled (site of spermatophore receipt), lined with smoother longitudinal ridges (Fig. 75C). Oviduct caecum absent. Bursa copulatrix duct long and slender, but not as slender as that of *Natalina*, running beside spermoviduct rather than within its coils; bursa copulatrix thin-walled, more or less ovate, situated posterior to pericardium. Spermoviduct relatively short, the lower half convoluted; hermaphrodite duct highly convoluted; ovotestis comprising a loose assemblage of slender acini, embedded in apical whorl of digestive gland.

Spermatophore (Figs 10A, 76): A single allospermatophore was found in a specimen of *Capitina calcicola* sp. n. collected in early October. It was in good condition, suggesting recent copulation and thus that mating occurs in spring, at least. Spermatophore tadpole-shaped (straightened length 8.2 mm) and situated in swollen, thick-walled, lower portion
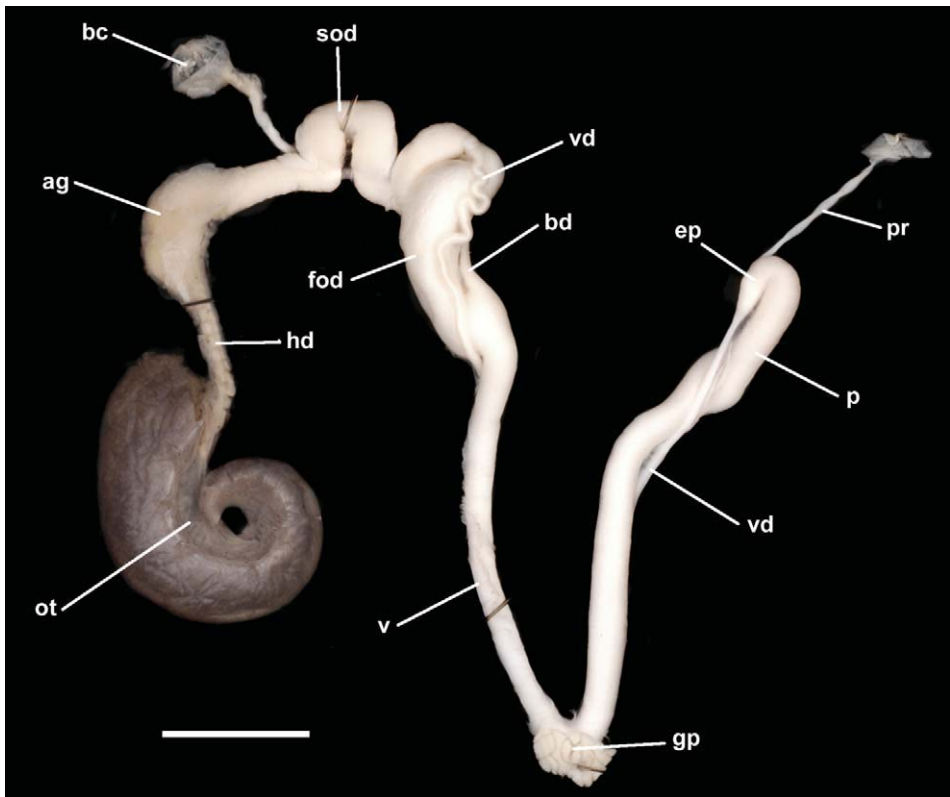
Fig. 74. *Capitina calcicola* sp. n., reproductive tract (paratype, NMSA W5670/T2265), scale bar = 5.0 mm. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bd – bursa copulatrix duct, ep – epiphallus, fod – free oviduct, gp – genital pore, hd – hermaphrodite duct, oc – oviduct caecum, ot – ovotestis, p – penis, pr – penial retractor muscle, sod – spermoviduct, v – vagina, vd – vas deferens.
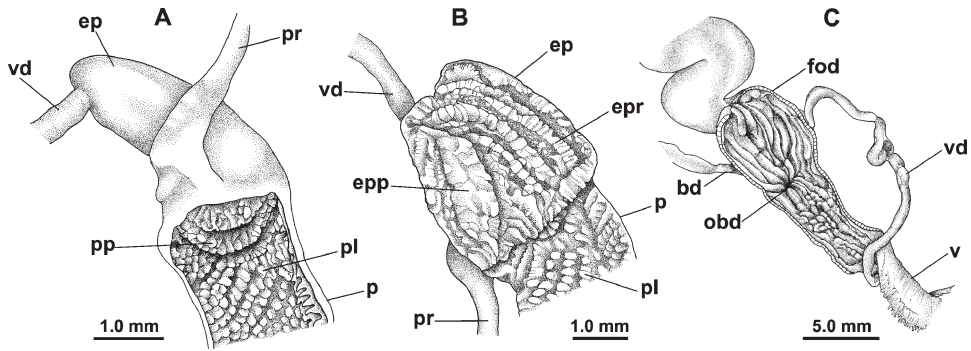
Fig. 75. Distal genitalia of *Capitina schaerfiae*, Oubos, Riviersonderendberge (NMSA W5672): (A) epi-
phallus–penis junction with penis dissected to show penis papilla and micropapillate lumen wall
(*in situ* the epiphallus lies beside the penis and is joined to it by a connective tissue web – not
shown); (B) epiphallus cut open longitudinally to shown internal pilaster and ridges; (C) female
tract with upper part of vagina and swollen free oviduct cut open to show internal structure. Ab-
breviations: bd – bursa copulatrix duct, ep – epiphallus, epp – epiphallus pilaster, epr – internal
epiphallus ridge, fod – free oviduct, obd – opening of bursa copulatrix duct, p – penis, pl – penis
lumen with micropapillate lining, pp – penis papilla, pr – penial retractor muscle, v – vagina, vd –
vas deferens.
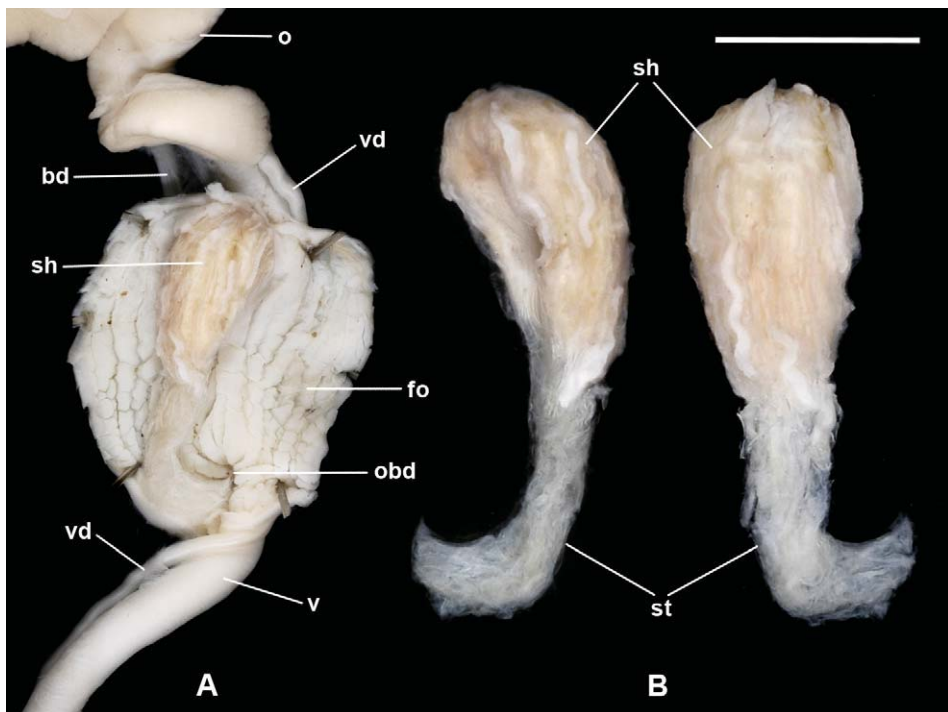
Fig. 76. *Capitina calcicola* sp. n., spermatophore, straightened length 8.2 mm (paratype, NMSA W5670/
T2265): (A) spermatophore *in situ* in dissected lower part of free oviduct; (B) two views of
extracted spermatophore, scale bar = 3.0 mm. Abbreviations: bd – bursa copulatrix duct, fo – free
oviduct wall with longitudinal folds, o – oviduct, obd – opening of bursa copulatrix duct, sh –
spermatophore head, st – spermatophore tail, v – vagina, vd – vas deferens.

of free oviduct. Head of spermatophore foremost, lying close to origin of free oviduct from spermoviduct, tail curving downward into opening of bursa duct. Spermatophore head pale orange-pink and hard, with numerous irregular, sometimes sinuous, longitudinal ridges; underside of the head concave, corresponding to tongue-like pilaster in epiphallus; internal contents of spermatophore head whitish; tail considerably thinner and without pink coloration or internal contents. No obvious vent evident, but central portion of concave underside of head thin-walled and possibly representing rupture site.

Notes: The phylogenetic analysis of morphological characters and DNA sequence data published by Moussalli *et al*. (2009) has shown that *Capitina* represents a highly distinctive lineage within *Natalina s. l.* As a result, we have proposed that the taxon be ranked as a genus in its own right. In terms of shell features, *Capitina* is characterised by the brown spiral lines on the adapical surface, wrinkled sculpture and thickened apertural lip of the adult. In addition, *Capitina* exhibits a number of distinct anatomical character states associated with the mantle edge, radula and distal genitalia which clearly distinguish it from *Natalina* and *Afrorhytida*.

The distribution of the genus is confined to the southern part of the south-western Cape and appears not to overlap with that of either *Natalina*[2] or *Afrorhytida*. It is the only genus of relatively large rhytidids known from the south-western Cape, west of 20°E. This, combined with the basal split between *Capitina* and (*Natalina + Afrorhytida*) (Moussalli *et al.* 2009) suggests that *Capitina* stems from an early divergence event which divided the ancestral *Natalina s. l.* stock into western and eastern lineages. Using a conservative mutation rate of 5 % pairwise, mtDNA sequence data places this basal split in the mid-Miocene (Moussalli *et al.* 2009). However, Spencer *et al*. (2006) suggested an even slower rate for COI evolution within the New Zealand rhytidid radiation, and there is thus a possibility that the initial split within *Natalina s.l.* may date from as far back as the early Miocene (Moussalli *et al*. 2009). It is interesting to note here in terms of an ancestral reconstruction, that the radula of *Capitina* is closer to that of the Australian *Strangesta* Iredale, 1933 (Smith 1979) and New Zealand *Schizoglossa* Hedley, 1892 (Powell 1930) than it is to either *Natalina* or *Afrorhytida*. However, such similarities may be diet-related homoplasies and need to be interpreted with caution.

When proposing *Capitina* as a new taxon, Watson (1934) included in it only '*Natalina*' *schaerfiae*, but noted the existence of light coloured specimens which Layard (in Benson 1864) had suggested were simply pale varieties or bleached specimens of the same species. Watson, however, observed additional differences in sculpture, shell proportions and protoconch size, and speculated that these specimens may ultimately prove to belong to a second and unnamed taxon. With considerably more material available and accurate locality data we are able to confirm Watson's observations and here describe this paler lineage as a new species.

The Agulhas Plain, to which this new species is limited, has experienced repeated Neogene marine transgressions of up to 200 m, with sea levels retreating to present levels only as recently as 2 Mya (Siesser & Dingle 1981; Linder 2003). Such transgressions may have constituted an effective isolating mechanism, restricting ancestral *Capitina* populations to refugial foci in the Riviersonderendberge and at higher elevations

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[2] Juvenile specimens of *Trigonephrus* species occurring in the Agulhas area can deceptively resemble juvenile specimens of *Natalina*.

on the Agulhas Plain, facilitating divergence within the ancestral stock. This is consistent with a Late Pliocene estimate for the divergence of the two lineages based on COI sequence data (unpubl. data).

Key to species of *Capitina*

1   Shell brown with darker brown spiral lines; periostracum well-developed; apex low (H:D=0.48–0.53) and shell thin; protoconch diameter 6.0–7.0 mm; radula with *ca* 30 teeth per half row. Riviersonderendberge .... **C. schaerfiae**

–   Shell typically pale usually with bold, darker brown spiral lines; periostracum weakly developed; apex higher (H:D=0.58–0.70) and shell somewhat thicker; protoconch diameter 4.0–5.3 mm; radula with *ca* 20 teeth per half row. Agulhas Plain ....

.... **C. calcicola** sp. n.

Capitina schaerfiae (Pfeiffer, 1861)

Figs 4C, 7C, 9C, 11A, 73A, B, 77, 78A, 79, 81

Helix schärfiae: Pfeiffer 1861: 73, pl. 2, figs 1–3; 1868: 242; Benson 1864: 494. Type loc.: Bredas Bosch, near Genadendal, W. Cape [Madame Schärf]. [*schärfiae* emended to *schaerfiae* following ICZN (1999), Art. 32.5.2.1]
Macrocyclis schaerfiae: Pfeiffer 1878 in 1878–81: 62.
Helix (*Ampelita*) *schaerfiae*: Pfeiffer 1879 in 1878–81: 184.
Helix schaerfiae: Kobelt 1886 in 1877–97: 615, pl. 178, figs 1–6.
Helix (*Ampelita*) *schaerfiae*: Pilsbry 1890 in 1890–91: 43, pl. 7, figs 95–97, 1, 2.
Rhytida schaerfiae: Melvill & Ponsonby 1898: 170.
?*Macrocyclis schaerfiae*: Sturany 1898: 33.
Natalina schaerfiae: Connolly 1912: 96 (in part); 1939: 116, pl. 4, figs 6–8, text-fig. 10 (in part); Barnard 1951: 142, pl. xxi, fig. 8.
Tulbaghinia schaerfiae: Connolly 1915: 174.
Natalina (*Capitina*) *schaerfiae*: Watson 1934: 153, pl. 19, figs 1–4.

Etymology: Named for 'Madame Sophie Schärf', perhaps connected with the Moravian Mission at Genadendal (Barnard 1965).
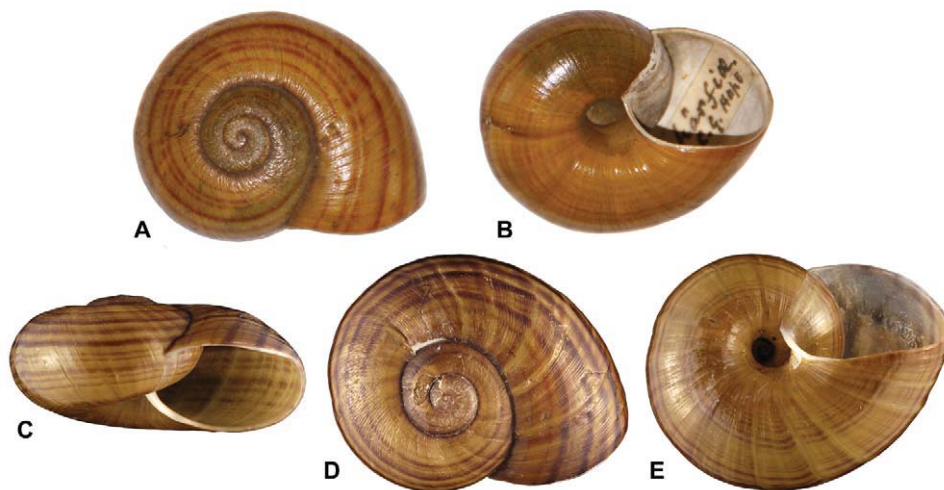
Fig. 77. *Capitina schaerfiae* (Pfeiffer, 1861): (A, B) lectotype of *Helix schärfiae* Pfeiffer, 1861, here designated (Polish Academy of Sciences 4295), diameter 31 mm (photographs courtesy of Dominika Mierzwa); (C–E) Oubos, Riviersonderendberge (NMSA W5672), diameter 29.7 mm.

Identification: More depressed and thinner-shelled than *Capitina calcicola* sp. n., and with a larger protoconch; umbilicus not obscured to any appreciable extent by reflected columella lip; periostracum darker and more obvious; spiral colour pattern usually less bold.

Description (Fig. 77): Shell lenticular to discoidal, spire low; comprising up to 4.5 whorls, last adult whorl expanding relatively rapidly and descending noticeably prior to aperture; apical surface lustreless, base glossy. Protoconch diameter 6.0–7.0 mm; sculptured primarily by close-set axial riblets (Fig. 4C), strongest adapically, but traces of spiral threads may also be present, particularly near periphery. Teleoconch sculptured initially by close-set axial riblets, these becoming less distinct with growth and tending to anastomose, producing a pitted or wrinkled sculpture; this sculpture evanescing at periphery, base smoother and more glossy with only weak growth-lines and fine spiral lirae. Aperture obliquely ovate-reniform; outer lip weakly, but distinctly thickened, white; basal lip almost straight in basal view; umbilicus of moderate width, not appreciably obscured by reflected upper part of columella lip.

Ground colour yellowish brown to mid brown with darker brown spiral lines, one line just above periphery usually more distinct; lines finer on base and usually absent in peri-umbilical area; periostracum relatively well developed, but not extending beyond aperture lip at maturity, honey-brown in fresh shells, though appearing darker in living specimens.

Dimensions: Largest specimen (NMSA B0031, Oubos), diameter 31.6 mm, H:D of adults 0.48–0.53 (N=6).

Living animal (Fig. 78A): Head-foot grey or brown to dark grey-brown, sometimes paler laterally and beneath shell; pedal margin tinged with or distinctly orange, orange colour usually more extensive on tail; tentacles generally greyish; paler longitudinal bands on neck not evident; mantle edge a darker shade of main body colour.

Radula (Figs 73A, B): See generic description; formula 1+~30 (N=2).

Type material: Originally in Szczecin (Stettin) Museum [H. Dohrn collection], Poland (Connolly 1912). Although Dance (1986) stated that the Dohrn collection was totally destroyed in the Second World War, we have established through Furth *et al*. (1994), that some entomological material from the Stettin Museum was transferred to the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw. Further enquiries have led to the discovery of a specimen labelled '*Helix schärfiae*' at the latter institution. This almost certainly represents a shell from the original sample and indicates that some Stettin Museum
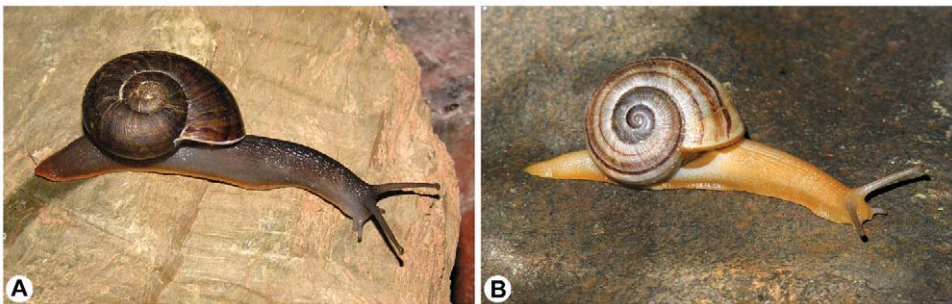

Fig. 78. *Capitina* species, living animals: (A) *Capitina schaerfiae* (Pfeiffer, 1861), Oubos, Riviersonderend-berge (NMSA W5672), shell diameter 28.0 mm; (B) *Capitina calcicola* sp. n., Gansbaai (paratype, NMSA W3201/T2269), shell diameter 22.8 mm.

molluscan material was transferred to the Institute of Zoology and is still extant. We designate this specimen as lectotype (Figs 77A, B).

Material examined: SOUTH AFRICA: *W. Cape*: Riviersonderendberge, Oubos (Oudebosch) (NMSA B0031 *ex* SAMC, BMNH 1937.12.30.1309–10); ditto (34.07702°S:19.82884°E), 370 m, Afrotemperate forest, in leaf-litter and under logs, D. Herbert & L. Davis, 11/x/2007 (NMSA W5672); 'Swellendam' *ex* E.L. Layard, purchased from Sowerby & Fulton, 1919 (NMSA 3125).

Distribution (Fig. 79): A narrow-range W. Cape endemic, known only from the southern slopes of the Riviersonderendberge. We consider records from Swellendam to be highly dubious. They relate to old specimens purchased from Sowerby & Fulton and the provenance given may simply refer to a then more well-known locality in the general area of occurrence. Records from the Bredasdorp area (Connolly 1912, 1939) refer to the following species.

Habitat: *Capitina schaerfiae* has been found only in patches of southern Afrotemperate forest in valleys on the south-facing slopes of the Riviersonderendberge. At Oubos [Oudebosch], where the material studied by Connolly and Watson originated, the species remains common, living under logs and forest floor debris (altitude 350–400 m).

Notes: In addition to being thinner-shelled, more depressed and generally less boldly marked than *Capitina calcicola* sp. n., in the present species the protoconch is larger, the head-foot darker and the radula has more teeth per row. Further comparative details are given under *C. calcicola*.

Conservation: The available data suggest that the distribution of *Capitina schaerfiae* is both fragmented and highly restricted. Its range in the Riviersonderendberge is essentially linear, and covers a west-east distance of only approx. 65 km. Even within this it evidently occurs only in forest fragments. The only locality at which it has been recorded within the last 50 years is at Oubos, where, for a moderately large predatory species, it seems
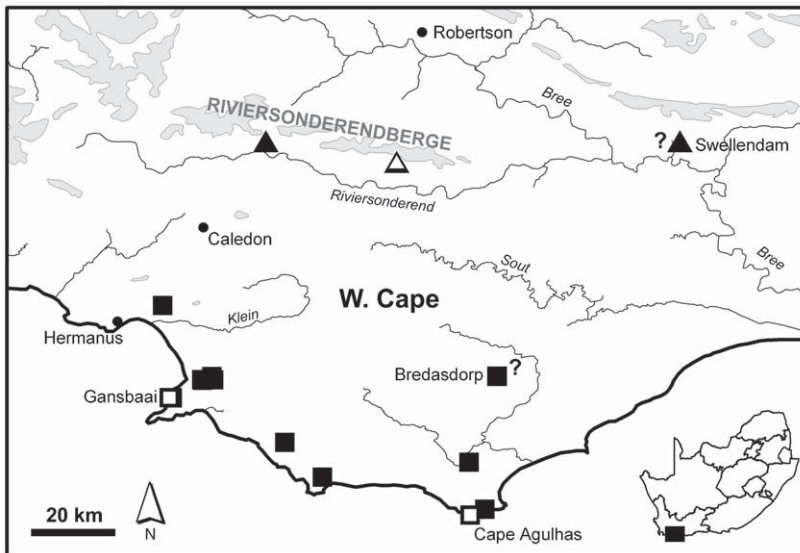
Fig. 79. Distribution of *Capitina* species: *C. schaerfiae* (Pfeiffer, 1861) (triangles), *C. calcicola* sp. n. (squares). Symbols with a white centre indicate localities for specimens used in DNA analyses (Moussalli *et al.* 2009). Contour at 1000 m.

to be relatively common. More field surveys are needed in order to clarify the current extent of its range, but it seems probable that other populations remain in forested valleys elsewhere on the southern slopes of these mountains. The area is not well sampled.

Large parts of the Riviersonderendberge fall within conservation areas (Greyton Nat. Res., Riviersonderend Provincial Nat. Res. and Riviersonderend Mountain Catchment Area) and are thus afforded some degree of protection.

Capitina calcicola sp. n.
Figs 6B, 8C, 10A, 73C, D, 74, 76, 78B, 79–81

Natalina schaerfiae [*non* Pfeiffer, 1861]: Connolly 1912: 96 (in part); 1939: 116 (in part), pl. 4, figs 9–11.
Natalina (*Capitina*) *schaerfiae*: Watson 1934: 153 (in part); Schileyko 2000: fig. 972A.

Etymology: From Latin *calx* (lime) and *cola* (an inhabitant); referring to its occurrence in calcium-rich habitats.

Identification (Fig. 80): *Capitina calcicola* is a distinctive taxon easily separated from *C. schaerfiae* by its paler, more elevated, thicker shell, frequently with a bolder spiral colour pattern. In addition, the sculpture is somewhat coarser, the protoconch smaller (diameter 4.0–5.3 mm), the head-foot coloration more orange and the radula has fewer teeth per transverse row.

Description: Shell subglobose to lenticular, spire low; comprising 4.5–5.0 whorls when adult; last adult whorl descending prior to aperture; apical surface lustreless, base glossy. Protoconch diameter 4.0–5.3 mm, sculptured by axial riblets, strongest below suture, and increasing in strength toward end of final whorl; one or more weak incised spiral lines may be present just above abapical suture/periphery, but these sometimes scarcely evident. Teleoconch with similar axial riblets, these interacting with irregular spiral elements to produce a pitted or wrinkled sculpture; this sculpture evanescing at periphery and base smoother and more glossy with only weak growth-lines and fine spiral lirae. Aperture variable in shape, generally obliquely ovate-reniform; outer lip weakly, but distinctly thickened, white; interior of aperture sometimes with a thickened subsutural spiral ridge set back some distance behind outer lip, a second similar ridge present on upper part of parietal lip, the two delimiting a distinct groove underlying the suture (this feature present only in adult specimens and then only in some individuals); umbilicus of moderate width, partially obscured by upper, reflected portion of columella lip. In sub-adult specimens (Fig. 80J) the basal and columella lips show some thickening, but the upper outer lip remains thin and descends only slightly, the thickening of the columella lip is also not completed and the umbilicus is therefore less obstructed.

Shell whitish, overlain by a pale straw-brown to light honey-brown periostracum; apical surface patterned with spiral lines of differing width, in various shades of brown, one or two lines just above periphery usually more distinct; lines weaker on base and usually absent in peri-umbilical area; periostracum not extending over aperture lip at maturity.

Dimensions: Holotype: diameter 28.0 mm, height 17.2 mm; largest specimen (NMSA W5670/T2265, Grootbos Nat. Res.), diameter 33.6 mm; H:D of adults 0.58–0.70 (N=22).

Living animal (Fig. 78B): Head-foot pale apricot to bright orange or brown, usually paler laterally and beneath shell; pedal margin and tail often slightly more intensely

coloured; tentacles somewhat paler or more greyish; no pale longitudinal bands evident on neck; mantle edge darker orange-brown.

Radula (Figs 73C, D): See generic description; formula 1+~20 (N=3) in adult, juveniles with fewer teeth in lateromarginal series.

Holotype (Figs 80A–C): SOUTH AFRICA: *W. Cape*: Die Dam region (34.7487°S:19.6708°E), coastal fynbos, A. Moussalli & D. Stuart-Fox, 14/ii/2005 (NMSA W6265/T2262).

Paratypes: SOUTH AFRICA: *W. Cape*: same data as holotype (NMSA W3354/T2276, 1 specimen; W3355/T2264, 5 specimens); Gansbaai (34.5794°S:19.3442°E), coastal dune scrub, dormant, buried in sand under vegetation, A. Moussalli & D. Stuart-Fox, 13/ii/2005 (NMSA W3201/T2269, 4 specimens; W3368/T2263, 1 specimen; W3369/T2268, 1 specimen); Gansbaai area, Grootbos Nat. Res. (34.53402°S:19.43480°E), 330 m, limestone fynbos, under vegetation beside rocks, D. Herbert & L. Davis, 08/x/2007 (ELM D15856, 2 specimens; BMNH 20100127, 1 specimen; NMSA W5670/T2265, 29 specimens; RMNH.MOL.121374, 1 specimen); Pearly Beach area, Bantamsklip (34.674772°S:19.590264°E), limestone hills, at base of or in restios, M. Picker, 29/ix/2007 (NMSA W5998/T2266, 3 specimens); Cape Agulhas (34.8293°S:19.9854°E), coastal dune scrub, buried deep in sand under small bush, A. Moussalli & D. Stuart-Fox, 14/ii/2005 (MVM F167491, 1 specimen; NMSA W3360/T2270, 1 specimen; W3365/T2267, 8 specimens); Cape Agulhas, V. Fitzsimons, x/1940, *ex* Transvaal Museum (NMSA 3978/T2271, 1 specimen); Bredasdorp, E.L. Layard (BMNH 1937.12.30.1311–13, 3 specimens).
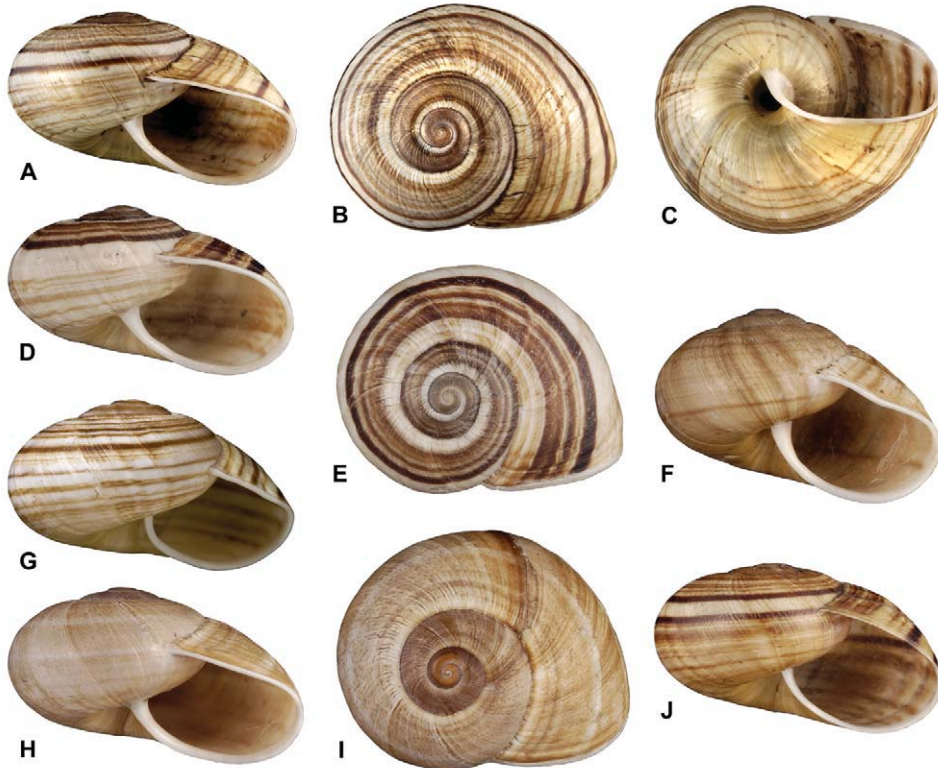
Fig. 80. *Capitina calcicola* sp. n. (all NMSA): (A–C) holotype, Cape Agulhas (W6265/T2262), diameter 28.0 mm; (D, E) boldly patterned specimen, Bantamsklip (paratype, W5998/T2266), diameter 28.4 mm; (F) elevated specimen, Cape Agulhas (paratype, W3360/T2270), diameter 28.0 mm; (G) Bredasdorp (paratype, BMNH 1937.12.30.1311–13), diameter 29.5 mm (photo courtesy of J. Ablett and P. Hurst); (H, I) weakly patterned specimen, Cape Agulhas (paratype, W3365/T2267), diameter 29.4 mm; (J) typical pattern, subadult specimen, Grootbos Private Nat. Res. (paratype, W5670/T2265), diameter 27.5 mm.

Additional material examined (all NMSA unless otherwise indicated): *W. Cape*: Hermanus, Maanskynkop (SAMC A8174); Gansbaai, M. Picker, 06/ix/2003 (W4854); Gansbaai area, Grootbos Nat. Res. (34.54205°S: 19.41529°E), 215 m, milkwood forest, dead in leaf-litter, D. Herbert & L. Davis, 07/x/2007 (W5664); ditto (34.54063°S:19.41318°E), 217 m, milkwood forest, in sandy leaf-litter, A. Moussalli & D. Stuart-Fox, 13/ ii/2005 (W5421); ditto (34.54135°S:19.43871°E), 325 m, Afrotemperate forest, in leaf-litter and under logs, D. Herbert & L. Davis, 08/x/2007 (W5919); Bredasdorp area, Soetendalsvlei, *ex* Transvaal Museum (B7315); l'Agulhas, in macchia veld, J.S. Taylor, 22/viii/1964 (4122); Cape Agulhas (34.8293°S:19.9854°E), coastal dune scrub, buried deep in sand under small bush, A. Moussalli & D. Stuart-Fox, 14/ii/2005 (W3359); Bredas-dorp District, Prof. de Villiers (BMNH 1937.12.30.1314–16).

Distribution (Fig. 79): Endemic to the Agulhas Plain, recorded only from the coastal region between Hermanus and Cape Agulhas, W. Cape. Records from Bredasdorp (e.g., Connolly 1939: pl. 4, figs 9–11), although perfectly plausible, require confirmation since all are early records and may simply cite the town due to its being the nearest well-known settlement. Recorded at altitudes from sea level to 330 m.

Habitat: Occurs primarily in coastal fynbos habitats (Agulhas Limestone fynbos and western Overberg dune strandveld, *sensu* Musina & Rutherford 2006), and can be common in limestone areas. Dead shells have also been found in coastal milkwood (*Sideroxylon*) forest, but much less commonly so. In the dry season the animals bury themselves deeply in sandy soil/litter beneath shrubs, but can be found on the surface beneath plants during wetter periods.

Notes: *Capitina calcicola* differs clearly and consistently from *C. schaerfiae*. Its shell is paler and more elevated (H:D=0.58–0.70 compared with 0.48–0.53 in *C. schaerfiae*, see Fig. 81), and the spiral colour bands are generally darker and more pronounced (ex-cepting occasional weakly patterned individuals). In addition, the protoconch is smaller (diameter 4.0–5.3 mm, compared with 6.0–7.0 mm in *C. schaerfiae*), the body coloration is paler and of a more orange hue, and the radula has fewer teeth (approx. 20 per half
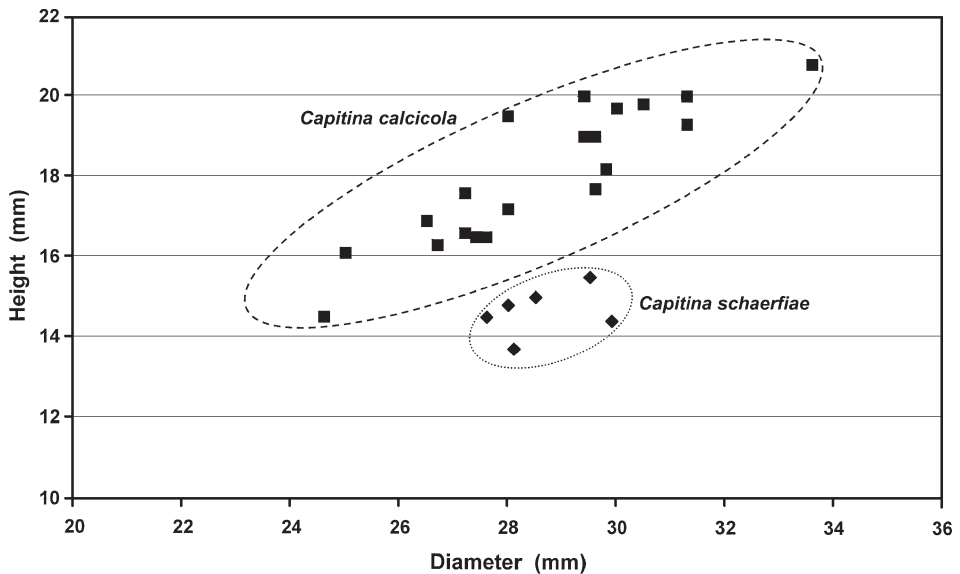

Fig. 81. Plot of height/diameter measurements of *Capitina* species, showing differing shell proportions in the two species. The largest specimen of *C. schaerfiae* (31.6 mm diameter) is missing its apex and cannot be included in this plot. Similarly, the height of the lectotype (31 mm diameter) cannot be measured from the photographs available.

row compared to approx. 30 in *C. schaerfiae*). *C. calcicola* is also generally thicker-shelled (perhaps due to the presence of environmental limestone) and the periostracal layer is paler and thinner, tending to flake off after death; it is however certainly present in living specimens (cf. Connolly 1939).

Since these differences are considerable and include features of the protoconch, teleo-conch and radula, we believe they are sufficient to warrant recognition of the two taxa as separate species. Molecular data likewise separate the two taxa (Moussalli *et al.* 2009), although at present, the level of genetic divergence between the two is difficult to assess given the limited number of specimens sequenced to date. This remains a topic needing to be investigated more thoroughly through the collection and sequencing of further samples of both species from additional localities, particularly for *C. schaerfiae*.

Conservation: Although not as narrowly endemic as *C. schaerfiae*, *C. calcicola* sp. n. too is evidently a species of restricted range. The known extent of occurrence is approx. 2500 km². It is recorded from or likely to occur in several formally protected areas and private nature reserves (Cape Agulhas National Park, Walker Bay Provincial Nat. Res. and Grootbos Private Nat. Res.). The continued preservation of pristine limestone fynbos habitats in the western Agulhas Plain is crucial to the on-going survival of this taxon. In this regard, habitat transformation resulting from the invasion of exotic *Acacia* species represents a potential threat.

BIOGEOGRAPHIC SUMMARY

Rhytidid snails represent a characteristic element of the palaeogenic invertebrate fauna of southern Africa (Stuckenberg 1962). The family is thought to be of Gondwanan origin and part of what Solem (1959) termed the 'southern relict fauna'. However, the Rhytididae has a somewhat restricted distribution within fragmented Gondwana, with representatives occurring only in southern Africa, Australasia and islands in the south-western Pacific (supposed rhytidids occurring in E. Africa, the Seychelles and Madagascar belong to other families, see Introduction). Strangely, they are absent from that part of Gondwana with which Africa had its most recent contact, namely South America (although their relationship to the South American Systrophiidae, which are also often included in the Rhytidoidea, needs to be further explored). A similar Gondwanan distribution that excludes South America is evident in sphaerotheriid millipedes and suggests an origin in eastern Gondwana (Wesener & VandenSpiegel 2009). However, sphaerotheriid millipedes are also known from India, Madagascar and south-east Asia, whereas rhytidid snails are not. The absence of rhytidids from the latter regions implies that their pre-fragmentation distribution in eastern Gondwana did not include those parts of the African plate abutting the Indo-Malagasy plate. This is consistent with the fact that, within Africa, rhytidids are [remain] restricted to the extreme south and south-east of the continent. The African distribution of peripatopsid Onychophora is similarly confined to this region, and they are also absent from India-Madagascar and south-east Asia, but unlike rhytidids and sphaerotheriids, the peripatopsids also occur in South America. Although the present-day global distribution of each of these low-vagility, Gondwanan invertebrate groups comprises a different assemblage of Gondwanan continental fragments, this does not detract from their hypothesised Gondwanan origins and probably strongly relates to the distribution of respective groups in pre-fragmentation Gondwana.

Within south-east Africa, the larger rhytidids are limited to those regions south and east of the Great Escarpment (Fig. 82) and the same is true for the smaller species (*Nata s. l.*), although new distribution data indicate that the latter penetrate further inland than indicated in the map provided by Bruggen (1978), further even than *Natalina s. l.* (unpubl. data). The north-eastern family boundary is defined by the low-lying Limpopo Valley, a geomorphic feature already in existence in the Cretaceous (Partridge & Maud 1987) and an effective biogeographic barrier since the early Tertiary (Stuckenberg 1962). Only at the coast has the family crossed this barrier, and then only marginally so. The range of the related chlamydephorid slugs and the African peripatopsid Onychophora is similarly restricted by the Great Escarpment (Hamer *et al*. 1997; Herbert 1997), but unlike the peripatopsids and rhytidids, the distribution of the chlamydephorids extends to the eastern highlands of Zimbabwe. African sphaerotheriid millipedes, though also largely confined to south-eastern Africa, range still further north, reaching Malawi (Wesener & Van den Spiegel 2009). It is possible that the restriction of these groups to the south and east of southern Africa is linked to the distribution of forests, but while this may have been true historically, it is not currently the case for either rhytidids or chlamydephorids as representatives of both occur in non-forest habitats such as open thicket and savannah, and even fynbos in the case of rhytidids.

Molecular evidence suggests that cladogenesis within *Natalina s. l.* probably predates the Pliocene (Moussalli *et al.* 2009) and may have been associated with major drying, contraction and fragmentation of mesic habitat in sub-Saharan Africa commencing in the mid-Miocene and extending into the Plio-Pleistocene, a phenomenon known to have had important evolutionary implications for many components of the regional biota (Mucina & Rutherford 2006; Tolley *et al.* 2008, 2009). The first lineage divergence appears to have split the ancestral stock into western (*Capitina*) and eastern lineages (*Afrorhytida* and *Natalina*). The boundary between the two is coincident with that between western (winter rainfall) and eastern (year-round rainfall) components of the
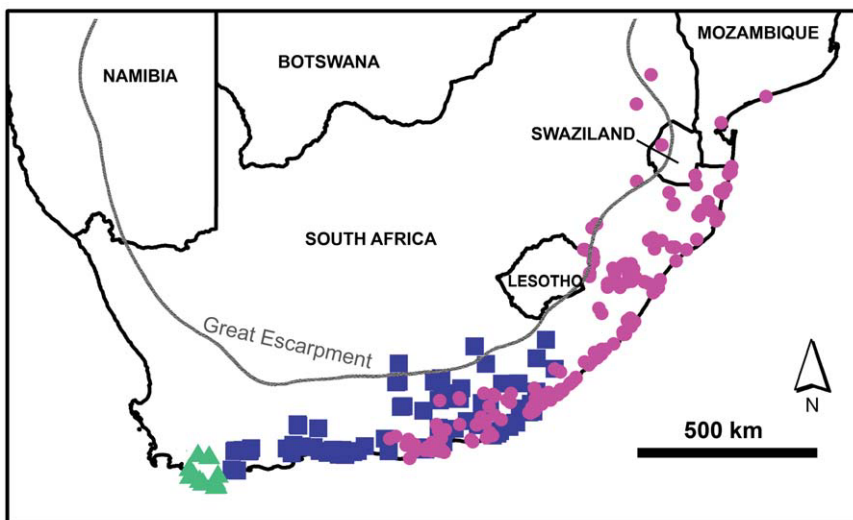
Fig. 82. Distribution of genera within *Natalina s.l.*: *Capitina* (triangles), *Afrorhytida* (squares), *Natalina* (circles).

Cape Floristic Region (CFR), in the region of the Breede River (Cowling & Richardson 1995) (Fig. 83), although the range of one *Afrorhytida* subspecies (*A. kraussi oraria*) lies just within the western CFR. Based on the present-day distribution of *Capitina*, this western lineage appears not to have crossed the Hottentots-Hollands Mountains (a sub-boundary within the western CFR), unlike *Nata s.l.,* the other southern African rhytidid radiation. *Capitina* remains an isolated lineage restricted to the Agulhas–Overberg region (the Bredasdorp Centre of plant endemism). Its distribution does not overlap with either *Afrorhytida* or *Natalina*. In contrast, the current distributions of *Afrorhytida* and *Natalina* overlap extensively (Fig. 82) and each has undergone moderate radiation in the year-round and summer rainfall regions south and east of the Great Escarpment.

Afrorhytida occurs only in the southern and eastern Cape, and the dominant biogeographic pattern is one of an west-east species turnover (Fig. 83). *Afrorhytida kraussi* occurs in the eastern CFR, reaching its easternmost limit just west of Port Elizabeth. East of this it is replaced by *A. knysnaensis*, the turnover zone being more or less coincident with the boundary between the Fynbos and Albany Thicket biomes (Mucina & Rutherford 2006), in the region of the Uitenhage Basin. *A. knysnaensis* is the sister taxon of *A. kraussi* from which it may have diverged due to selection pressures associated with the increasingly open and drier habitats emerging during the Plio-Pleistocene aridification. Certainly, *A. knysnaensis* is now more tolerant of drier conditions than is *A. kraussi*, and its distribution extends a considerable distance further inland, essentially tracking the Albany Thicket biome, a recognised centre of endemism for plants (van Wyk & Smith 2001), molluscs (Govender 2007) and millipedes (Hamer & Slotow 2002).

To the east, *A. burseyae* replaces *A. knysnaensis* at the boundary between the Albany Thicket and the southern parts of the Grassland and Savannah biomes. Their distributions coincide also with river catchments, *A. knysnaensis* occurring in the Sundays and Great Fish catchments and *A. burseyae*, largely in the Kei and Mbashe catchments. It appears therefore that for these two non-forest species, it is the catchment boundaries that may be the limiting biogeographical features in this instance. Although these two taxa are not sister species and the boundary between the Great Fish and Kei catchments therefore not a vicariant feature contributing to speciation, it may well now limit dispersal and maintain the allopatry of these lineages. The high altitude, open grassy habitats of the Winterberge and Amathole Mountains could be an effective barrier to dispersal in the inland region. Although river catchments often define species boundaries in freshwater groups, they are rarely cited as being significant for fully terrestrial taxa, but Price *et al*. (2007) have postulated similar catchment-delimited boundaries between lineages of the cicada *Platypleura stridula* (L., 1758) in the south-western Cape. Relative to the preceding *Afrorhytida* species, *A. trimeni* has a more restricted range, limited to the coastal region of the Albany Thicket. It is not, however, a thicket species, occurring instead in forest patches within the broader thicket biome and thus its distribution is limited to the higher rainfall coastal regions suitable for forest persistence.

Phylogenetic diversity within *Afrorhytida* is evidently considerable, as indicated by the relatively deep divergence of the major clades and long branch lengths subtending the terminal taxa in all lineages except *A. trimeni* (Fig. 1). This suggests that the lineages are relatively old, and that gene flow within them has been historically interrupted (less so in *A. trimeni*), in which case phylogeographical substructure should be evident (e.g.,

A. kraussi). Alternatively, high within-clade diversity without obvious geographical substructure (*A. knysnaensis*) may result from the persistence of a single large or several well connected populations combined with the retention of ancestral polymorphisms. Additional fine-scaled molecular analysis with greater specimen representation is needed to resolve these competing hypothesis.

The distribution of *Natalina* overlaps extensively with that of *Afrorhytida* in Eastern Cape, but extends much further to the north-east, reaching the Limpopo River valley in southern Mozambique. The most basal divergence is that of the morphologically distinct *N.* (*Tongalina*) *wesseliana*, the only *Natalina* lineage occurring in the subtropical north-eastern coastal region (Fig. 84). Its distribution closely matches that of the Maputaland centre of endemism (van Wyk & Smith 2001). However, whereas most species endemic to this centre are of Afrotropical origin (van Wyk & Smith 2001), *N. wesseliana* is clearly derived from southern stock. Since the forests of the Indian Ocean Belt are thought to have expanded in to this region only after the last Glacial Maximum (Eeley *et al*. 1999; Lawes *et al*. 2007), it seems probable that *N. wesseliana*, a largely forest-dependent species, persisted as relict populations along the coastal scarp in northern Zululand during the last hypothermal, expanding northwards and coastwards as forest cover increased. Although represented by relatively few individuals in our molecular phylogeny, there is some geographic substructure within this clade which, combined with the comparatively long branch lengths, suggests some historical inter-ruption in gene flow and fragmentation of the refugial population.

Subsequent cladogenesis within *Natalina* (i.e. within *Natalina s. s.*) resulted in the evolution of two distinct lineages, the small-shelled *N. quekettiana* complex and the
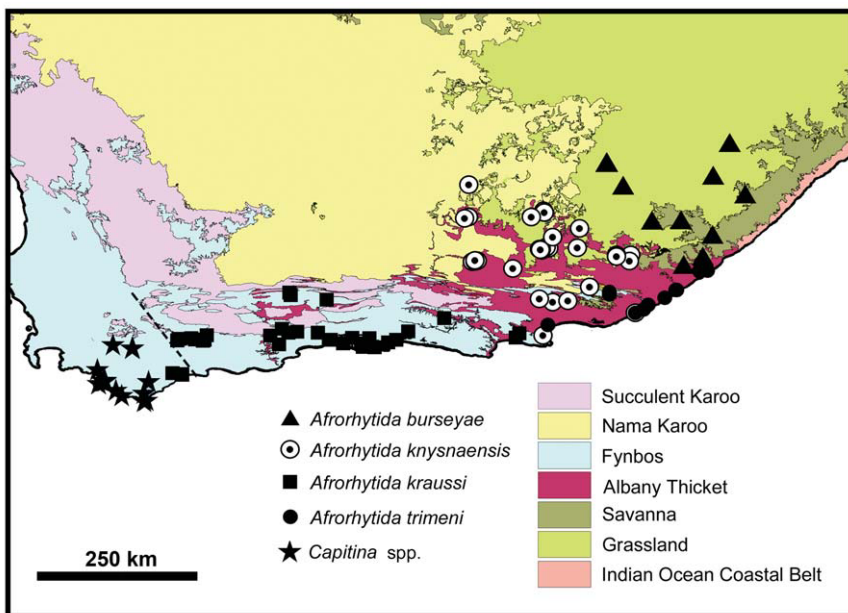
Fig. 83. Distribution of *Afrorhytida* and *Capitina* species in relation to biome type (Mucina & Rutherford 2006). The dashed line represents the approximate boundary between the western and eastern Cape Floristic Region.

large-shelled *N. cafra−beyrichi* clade. The distribution of the former is tied to the forest biome along the north-eastern section of the Great Escarpment, extending to lower altitude mist-belt and scarp forests (Fig. 84), and mirrors a pattern evident in the forest-dependent dwarf chameleons (*Bradypodion* spp.) of KwaZulu-Natal and the northern Drakensberg (Tolley *et al.* 2004, 2006). The basal divergence of the two montane lineages in this clade (Fig. 1) might be taken to suggest that the complex as a whole originated at high altitudes, with subsequent dispersal into mist-belt and scarp forests. However, the idea that the geographical location of the basal taxon within a clade reflects the centre of origin of that clade is controversial. Sequential localised differentiation within a widespread ancestral population may achieve a similar result (Heads 2009). In this case, dispersal from montane forests to mist-belt and scarp forest would run counter to the general pattern evident in eastern South Africa, i.e. post-Last Glacial Maximum (LGM) dispersal from scarp forest refugia into higher altitude forests (Lawes *et al.* 2007). Although, under such a scenario one might expect the lineages in the lower altitude forests to be basal. In fact, given the considerable genetic divergence evident within this clade, it seems likely that the early divergence of both montane lineages considerably predates the LGM (estimated to date from the Pliocene based on the conservative 5 % mutation rate for mtDNA used here – see Moussalli *et al.* (2009) for further detail). Thus the branching pattern evident in this group probably reflects sequential vicariant cladogenic events resulting from repeated expansion and contraction of Afrotemperate forests during the Plio-Pleistocene, perhaps from lower altitude scarp
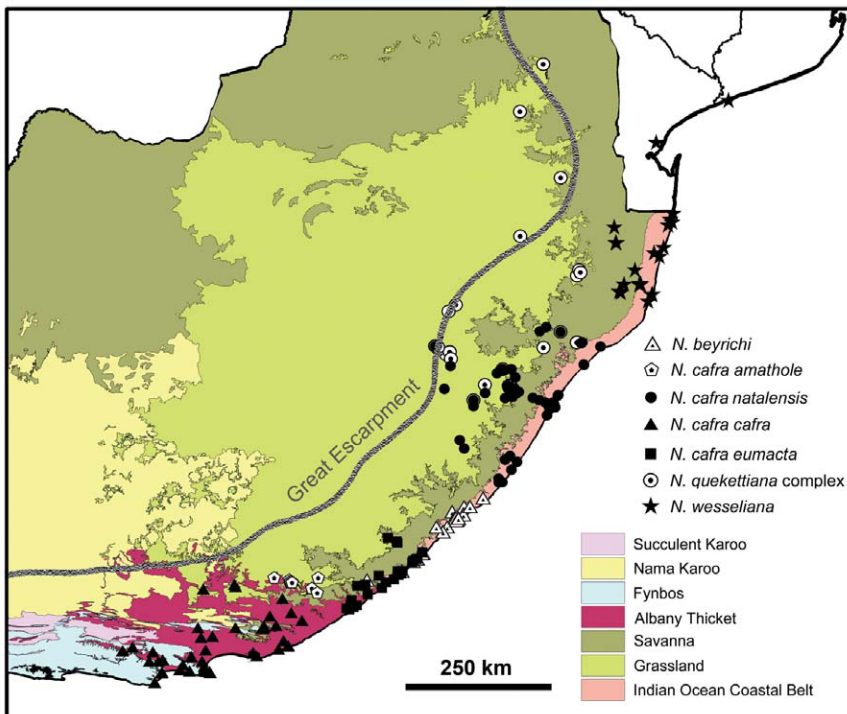
Fig. 84. Distribution of *Natalina* species in relation to biome type (Mucina & Rutherford 2006).

forest refugia. Evidently the forests in the Cathedral Peak–Injasuthi area have persisted through these climatic fluctuations, retaining lineages from previous interglacial expansions. The fact that these forests also contain narrow-range, forest-dependent chameleons (Tolley & Burger 2007), spiders (Griswold 1985) and achatinid snails (Bruggen 1965) provides further support for their long term persistence. Millipedes of the genus *Doratogonus* Attems, 1914, show similar narrow-range endemism associated with high altitude forests in the KwaZulu-Natal Drakensberg (Hamer 2000), although it is not clear whether the species concerned constitute a monophyletic lineage.

With regard to the *Natalina cafra–beyrichi* complex, the low levels of phylogenetic diversity evident in this clade point to relatively recent radiation (Moussalli *et al.* 2009 and Fig. 1). The primary divergence within this complex relates to a cladogenic event in the north-eastern E. Cape, separating well-supported, north-eastern (KwaZulu-Natal) and southern (E. Cape) lineages (Fig. 1). *N. beyrichi* then diverged from the main E. Cape lineage in the Pondoland region (Fig. 84), an area known to be rich in neoendemics of Cape origin (van Wyk & Smith 2001) and a focus of endemism in other molluscan genera (Bursey & Herbert 2004; Govender 2007; Cole & Herbert 2009). Subsequently, the remaining E. Cape *N. cafra* stock has diverged in to three further lineages. One is an ecologically tolerant form that is broadly distributed in the more mesic southern parts of the Albany Thicket (*N. cafra cafra*), whereas the other two are generally (though not exclusively in the case of *N. cafra eumacta*) associated with forest habitats in the Amathole Mountains (*N. cafra amathole*) and the East London–southern Transkei coastal belt (*N. cafra eumacta*). The forests in the Amathole region are known to contain additional narrowly endemic, forest-dependent taxa belonging to other low-vagility groups, e.g., forest floor spiders (*Microstigmata amatola* Griswold, 1985) and frogs (*Anhydrophryne rattrayi* Hewitt, 1919). These forests straddle the catchment boundary between the Kei River on the one hand and the Great Fish River and smaller coastal catchments (Keiskamma and Buffalo) on the other. Griswold (1985) considered the deep, relatively arid and thicket-filled valleys of these two large drainage systems to be important barriers, isolating the forests and forest-associated animals of the Amathole Mountains. Significantly, his work on the spider genus *Microstigmata* (Griswold 1985) revealed a similar spatio-temporal pattern of cladogenic events, with the KZN species occupying basal positions relative to a younger radiation in E. Cape, which in turn has foci of distribution west of the Great Fish River, in the Amathole Mountains, and in Transkei. Given these concordant patterns, it is possible that the basally divergent *N. cafra natalensis* represents a separate, highly cryptic species.

From the above biogeographic summary, it is evident that the spatial distribution of all the species and subspecies under consideration is correlated and congruent with the broader patterns of floristic endemism in the southern Africa, south and east of the Great Escarpment. Evidently, the historical evolutionary process that have shaped floral diversity in the region have had a similar influence on speciation in these carnivorous snails. Further studies need to focus on the more deeply divergent lineages such as *Afrorhytida burseyae*, *A. knysnaensis*, *A. kraussi* and the *Natalina quekettiana* complex, in order to improve sister-group resolution and to search for finer-level phylogeographic structuring and cryptic species. In addition, the patterns evident in *Afrorhytida*, *Capitina* and *Natalina* need to be compared with the growing body of information on other taxa of limited vagility (Griswold 1985; Hamer & Slotow 2000; Tolley *et al.* 2006; Daniels

et al. 2009), so as to identify concordant spatial patterns across unrelated groups. It is these taxa with limited dispersal capacity that are likely to retain the strongest biogeographic signal reflecting historical evolutionary processes at a regional scale (Hugall *et al.* 2002, 2003). At a broader scale, the analysis of molecular data needs to be expanded to include a wider spectrum of genera from the broader Australasian region in order to explore Gondwanan relationships and to test whether the southern African rhytidid radiation is indeed monophyletic.

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