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Revision of the dwarf cannibal snails (*Nata s.l.*) of southern Africa—*Nata s.s.* and *Natella* (Mollusca: Gastropoda: Rhytididae), with description of three new species

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Abstract

This paper represents the second part of our revisionary studies on the rhytidid fauna of southern Africa. The species discussed belong to the taxon *Nata s.l.* in which we recognise two genus-level lineages, *Nata s.s.* and *Natella* with six (three new) and one species respectively. We update the species-level taxonomy extensively in the light of new molecular and morphological data, and provide a comprehensive revision of all species, including keys. Detailed comparative morphological observations are provided for the distal reproductive tract, 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 items and mating behaviour. Although the two genera are well circumscribed in terms of both internal anatomy and molecular data, shell morphology is highly conserved, and species discrimination using shell characters alone is difficult. We have discovered three undescribed species within *Nata* and there is evidence that further research of a phylogeographic nature may uncover additional cryptic diversity. The geographic distributions of the species are discussed in relation to regional vegetation patterns and, as with the larger cannibal snail radiation, the Albany Thicket Biome emerges as a focus of endemism. Observations on the conservation status of all species are provided.

New species: *Nata aequiplicata* **sp. nov.**, *Nata erugata* **sp. nov.** and *Nata watsoni* **sp. nov.** Revised status: *Natalina caffrula* Melvill & Ponsonby, 1898 is transferred to the genus *Nata* and thought to be a synonym of *Nata dumeticola* (Benson, 1851).

Key words: biogeography, conservation, diet, distal genitalia, keys, protoconch, radula, taxonomy

Introduction

The genus *Nata s.l.* Watson, 1934 represents a radiation of smaller-sized rhytidid snails from southern Africa, the so-called ‘dwarf cannibal snails’. They include widespread, environmentally tolerant species that are amongst the most frequently encountered terrestrial snails in the mesic southern and eastern parts of the region, as well as rare, narrowly endemic species of conservation concern. The larger cannibal snails belonging to the genera *Afrorhytida* Möllendorff, 1903, *Capitina* Watson, 1934 and *Natalina* Pilsbry, 1893 were revised by Herbert & Moussalli (2010). The present paper represents the second part of our revision of the Rhytididae fauna of southern Africa. Introductory remarks concerning the family as a whole were provided in the first part of our revision and need not be repeated. Watson (1934) erected *Nata* to accommodate several smaller rhytidid species that differed significantly, both in shell form and internal anatomy, from the larger species (*Natalina s.l.*), notably in relation to features of the protoconch, radula, kidney, distal reproductive tract and pedal mucus gland. Analysis of DNA sequence data has subsequently confirmed that *Nata s.l.* represents a lineage quite distinct from *Natalina s.l.* (Moussalli *et al*. 2009; Moussalli & Herbert 2016).

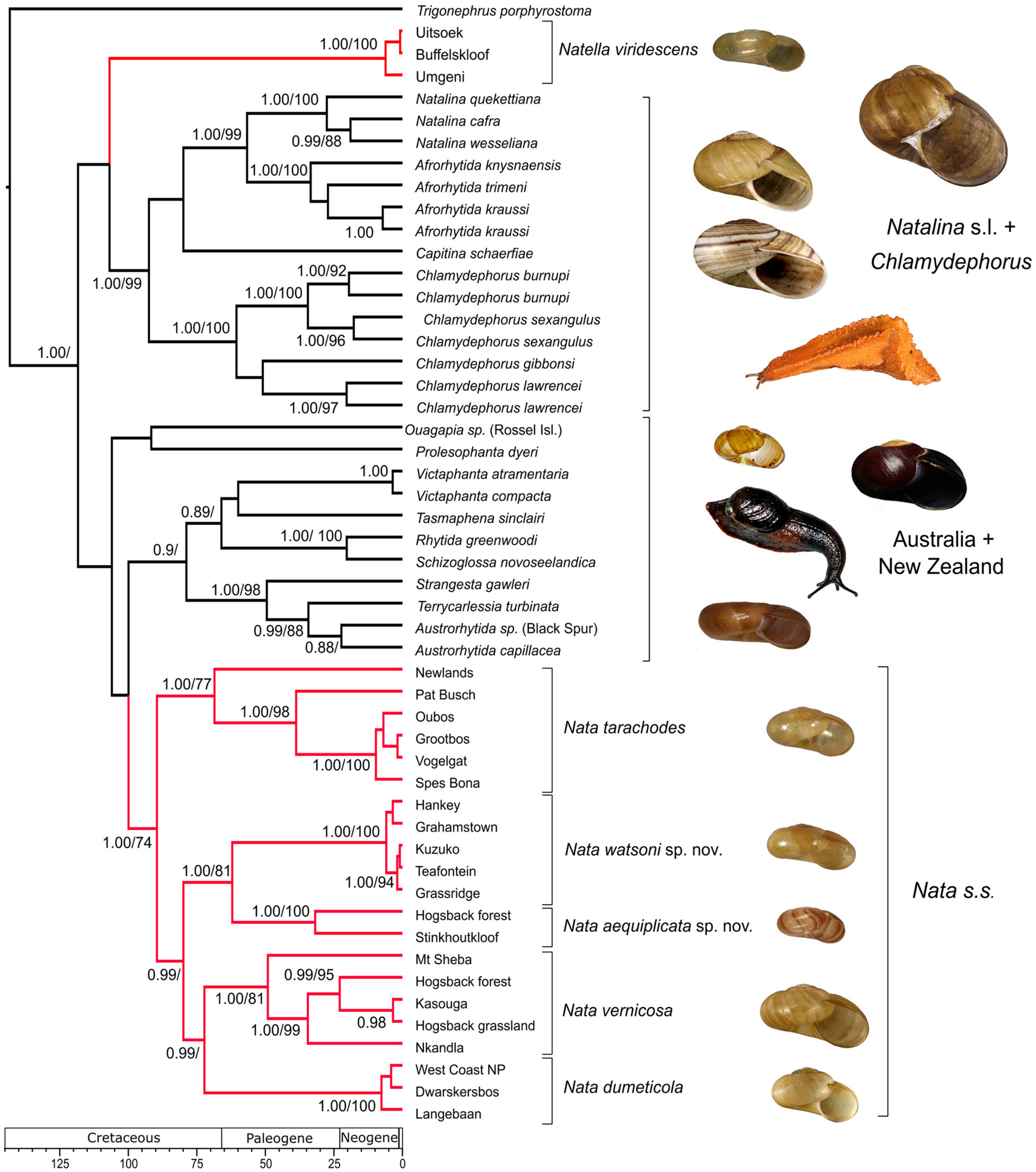

FIGURE 1. Phylogenetic estimate using BEAST uncorrelated (lognormal) relaxed clock model based on two nuclear and two mitochondrial genes (modified from Moussalli & Herbert 2016). A biogeographic calibration was applied to the base of the Rhytididae, representing the East–West Gondwana split (approx. 120 Mya). Nodal support represents posterior probabilities (only PP ≥0.90 shown) followed by likelihood bootstrap support (only BS ≥75 shown). Images are reflective of size, but not accurately to scale.

Although *Nata s.l.* is relatively easy to discriminate from *Natalina s.l.* on shell characters alone (*inter alia* its small, smooth protoconch), the species level taxonomy of the genus remains poorly resolved. When describing *Nata*, Watson (1934) divided it into two sections *Nata s.s.* and *Natella* Watson, 1934, which have since been regarded as subgenera. The bulk of species he placed in *Nata s.s.*, proposing *Natella* solely for *Nata viridescens* (Melvill & Ponsonby, 1891), which he showed differed significantly from the remaining species in terms of its soft-part morphology. Subsequent authors have followed Watson's lead (Connolly 1939; Zilch 1959–1960; Schileyko 2000). However, discriminating between the nominal species belonging to *Nata s.s.* has proved troublesome, due to the simple and conservative morphology of the shell, and the existence of considerable intraspecific variation. Watson (1934) believed that several of the names proposed by Melvill & Ponsonby (1892a, 1894) were merely synonyms of the widespread and variable *Nata vernicosa* (Krauss, 1848). Bruggen (1985) went even further, suggesting that *Nata s.s.* might be a super species distributed from the Cape Peninsula to Zululand and northern South Africa. For further clarification he recommended that future studies should be based on more abundant material from throughout the distributional range and should include anatomical data. A great deal more material has been collected in the intervening 30 years and now, with over 830 samples available, many with preserved soft-parts, we are able to re-evaluate the taxonomy of the dwarf cannibal snails of southern Africa and provide a revision of the species based on integrated data derived from morphological and molecular datasets.

Following on from earlier molecular work on *Natalina s.l.*, we have undertaken a similar study of *Nata s.l.*, but including a broader spectrum of rhytidid diversity as well as chlamydephorid slugs (Moussalli & Herbert 2016). The resultant phylogeny, reproduced here in Figure 1, revealed that whereas *Nata s.s.* forms a well-supported monophyletic entity (PP = 1.0; BS = 74), *Natella* is a deeply divergent lineage occupying a basal position within the Rhytididae. The phylogeny also confirms that chlamydephorid slugs are closely related to the larger cannibal snails (*Natalina s.l.*) and are in fact limaciform rhytidids rather than a separate family of slugs. Although phylogenetic relationships between the major lineages, including *Nata s.s.* and *Natella*, remain unresolved, the very deep divergence and distinct morphology strongly supports the recognition of *Natella* as a separate genus. When viewed in conjunction with phenotypic variation, our molecular analysis highlighted the remarkable levels of morphological conservatism within *Nata s.l.*, spanning considerable evolutionary depth, including within *Nata s.s*.

Combining this new molecular data with detailed morphological studies, we update the species-level taxonomy of *Nata s.l.* extensively and provide a comprehensive revision of all species, including keys. Detailed comparative morphological observations are provided for the distal reproductive tract (including spermatophores when available), pulmonary cavity, mantle edge, radula and suprapedal gland.

Material and methods

The bulk of the material examined is housed in the KwaZulu-Natal Museum, Pietermaritzburg, South Africa. This material has been accumulated over more than a century of collecting activity, but has been greatly augmented by recent field surveys undertaken by the authors together with Mary Cole (East London Museum) and Linda Davis (KwaZulu-Natal Museum). The specimens thus acquired have much more accurate 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 of such taxa was kept to a minimum. Additional material housed in ELM, NHMUK, SAMC and SMNH was also examined. Material cited by Connolly in his monograph (Connolly 1939), when not present in the NMSA or SAMC, is generally to be found in the NHMUK. 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. 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 Hitachi S–570 SEM, Philips XL30 ESEM and Zeiss EVO 10LS scanning electron microscopes. Photographs of shells were taken with a Nikon D70 camera and those of living specimens with a Nikon CoolPix 8800. Photographs of everted penises were taken using a Zeiss Stemi 2000-C dissecting microscope with AxioCam ERc5s digital camera and stacked images were then combined using Helicon Focus Pro (Helicon Soft Ltd) to provide extended depth of field. Light micrographs of stained radula slides were taken using an Olympus AX70 Compound Fluorescence Light Microscope with a Nikon DS-Ri1 camera and NIS Elements Imaging Software. Shell measurements were taken following the methods described earlier (Herbert & Moussalli 2010). Figures relating to the number of protoconch whorls exclude the nucleus or apical cap (± 0.5 whorls). Immature shells were excluded from the data used to calculate H:D ratios.

Abbreviations: ELM, East London Museum, East London, South Africa; H:D, shell height: diameter ratio; MV, Museum Victoria, Melbourne, Australia; NHMUK, Natural History Museum, London, U.K.; NMSA, KwaZulu-Natal Museum, Pietermaritzburg, South Africa; NMW, National Museum of Wales, Cardiff, U.K.; RMNH, Naturalis Biodiversity Center, Leiden, The Netherlands; SAMC, South African Museum, Cape Town, South Africa; SMNH, Swedish Museum of Natural History, Stockholm, Sweden.

Biological observations

General observations on the biology and ecology of southern African rhytidid snails were provided by Herbert & Moussalli (2010) in relation to the larger species. Much of what was stated therein is relevant here and need not be repeated. For the most part, however, rather less is known of the biology of the smaller species. Like the larger cannibal snails, they occur primarily to the south and east of the Great Escarpment. Within this region, however, they occur in a wide variety of habitats, from wet mistbelt forest to thicket, open savannah and fynbos, and they range considerably further inland into the Karoo and Highveld regions than was previously thought (Bruggen 1978) [discussed further in the concluding biogeographic discussion below]. The ecological tolerance of the individual species is variable. Most are catholic in their requirements and occur in forest habitats as well as thicket and more open savannah environments (e.g. *Nata vernicosa, N. watsoni* **sp. nov.**, and *Natella viridescens*), whereas others appear more specialised and favour particular habitats types, such as forest (e.g. *Nata aequiplicata* **sp. nov.**) or coastal scrub and fynbos (e.g. *Nata dumeticola*).

Feeding. The diet is again thought to comprise chiefly of soft-bodied invertebrates, but published observations on feeding and prey items are few. Edgar Layard (in Cooke 1895: 54) reported *Nata dumeticola* and *N. vernicosa* preying upon *Cyclostoma affine* [=*Tropidophora ligata*], *Helix capensis* [=*Trachycystis capensis*] and *H. cotyledonis* [= *Sheldonia cotyledonis*]. Similarly, we have found that *N. vernicosa* will attack small to medium-sized snails such as species of *Gittenedouardia*, *Sheldonia* and *Trachycystis* with vigour, as well as slugs and earthworms. Without doubt *N. vernicosa* is a voracious predator of other molluscs and care has to be taken to keep living specimens of this species separate from other snails when collecting in the field. They will even attempt to attack prey items much larger than themselves, such as achatinid snails (Herbert & Kilburn 2004). Table 1 lists the prey items so far observed for dwarf cannibal snails. Although the data available are not extensive, it seems that differences in radula morphology do not reflect differences in diet, for even *N. watsoni* **sp. nov.**, with its aberrant, fine-toothed radula, feeds on snails. No observations are available for *Natella viridescens*.

TABLE 1. Summary of information concerning the diet of species of *Nata.*

Species	Prey	Reference
Nata aequiplicata **sp. nov.**	*Trachycystis* sp.	herein
Nata dumeticola	*Sheldonia cotyledonis* (Benson, 1850) *Trachycytsis capensis* (Pfeiffer, 1841) *Tropidophora ligata* (Müller, 1774)	E. Layard (in Cooke, 1895)
	Theba pisana (Müller, 1774)	W. Sirgel (pers. comm., 2012)
Nata erugata **sp. nov.**	*Opeas* cf. *florentiae* (Melvill & Ponsonby, 1901)	herein
Nata tarachodes	*Trachycystis* sp.	W. Sirgel (pers. comm., 2012)
Nata vernicosa	*Gittenedouardia* spp., *Sheldonia* spp., *Trachycystis* spp., *Elisolimax flavescens* (Keferstein, 1866), earthworms	Herbert & Kilburn (2004), herein and L. Davis (pers. comm., i/2013)
Nata watsoni **sp. nov.**	*Sheldonia asthenes* (Melvill & Ponsonby, 1907)	herein

Olfactory capacity in these snails is evidently acute and feeding behaviour is elicited almost immediately upon contact with prey. Unlike the larger cannibal snails, there are no labial palps in species of *Nata* or *Natella* and prey detection is perhaps chiefly mediated by the inferior tentacles. Whether prey is initially located by trail-following is not known, but this seems likely. In *Nata vernicosa*, once contact is made with the prey item, the predator draws its head back fractionally, at the same time exposing and slightly protruding the whitish lips and inner oral area. It then lunges forward, thrusting the odontophore out through the mouth to make contact with the prey. The bristling radula teeth at the end of the odontophore penetrate the victim's flesh, gripping and tearing off pieces of tissue as the odontophore is withdrawn. Through repeated protrusion and withdrawal of the odontophore and radula, the predator is able to consume its prey in a piece-meal fashion over a perhaps extended period of time. Whether *Nata*, like *Natalina* is able to extract the calcium from the prey snail's shell once its flesh has been consumed is not known.

In *Nata*, as with the larger southern African rhytidids, there is no evidence of a proboscis-like structure. Such a structure may be present in *Natella*, however, in which a drowning individual of *Natella viridescens* was seen to evert a cylindrical extension of the oral tube, well beyond the mouth (Fig. 2A). This may be another distinguishing feature of *Natella*, but is one that needs to be investigated more fully. Currently the availability of well-preserved specimens is insufficient. Such a structure is also present in species of *Ouagapia* (Kondo 1943).

While the predator has acute olfactory capacity, so does the prey, and the initial contact with the predator may elicit an immediate and distinct escape response. Resting specimens of *Sheldonia* are roused instantly when touched on almost any part of the body by *Nata vernicosa*, and crawl away at surprising speed, waging their tail vigorously. In *Gittenedouardia* and some *Trachycystis* species the response to contact is a vigorous twisting of the shell, and occasionally a foot-thrashing behaviour where the extended foot is flicked rapidly from side to side, overbalancing the shell and allowing the snail to hastily flip-flop away from the predator, righting itself soon thereafter and crawling off to safety. If, however, the predator manages to effect a good initial bite, the prey is usually unable to escape and it withdraws rapidly into its shell to await the inevitable.

*Reproductive biology***.** Information on the reproductive biology and behaviour of *Nata* is scant and that of *Natella* is unknown. Though specimens have been found *in copulo* in the field (February), the preceding courtship behaviour, if such exists, has not been witnessed. Mating itself involves shell mounting (Fig. 2B), as is the case in *Natalina*, which is evidently atypical for low-spired snails (Asami *et al.* 1998). Mating events, however, require more careful scrutiny in order to establish whether sperm transfer is reciprocal or unilateral (Davison *et al.* 2005). Egg-laying was recorded for *Nata vernicosa* by Herbert & Kilburn (2004) who observed an individual laying a clutch of approx. 25 eggs in small hollow that it had excavated in the surface soil. The eggs, measuring about 1.8 mm in diameter, were each encased in a thin, brittle, white to yellow-brown, calcareous shell, bearing microscopic spicules on the surface. Hatching time may be as little as 32 days in the summer (Herbert & Kilburn 2004) with development extending slightly beyond the protoconch such that hatchlings emerge with approximately one-quarter of the first teleoconch whorl already laid down.

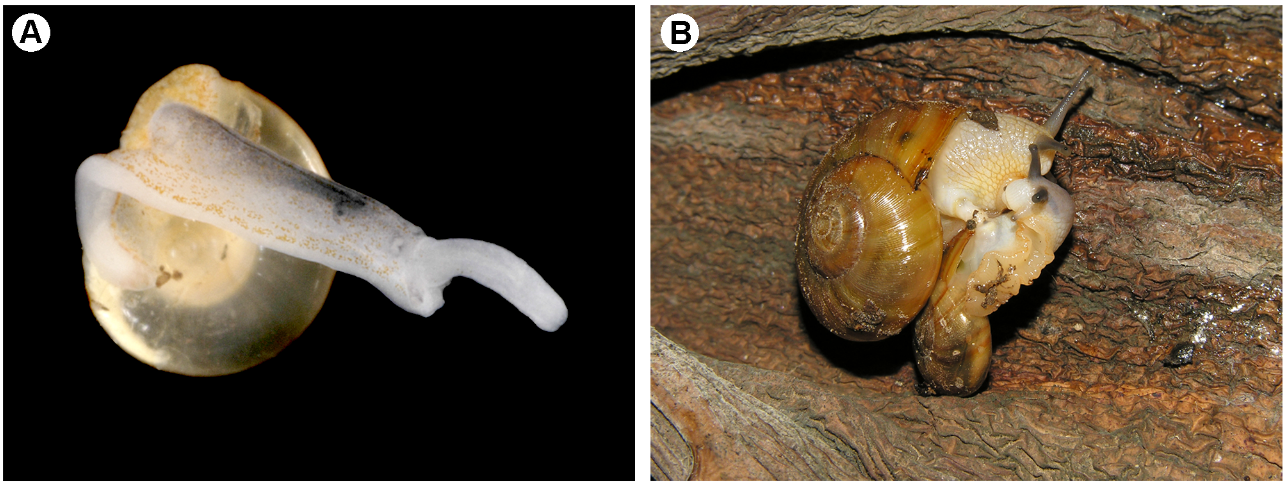

FIGURE 2. A, *Natella viridescens* (Melvill & Ponsonby, 1891), drowning individual with proboscis everted, Ithala Game Res., KwaZulu-Natal, shell diameter 3.7 mm (NMSA W7263). **B,** *Nata vernicosa* (Krauss, 1848), mating pair, Qora River mouth, E. Cape, respective shell diameter 20.5 mm and 14 mm (NMSA W4015).

Comparative morphological observations

The considerable morphological conservatism evident in southern Africa's dwarf cannibal snails was mentioned in the Introduction. This conservatism, however, particularly regarding the morphology of the shell, is not restricted to *Nata s.l.* It extends also to components of the Australian rhytidid radiation and includes genera such as *Altidelos* Stanisic, 2010, *Austrorhytida* Smith, 1987, *Echotrida* Iredale, 1933, *Montedelos* Iredale, 1943, *Saladelos* Iredale, 1933, *Scagacola* Stanisic, 2010 and *Vitelledelos* Stanisic, 2010 (Stanisic *et al.* 2010). Specimens of the common and widespread *Nata vernicosa* would not look at all out of place in an Australian rainforest, wet sclerophyll forest or vine thicket. Indeed, comparison might also be drawn with South American systrophiids, North American haplotrematids, European oxychilids and perhaps even helicoid streptaxids from East Africa (e.g. species of *Tayloria* Bourguignat, 1889). This broader conservatism is clearly convergent, but it surely attests to the evolutionary success of a shell that is low spired, relatively broadly umbilicate, rather uniformly yellowish-brown, weakly sculptured and often glossy—a shell morphology that has evidently proved suitable to a carnivorous mode of life.

Protoconch (Fig. 3). One of the most distinctive features serving to distinguish the smaller-shelled southern African rhytidid radiation from the larger-shelled one is the form of the protoconch. Although the shape and number of whorls is similar in both, the size and sculpture vary considerably. In the smaller species discussed here the protoconch is small (diameter <2.6 mm, and usually <2.0 mm) and consistently smooth, whereas the larger-shelled species generally have a considerably larger protoconch (diameter 2.5–8.5 mm), the bulk of which is sculptured by close-set axial riblets (Herbert & Moussalli 2010). Within the *Nata–Natella* radiation, however, the largely featureless protoconch offers little in the way of useful taxonomic characters. Its size varies with the species and is clearly linked to the maximum adult shell size attained, but there is considerable interspecific overlap in protoconch diameter ranges (Table 2). The number of protoconch whorls is often difficult to determine with precision, depending upon the definition of the apical cap and delimitation of the terminal lip, but typically ranges from 1.0 to 1.25 whorls beyond to the apical cap.

TABLE 2. *Nata* and *Natella* species: comparative shell morphology data.

Species	max shell diameter (mm)	nº of whorls	protoconch diameter (mm)	H:D
Nata aequiplicata **sp. nov.**	6.7	2.75	0.7–0.9	0.53–0.59
Nata caffrula	12.4	2.75	1.5–1.6	0.63–0.70
Nata dumeticola	14.3	3.25	1.6–2.0	0.57–0.78
Nata erugata **sp. nov.**	21.0	3.5	1.0–1.9	0.46–0.60
Nata tarachodes	12.6	2.75	0.9–1.2	0.51–0.63
Nata vernicosa	24.5	3.75	1.1–2.6	0.49–0.71
Nata watsoni **sp. nov.**	16.0	3.75	1.0–1.4	0.48–0.60
Natella viridescens	5.3	2.0	0.7–1.0	0.42–0.47

Head-foot (Fig. 4). The head-foot of *Nata* and *Natella* exhibits a trait common in carnivorous snails in which the neck region is notably elongate (Watson 1915; Herbert & Moussalli 2010). This is partly due to the length of the long, muscular odontophore that has to be accommodated within the neck when the animal is active, but at the same time, a long slender neck also facilitates probing into burrows and crevices in search of prey, and extracting tissue from within the shell of molluscan victims. In contrast, the tail is usually short, normally projecting little beyond the posterior margin of the shell. A pair of conspicuous longitudinal grooves extends along the neck, one either side of the dorsal mid-line. Skin texture is variable, appearing relatively smooth in the smaller species such as *Nata tarachodes* and *Natella viridescens* (Fig. 4D, H), whereas in the larger *Nata* species, particularly *N. dumeticola* and *N. erugata* **sp. nov.**, the skin grooves are more pronounced, sometimes distinctly so (Fig. 4B, C). The foot is holopodous, the sole undivided and the tip of the tail is simple, having neither a caudal pore nor an appendage. The optic and inferior tentacles are well developed, and in the larger species a slight downwardly directed bulb may be evident beneath the eye (less obvious in the smaller species).

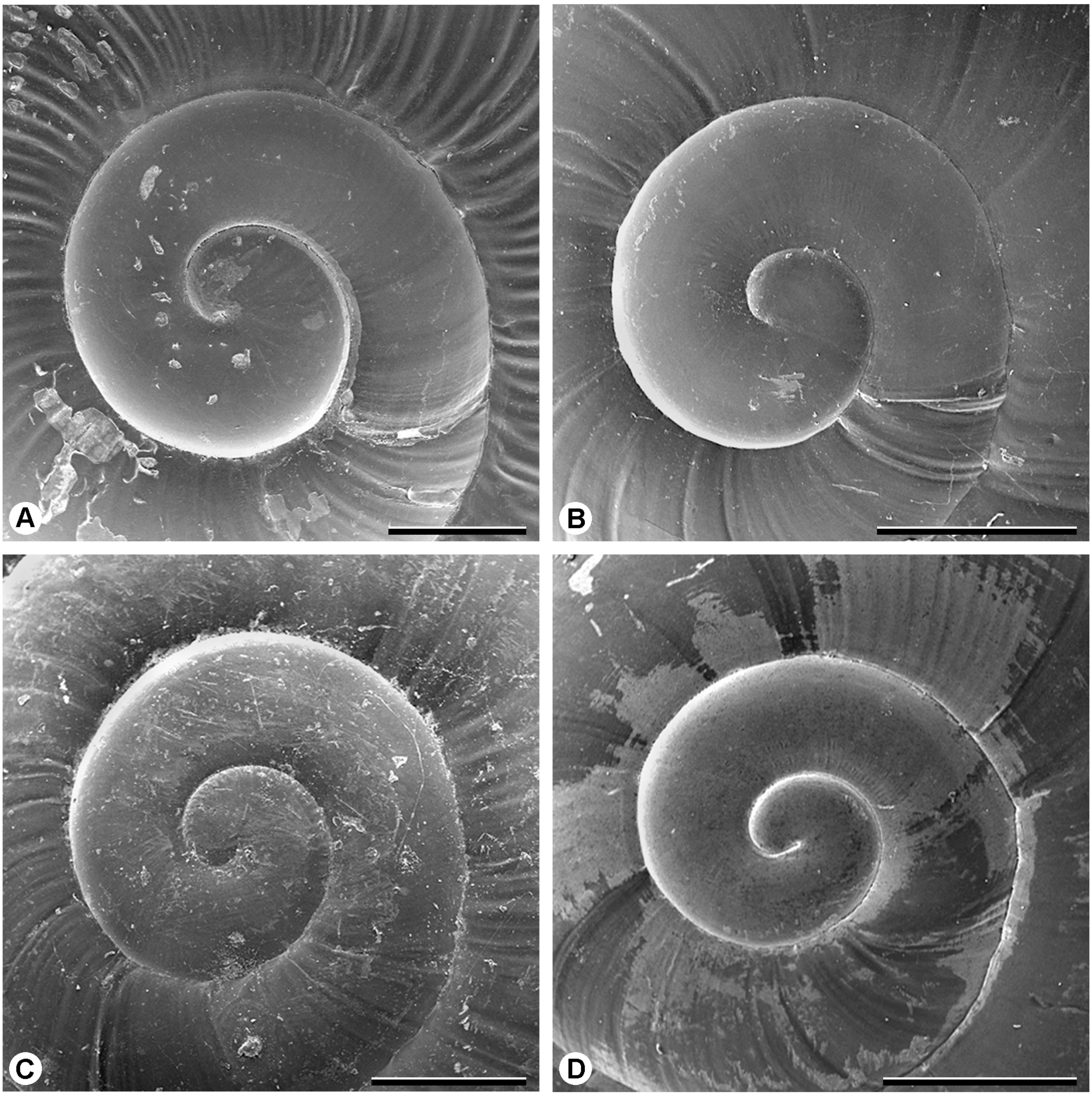

FIGURE 3. Protoconchs of *Nata* and *Natella*. **A,** *Nata dumeticola*, Kommetjie, W. Cape (NMSA 2767). **B,** *Nata tarachodes*, Spes Bona bush, Cape Peninsula (NMSA V9848). **C,** *Nata vernicosa*, Pietermaritzburg, KwaZulu-Natal (NMSA A7114). **D,** *Natella viridescens*, Ithala Game Res., KwaZulu-Natal (NMSA V2530). Scale bars = 0.5 mm.

As indicated above in relation to feeding behaviour, there are no labial palps associated with the mouth, another feature that distinguishes the dwarf cannibal snails from their larger counterparts (Herbert & Moussalli 2010). The edge of the mantle skirt is divided into left and right lobes, the form of which most closely resembles the condition in *Natalina s.s.* and *Afrorhytida*, in which the left lobe is divided into two smaller lobes. In both *Nata* and *Natella*, however, the lower left lobe has a narrow base and bears lateral flanges on both sides (Fig. 5A) (only on the right in *Natalina s.s.* and *Afrorhytida*). The genital pore is usually situated ventral to the pneumostome (see distal reproductive tract below).

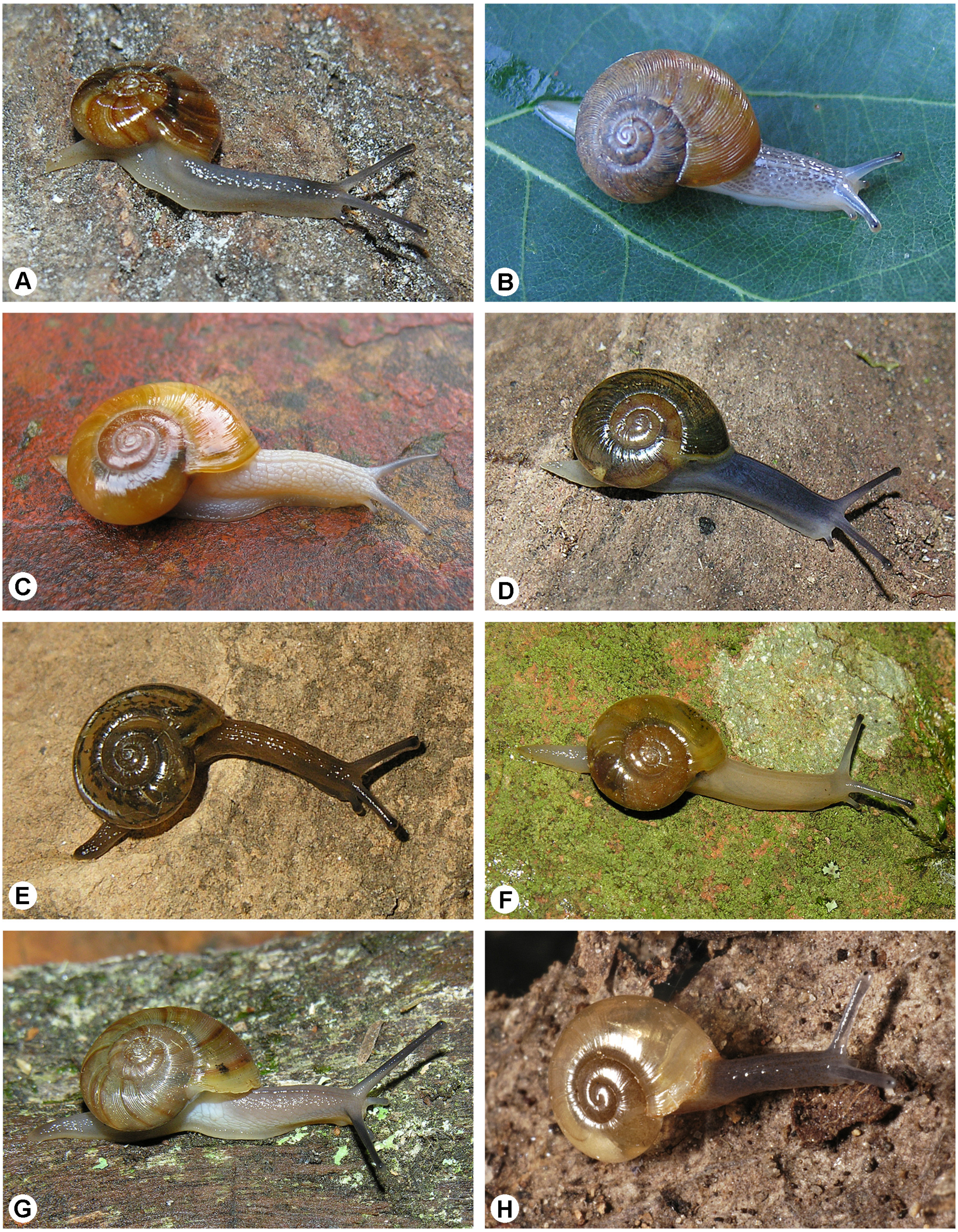

FIGURE 4. Living animals of *Nata* and *Natella*. **A,** *Nata aequiplicata* **sp. nov.**, holotype, Stinkhoutkloof, E. Cape, shell diameter 6.5 mm (NMSA W9248/T3066). **B,** *Nata dumeticola*, West Coast National Park, W. Cape, shell diameter 10.8 mm (NMSA W3224). **C,** *Nata erugata* **sp. nov.**, Tullach-Mohr, Nelspruit area, Mpumalanga, shell diameter 20 mm (MV *ex* NMSA W3301). **D,** *Nata tarachodes*, Grootbos Private Nat. Res., Gansbaai, W. Cape, shell diameter 7.7 mm (NMSA W5658). **E,** *Nata watsoni* **sp. nov.**, Hankey, E. Cape, shell diameter 7.5 mm (paratype NMSA W6524/T3921). **F,** *Nata watsoni* **sp. nov.** Camdeboo National Park, Graaff-Reinet, E. Cape, shell diameter 13.0 mm (paratype, NMSA W6091/T2303). **G,** *Nata vernicosa*, Vernon Crookes Nat. Res., KwaZulu-Natal, shell diameter 14.0 mm (NMSA W8020). **H,** *Natella viridescens*, Ithala Game Res., KwaZulu-Natal, shell diameter 3.7 mm (NMSA W7263).

In terms of body colour, most species exhibit some variation in head-foot coloration, particularly *Nata vernicosa* in which the head-neck ranges from pale grey to dark charcoal-grey. The mantle edge is usually a slightly paler shade of the head-foot colour and the optic tentacles a darker shade. In most species some individuals also possess conspicuous orange coloration due to the presence of numerous microscopic orange pigment granules in the skin, particularly along the margins of the foot and tail, and the mantle edge. Similar orange pigmentation may be present in the larger cannibal snails and was discussed in greater detail by Herbert & Moussalli (2010). The dorsal neck grooves are never differentially coloured as they are in some Australian species (Stanisic *et al*. 2010).

Pulmonary anatomy (Fig. 5). The renal system is sigmurethrous. The shape of the kidney ranges from trigonal (*Nata*, Fig. 5B) to bean-shaped (*Natella*, Fig. 5C), the anterior portion curving to the left, over the pericardium. The primary ureter, arising anterior to the auricle, is recurved around the anterior portion of the kidney and follows the right kidney margin to its posterior edge where it vents close to the posterior limit of the pulmonary cavity. The continuing secondary ureter is an ill-defined, open conduit that runs forwards beside the rectum to the pneumostome. The recurved anterior portion of the kidney and primary ureter is a feature not seen in the *Natalina s.l.* radiation (Watson 1934; Herbert & Moussalli 2010). The blood vessels lining the pulmonary cavity are not conspicuous, often only the pulmonary vein is evident. In some species, notably *Nata tarachodes*, the whitish coloration of the kidney is noticeable externally, through the translucent shell (Fig. 20B).

Pigmentation of the pulmonary wall is usually limited except in *Nata tarachodes* in which there may be extensive black pigmentation, particularly just prior to the mantle edge (Fig. 4D). Some individuals of *N. watsoni* **sp. nov.** may also exhibit conspicuous dark pigmentation of the pulmonary wall, whereas others may have only a few black spots (compare Figs 4E and F). *N. vernicosa* rarely exhibits much pigmentation in this region, but it commonly (perhaps invariably) has a small black blotch just above and to the left of the pneumostome (Figs 4G, 26). Freshly preserved specimens of this species also frequently exhibit a bluish tinge in the mantle collar in the pneumostomal area, perhaps related to the presence of mucus glands in the mantle edge. This colour, however, is lost with time in ethanol-preserved specimens.

Radula (Fig. 6). As in other rhytidid genera, and carnivorous snails in general, species of *Nata* and *Natella* lack a jaw and have a beloglossan radula (for further discussion see Herbert & Moussalli, 2010). However, whereas the larger southern African rhytidids possess a rachidian tooth, most of the smaller species lack this tooth, with the exception of *Nata aequiplicata* **sp. nov.**, *Natella viridescens* and some unusual specimens tentatively identified with *Nata tarachodes*. Although there is often considerable variation in tooth size across the width of the radula, there is usually no obvious feature that can be used to distinguish lateral and marginal series. Frequently, however, one tooth in each half-row is clearly identifiable as the largest tooth (Fig. 6A, C, D, F) and we treat this as the outermost lateral tooth. This distinction is admittedly arbitrary, for the first marginal is often of similar appearance, but it facilitates description of radula characters. Only in *Nata dumeticola* and *N. watsoni* **sp. nov.** (Figs 6B, E) can no one tooth be identified as the largest and in these we consider all the teeth to belong to one series. Comparative data relating to radula dentition is provided in Table 3 and light micrographs of stained radula mounts are provided in Figure 6. Additional figures, mostly SEM images are provided with the species descriptions. In all species there is a reduction in the number of teeth and an increase in the size of the teeth from the anterior to the posterior of the radula. Thus as the animal grows its radula teeth become fewer in number but larger, and it is therefore presumably able to consume prey more rapidly and may also be capable of dealing with larger prey items.

TABLE 3. *Nata* and *Natella*, interspecific variation in radula statistics.

Species	radula formula	n° teeth/row	n° of rows
Nata aequiplicata **sp. nov.**	1+(6–7)+(8–10)	26–32	37–42
Nata dumeticola	0+(14–22)	28–44	55
Nata erugata **sp. nov.**	0+(7–8)+(3–4)	20–24	24–33
Nata tarachodes	0+(7–9)+(4–5)	22–28	29–35
Nata watsoni **sp. nov.**	0+(19–33)	38–66	44–60
Nata vernicosa	0+(8–11)+(3–4)	22–30	23–32
Natella viridescens	1+7+(3–4)	20–22	27–32

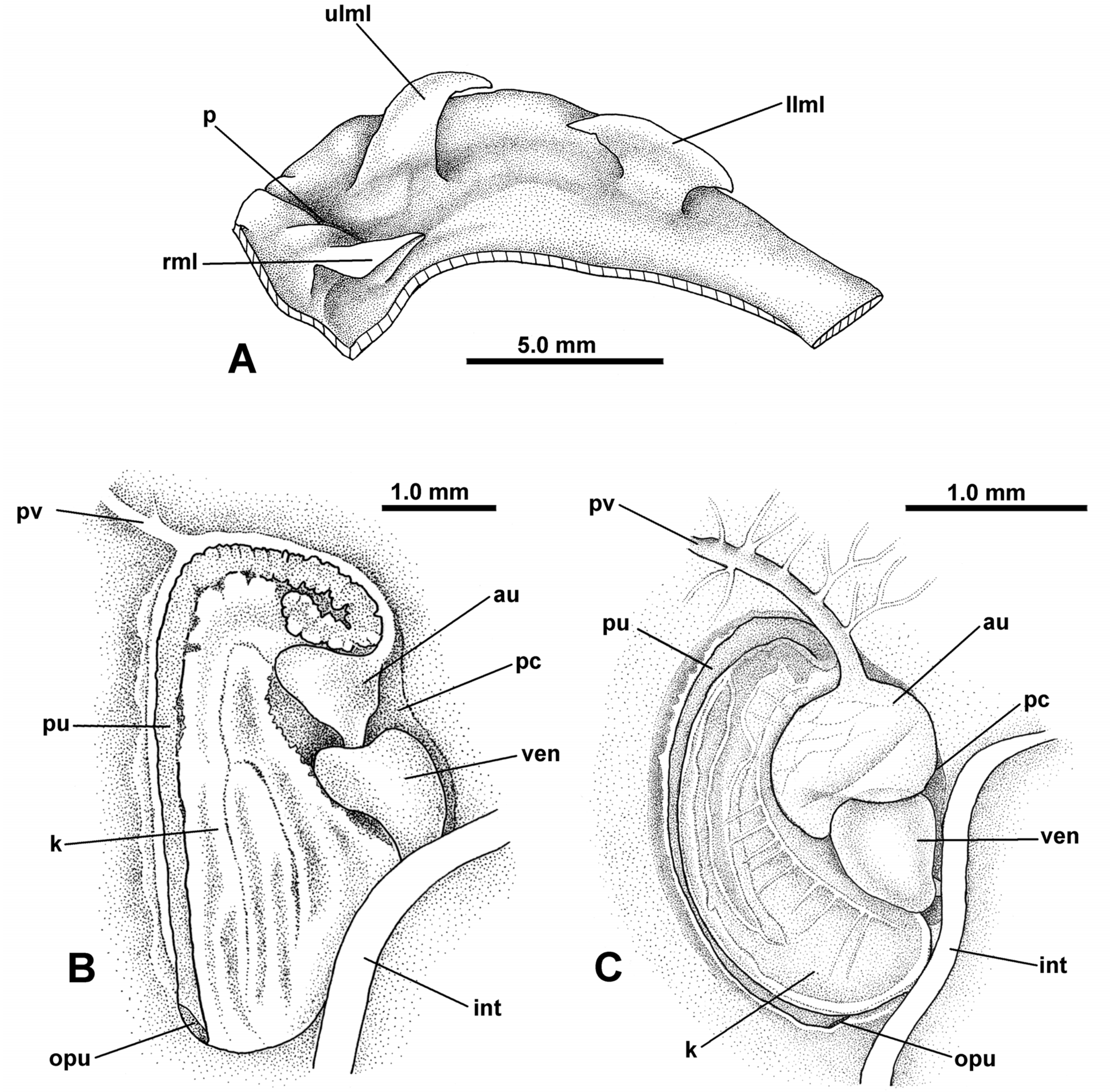

FIGURE 5. Morphology of mantle edge and reno-pericardial system (ventral aspect). **A,** *Nata vernicosa*, mantle edge showing structure of upper and lower left mantle lobes, The Haven, E. Cape (NMSA W4151). **B,** *Nata tarachodes*, reno-pericardial system, Oubos, W. Cape (NMSA W5671). **C,** *Natella viridescens*, reno-pericardial system, Ithala Game Res., KwaZulu-Natal (NMSA V3177). Abbreviations: au, auricle; int, intestine; k, kidney; llml, lower left mantle lobe; opu, opening of primary ureter; p, pneumostome; pc, pericardium; pu, primary ureter; pv, pulmonary vein; rml, right mantle lobe; ulml, upper left mantle lobe; ven, ventricle.

The rachidian when present is small and narrow (Fig. 6A, F). In *Nata aequiplicata* **sp. nov.** it is particularly small, perhaps vestigial and probably of limited functional significance. It is somewhat larger in *Natella viridescens* and, when describing the taxon *Natella*, Watson (1934) listed its possession of a rachidian as a distinctive character. However, since a rachidian is also present in *Nata aequiplicata* **sp. nov.**, which genital characters and DNA sequence data show to be species of *Nata*, retention of the rachidian is not unique to *Natella* amongst southern Africa's dwarf cannibal snails. Given that the rachidian is also retained in all three of the larger southern African cannibal snail genera, as well as many of the Australasian genera for which radula information is available [e.g. *Rhytida* and *Wainuia* (Powell 1930); *Austrorhytida*, *Macrodelos*, *Murphitella* and *Tasmaphena* (Smith 1979, 1987); *Diplomphalus* (Hausdorf 2013); *Schizoglossa* and *Strangesta* (unpublished obs.)] this is probably the ancestral character state. Furthermore, Kondo (1943) observed that whereas adult specimens of

Ouagapia ratusukuni Cooke, 1942 lack the rachidian tooth, such a tooth is present in juveniles. Although we have looked for this in juvenile *Nata vernicosa*, but not found the same, it does suggest that the loss of this tooth may reflect ontogenetic phenomena rather than phylogeny alone. Similarly, the presence/absence of a rachidian is thought to have little phylogenetic significance in the Streptaxidae (Bequaert & Clench 1936; Rowson 2010).

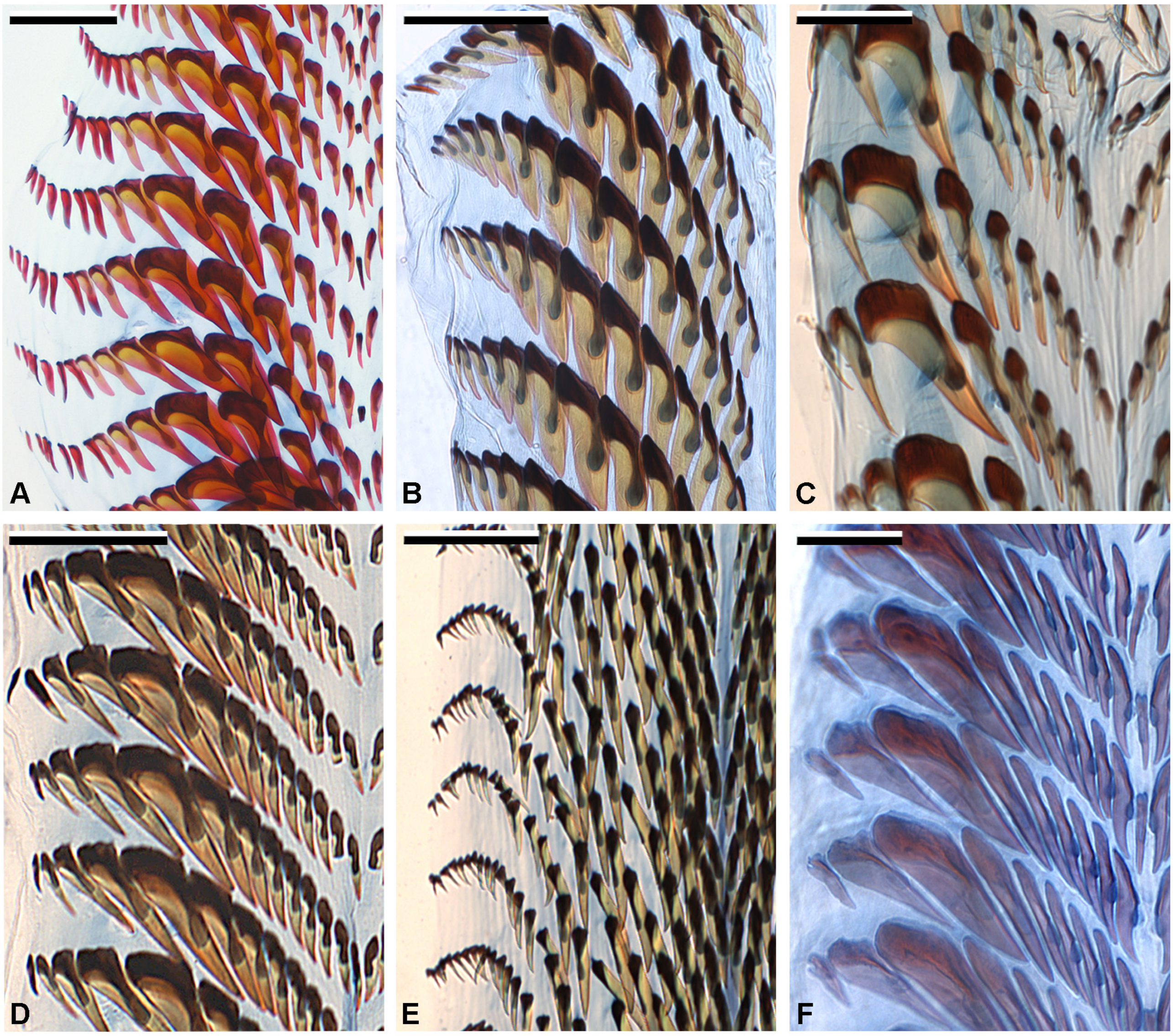

FIGURE 6. Radulae of *Nata* and *Natella*, automontage light micrographs of half-row portions of stained radula mounts. **A,** *Nata aequiplicata* **sp. nov.**, type locality (paratype, NMSA W9249/T3067). **B,** *Nata dumeticola*, Jacobsbaai, W. Cape (NMSA V7760). **C,** *Nata erugata* **sp. nov.**, Golden Gate Highlands National Park, Free State (paratype, NMSA W4243/T3913). **D,** *Nata tarachodes*, Oubos, W. Cape (NMSA W5671). **E,** *Nata watsoni* **sp. nov.**, Graaff-Reinet, E. Cape (paratype, NMSA W6091/T2303). **F,** *Natella viridescens*, Ithala Game Res., KwaZulu-Natal (NMSA V2530). Scale bars: A = 100 µm; B = 200 µm; C–E = 250 µm; F= 50 µm.

In species where one lateral tooth is clearly the largest, the inner lateral teeth are slender and increase in size away from the mid-line, gradually at first, but ultimately rapidly so, culminating in several robust, sharply pointed teeth, including the largest one, between half and two-thirds of the way along the row from the mid-line. Smith (1987) referred to this largest tooth as the 'fang' tooth. Three to ten marginal teeth lie beyond this largest tooth, often rapidly decreasing in size to the minute outermost one. Compared to other southern African rhytidid genera, this type of radula is closest to that of *Afrorhytida* though the teeth are more numerous in that genus and a rachidian is always present (Herbert & Moussalli 2010). It is also close to that of *Austrorhytida* from Australia (Smith 1987) and *Rhytida* from New Zealand (Powell 1930).

In *Nata dumeticola* and *N. watsoni* **sp. nov.**, in which the within-row progression in tooth size is more gradual and no one tooth clearly stands out as being the largest, the number of teeth per row and the total number of tooth rows in the radula is high relative to the other species (Table 3). The short, broad radula teeth of *N. dumeticola* resemble those of *Delos* (Powell 1930).

Distal reproductive tract (Fig. 7). Significant amongst the distinctive features of the *Nata s.l.* radiation is the position of the genital pore, which occupies a posterior location, ventral to the pneumostome, rather than being adjacent to the right optic tentacle (as in *Natalina s.l.*). We have found this to be consistently true in the larger number of species studied here, except in the case of *Nata dumeticola* in which the genital pore lies somewhat further forward, approximately midway between the pneumostome and the optic tentacles. Other distinctive features of *Nata* noted by Watson and confirmed here include the absence of convolutions in the spermoviduct (it may be sinuous and the oviduct may bear superficial folds, but it is not convoluted as in *Natalina s.s.* cf. Herbert & Moussalli 2010: fig. 12), a shorter bursa copulatrix duct that is broader basally, the lack of an oviduct caecum, a very short vagina (sometimes not evident at all) and the epiphallus, if present, is short and usually considerably narrower than the penis.

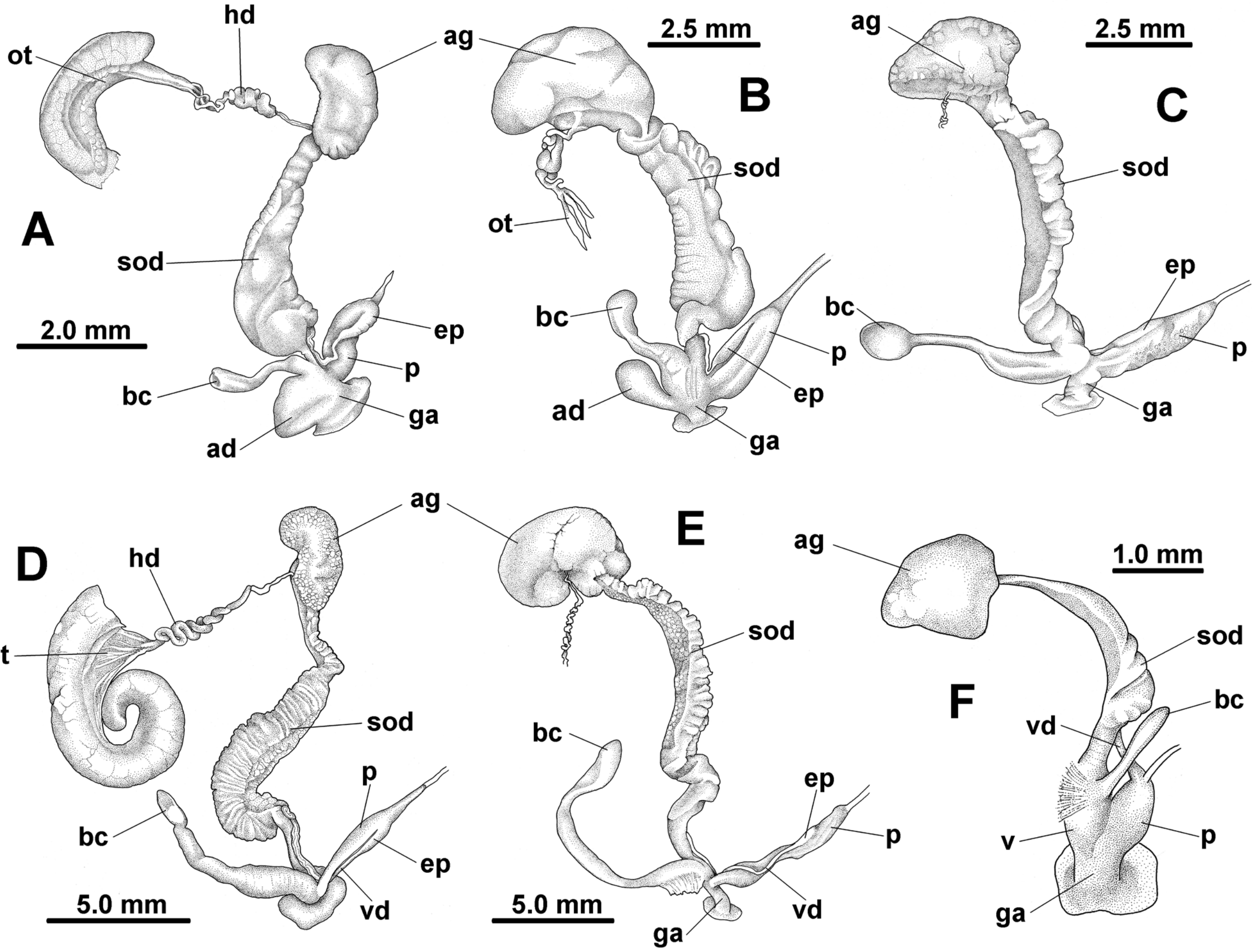

FIGURE 7. Reproductive tract of *Nata* and *Natella*. **A,** *Nata aequiplicata* **sp. nov.** (paratype, NMSA W9249/T3067). **B,** *Nata tarachodes* (NMSA W9118). **C,** *Nata dumeticola* (NMSA W8258). **D,** *Nata vernicosa* (NMSA W9322). **E,** *Nata watsoni* **sp. nov.** (holotype). **F,** *Natella viridescens* (NMSA V31770). Abbreviations: ad, atrial diverticulum; ag, albumen gland; bc, bursa copulatrix; ep, epiphallus; ga, genital atrium; hd, hermaphrodite duct; ot, ovotestis; p, penis; sod, spermoviduct; v, vagina; vd, vas deferens.

In *Nata s.s.* the distal reproductive tract is relatively simple in all species, but is at its simplest in the larger ones (*dumeticola*, *erugata* **sp. nov.**, *vernicosa* and *watsoni* **sp. nov.**, Figs 7C–E). In these the penis is generally elongate, though its shape in preserved specimens is much dependent on the degree of contraction/relaxation of the animal when preserved. The vas deferens lies adnate to the penis, but is not firmly adherent to it. Its distal region is somewhat swollen and forms an indistinct epiphallus that inserts laterally between one-third and three-quarters of length of the penis from its base. Internally the penis lumen bears numerous small papillae that may be arranged in ill-defined radiating ridges around the opening of the epiphallus. In its contracted state, there may also be some longitudinal folds in the penis wall. When the penis is everted, the papillae project from its surface (Fig. 8A, B). Running to the base of the penis, the vas deferens reflexes alongside the free oviduct, in which region it is frequently somewhat sinuous prior to its origin at the base of the prostatic portion of the spermoviduct. The free oviduct and the bursa copulatrix duct arise almost side by side directly from the genital atrium and the vagina is short or virtually absent. The bursa and its duct are between half to two-thirds the length of the spermoviduct (including the free oviduct), and the basal region of the duct is usually quite distinctly broader. The bursa itself is generally small and often has an oval whitish mass inside. Whereas the vagina is very short, the free oviduct is considerably longer—this being the reverse of that observed in the larger southern African rhytidids (Herbert & Moussalli 2010).

The smaller species of *Nata* (*aequiplicata* **sp. nov.** and the type species, *tarachodes*, Fig. 7A, B) exhibit slight modifications of this plan in that the penis is more stout, the bursa copulatrix duct shorter and there is a lateral diverticulum (the vaginal appendix of Watson 1934) on the genital atrium associated with the base of the bursa duct. The epiphallus, however, still inserts laterally on to the penis and the vas deferens follows the same reflexed course beside the penis and free oviduct.

In *Natella* (Fig. 7F) there are additional differences that set this genus apart from *Nata*. The penis is very short and squat and there is no epiphallus evident. Instead, the vas deferens is much shorter and follows a more or less direct route from the base of the prostatic portion of the spermoviduct to the penis. It does not pass down the free oviduct and beside the penis. The penis is not internally papillate and has a well-developed apical verge. Furthermore, there is a more distinct, somewhat swollen vaginal region leading to the free oviduct, from the side of which arises a short bursa copulatrix duct with an elongate bursa.

In all cases the penis lies to the right of the retractor muscle of the right optic tentacle. The spermoviduct is usually sinuous, correlating with its spiral course within the viscera, and the prostatic and oviductal portions are generally distinct. The albumen gland varies considerably in size and shape, and has a soft texture. The hermaphrodite duct is long, and thickened and convoluted in its mid region. The ovotestis comprises a small number of fusiform lobes embedded in the uppermost whorl of the digestive gland.

Spermatophores (Fig. 8C). A single well preserved spermatophore has been found in a specimen of *Nata watsoni* **sp. nov.** This was a simple, slender, tadpole-shaped structure with an elongate-ovate head tapering to a narrow tail. The surface was smooth, with no evidence of ridges or spines. In this instance it was an allospermatophore and was found with the head in the bursa copulatrix and the tail extending down into the bursa duct. Similar ovate spermatophore-like masses have been found associated with the bursa copulatrix and its duct in other species, but degradation had progressed to a stage where little detail was apparent. In *N. erugata* **sp. nov.** these structures were observed in the swollen basal part of the bursa duct.

Compared to the spermatophores of *Afrorhytida* and *Natalina* (Herbert & Moussalli 2010), that of *Nata* is far less elaborate. The tadpole form is closer to that of *Capitina*, but in *Nata* the surface is not sculptured. Barker (2001: 95) has suggested that such simplification of the spermatophore is a derived condition leading to spermatophore reduction and ultimately to spermatophore loss. Few mature specimens of *Natella viridescens* have been examined and no information on the spermatophore is available for that species. However, given that the epiphallus appears to be lacking, it is possible that a discrete spermatophore is not produced and sperm is transferred as an un-encapsulated seminal mass.

In *Nata*, where the vagina is short or non-existent, it seems probable that the everted penis is inserted into the swollen basal portion of the bursa copulatrix duct or into the atrial diverticulum if this is present, and the spermatophore deposited in either of these structures. This contrasts with the situation in the larger *Natalina s.l.* species where the penis and vagina are both long and the former is inserted into the latter, with the site of spermatophore receipt being the oviduct caecum (*Natalina s.s.*) or the free oviduct and upper vagina (*Afrorhytida* and *Capitina*). A similar situation may occur in *Natella*, where the structure of the genitalia suggests that the penis inserts into the similarly shaped vagina, with the seminal mass being deposited close to the origin of both the bursa duct and the free oviduct.

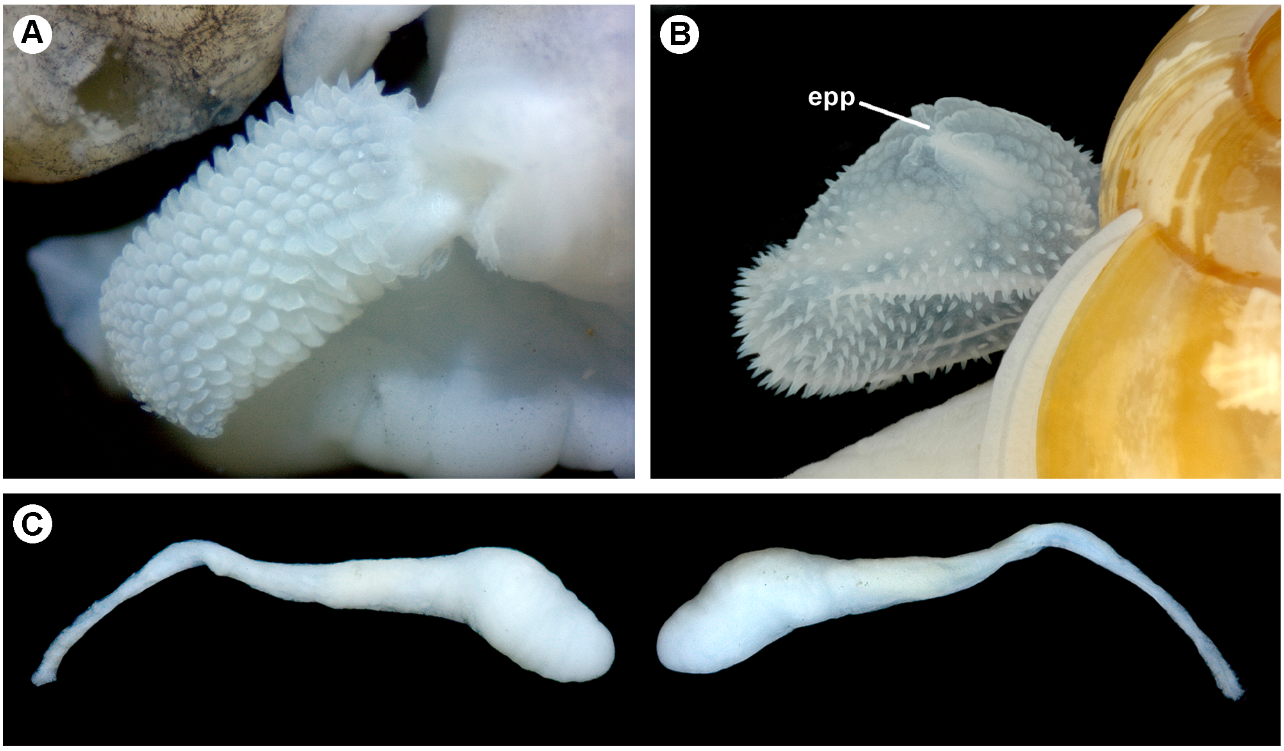

FIGURE 8. A, *Nata tarachodes* (Connolly, 1912), everted penis, penis length 2.3 mm, Oubos, Riviersonderendberge, W. Cape (NMSA W5671). **B,** *Nata vernicosa* (Krauss, 1848), everted penis, penis length 3.3 mm, Pietermaritzburg, KwaZulu-Natal (NMSA W3910). **C,** spermatophore of *Nata watsoni* **sp. nov.**, left and right sides, extended length 6.6. mm, Alexandra Forest, E. Cape (NMSA W9173). Abbreviations: epp, epiphallus pore.

Suprapedal gland (Fig. 9). As is typical of rhytidids in general, the suprapedal mucus gland of *Nata* and *Natella* is well developed. It lies on the floor of the body cavity, beneath the buccal mass, and is loosely attached to the pedal musculature by scattered connective tissue strands. It is never as long and convoluted as in species of *Natalina*, and is closer to that of *Afrorhytida* and *Capitina*. It opens at the anterior limit of the foot, beneath the oral region, and extends posteriorly for a distance approximately equal to the length of the buccal mass. For about three-quarters of its length, the central duct is lined laterally and ventrally by glandular tissue, but the posterior portion lacks gland cells and comprises only the thin-walled duct, ending blindly in a slightly swollen terminal bulb. This flimsy posterior portion is often kinked or slightly twisted. The terminal bulb has a small white mass of tissue on what is usually the postero-dorsal surface of the lumen (sometimes ventral if the duct is twisted). This is very closely applied to, and probably confluent, with the pedal artery which runs along the dorsal surface of the gland before descending beneath the terminal bulb and into the posterior pedal musculature. A similar structure is also present at the posterior extremity of the suprapedal gland of *Afrorhytida*, *Capitina* and *Natalina*, but in these genera it is less conspicuous because the glandular tissue continues to the end of the duct (Watson 1915; D. Herbert, pers. obs.). Collinge (1901) has illustrated what is evidently the same structure in *Rhytida* and *Paryphanta* and Watson (1915) provided a detailed discussion of its occurrence in chlamydephorid slugs, comparing it to a typhlosole. The function of this component of the suprapedal gland is not known, but the observations on other stylommatophorans reported by Barr (1926) suggest that it may play a role in excretion.

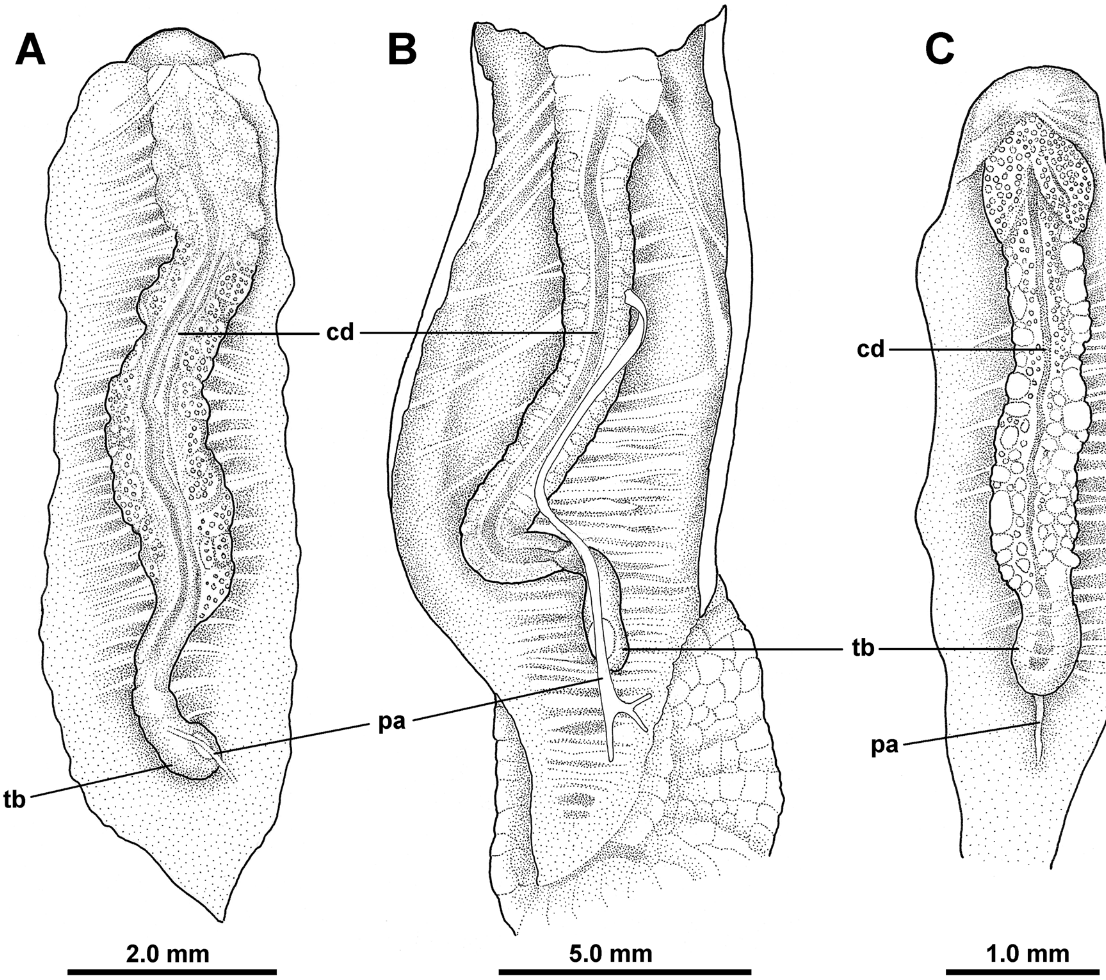

FIGURE 9. Suprapedal gland of *Nata* and *Natella*. **A,** *Nata tarachodes*, Oubos, W. Cape (NMSA W5671). **B,** *Nata vernicosa* Kelso Junction, KwaZulu-Natal (NMSA V7940). **C,** *Natella viridescens*, Ithala Game Res., KwaZulu-Natal (NMSA V3177). Abbreviations: cd, central duct; pa, posterior aorta; tb, terminal bulb.

Systematic descriptions

Superfamily Rhytidoidea Pilsbry, 1893

Family Rhytididae Pilsbry, 1893

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

For diagnosis see Herbert & Moussalli (2010).

Key to genera within *Nata s.l.*

1. Epiphallus present, inserting laterally into penis; vas deferens reflexed; vagina short or non-existent; base of bursa copulatrix duct swollen or with an associated atrial diverticulum; kidney trigonal. . . . . *Nata*

– Epiphallus absent; vas deferens not reflexed, inserting at penis apex; vagina and penis of more or less equal length; base of bursa copulatrix duct not swollen and without an associated atrial diverticulum; kidney bean-shaped. . . . . *Natella*

Genus *Nata* Watson, 1934

Nata Watson, 1934: 158. Type species (by original designation): *Natalina tarachodes* Connolly, 1912.

Diagnosis. Shell small to moderate in size (adult diameter 6–25 mm), thin, subglobose to discoidal, yellowish-brown to honey-brown, frequently with uneven darker axial bands, but lacking spiral colour pattern; apical surface with close-set axial (collabral) riblets or smooth, sculptured only by weak growth-lines, spiral sculpture mostly lacking; usually glossy, occasionally lustreless; base generally smoother and more glossy; peristome interrupted in parietal region; outer lip thin with membranous periostracal fringe, never thickened; umbilicus open, width moderate to wide; protoconch smooth, comprising 1.0–1.25 whorls, diameter 0.7–2.6 mm (rarely more than 2.0 mm).

Radula beloglossan, but tooth morphology variable; labial palps not evident; epiphallus present but usually small, inserting laterally into penis; penis lumen papillate, epiphallus pore may be somewhat raised or surrounded by a flange-like disc, but a verge-like structure is absent; retractor muscle of right optic tentacle passes to left of penis; vas deferens reflexed, passing down penis then back along free oviduct; vagina short or absent; bursa copulatrix duct broader basally; no oviduct caecum present; atrial diverticulum sometimes present; kidney trigonal, primary ureter reflexed around anterior of kidney; suprapedal mucus gland not convoluted, the posterior portion lacking glandular tissue.

Remarks. As indicated in the Introduction, following our previous work (Moussalli & Herbert 2016), we employ the genus *Nata* in a restricted sense, and treat *Natella* as a separate genus. There are significant morphological differences between the two and molecular data demonstrate that *Natella* constitutes a deeply divergent, basal lineage within the Rhytididae.

Nata is endemic to southern Africa, occurring mostly to the south and east of the Great Escarpment and ranging from the south-western Cape to the Soutpansberg in Limpopo (23°S) and Inhambane in southern Mozambique (24°S). The range of one species also extends into the Highveld of Gauteng, Free State and Lesotho.

Key to species of *Nata*

1. Shell small with distinct, evenly and quite widely spaced, axial pliculae that extend around periphery and into umbilicus; restricted to the area just west of Port Elizabeth . . . . **Nata aequiplicata sp. nov.**

\- Shell small to moderate in size, sculpture weak (essentially growth-lines only), or with close-set axial riblets that evanesce at periphery, the base with weak growth-lines only. 2

2\. Shell lacking distinct and regular axial riblets, sculpture largely consisting only of relatively fine, irregularly spaced growth-lines. 3

\- Strength of shell sculpture variable, but adapical surface (or at least the subsutural part thereof) always with some evidence of close-set axial riblets 4

3\. Radula with ≥19 teeth per half-row, lacking a distinct fang tooth; largely confined to the Albany Thicket Biome . . . . ***Nata watsoni* sp. nov.**

\- Radula with ≤12 teeth per half-row, one of which (the fang tooth) is clearly larger than the others; inland and montane regions of eastern South Africa and Lesotho (mostly above 1000 m), as well as at lower altitudes in Maputaland and the Lowveld of Mpumalanga . . . . ***Nata erugata* sp. nov.**

4\. Adult diameter >20 mm; widespread throughout southern and eastern South Africa . . . . *Nata vernicosa*

\- Adult diameter <15 mm; W. Cape only 5

5\. Shell with relatively strong, crisp, evenly spaced and close-set axial riblets on the adapical surface, often lustreless; adult shell with rather globose profile and compact whorls; Cape Peninsula and Atlantic Cape coast. . . . . *Nata dumeticola*

\- Shell with less regular axial riblets, usually glossy; profile somewhat depressed and whorls comparatively rapidly expanding; more widely distributed in south-western Cape . . . . *Nata tarachodes*

Nata aequiplicata sp. nov.

Figures 4A, 6A, 7A, 10–13

Etymology. From *aequalis* (L.)—equal, uniform; and *plico* (L.)—to fold, *plicatus*—folded; with reference to the distinctive shell sculpture.

Type material. Holotype (Fig. 4A, 10A–C): SOUTH AFRICA: E. CAPE: Loerie area, Longmore, Stinkhoutkloof (33.79940°S: 25.09698°E), 540 m, indigenous forest, under logs, D. Herbert, L. Davis & M. Cole, st'n 12-45, 17/xi/2012 (NMSA W9248/T3066).

Paratypes: SOUTH AFRICA: E. CAPE: same data as holotype, in leaf-litter and under logs (NMSA W9249/T3067, three specimens); Van Stadens Wild Flower Res. (33.91200°S: 25.20507°E), 175 m, gorge forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, st'n 08-56, 22/ix/2008 (ELM D15970/T032, two specimens); ditto (33.91165°S: 25.20465°E), 190 m, indigenous forest on steep rocky slope, in leaf-litter, D. Herbert, L. Davis & M. Cole, st'n 11-21, 27/ix/2011 (NMSA W8356/T3897, one specimen); Ferndale, near Patensie (33.71642°S: 24.85030), 160 m, riverine woodland, in leaf-litter, D. Herbert, L. Davis & M. Cole, st'n 11-25, 28/ix/2011 (NMSA W8320/T3898, two specimens).

Other material examined: (all NMSA): SOUTH AFRICA: E. CAPE: Same data as holotype (W9206); Thornhill area, valley of Berg River (33.87457°S: 25.11965°E), 155 m, indigenous forest, in leaf-litter, D. Herbert & L. Davis, st'n 12-44, 17/xi/2012 (W9199); Van Stadens River gorge (33.90937°S: 25.19090°E), 130 m, indigenous forest, in leaf-litter, D. Herbert & L. Davis, st'n 12-42, 16/xi/2012 (W9229); Van Stadens Wild Flower Res. (33.91200°S: 25.20507°E), 175 m, gorge forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, st'n 08-56, 22/ix/2008 (W6485).

Identification. Shell superficially similar to that of other *Nata* species, but distinguished by its small size and the evenly plicate axial sculpture that extends around the periphery and into the umbilicus.

Shell (Fig. 10): Discoidal, last adult whorl somewhat tumescent, spire low to almost flat; largest specimens comprising 2.50–2.75 teleoconch whorls; suture well above periphery, not noticeably descendant prior to aperture; periphery slightly below mid-whorl; surface glossy throughout. Protoconch very small, diameter 0.7–0.9 mm, comprising ±1.0 whorl, but junction with teleoconch usually not clear; for the most part smooth and glossy, but developing collabral growth-lines toward junction with teleoconch. Teleoconch relatively strongly sculptured with distinct, evenly spaced, axial pliculae that continue around periphery, onto base and into umbilicus. Aperture roundly ovate; peristome interrupted by bulging parietal region; outer lip thin with membranous periostracal fringe where undamaged, its adapical edge strongly convex in profile; base and umbilical margin evenly rounded; umbilicus relatively narrow and steep-sided, patent to apex; columella lip not reflected.

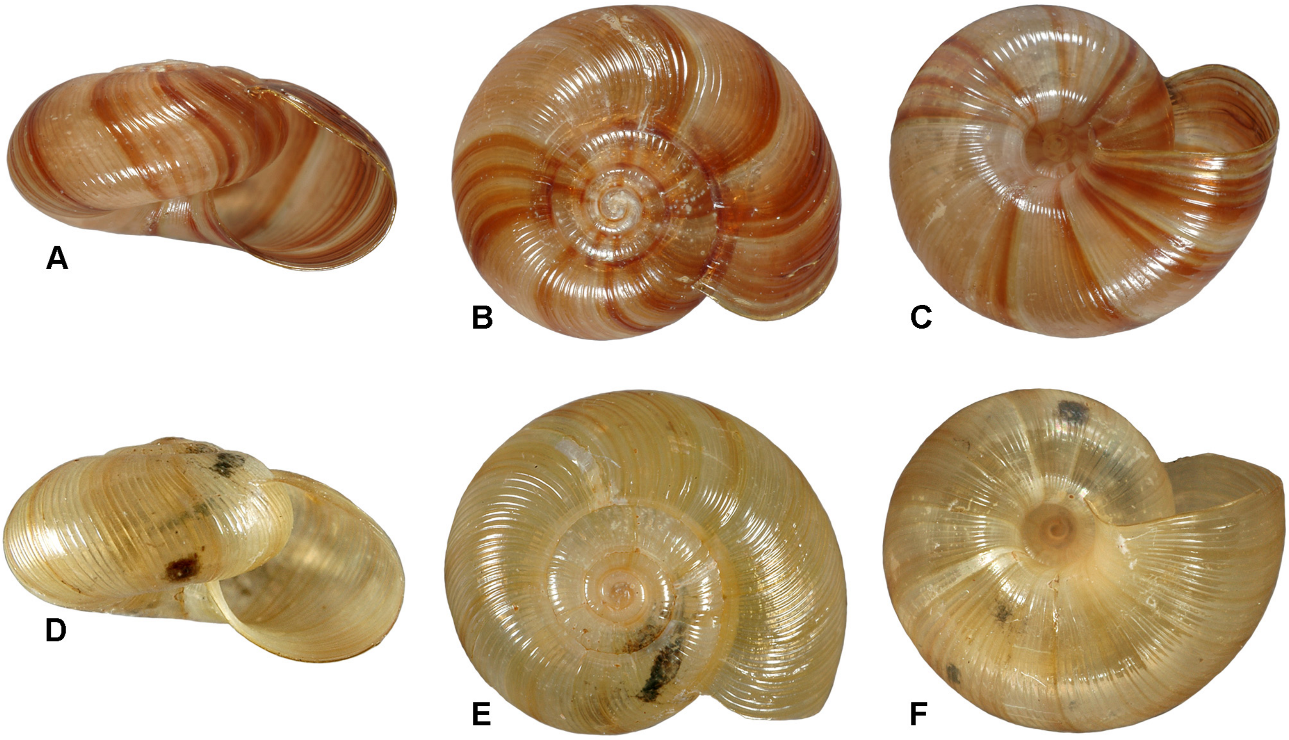

FIGURE 10. *Nata aequiplicata* **sp. nov. A–C,** holotype, diameter 6.5 mm (NMSA W9248/T3066). **D–F,** paratype, Van Stadens Wild Flower Res., diameter 6.7 mm (paratype, ELM D15970/T032).

Translucent, pale corneous brown with distinct, irregularly spaced, darker brown, axial bands when fresh, but colour pattern fading to pale yellowish-buff in dead shells.

Dimensions: Holotype, diameter 6.5 mm, height 3.6 mm; largest specimen, diameter 6.7 mm, height 3.7 mm; H:D of adults 0.535–0.585 (N=6).

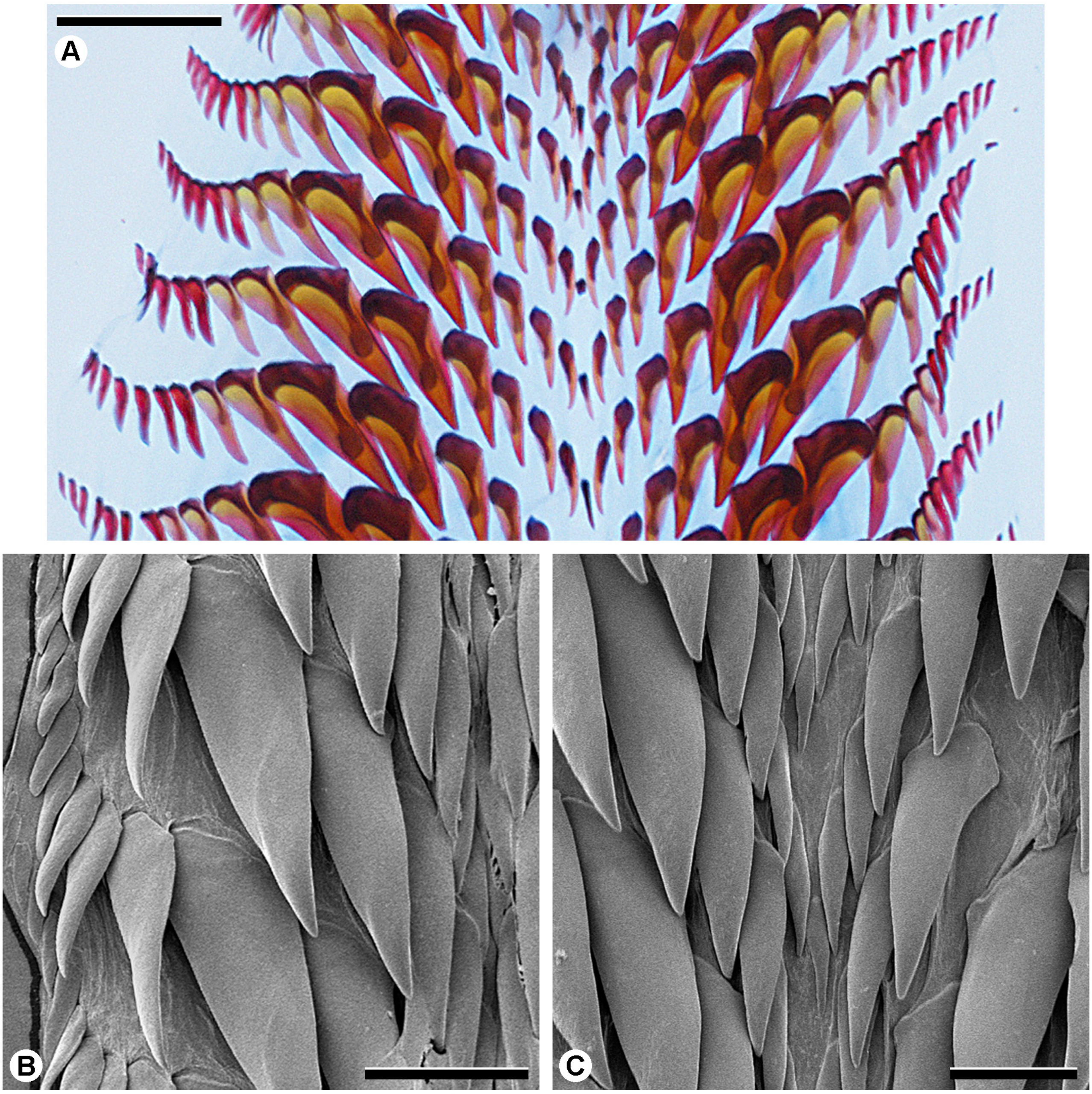

FIGURE 11. *Nata aequiplicata* **sp. nov.**, radula. **A,** light micrograph of stained preparation, anterior third of radula (paratype, NMSA W9249/T3067). **B,** outer lateral and marginal teeth, posterior third of radula (holotype). **C,** rachidian and inner lateral teeth, anterior third of radula (holotype). Specimen A considerably smaller than holotype and radula teeth thus proportionately smaller. Scale bars: A, B = 100 µm; C = 50 µm.

Living animal (Fig. 4A): Head and neck grey, darker anteriorly and on tentacles; foot paler ventrally and beneath shell; tail of foot relatively short, greyish-white; skin texture fine, somewhat coarser on neck; mantle edge greyish-white; lower left mantle lobe broad with relatively small lateral flanges; lining of mantle cavity not strongly marked but with some dark pigmentation, particularly bordering the pulmonary vein; kidney trigonal, pale buff, not conspicuous through shell.

Radula (Figs 6A, 11): Formula 1+(6–7)+(8–10); length up to 4.5 mm, with 37–42 broadly V-shaped rows of teeth; teeth progressively larger from anterior to posterior of radula, approx. 13 rows/mm anteriorly, approx. 7

rows/mm posteriorly; largest lateral tooth increasing up to 45% in size from anterior to posterior of radula; rachidian small, narrowly lanceolate and sharply pointed; innermost laterals small, but distinctly larger than rachidian, subsequent laterals progressively increasing in size, with teeth 5–6 (7 as well toward posterior of radula) much larger; inner laterals lanceolate, teeth 5–7 much broader and more trigonal; marginal series beginning beyond lateral 6–7, progressively decreasing in size, these teeth, 8–10 in number, are initially knife-shaped with a broader base and up-curved tip, but become shorter and more spathulate toward radula margin. Basal attachment of larger teeth L-shaped.

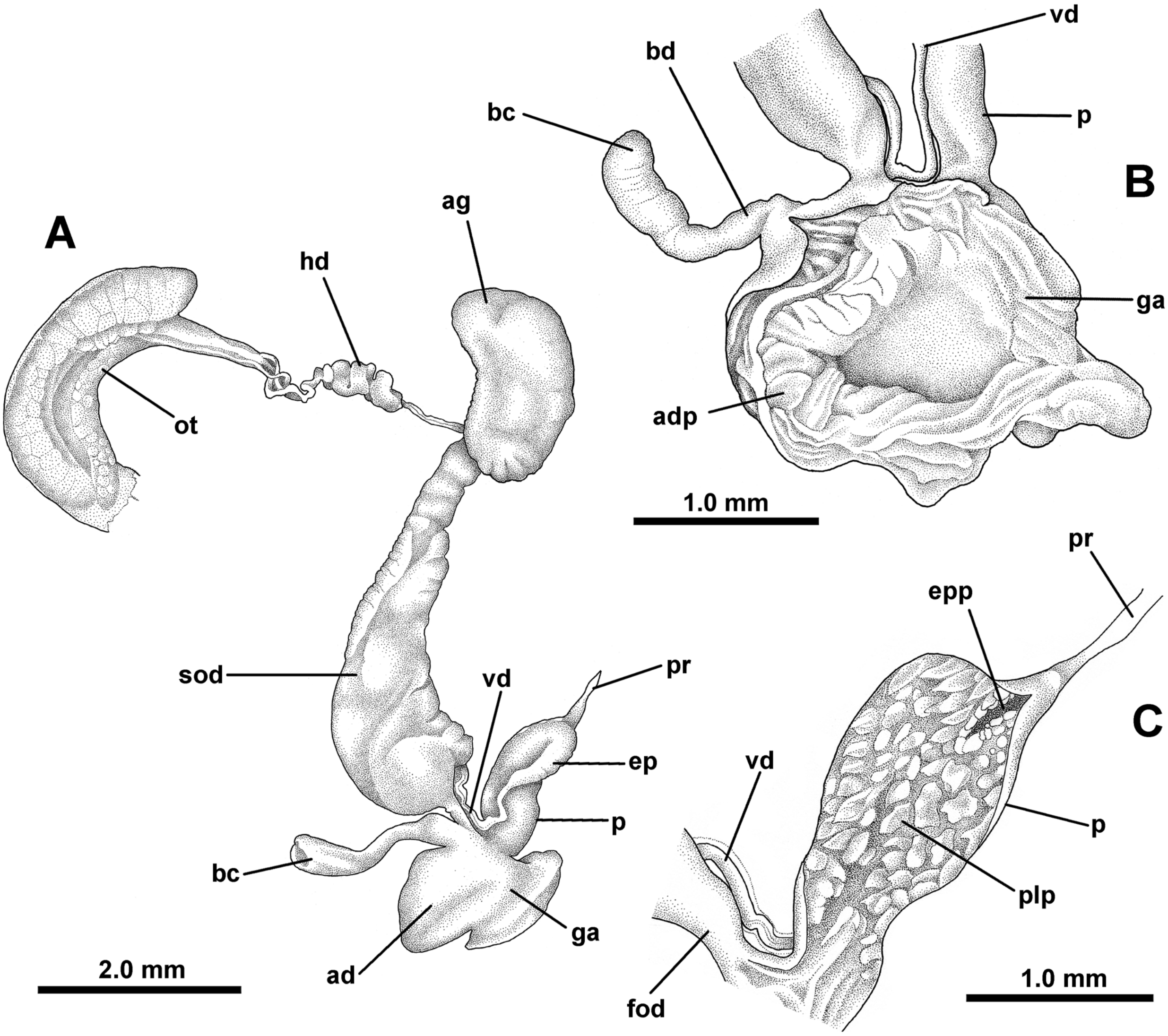

FIGURE 12. *Nata aequiplicata* **sp. nov.**, genitalia. **A,** entire genital tract (paratype, NMSA W9249/T3067). **B,** dissection of genital atrium and its diverticulum showing raised ridge-like pleat (holotype). **C,** longitudinal dissection of penis showing papillate lumen (holotype). Abbreviations: ad, atrial diverticulum; adp, pleat of atrial diverticulum; ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; ep, epiphallus; epp, epiphallus pore; fod, free oviduct; ga, genital atrium; hd, hermaphrodite duct; ot, ovotestis on inner margin of digestive gland; p, penis; plp, papillate lumen of penis; pr, penial retractor muscle; sod, spermoviduct; vd, vas deferens.

Distal genitalia (Fig. 12): Genital pore ventral to pneumostome; right optic tentacle retractor passing to left of penis. Penis relatively short and stout (length ±2.0 mm), broadest in mid region; its wall not conspicuously muscular, lumen lined with relatively coarse papillae; epiphallus pore simple, subapical. Penial retractor muscle attached at apex of penis; epiphallus present, one-third to half length of penis; adherent to side of penis and inserting subapically; vas deferens continues to penis base before running alongside free oviduct to join spermoviduct. Genital atrium simple and vagina almost non-existent, the free oviduct and bursa copulatrix duct seeming to arise directly from atrium, as does the penis. Atrial wall with indistinct longitudinal folds, becoming stronger near base of free oviduct and bursa copulatrix duct. Bursa copulatrix and its duct about one-quarter to one-third length of spermoviduct; basal portion of duct broader, lined internally with longitudinal folds originating in atrium; duct narrowing in mid region before bursa; bursa itself ovate, thin-walled and approx. half length of its duct. Genital atrium also with a relatively large, globose, lateral diverticulum, similar to but larger than that adjacent to base of bursa duct in *Nata tarachodes*; diverticulum with a prominent internal pleat forming a raised U-shaped ridge extending from close to genital pore, into diverticulum and ending adjacent to origin of bursa duct; crest of ridge bearing irregular transverse folds.

Distribution (Fig. 13): Known only from E. Cape, South Africa; evidently a restricted-range endemic, confined to a small area of the coastal hinterland between Jeffreys Bay and the eastern limit of the Cape Fold Mountains (Elandsberge); 130–540 m.

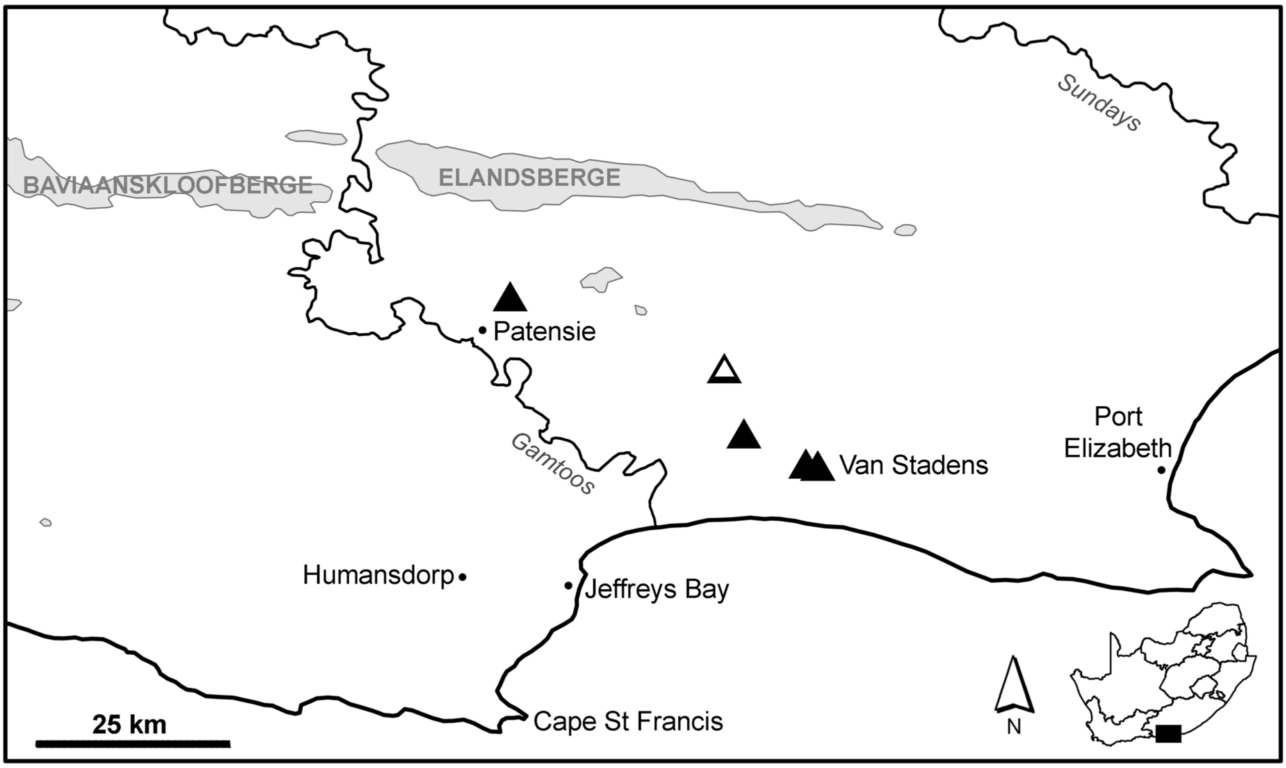

FIGURE 13. Distribution of *Nata aequiplicata* **sp. nov.** Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli & Herbert 2016); contour at 1000 m.

Habitat. Southern Coastal Forest in the Van Stadens River gorge and Southern Temperate Forest further inland on the south-facing portion of the Elandsberge (Mucina & Rutherford 2006); living in leaf-litter and under logs.

Remarks. *Nata aequiplicata* **sp. nov.** is one of the smallest species of *Nata*, but it is relatively easily distinguished on account of its strong, regularly and quite widely spaced axial pliculae and the fact that this axial sculpture extends around the periphery and into the umbilicus. The colour pattern of living individuals is also bolder than all except occasional specimens of *Nata vernicosa*. It is unusual in that the radula retains a rachidian tooth, as does that of *Natella viridescens*. The reproductive system, however, is similar to that of *Nata tarachodes*, and molecular data group the species with *Nata s.s.* (Moussalli & Herbert 2016).

An additional juvenile specimen from Hogsback, E. Cape, included in our molecular phylogeny clustered together with the present species. However, no voucher shell or soft parts are available and it is not possible to establish whether it is morphologically referable to *Nata aequiplicata* **sp. nov.** Further targeted field work in the Hogsback area has not brought to light any material resembling *Nata aequiplicata* **sp. nov.** suggesting that this specimen may represent a distinct entity requiring further investigation.

Conservation. Although *Nata aequiplicata* **sp. nov.** is small and thus easily overlooked, the E. Cape of South Africa is a relatively well-collected region and the absence of records of the species from much of the province suggests that its distribution is genuinely restricted to a small area in the south-west of the province. Further survey work is needed, particularly in forest habitats on the south facing slopes of the mountains of the eastern Cape Fold

Belt, to establish whether the species ranges further to the west. The data currently available indicate that this is a species of conservation concern, for which the preservation of indigenous forests in the area between the Gamtoos River valley and Port Elizabeth is likely to be critical.

Nata caffrula **(Melvill & Ponsonby, 1898) comb. nov.**
Figure 14

Natalina caffrula Melvill & Ponsonby, 1898a: 24, pl. 8, fig. 1. Melvill & Ponsonby, 1898b: 170. Möllendorff, 1903 in Möllendorff & Kobelt, 1903–1905: 23, pl. 4, figs 4, 5. Kobelt, 1909: 53. Connolly, 1912: 91. Connolly, 1925: 122. Connolly, 1939: 110. Richardson, 1986: 48. Type loc.: Knysna, W. Cape.

Not *Natalina caffrula*—Sturany, 1898: 32. Germain, 1935: 5. Haas, 1936: 18 [=*Nata vernicosa* and *N. erugata* **sp. nov.**].

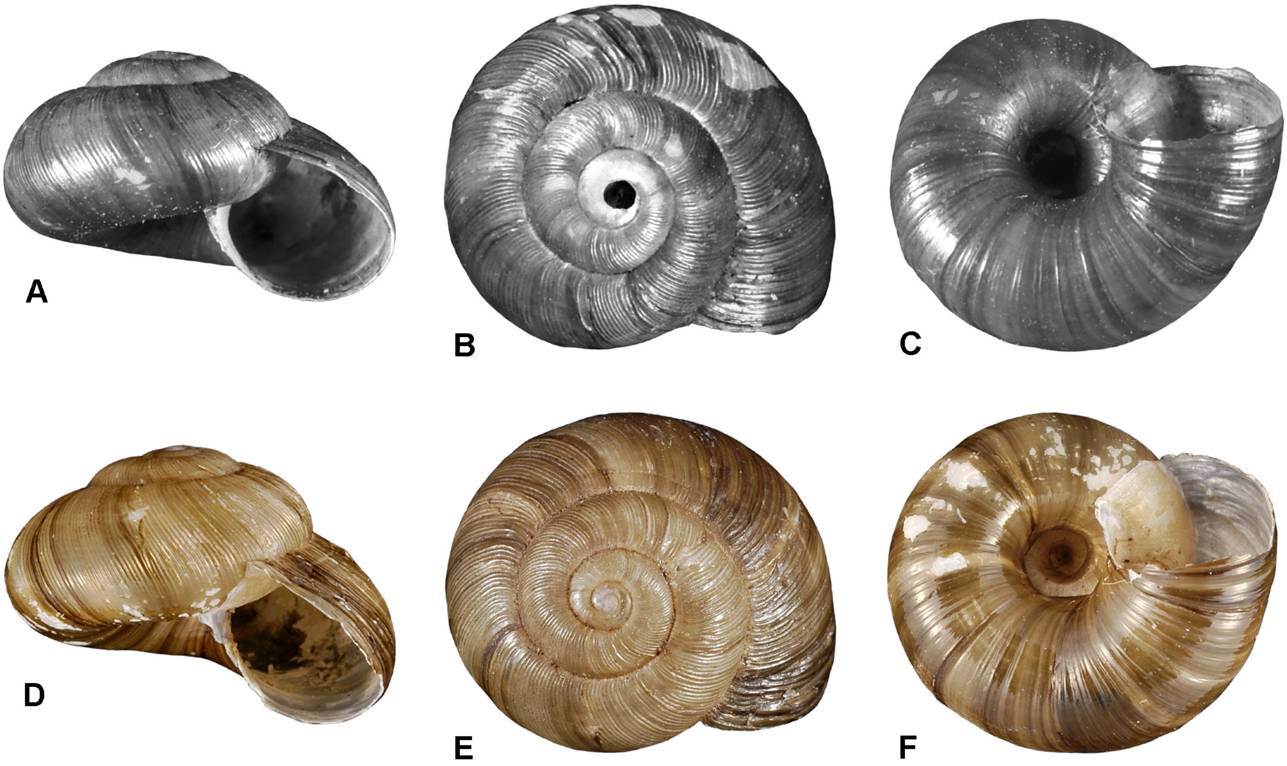

FIGURE 14. *Nata caffrula* (Melvill & Ponsonby, 1898), type material. **A–C,** holotype of *Natalina caffrula* Melvill & Ponsonby, 1898, diameter 11.2 mm (NHMUK 1911.8.8.10). **D–F,** paratype of *Natalina caffrula* Melvill & Ponsonby, 1898, diameter 12.5 mm (SAMC 2369).

Etymology. Diminutive of the Latinized form of the Arabic *kafir* (unbeliever); in reference to its resemblance to *Natalina cafra* (Férussac, 1821).

Type material. Holotype (Fig. 14A–C) in NHMUK (1911.8.8.10), diameter 11.2 mm [given as 11.5 mm by Melvill & Ponsonby 1898a]; two paratypes in SAMC (2369), one here figured (Fig. 14D–F).

Distribution: Connolly (1912) cited Crawford material from Port Elizabeth, but subsequently doubted its provenance (Connolly 1939). Records from Durban, Zululand and southern Mozambique (Sturany 1898; Germain 1935; Haas 1936) are erroneous and almost certainly represent misidentified specimens of *Nata vernicosa s.l.* Thus the only seemingly reliable record is that given as the type locality, but even this is suspect (see Remarks below).

Habitat. Unknown.

Remarks. Despite its small size, Connolly (1939) maintained this species in the genus *Natalina*, commenting that it resembled a miniature version of *Natalina cafra*. However, this decision is puzzling since he observed that the apical whorls of the holotype (the only specimen known to him), although defective, were 'apparently smooth'. In fact the protoconch of the holotype is effectively missing, but Connolly was evidently unaware of the existence of two paratypes in the SAMC. These have intact apices with a protoconch that is both small (diameter 1.5–1.6 mm) and smooth. Such an apex is typical of *Nata s.l.* rather than *Natalina s.l.*, species of which have a much larger (diameter >2.5 mm), axially ribbed protoconch (Herbert & Moussalli 2010). It is thus clear that the taxon should be transferred to the genus *Nata*. Its relatively small size is also consistent with a position in *Nata*, species of which are invariably smaller-shelled than any of the genera now recognised within *Natalina s.l.* (Herbert & Moussalli 2010).

The type specimens of this species remain the only material available. In terms of size, sculpture and proportions, they exhibit a very close resemblance to larger specimens of *Nata dumeticola* from the Saldanha Bay area, differing only in colour, having a somewhat more olive-green hue. Connolly (1939) rightly questioned the validity of records of *N. caffrula* from Mozambique and KwaZulu-Natal, and also doubted Port Elizabeth, evidently believing only the type locality (Knysna) to be reliable. However, no further specimens have come to light from the Knysna area. We strongly suspect that *N. caffrula* is a synonym of *N. dumeticola* and, since the latter is known only from the Cape Peninsula and the Atlantic coast of W. Cape, the provenance of the types of *N. caffrula* must also be considered dubious. The specimens were presented (and almost certainly collected) by W.F. Purcell (L. Hoenson, pers. comm., xi/2012) an employee of SAMC (1896–1905) who is known to have collected primarily in the south-western Cape (Summers 1975; Glen & Germishuizen 2010). Nevertheless, the Knysna area is not well surveyed and there remains a possibility that further material may be found there.

***Nata dumeticola* (Benson, 1851)**

Figures 3A, 4B, 6B, 7C, 15–18

Helix dumeticola Benson, 1851: 106. Krauss, 1852: 32. Pfeiffer, 1853: 93. Reeve, 1853: sp. 1172. Pfeiffer, 1854 in 1853–1860: 390, nº 937, pl. 143, figs 16–18. Benson, 1856: 437. Type loc.: various localities in the Cape Town–False Bay area cited; said to be 'frequent in littoral thickets near Simon's Town' and this here selected to be the type locality.

Helix (*Pella*) *dumeticola*—Pfeiffer, 1879 in 1878–1881: 102. Tryon, 1887: 106, pl. 20, fig. 79.

Rhytida vernicosa [*non* Krauss, 1848]—Binney, 1879: 355, pl. 14, fig. 1 (radula). Binney, 1884: 82, pl. 17, fig. L (radula).

Natalina dumeticola—Pilsbry, 1893 in 1892–1893: 135. Melvill & Ponsonby, 1898b: 170. Sturany, 1898: 32. Connolly, 1912: 93.

?*Natalina caffrula* Melvill & Ponsonby, 1898a: 24, pl. 8, fig. 1 [see above].

Rhytida (*Macrocycloides*) *dumeticola*—Möllendorff & Kobelt, 1903, in 1903–1905: 59, pl. 10, figs 20–22. Kobelt, 1909: 53.

Nata dumeticola—Watson, 1934: 158, pl. 19, fig. 9 (radula tooth). Connolly, 1939: 101. Richardson, 1989: 45. Schileyko, 2000: 747, fig. 973C.

Etymology. From *dumetum* (L.)–a thicket, *dumeticola*–thicket dweller; with reference to its coastal scrub habitat.

Type material. Three probable syntypes in NHMUK (1912.8.16.206–8), labelled 'S. Africa' 'Benson's types'. Connolly's statement 'type in British Museum' (Connolly 1912: 93, repeated 1939: 102) does not constitute a lectotype designation as no one individual was clearly specified. The largest of the three is here illustrated (Fig. 15A–C) and designated as the lectotype (diameter 11.4 mm).

Additional material examined and literature records: See Appendix 1.

Identification. The relatively strong, crisp and close-set axial riblets on the adapical surface, combined with the rather globose profile of adult specimens renders this species distinctive. Juveniles and subadults may resemble *N. aequiplicata* **sp. nov.**, but in that species the axial riblets are more widely spaced and remain distinct on the base, and its protoconch is considerably smaller. *N. tarachodes* has more rapidly expanding whorls, less regular axial sculpture and is more depressed.

Shell (Fig. 15): Lenticular to sub-globose, spire frequently relatively elevated; largest specimens comprising ±3.25 teleoconch whorls; periphery close to mid-whorl in small specimens (diameter <10.0 mm) but usually well below mid-whorl in the largest individuals; suture just above periphery, slightly descendant prior to aperture in some large specimens. Protoconch 1.6–2.0 mm in diameter, comprising ±1.0 whorl, smooth and glossy, junction with teleoconch usually evident. Apical surface of teleoconch sculptured with distinct, close-set, axial riblets; riblets evanesce at periphery and base smoother, sculptured primarily by uneven growth-lines. Aperture roundly ovate; peristome interrupted by bulging parietal region; outer lip thin with membranous periostracal fringe (commonly lost); base and umbilical margin evenly rounded; umbilicus relatively narrow and steep-sided, particularly in large individuals; columella lip weakly reflected, but only in large specimens

Shell translucent milky-white; periostracum semi-matt to glossy, straw-yellow to olive-brown or tan, usually with some slight axial variation in intensity.

Dimensions: Largest specimen, diameter 14.3 mm, height 9.1 mm; H:D of adults 0.57–0.78 [N=22].

Living animal (Fig. 4B): Head-foot pale grey, neck region with relatively coarse, darker grey skin granules; longitudinal mid-line grooves somewhat fragmented by granulation; optic tentacles smooth, with dark grey retractor muscles (data from one individual).

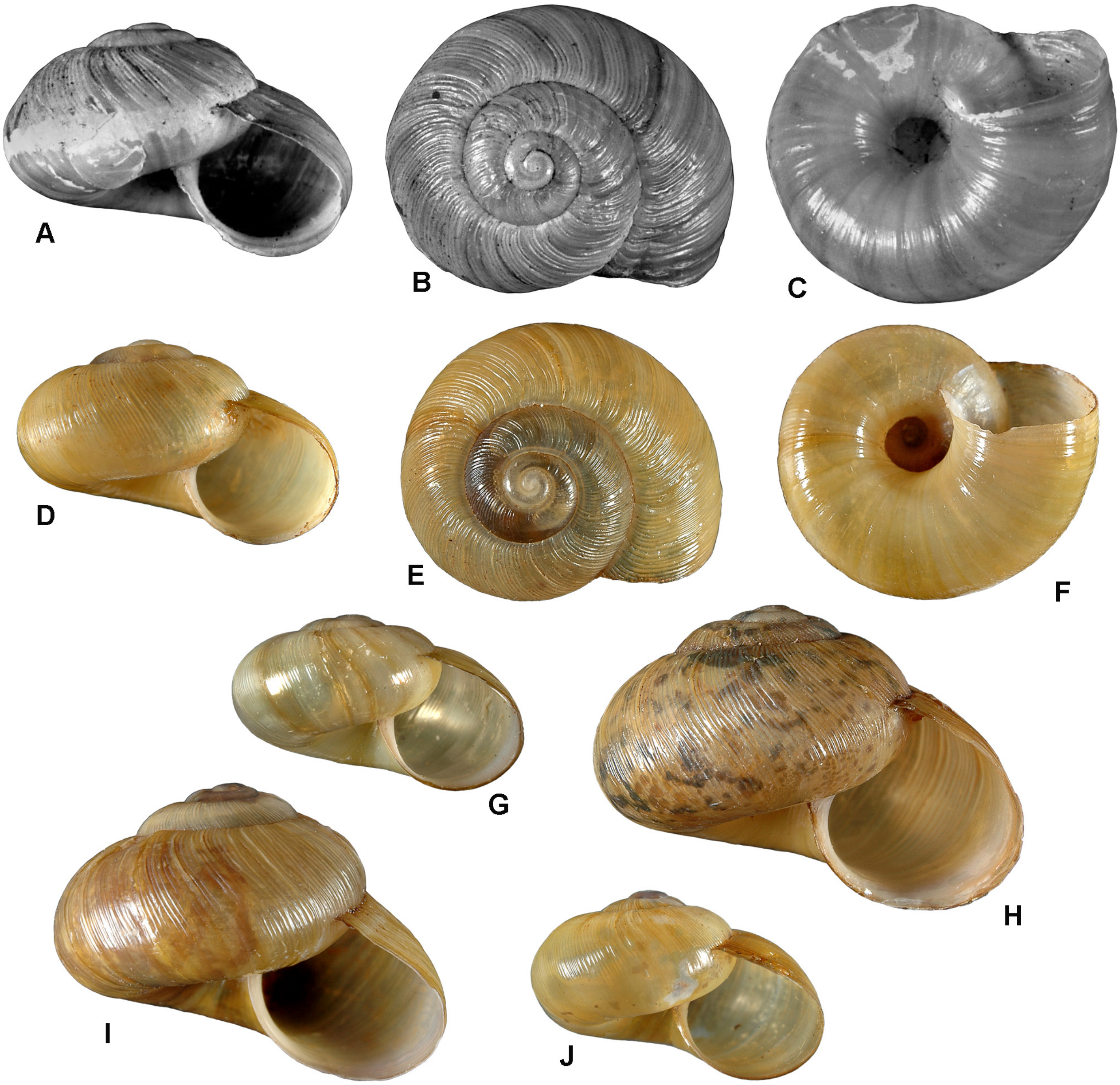

FIGURE 15. *Nata dumeticola* (Benson, 1851). **A–C,** lectotype of *Helix dumeticola* Benson, 1851, 'S. Africa', diameter 11.4 mm (NHMUK 1912.8.16.206–208). **D–F,** Robben Island, mid-sized specimen, diameter 10.4 mm (NMSA V8258). **G,** Strandfontein, lenticular subadult specimen, diameter 9.6 mm (NMSA W7522). **H, I,** Saldanha Bay area, Jacobsbaai, large subglobose specimens, diameter respectively 14.2 mm and 12.8 mm (NMSA V7760). **J,** Cape Peninsula, Connolly, diameter 9.6 mm (NHMUK 1937.12.30.1360–66).

Radula (Figs 6B, 16): Formula 0+(14–22); length up to 5.7 mm, with approx. 55 broadly V-shaped rows of teeth; no obvious distinction between lateral and marginal series; teeth progressively increasing in length and width, then decreasing in size, and more rapidly so toward radula margin; inner teeth with curved, claw-like cusp; subsequent mid-series teeth progressively larger, broader and more quadrate with a curved outer cutting edge, sometimes leading to an ill-defined apical cusp; outer teeth progressively smaller, lanceolate to spathulate, the outermost one minute.

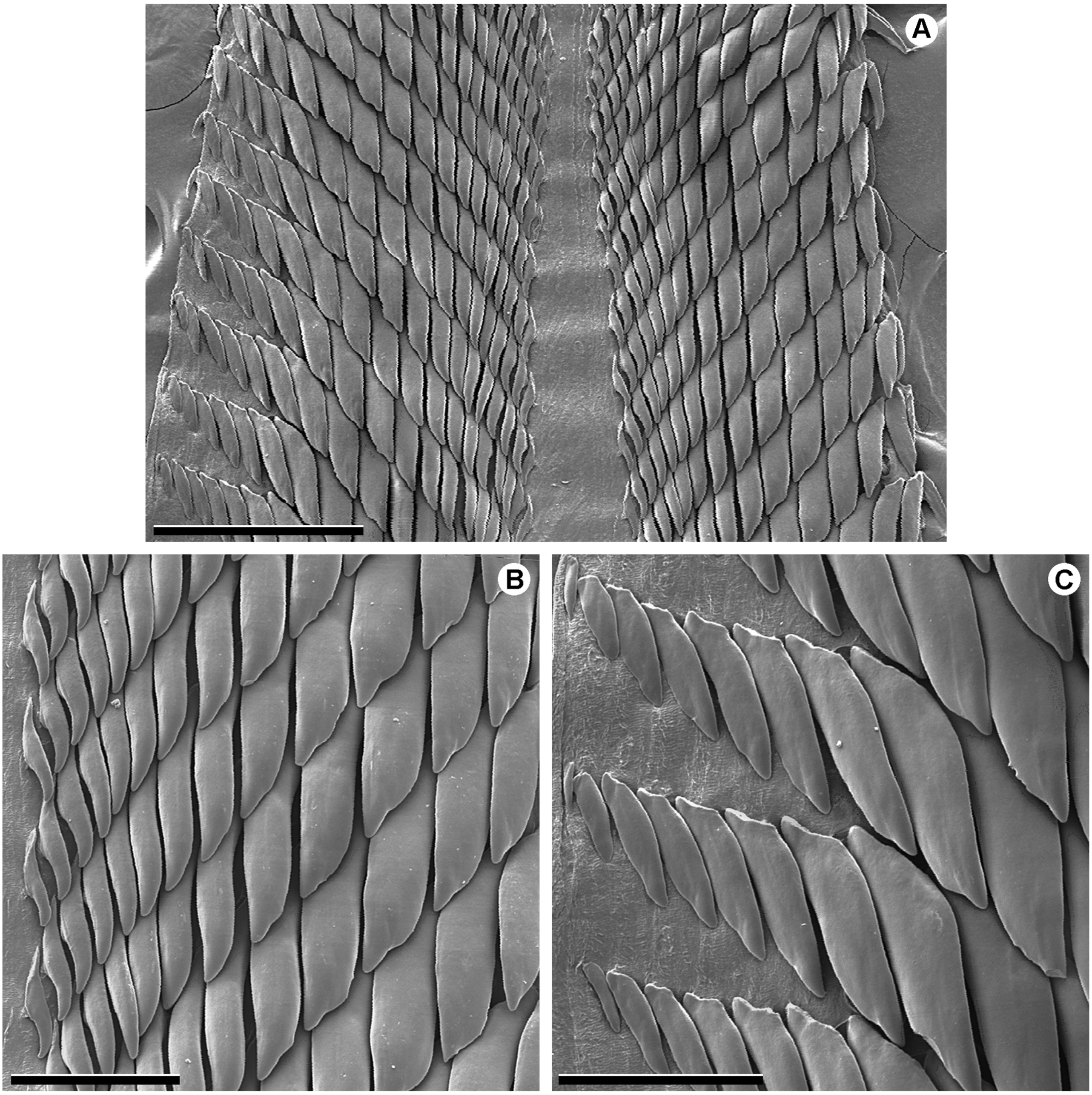

FIGURE 16. *Nata dumeticola* (Benson, 1851), radula, Saldanha Bay area, Jacobsbaai (NMSA V7760). **A,** whole width of radula approx. one-quarter to one-third of length from anterior end, the wide median gap is an artefact of preparation. **B,** right inner latero-marginal series. **C,** left outer latero-marginal series. Scale bars: A = 250 µm; B, C = 100 µm.

Teeth at anterior of radula smaller and more numerous, becoming fewer and larger toward posterior. In one specimen, near the anterior of the radula (juvenile portion) the largest teeth in each half-row were numbers 13–15 (of 22), in the mid region numbers 8–10 (of 18) and in the posterior third numbers 6–8 (of 15). The dentition thus becomes coarser and more robust as the animal grows.

Watson (1934) has pointed out that the radula illustrated by Binney (1879, 1884) as that of *Nata vernicosa* was certainly not correctly identified and in all probability belonged to a specimen of *Nata dumeticola*, although puzzlingly his figure did not show the L-shaped basal attachment of the larger teeth (Fig. 6B), probably due to the use of different staining methods.

Distal genitalia (Fig. 17): Genital pore situated approx. midway between pneumostome and tentacles; right optic tentacle retractor passing to left of penis. Penis of moderate length (±2.7 mm), broadest in apical half with basal region conspicuously narrow in some specimens; insertion of epiphallus lateral, approx. one-third length of penis from its apex; interior of penis with a raised pilaster overlying adnate epiphallus; an elongate subapical pore opens on pilaster crest; pore with lobate lips; interior of pore with a second set of lips surrounding narrowly elongate opening of epiphallus; remainder of swollen apical half of penis lumen covered with micropapillae; basal half of penis with fine, ill-defined longitudinal folds. Penial retractor muscle attached at apex of penis; epiphallus one-third to half length of penis; vas deferens passes down to penis base and then runs somewhat sinuously beside free oviduct before joining spermoviduct. Genital atrium simple and vagina almost non-existent, the free oviduct and bursa copulatrix duct seeming to arise directly from upper part of atrium. Bursa copulatrix and its duct about three-quarters length of spermoviduct, basal half of duct swollen, lined internally with ill-defined longitudinal folds, distal half narrow; bursa copulatrix itself ovate, thin-walled.

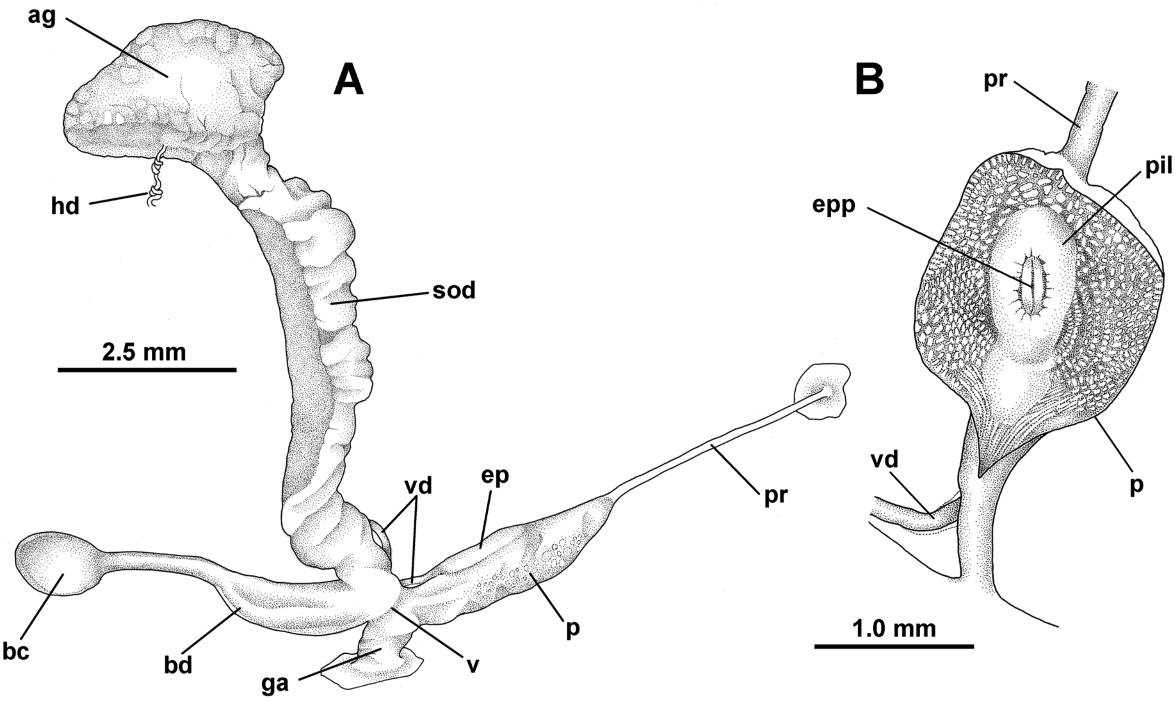

FIGURE 17. *Nata dumeticola* (Benson, 1851), genitalia. **A,** entire genital tract, minus ovotestis (NMSA V8258). **B,** internal features of penis (NMSA W3224). Abbreviations: ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; ep, epiphallus; epp, epiphallus pore; ga, genital atrium; hd, hermaphrodite duct; p, penis; pil, penis pilaster; pr, penial retractor muscle; sod, spermoviduct; v, vagina; vd, vas deferens.

Distribution (Fig. 18): Known primarily from the coastal hinterland along the Atlantic Cape coast, from St Helena Bay south to the Cape Peninsula and north-western shores of False Bay. An additional record from Garies in Namaqualand (SAMC A7719), though not impossible, is substantially further to the north and requires confirmation.

Habitat. Coastal scrub and fynbos; in sandy soil and accumulations of plant debris beneath shrubs and bushes.

Remarks. A variable species in terms of shell proportions. Juvenile and subadult specimens are relatively low and lenticular (Fig. 15G, J), but in larger individuals the last adult whorl is considerably deeper and its periphery usually situated well below mid-whorl, giving the shell a more elevated and more globose form (Fig. 15A, H, I).

Nata dumeticola is the only rhytidid occurring on the Atlantic Cape coast north of Table Mountain and the Cape Peninsula. Although the range of *N. tarachodes* extends westward to the Cape Peninsula, in these areas it is generally found at higher altitudes and further from the coast than *N. dumeticola*, and the two species evidently rarely co-occur. Has been observed feeding on the invasive snail *Theba pisana* (Müller, 1774) (W. Sirgel, *in lit.*, vii/ 2012).

Conservation. Preservation of the delicate strandveld and sand fynbos habitats on the Atlantic Cape coast between Cape Point and St Helena Bay will be necessary for the conservation of this species. Much of the remaining natural habitat in this area is considered vulnerable or endangered (Mucina & Rutherford 2006). The West Coast National Park and the coastal parts of Table Mountain National Park have a significant role to play in this regard.

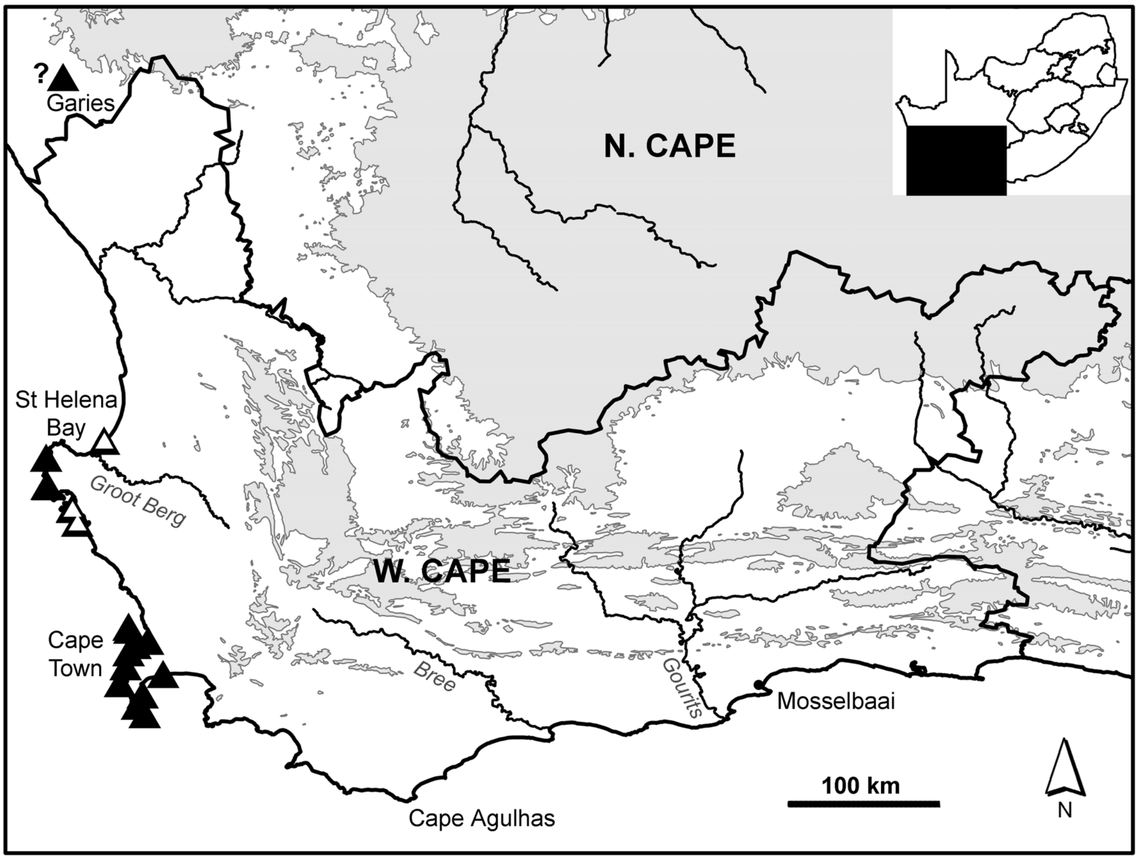

FIGURE 18. Distribution of *Nata dumeticola* (Benson, 1851). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli & Herbert 2016); contour at 1000 m.

Nata tarachodes (Connolly, 1912)
Figures 4D, 5B, 6D, 7B, 8A, 9A, 19–23

?*Helix vernicosa* [*non* Krauss, 1848]—Benson, 1850: 254.
Natalina tarachodes Connolly, 1912: 96, pl. 2, fig. 4. Type loc.: Cape Peninsula (generally distributed).
Macrocycloides cosmia [*non* Pfeiffer, 1852]—Thiele, 1931: 725, fig. 765.
Nata tarachodes—Watson, 1934: 158, 161, pl. 19, figs 6–8. Connolly, 1939: 102. Bruggen, 1970a: 468. Richardson, 1989: 45. Schileyko, 2000: 747, fig. 973A, B.

Etymology. From *tarache* (Gr.)–disturbance, confusion; presumably referring to the fact that the species was previously confused with *Nata vernicosa*.

Type material. Holotype (Fig. 19A–C) in NHMUK (1912.4.27.14), diameter 7.2 mm (8.0 mm *fide* Connolly 1939), plus five paratypes (1937.12.30.1346–51).

Additional material examined and literature records: See Appendix 2.

Identification. Characterised by its small size, thin shell, low spire, relatively rapidly expanding whorls, and glossy, almost uniformly coloured shell with distinct but rather uneven axial riblets.

Shell (Fig. 19): Lenticular to discoidal, thin, spire low; largest specimens comprising 2.5–2.75 teleoconch whorls; whorls expanding relatively rapidly; periphery close to mid-whorl; suture well above periphery. Protoconch 0.90–1.15 mm in diameter, comprising ±1.0 whorl, smooth and glossy, junction with teleoconch usually distinct. Apical surface of teleoconch sculptured with close-set, axial riblets of uneven strength, often with additional growth scars; riblets evanesce at periphery and base smoother, sculptured by irregular growth-lines. Aperture subcircular to ovate, but peristome interrupted by bulging parietal region; outer lip thin with membranous periostracal fringe; base and umbilical margin evenly rounded; umbilicus moderately wide; columella lip not reflected.

Shell glossy throughout, translucent with honey-gold periostracum when fresh; pigmentation of underlying tissue clearly visible.

Dimensions: Largest specimen, diameter 12.6 mm, height 6.6 mm, but diameter mostly <10 mm; H:D of adults 0.51–0.63 [N=17].

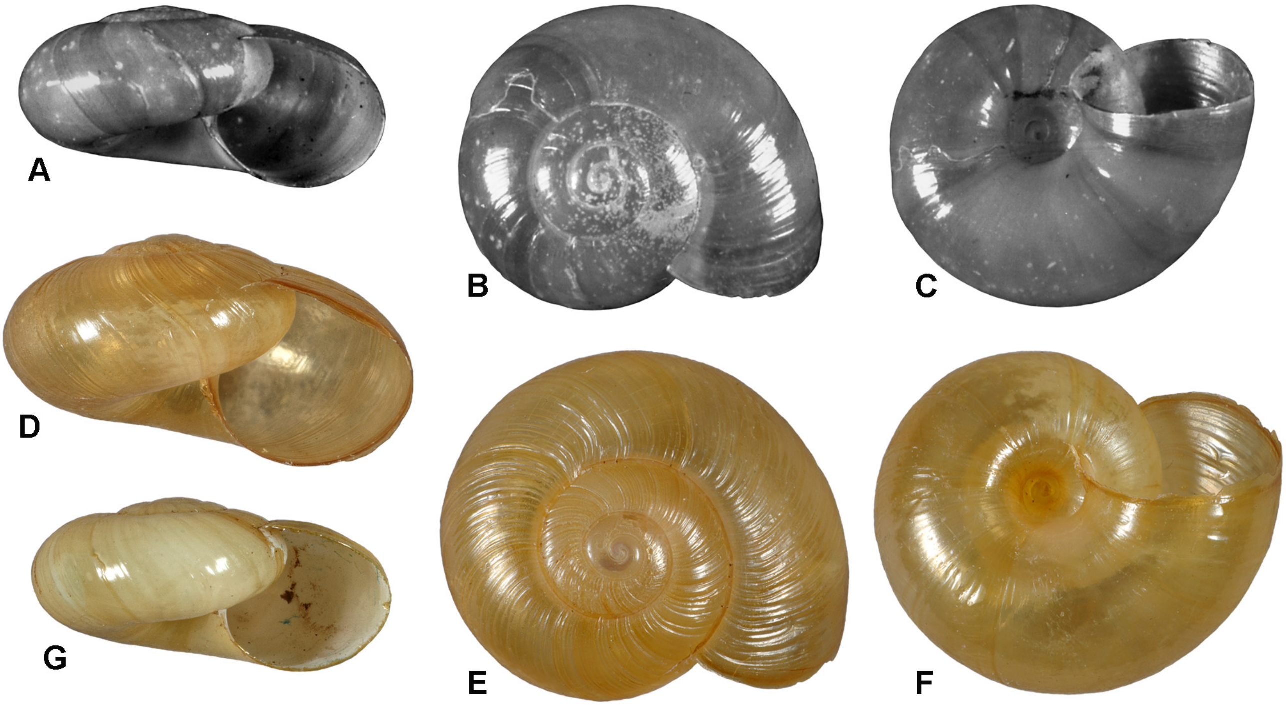

FIGURE 19. *Nata tarachodes* (Connolly, 1912). **A–C,** holotype of *Natalina tarachodes* Connolly, 1912, diameter 7.2 mm (NHMUK 1912.4.27.14). **D–F,** elevated specimen with distinct axial riblets, Grootbos Private Nat. Res., Gansbaai, W. Cape, diameter 8.0 mm (NMSA W5658). **G**, depressed specimen, faded, Kalk Bay Mountain, W. Cape, diameter 7.1 mm (SAMC 8299).

Living animal (Figs 4D, 20): Body colour rather variable; head and neck grey to dark bluish-grey, often with some microscopic orange pigment granules; tentacles of similar colour, darker toward the tip; foot paler ventrally; tail of foot short, commonly greyish white; skin texture relatively smooth; mantle edge yellowish-grey, with a broad, dark subterminal band; lining of mantle cavity with irregular blackish markings (particularly dense in specimens from the Gansbaai area), the kidney showing through as a whitish trigonal structure (Fig. 20B). Some populations (e.g. in the forests of the Riviersonderendberge) with tail and mantle edge conspicuously orange (Fig. 20A).

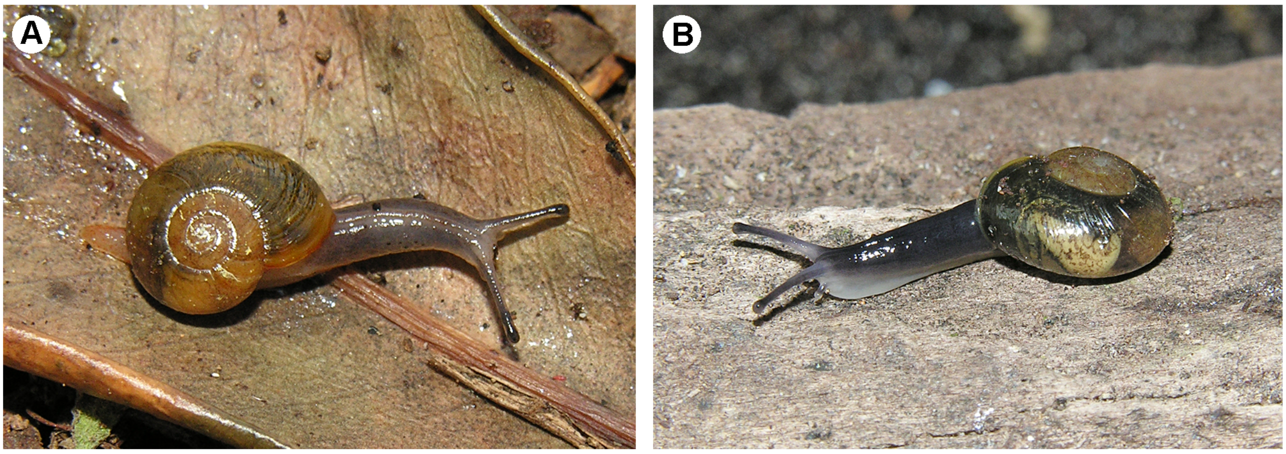

FIGURE 20. *Nata tarachodes* (Connolly, 1912), living animals. **A,** Oubos, Riviersonderendberge, W. Cape (NMSA W5671). **B,** Grootbos Private Nat. Res., Gansbaai, W. Cape (NMSA W5658). Note relatively dense pigmentation of pulmonary lining and conspicuous pale kidney in B. Shell diameter of both specimens 7.7 mm.

Radula (Figs 6D, 21): Formula 0+(7–9)+(4–5); length up to 6.0 mm, with 29–35 V-shaped rows of teeth; teeth progressively larger from anterior to posterior of radula, with up to 10 rows/mm anteriorly, approx. 5 rows/mm posteriorly; largest lateral tooth increasing up to 100% in size; rachidian absent; lateral teeth progressively larger moving away from mid-line, one tooth clearly the largest (fang tooth), this taken to be outermost lateral (tooth nº 7, 8 or 9, may differ on left and right side of radula); inner lateral teeth elongate-lanceolate, fang tooth robust, narrowly trigonal, with slightly in-curved tip giving it a blade-like profile; 4–5 teeth (marginals) beyond largest lateral, the first only slightly shorter than largest lateral, but more slender, remaining marginals decreasing rapidly in size, the outer one minute.

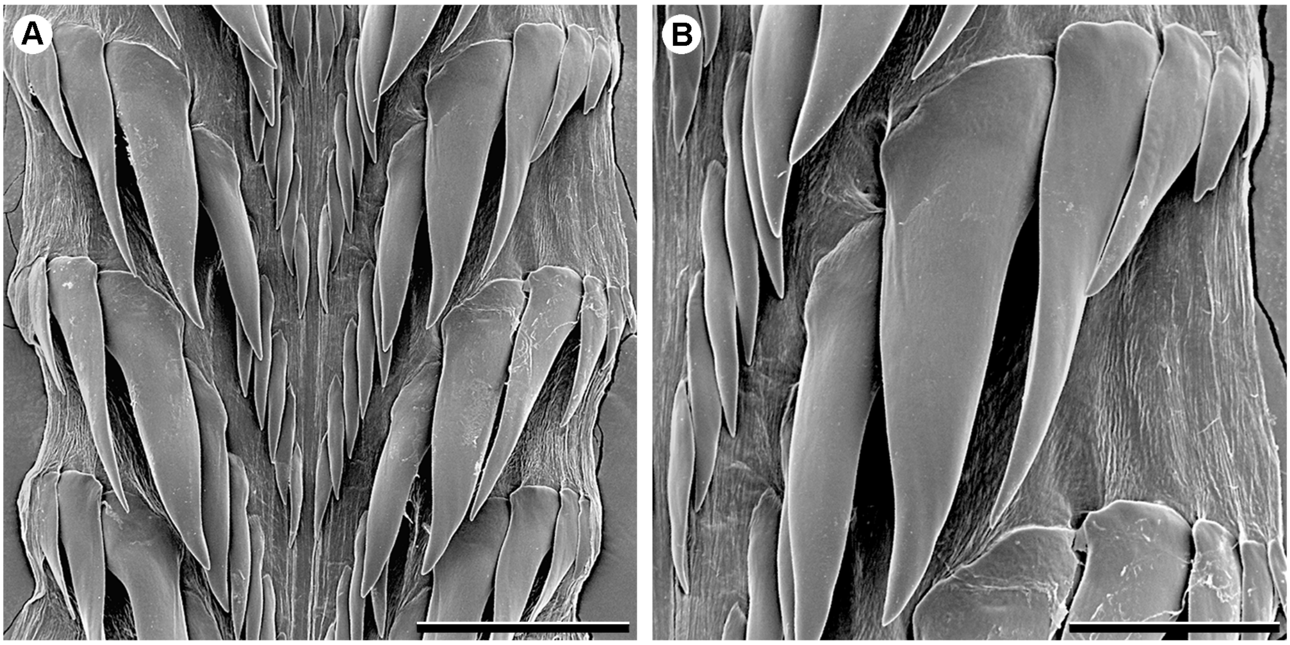

FIGURE 21. *Nata tarachodes* (Connolly, 1912), radula, Grootbos Private Nat. Res., Gansbaai (NMSA W5658). **A,** whole width of radula. **B,** half width of radula showing large teeth (numbers 6–8), fang tooth is tooth nº 7 in this case. Scale bars: A = 200 µm; B = 100 µm.

Distal genitalia (Figs 7B, 8A, 22): Genital pore ventral to pneumostome; right optic tentacle retractor passing to left of penis. Penis relatively short and stout (length ±2.5 mm), narrowing basally; its wall not conspicuously muscular and lined internally with relatively coarse (stout), close-set papillae (Fig. 8A shows these in the everted state); epiphallus pore surrounded by a slightly raised lip, but not forming an enlarged papilla or verge. Penial retractor muscle attached at apex of penis; epiphallus distinct and comparatively large, ±0.75 length of penis, adnate to side of penis and inserting just below its apex; epiphallus internally papillate, papillae somewhat smaller than those of penis and aligned longitudinally; vas deferens running beside free oviduct before joining spermoviduct. Genital atrium simple and vagina almost non-existent, the free oviduct and bursa copulatrix duct seeming to arise directly from atrium. Bursa copulatrix and its duct about one-third to half length of spermoviduct, basal portion of duct markedly swollen, lined internally with well-developed longitudinal folds, often visible by transparency; duct narrowing distally toward bursa copulatrix; bursa itself ovate, thin-walled and of rather variable size. Genital atrium with a lateral diverticulum arising near base of bursa duct; diverticulum of variable size, well developed in some specimens, but little more than a small pouch in others; internally papillate. [This structure was termed a vaginal appendix by Watson (1934), but a vagina *per se* is hard to delimit and in the material examined herein the diverticulum appears to derive from the genital atrium, close to the base of the bursa duct.]

Distribution (Fig. 23): Probably endemic to the south-western Cape, from the southern Swartland (Kasteelberg) south to the Cape Peninsula and east to the central Langeberge. Literature records (Connolly 1939) from further east (E. Cape and Lesotho, see Appendix 2) must be considered dubious. It seems probable that these represent misidentified specimens.

Habitat. Occurs in a wide variety of habitats, ranging from fynbos to forest and from the coast to 1500 m in the western Riviersonderendberge (Jonaskop); usually found in accumulations of plant debris beneath shrubs and in forest floor leaf-litter.

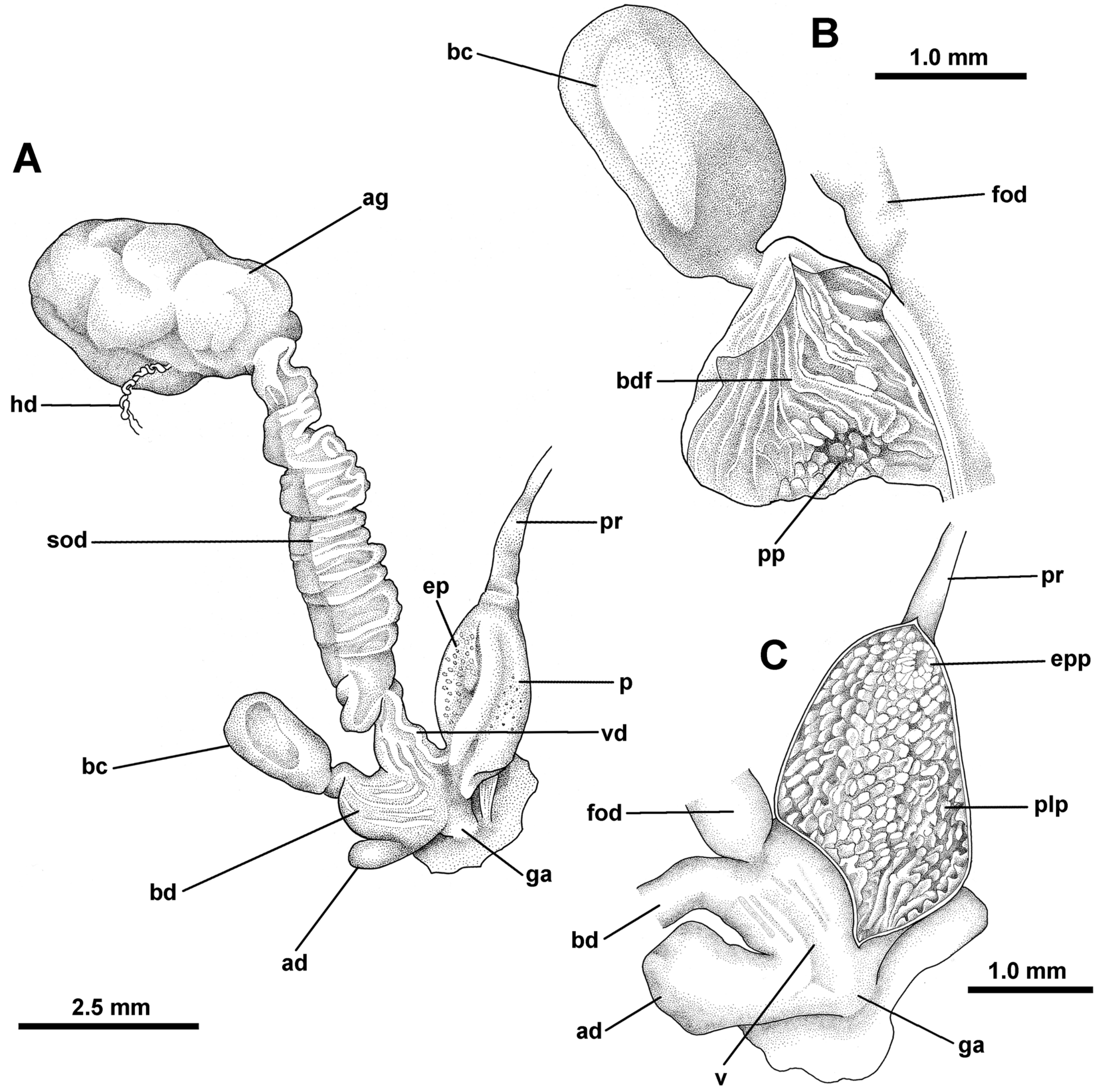

FIGURE 22. *Nata tarachodes* (Connolly, 1912), genitalia. **A,** entire genital tract, minus ovotestis (NMSA W5671). **B,** dissection of basal portion of bursa copulatrix duct showing folds on lumen wall and papillate pocket of atrial diverticulum (NMSA W5671). **C,** longitudinal dissection of penis showing papillate lumen, atrial diverticulum large in this individual (NMSA W9118). Abbreviations: ad, atrial diverticulum; ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; bdf, folds in wall of bursa copulatrix duct; ep, epiphallus; epp, epiphallus pore; fod, free oviduct; ga, genital atrium; hd, hermaphrodite duct; p, penis; plp, papillate lumen of penis; pp, papillate pocket of atrial diverticulum; pr, penial retractor muscle; sod, spermoviduct; v, vagina; vd, vas deferens.

Remarks. On the Cape Peninsula the range of *Nata tarachodes* overlaps with that of *Nata dumeticola* (see Remarks thereunder), but that species has a deeper shell with stronger, more regular axial riblets, and is usually larger (diameter up to 14.3 mm).

The radula of *Nata tarachodes* is clearly similar to that of *Nata vernicosa*, but the distal reproductive tract differs noticeably, particularly with regard to the proportionally larger epiphallus which inserts laterally near the apex of the penis (rather than some distance below the penis apex), and the presence of an atrial diverticulum near the base of the bursa copulatrix duct. A specimen has been observed feeding on a much larger species of *Trachycystis* in the Koegelberg Nature Reserve (W. Sirgel, *in lit*., vii/2012).

In addition to the material discussed above, there are three further samples (locality details below) that we initially identified as *Nata tarachodes*, based on conchological features, but which exhibit unusual radula characters for this species. Firstly a specimen from Newlands Forest [beside contour path, at beginning of Newlands Ravine pathway (33.9628°S: 18.43902°E), 360 m, under logs, D. Raharinjanahary, 10/xii/2006 (NMSA W6601)] is unusual in that the radula formula is 0+6+7, i.e. there are fewer lateral teeth and more marginal teeth than is usual for this species, to such an extent that the number of marginals exceeds the number of laterals. Furthermore, the sequence data for this specimen shows its relationship to other *Nata tarachodes* material to be rather distant and weakly supported (Moussalli & Herbert 2016).

Secondly, two samples from the Klein Karoo [Calitzdorp area, Matjiesvlei (33.44525°S: 21.65388°E), 360 m, rocky hillside with succulents and aloes, D. Herbert, L. Davis, M. & K. Cole, 04/xi/2013 (NMSA W9588); Gamkaberg Nat. Res., Tierkloof (33.69003°S: 21.90158°E), 440 m, in leaf-litter beneath trees and shrubs, D. Herbert, L. Davis, M. & K. Cole, 07/xi/2013 (NMSA W9548)] are geographically distant from the remaining *Nata tarachodes* material (localities marked with ? in Fig. 23), though the distance is not great and a range extension of this magnitude would not in itself seem unlikely. However, in this material the radula possesses a rachidian tooth [formula: 1+(9–11)+(4–5)] and the number of laterals is larger than is usual for *Nata tarachodes*. These features render the specimens distinct from typical *Nata tarachodes* and they are thus questionably referable to the species. Unfortunately the individuals were immature and the distal genitalia were not sufficiently well developed to permit comparison. As yet no molecular data is available for this material.

In both of these cases, definitive conclusions regarding the affinity of the specimens with *Nata tarachodes* (or otherwise) must await additional sampling and additional comparative data. The possibility exists that one or both may represent unrecognised cryptic species of *Nata*.

Conservation. Although restricted to the south-western Cape, *Nata tarachodes* is evidently catholic in its habitat preferences and may be locally common. It is recorded from a number of national parks and nature reserves that span much of its range. Its conservation is thus currently not an issue of concern.

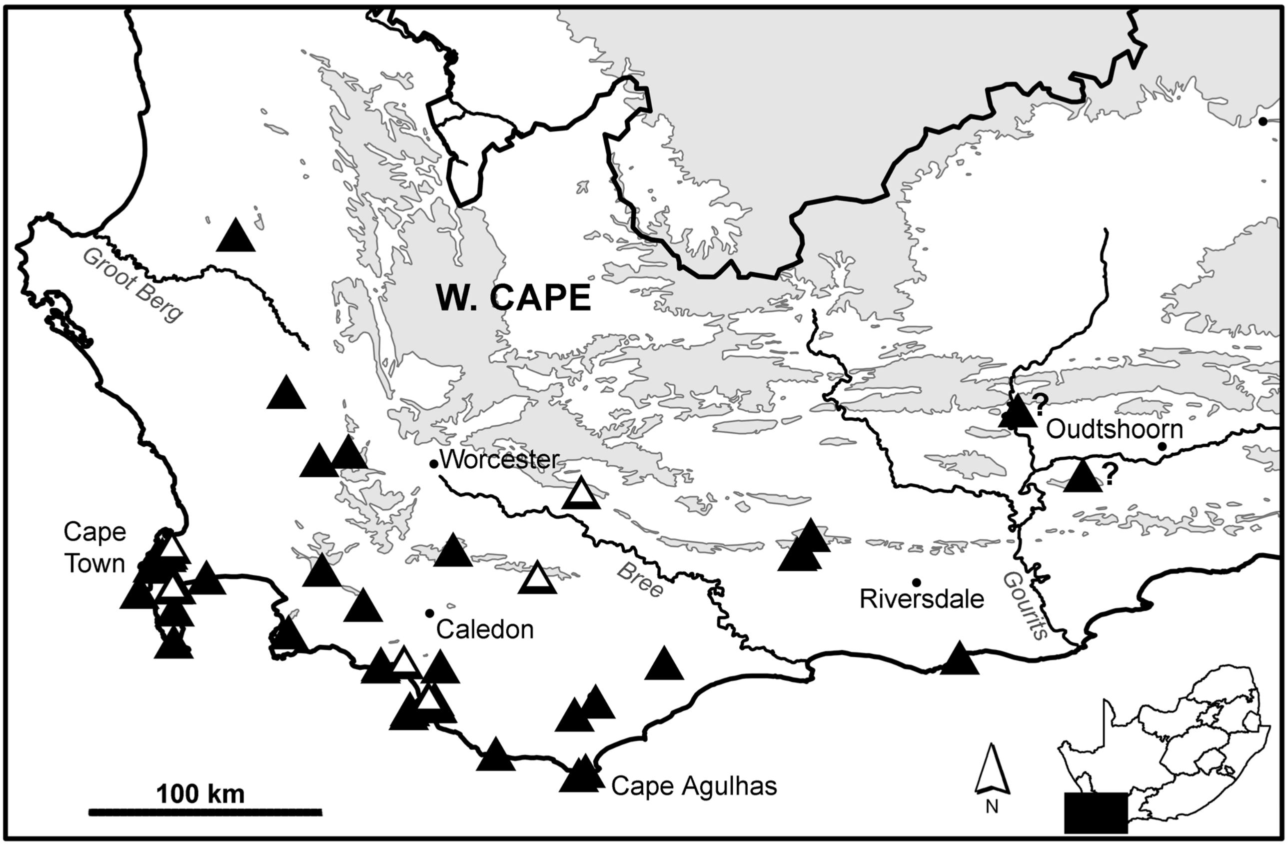

FIGURE 23. Distribution of *Nata tarachodes* (Connolly, 1912). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli & Herbert 2016); contour at 1000 m.

Nata vernicosa (Krauss, 1848) *sensu lato*

Figure 24

Helix vernicosa Krauss, 1848: 76, pl. 4, fig. 23. Pfeiffer, 1849: 93. Reeve, 1851: sp. 198, pl. 43. Morelet, 1889: 19. Herbert & Warén, 1998: 235. Type loc.: '*in terra natalensi*' [Wahlberg].
Helix vernicosa β. *minor* Pfeiffer, 1853: 95. Type loc.: '*Natal Africae meridionalis*'.
Helix (*Pella*) *vernicosa*—Pfeiffer, 1879 in 1878–1881: 102.
Elaea vernicosa—Tryon, 1885: 130, pl. 28, figs 52–54 [as *E. verrucosa* [*sic*] in plate legend].
Elaea vernicosa var. *minor*—Tryon, 1885: 131.
Helix (*Macrocyclis*) *caenotera* Melvill & Ponsonby, 1892b: 238, pl. 13, fig. 2. Type loc.: 'Tharfield', E. Cape [Dr Schönland].
Helix (*Macrocyclis*) *liparoxantha* Melvill & Ponsonby, 1892b: 238, pl. 13, fig. 3. Type loc.: 'Maritzburg' [H.C. Burnup].
Natalina caenotera—Pilsbry, 1893 in 1892–1893: 135. Melvill & Ponsonby, 1898b: 170. Connolly, 1912: 92.
Natalina liparoxantha—Pilsbry, 1893 in 1892–1893: 135. Melvill & Ponsonby, 1898b: 170. Connolly, 1912: 96.
Natalina vernicosa—Pilsbry, 1893 in 1892–1893: 135. Sturany, 1898: 31. Connolly, 1912: 97.
Natalina chaplini Melvill & Ponsonby, 1894: 91, pl. 1, fig. 3. Melvill & Ponsonby, 1895: 165, pl. 12, figs 5, 5b. Melvill & Ponsonby, 1898b: 170. Sturany, 1898: 31. Connolly, 1912: 92. Type loc.: 'Karnachs' [?=Kamesh], near Port Elizabeth, E. Cape [J. Crawford].
Rhytida kraussi [*non* Pfeiffer, 1846]—Moss, 1894: 25, pl. 1, fig. 3.
Rhytida Kraussii [*sic*] [*non* Pfeiffer, 1846]—Cooke, 1895: 232, fig. 139.
Macrocyclis coenotera [*sic*]—Sturany, 1898: 32.
Macrocyclis liparoxantha—Sturany, 1898: 33.
Natalina caffrula [*non* Melvill & Ponsonby, 1898]—Sturany, 1898: 32. Germain, 1935: 5: Haas, 1936: 18 (in part, Umfolozi).
Rhytida vernicosa—Melvill & Ponsonby, 1898b: 170.
Rhytida (*Macrocycloides*) *vernicosa*—Möllendorff & Kobelt, 1903, in 1903–1905: 57, pl. 10, figs 12–14. Kobelt, 1909: 53.
Rhytida (*Macrocycloides*) *chaplini*—Möllendorff & Kobelt, 1903, in 1903–1905: 58, pl. 10, fig. 15–17. Kobelt, 1909: 53.
Rhytida (*Macrocycloides*) *liparoxantha*—Möllendorff & Kobelt, 1903, in 1903–1905: 58, pl. 10, fig. 18. Kobelt, 1909: 53.
Rhytida (*Macrocycloides*) *coenotera* [*sic*]—Möllendorff & Kobelt, 1903, in 1903–1905: 59, pl. 10, fig. 19. Kobelt, 1909: 53.
Natalina vernicosa var. *minor*—Connolly, 1912: 98.
Nata vernicosa—Watson, 1934: 161. Connolly, 1939: 99, pl. 4, figs 4, 5, text fig. 6. Zilch, 1959–60: 554, fig. 1936. Bruggen, 1966: 376, fig. 54. Bruggen, 1967: 29. Bruggen, 1969: 37. Bruggen, 1970: 468. Bruggen, 1978: fig. 3i. Bruggen, 1985: 286. Bruggen & Appleton, 1977: 32. Richardson, 1989: 45. Herbert, 1991: 11. Herbert & Kilburn, 2004: 219.
Nata liparoxantha—Connolly, 1939: 101, pl. 3, figs 4–6. Richardson, 1989: 46.
Nata minor—Connolly, 1939: 100, pl. 2, figs 9–11. Richardson, 1989: 46.
Helix (*Nata*) *liparoxantha*—Bruggen, 1967: 29 [syn. nov. of *Nata vernicosa*]
Nata caerotera [*sic*]—Richardson, 1989: 46.
Nata chaplini—Richardson, 1989: 46.

Not *Rhytida vernicosa*—Binney, 1879: 355 pl. 14, fig. 1. Binney, 1884: 82, pl. 17, fig. L [=*Nata dumeticola*].

The taxonomy of *Nata vernicosa* is complex and confusing. Connolly (1939) provided the first revisionary comment on the species and noted that the E. Cape taxa *Helix caenotera* Melvill & Ponsonby, 1892 and *Natalina chaplini* Melvill & Ponsonby, 1894 were inseparable from *Nata vernicosa* and thus considered them to be junior synonyms thereof. He treated *Helix liparoxantha* Melvill & Ponsonby, 1892 from KwaZulu-Natal as a distinct species, also referring it to *Nata*, as had Watson (1934). Connolly observed, however, that although *N. liparoxantha* attains a slightly larger size and has somewhat weaker axial sculpture than *N. vernicosa*, it may in fact represent the same species. Pfeiffer's *N. vernicosa* var. *minor* he considered to be another distinct species with a smaller, smoother shell. Subsequently, Bruggen (1967: 29) placed *N. liparoxantha* in synonymy with *N. vernicosa*, and later (Bruggen 1985) suggested that *N. vernicosa* might be considered a single wide-ranging and conchologically variable species encompassing all the taxa referred to *Nata s.s.* by Connolly (1939) [see Introduction], noting at the same time that more conchological and anatomical information was needed.

While the availability of additional material has enabled us to establish that *Nata s.s.* genuinely does encompass several distinct, highly genetically divergent species, circumscription of *N. vernicosa* itself has proven more difficult. In recent years, as a practical solution, material that was not clearly referable to any of the other species has been identified as *N. vernicosa s.l.*, including *N. liparoxantha* and *N. minor* (both *sensu* Connolly, 1939), as for example in Herbert & Kilburn (2004). This, however, includes specimens exhibiting considerable variation in conchological characters, ranging from low, discoidal specimens virtually devoid of axial riblets, to globose-lenticular (deep-whorled) specimens with strong, axial riblets. From an anatomical perspective, this material exhibits no distinctive characters or consistent patterns of variation in either the radula or the distal genitalia that point to there being more than one species involved. Nonetheless, closer scrutiny of the greater amount of material now available has enabled us to identify within *N. vernicosa s.l.* a separate, consistently smooth-shelled species that is geographically circumscribed and for the most part allopatric. This we describe below as *Nata erugata* **sp. nov.** To date, only a single specimen (NMSA W3343, from Mt Sheba, Mpumalanga) of this species has been included in the molecular work (see Fig. 1). While this specimen clustered as the most basally divergent individual in the *N. vernicosa* clade (Moussalli & Herbert 2016), additional material spanning the full range of the species will need to be included in future studies.

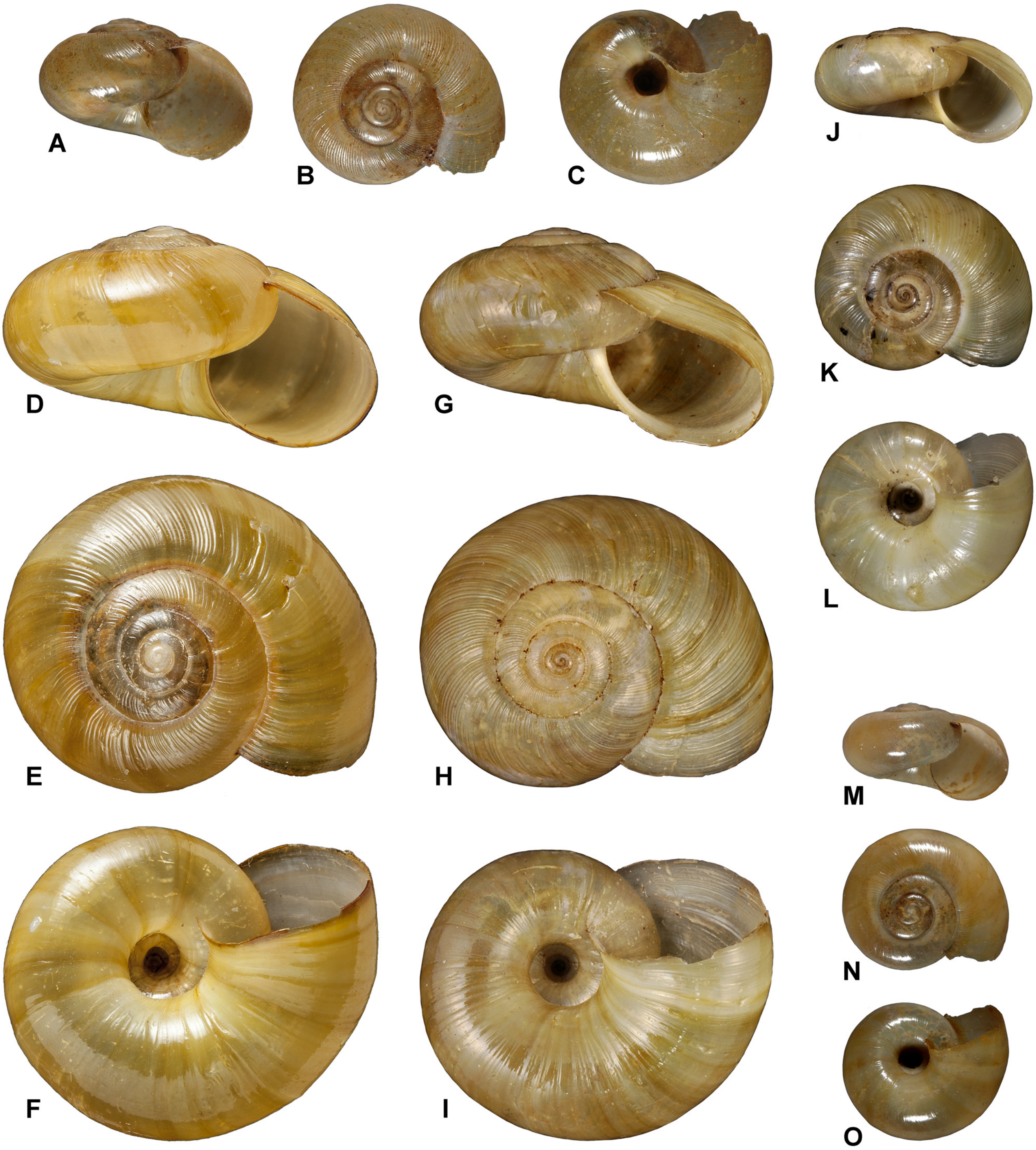

FIGURE 24. Type material of *Nata vernicosa* and synonyms. **A–C,** *Helix vernicosa* Krauss, 1848, lectotype (here designated), diameter 10.2 mm (SMNH 4965). **D–F,** *Helix* (*Macrocyclis*) *liparoxantha* Melvill & Ponsonby, 1892, lectotype, diameter 18.0 mm (NHMUK 1911.8.8.7). **G–I,** *Helix* (*Macrocyclis*) *caenotera* Melvill & Ponsonby, 1892, lectotype, diameter 17.0 mm (NHMUK 1911.8.8.8). **J–L,** *Natalina chaplini* Melvill & Ponsonby, 1894, lectotype, diameter 10.4 mm (NHMUK 1911.8.8.9). **M–O,** *Helix vernicosa* var. *minor* Pfeiffer, 1853, lectotype, diameter 8.0 mm (SMNH 4965).

The remaining *Nata vernicosa s.l.* material, however, continues to be problematic. Although highly variable in conchological features, we have been unable to discern any clear and consistent patterns in shell morphology that do not seem to intergrade. This variation intergrades both across the landscape and often also at individual localities, in an evidently seamless manner and it encompasses the variation exhibited by all the nominal taxa currently considered to be synonyms of *N. vernicosa*. The extent of this variation, both between and within populations of *N. vernicosa*, however, emphasises the significance of the morphological consistency underpinning *N. erugata* **sp. nov.** If further cryptic species are present within *N. vernicosa*, the most promising option for their discovery is likely to lie in molecular studies of a phylogeographic nature. Thus even though we have identified a new species amidst the confusion that has long surrounded *N. vernicosa s.l.*, we are still left with a morphologically diverse assemblage that requires further study using additional techniques.

Type material of *Helix vernicosa*: Connolly (1939) stated that the 'type' of *Helix vernicosa* Krauss, 1848 was in the Stuttgart Museum and gave its dimensions as 'diam. 14.8 x 12.0; alt. 7.6 mm'. Krauss, however, gave the dimensions as 'diam. 5 x 4, alt. 3.3 lines' (=11.28 x 9.02, alt. 7.44 mm)[1]. The Stuttgart specimen which Connolly considered to be the type was thus both significantly larger and more depressed than the material seen by Krauss (H:Dmax = 0.514 vs. 0.660). Connolly's reason for considering this to be the type was not stated and evidently it was an unjustified assumption.

In the SMNH, which contains much original Wahlberg material, there is a lot containing four specimens that Herbert & Warén (1999) treated as possible paralectotypes of *Helix vernicosa* (SMNH 4965), believing Connolly's discussion of 'the type' to constitute a lectotype designation. Since the latter was evidently unjustified on the grounds of the specimen's dimensions and proportions, the type status of the SMNH specimens needs to be re-evaluated. The largest specimen is again larger and more depressed than the Krauss material (max. diameter 13.3 mm; H:Dmax 0.586) and thus unlikely to have been seen by Krauss. However, in his remarks following the Latin description of *Helix vernicosa*, Krauss stated that 'the largest specimens were more costulate than the younger and as a result slightly semi-gloss.....the ribs are rather sharply raised and close-set.....', and these comments apply well to the three remaining specimens in this SMNH lot. The two largest of these have crisp, close-set riblets and are lustreless, while the third one is smaller (younger) and has weaker riblets and is more glossy. These two larger lustreless specimens are relatively deep-whorled shells, the proportions of which fit well with measurements given by Krauss and with his original illustration [H:Dmax 0.676 and 0.670 compared with 0.660 for Krauss's dimensions and 0.659 for his figure]. They are somewhat smaller than the measurements given by Krauss (Dmax 10.2 and 9.7, compared with 11.28 given by Krauss, but a difference of ±10% for the larger of the two is perhaps an acceptable error margin, allowing for differences in measuring methods.

The remaining smaller, more glossy shell (Fig. 24M–O) fits Pfeiffer's description '*costulis superficiei obsoletioribus*' for his variety β. *minor* (Pfeiffer 1853), since its sculpture is very much weaker than in the other specimens. It was redescribed in more detail and figured by Connolly (1939) and Herbert & Warén (1999) considered that it may justifiably be considered the lectotype for Pfeiffer's variety *minor.*

Since it is important to clarify which taxon is actually represented by the name *Helix vernicosa* (see below), it is necessary that a lectotype be designated. In light of the above observations, we select the larger of the two deep-shelled, strongly ribbed specimens as the lectotype (Fig. 24A–C). It was collected by Wahlberg in Natal, its dimensions and proportions are similar to those cited in the original description, it closely resembles the original figure and it matches the additional descriptive comments provided by Krauss.

Type material of synonyms: Lectotype of *Helix* (*Macrocyclis*) *caenotera* Melvill & Ponsonby, 1892 (designated Connolly 1912: 92) in NHMUK (1911.8.8.8) (Fig. 24G–I), diameter 17.0 mm (the original description mentioned six specimens, but the whereabouts of the other five is not known). Lectotype of *Helix* (*Macrocyclis*) *liparoxantha* Melvill & Ponsonby, 1892 (designated Connolly 1912: 96) in NHMUK (1911.8.8.7) (Fig. 24D–F), diameter 18.0 mm; the original description mentioned four specimens, thus three paralectotypes may also exist, two of these may be specimens in the Melvill-Tomlin Collection (NMW.1958.158) collected by H.C. Burnup in Port Shepstone [Rowson pers. comm., xii/2015]. Lectotype of *Natalina chaplini* Melvill & Ponsonby, 1894 (designated Connolly 1912: 92) in NHMUK (1911.8.8.9) (Fig. 24J–L), diameter 10.4 mm, label gives locality as 'Cape Colony', but original description states 'Karnachs, near Port Elizabeth (J. Crawford)', (the original description mentioned three specimens, but the whereabouts of the other two is not known).

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[1] In the foreword to Krauss (1848) he stated that the measurements given were in 'Pariser Zollen und linien'. [1.0 Paris ligne = 2.256 mm].

Nata vernicosa (Krauss, 1848)

Figures 2B, 3C, 4G, 5A, 7D, 8B, 9B, 24–29

Etymology. From *vernix* (L.)—varnish; presumably in reference to the periostracum, which can be glossy and lacquer-like.

Selected locality data for material examined: See Appendix 3.

Identification. The shell characters that most readily distinguish this species from its congeners are its relatively large size and its sculpture of axial riblets (weak or strong). Other species with axial riblets are considerably smaller at adult size, whereas other similarly-sized species are smoother, with a sculpture that primarily comprises growth-lines only. Juveniles can be difficult to identify, but beyond W. Cape *N. vernicosa* is the only species with axial riblets except for *N. aequiplicata* **sp. nov.** That species is very much smaller, has axial sculpture that continues onto the base and into the umbilicus, and is narrowly endemic to a small part of E. Cape.

Shell (Figs 24, 25): Lenticular to globose-lenticular, proportions very variable (H:D 0.49–0.71), some specimens with depressed whorls and a low spire (Fig. 25D), others with deep whorls and a more prominent spire (Fig. 25G); largest specimens comprising up to 3.75 teleoconch whorls; periphery at mid-whorl, occasionally somewhat below it (Fig. 25O); suture well above periphery, slightly descendant prior to aperture in some large specimens. Protoconch size very variable, diameter 1.1–2.6 mm, comprising ±1.0 whorl, smooth and glossy, junction with teleoconch often ill-defined. Apical surface of teleoconch sculptured with axial riblets, relatively weak in some specimens, crisp and close-set in others; shell commonly glossy, but tending to be lustreless when sculpture stronger (Fig. 25A, B, G, H); riblets evanesce at periphery and base smoother, sculptured primarily by uneven growth-lines. Base and umbilical margin evenly rounded; umbilicus of moderate width, steep-sided, with axial riblets usually reappearing to some extent within. Aperture roundly to obliquely ovate; peristome interrupted by bulging parietal region; outer lip thin with membranous periostracal fringe (commonly lost); upper part of columella lip extending forward and a little reflected.

Shell translucent milky-white; periostracum pale straw-brown to pale olive-green, honey-gold or olive-brown, usually with some axial variation in intensity, producing unevenly spaced, slightly darker axial banding.

Dimensions: Largest specimen, diameter 24.5 mm, height 16.1 mm; H:D of adults 0.49–0.71 [N=100].

Living animal (Figs 4G, 26): Body colour very variable; head and neck ranging from pale grey (Fig. 26C) to brownish-grey (Fig. 26A), bluish-grey and even dark charcoal grey (Fig. 26B); foot paler ventrally and beneath shell; commonly with some microscopic orange pigment granules, particularly on tail, ventral margins of foot and mantle edge (Fig. 26F); tentacles usually a darker shade of body colour. Tail of foot short, narrowly acuminate; skin grooves coarse and well defined in some individuals, less so in others; mantle edge generally pale; lining of mantle cavity mostly lacking black markings, but commonly (perhaps invariably) with a black blotch inset a short distance above pneumostome (Fig. 26A, B, D); kidney not clearly visible by transparency. In some populations (e.g. from Ngome Forest, KwaZulu-Natal) orange pigmentation on tail and mantle edge is conspicuous. Freshly preserved specimens frequently with a bluish tinge in pneumostomal area of mantle collar, perhaps related to the presence of underlying mucus glands.

Radula (Fig. 27): Formula 0+(8–11)+(3–4); length up to 15.5 mm, with 23–32 V-shaped rows of teeth in larger specimens (more in smaller ones); teeth progressively larger from anterior to posterior of radula; tooth form essentially similar to that of *Nata tarachodes*; rachidian absent; largest tooth, the fang tooth (number 8–11) taken to delineate limit of lateral series; fang tooth elongate-trigonal, with a sharply pointed tip and a substantial base-plate; middle laterals much more slender and narrowly acuminate, the tips sometimes curving inwards. Specimens from KwaZulu-Natal and the Cape usually with 8–9 laterals (Fig. 27A), those from Mpumalanga and Limpopo usually, but not invariably, with 10–11 laterals (Fig. 27C).

Distal genitalia (Figs 8B, 28): Genital pore ventral to pneumostome; right optic tentacle retractor passing to left of penis. Penis shape variable, ranging from long and slender to clavate or ovate-fusiform, frequently somewhat sinuous; length up to 6.0 mm; penis wall not conspicuously muscular, internally with numerous small papillae arranged in ill-defined radiating ridges around epiphallus pore and sometimes aligned on low longitudinal folds (Fig. 8B shows these in the everted state). Penial retractor muscle attached at apex of penis; epiphallus present, approx. one-third length of penis, inserting laterally; point of insertion variable, between one-third and three-quarters length of penis from its base; vas deferens and epiphallus loosely adnate to side of penis, but not fused to it; vas deferens continues to penis base before running alongside free oviduct to join spermoviduct, frequently sinuous beside free oviduct. Genital atrium simple and vagina short or scarcely evident, the free oviduct

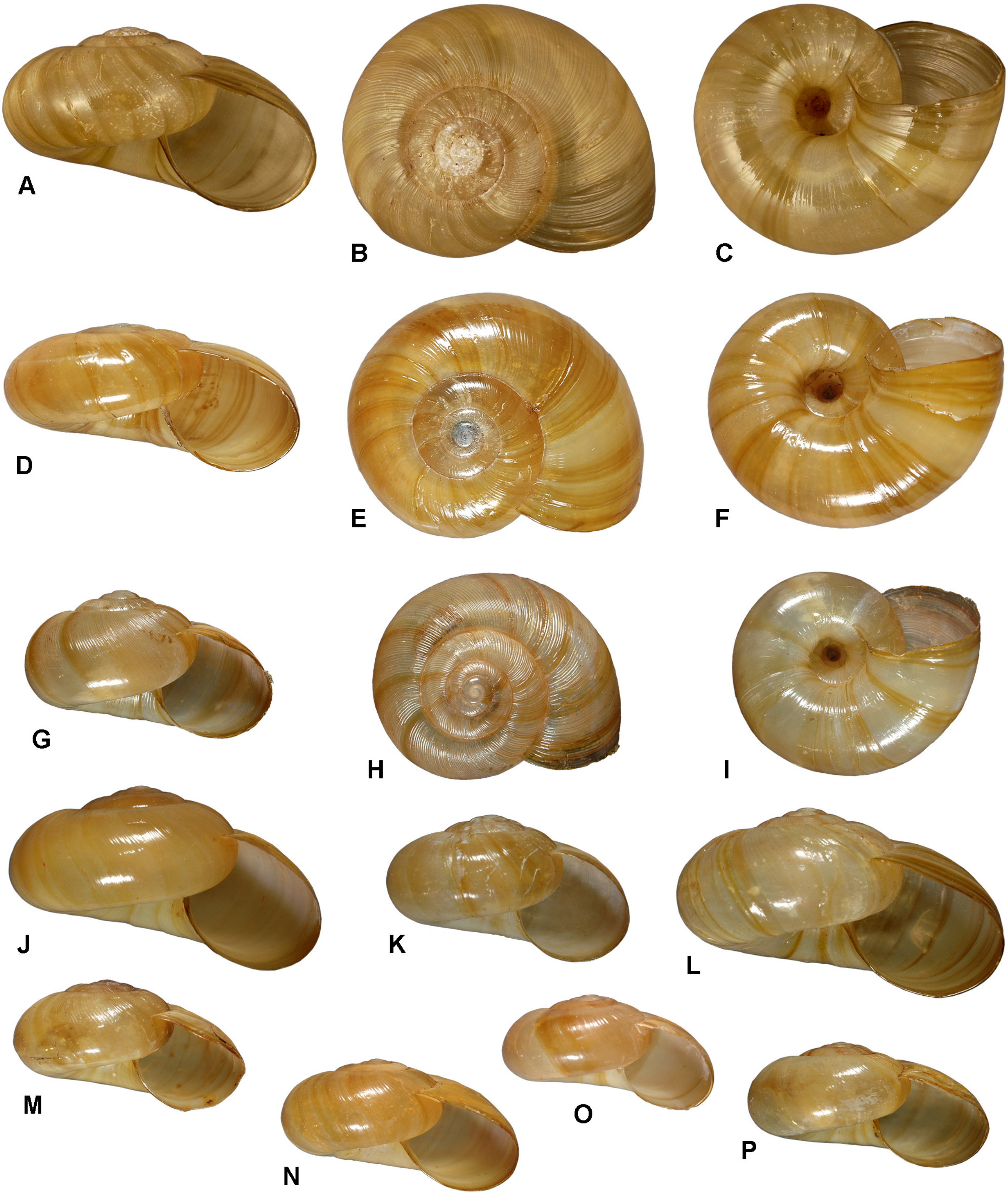

FIGURE 25. *Nata vernicosa* (Krauss, 1848). **A–C,** large typical specimen with strong sculpture, Mbotyi, E. Cape, diameter 20.7 mm (NMSA W4119). **D–F,** large low-spired, weakly sculptured, glossy specimen, *liparoxantha* morph, Umtamvuna Nat. Res., KwaZulu-Natal, diameter 19.5 mm (NMSA W7901). **G–I,** strongly sculptured, deep-whorled specimen, Kelso, KwaZulu-Natal, diameter 16.3 mm (NMSA W7940). **J–P,** additional specimens from throughout the range of the species [**J,** Lekgalameetse Nat. Res., Limpopo, diameter 20.6 mm (NMSA V5544). **K,** Mount Sheba, Mpumalanga diameter 16.0 mm (NMSA W3344). **L,** Hluhluwe Game Res., KwaZulu-Natal, diameter 21.7 mm (NMSA V571). **M,** Grahamstown, E. Cape, diameter 15.3 mm (NMSA W4198). **N,** Van Stadens Wild Flower Res., E. Cape, diameter 15.5 mm (NMSA W8359). **O,** Ferndale, E. Cape, diameter 14.0 mm (NMSA W8436). **P,** Fig Tree, Addo Elephant Park, E. Cape, diameter 15.9 mm (NMSA W4221)].

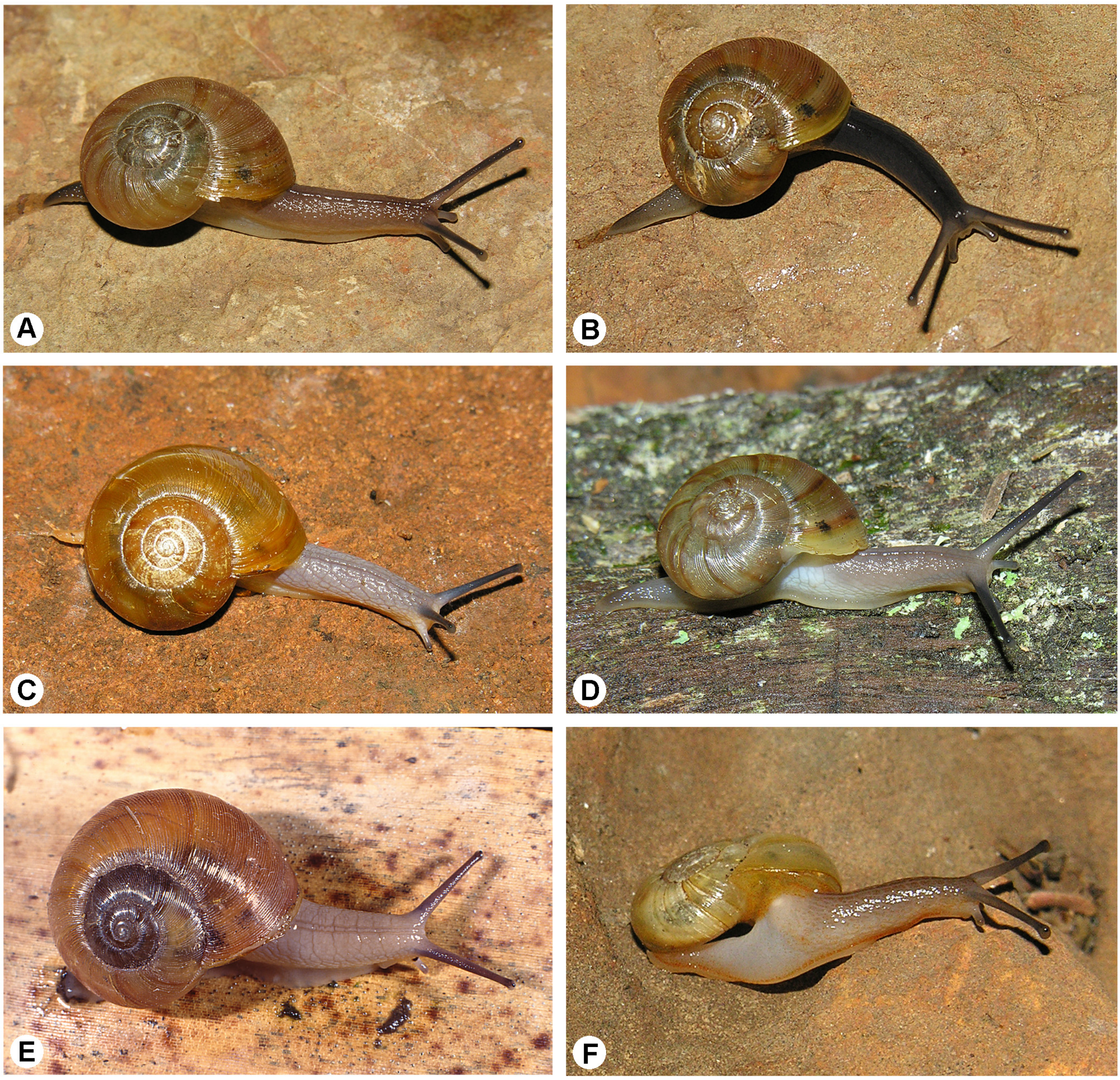

FIGURE 26. *Nata vernicosa* (Krauss, 1848), living animals. **A, B,** Empisini Nat. Res., Umkomaas, KwaZulu-Natal, shell diameter 15.7 mm and 11.8 mm respectively (NMSA W4399). **C,** Ferncliffe Nat. Res., Pietermaritzburg, KwaZulu-Natal, shell diameter 16.4 mm (NMSA W6647). **D,** Vernon Crookes Nat. Res., Umzinto KwaZulu-Natal, shell diameter 14.0 mm (NMSA W8020). **E,** Umtamvuna Nat. Res., KwaZulu-Natal, shell diameter 18.5 mm (NMSA V2089). **F,** Irma Booysen Flora Res., Cape St Francis, E. Cape, shell diameter 10.0 mm (NMSA W6382).

and bursa copulatrix duct seeming to arise side-by-side from atrium. Bursa copulatrix and its duct about half length of spermoviduct; basal half to three-quarters of duct broader, subcylindrical, sometimes narrowing slightly prior to insertion into atrium; distal portion of duct narrower and usually somewhat constricted at junction with bursa; broader portion of duct lined internally with numerous fine, close-set, wavy longitudinal folds, these becoming fewer and thicker in narrower section preceding bursa; bursa itself elongate-ovate, thin-walled and small, one-quarter or less length of its duct. Length of free oviduct variable; spermoviduct not convoluted, but usually sinuous; oviductal and prostatic portions distinct, the former with superficial folds. Albumen gland reniform, its size related to reproductive state; proximal half of hermaphrodite duct thicker and convoluted; ovotestis comprising approx. six fusiform lobes embedded in apical part of digestive gland.

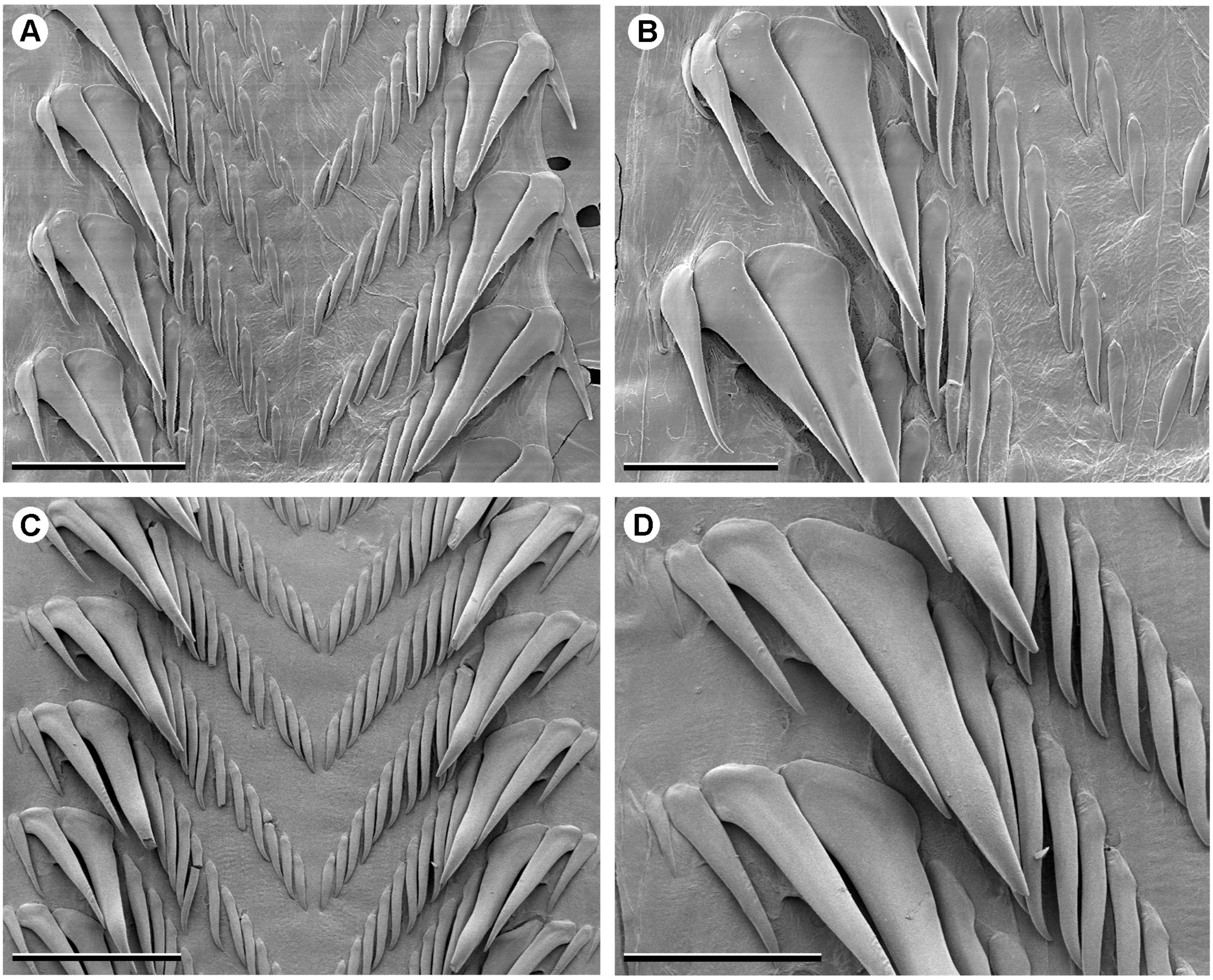

FIGURE 27. *Nata vernicosa* (Krauss, 1848), radula. **A, B,** Haven, E. Cape (NMSA W4151). **C, D,** Mount Sheba, Mpumalanga (NMSA W3344). Scale bars: A, C = 500 µm; B, D = 250 µm.

Distribution (Fig. 29): Widely distributed over much of eastern South Africa, from Mossel Bay in the west, through E. Cape and KwaZulu-Natal, to Mpumalanga, Limpopo and Swaziland; mostly in the coastal hinterland and inland to altitudes of approximately 1000 m, rarely more. However, in the northern part of its range the species is mostly associated with the Soutpansberg, Wolkberg and northernmost Drakensberg escarpment, where it primarily occurs at altitudes of 1000–1750 m. In addition, there is also a population occurring in suburban gardens in the environs of Cape Town, but this is almost certainly derived from translocated individuals.

Habitat. One of the most ecologically tolerant of all South African land snails; occurs in a wide variety of habitats ranging from open savannah, thornveld, coastal scrub and thicket to riverine woodland and dune, coastal scarp and afrotemperate forests, as well as *Eucalyptus* plantations, and suburban parks and gardens.

Remarks. The considerable variability in shell form exhibited by this species has been mentioned above. Further assessment of this variation needs to be undertaken in conjunction with phylogeographic analysis of molecular data. It is quite possible that additional cryptic species may be found to exist within what we here treat as a single variable entity.

Conservation. As currently interpreted, *Nata vernicosa* is one of the most widespread and commonly encountered snails in natural habitats in the south-eastern parts of South Africa. It is also tolerant of transformed habitats, particularly suburban gardens where the rather more well-watered conditions are favourable to both it and its prey. The conservation of the species is thus not a matter of concern. It is, however, a species that should be nurtured on account of its potential to reduce introduced pestiferous snail and slug populations.

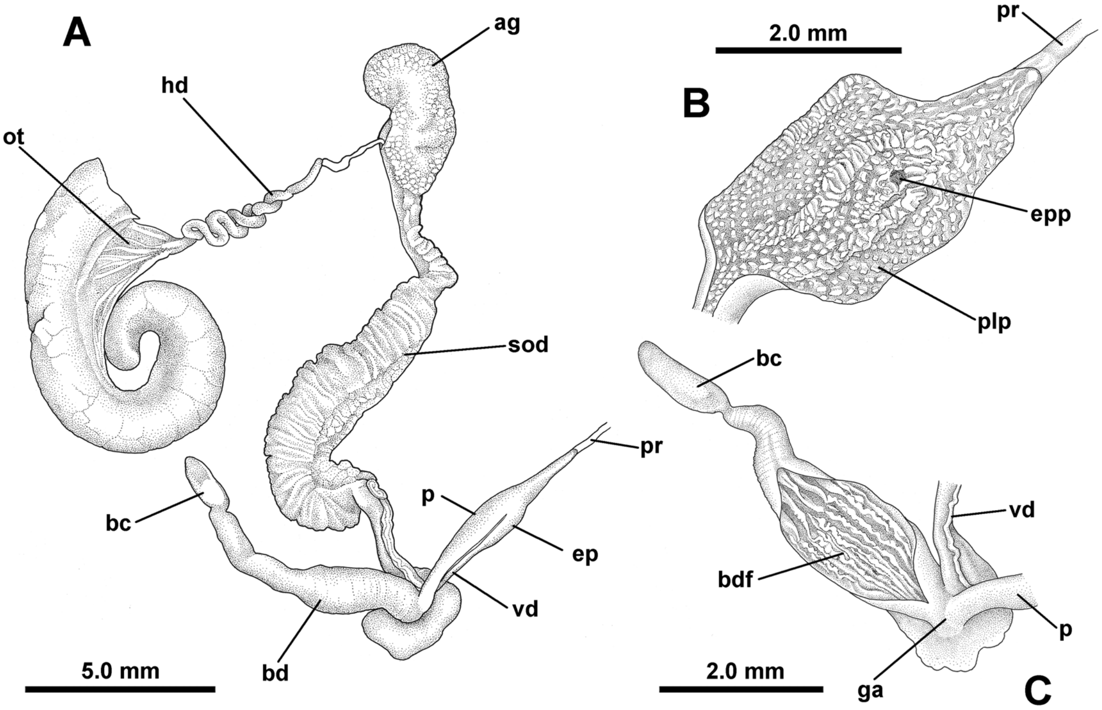

FIGURE 28. *Nata vernicosa* (Krauss, 1848), genitalia (NMSA W9322). **A,** entire genital tract. **B,** longitudinal dissection of penis showing papillate lumen. **C,** dissection of broader basal portion of bursa copulatrix duct showing fine folds on lumen wall. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; bdf, folds in wall of basal bursa copulatrix duct; ep, epiphallus; epp, epiphallus pore; ga, genital atrium; hd, hermaphrodite duct; p, penis; plp, papillate lumen of penis; pr, penial retractor muscle; sod, spermoviduct; vd, vas deferens.

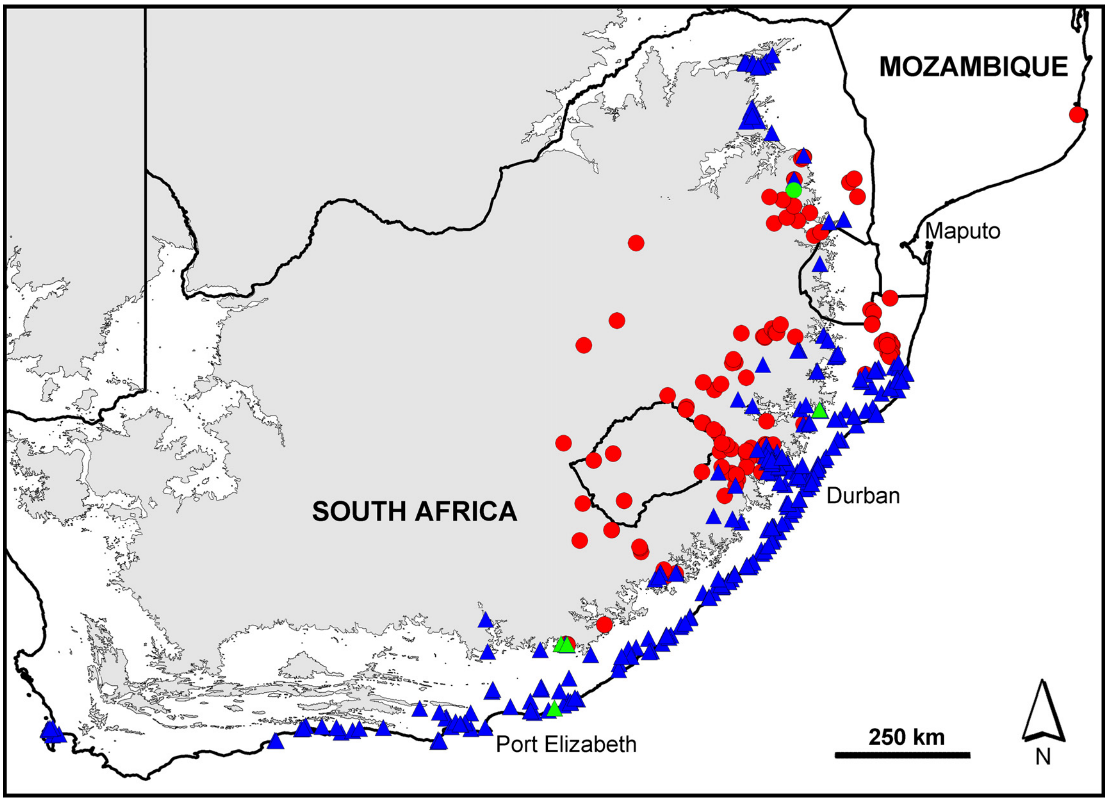

FIGURE 29. Comparison of distributions of *Nata vernicosa* (triangles) and *Nata erugata* **sp. nov.** (circles). Green symbols indicate localities for specimens used in DNA analyses (Moussalli & Herbert 2016); contour at 1000 m. The isolated population of *Nata vernicosa* in the Cape Town is considered to be derived from translocated individuals.

Nata erugata sp. nov.

Figures 4C, 6C, 29–32

Natalina caffrula—Haas, 1936: 18 (in part, Mkuzi).

Nata vernicosa—Bruggen, 1966: 376, fig. 54. Bruggen, 1969: 37. Bruggen, 1970a: 468 (in part). Bruggen, 1970b: 59. Bruggen, 1985: 286 (in part).

Etymology. From *erugo* (L.)—to clear of wrinkles, *erugatus* (L.)–without wrinkles, smooth.

Type material. Holotype (Fig. 30A–C): SOUTH AFRICA: KWAZULU-NATAL: Monk's Cowl area (29.05479°S: 29.38287°E), 1625 m, indigenous forest, in leaf-litter, F78, M. Hamer *et al*., 16/iii/2006 (NMSA W5599/T3906).

Paratypes (all NMSA unless indicated otherwise): SOUTH AFRICA: KWAZULU-NATAL: Pongola Bush Nat. Res. (27.323°S: 30.4817°E), 1300 m, montane *Podocarpus* forest, in leaf-litter and under logs, D. Herbert & NPB, 19/i/1995 (V776/T3915, one adult and three juvenile specimens; ELM D18003/T031, one specimen); Majuba area (27.477°S: 29.685°E), 1700 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, 28/i/1998 (V5932/T3909, one adult and three juvenile specimens); De Beers farm, approx. 15 km NE of Van Reenen (28.30403°S: 29.50240°E), 1841 m, afrotemperate forest, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Cunningham, 9/x/2006 (W4688/T3910, one specimen); Van Reenen (28.405°S; 29.390°E), iii/1918 (A7069/T3911, five specimens; ELM D18002/T030, one specimen); Kranskop (28.967°S: 30.863°E), Falcon coll'n, i/1922 (NMSA A7070/T3912, three specimens). FREE STATE: Platberg Nat. Res. (28.27631°S: 29.20772°E), 2100 m, montane shrubland/grassland, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Cunningham, 11/xii/2006 (W5621/T3908, two specimens); Golden Gate Highlands National Park (28.49430°S: 28.61868°E), 2000 m, gully thicket/grassland, buried in shrubs, A. Moussalli & D. Stuart-Fox, 28/xii/2005 (W4243/T3913, one specimen); Zastron area, Mapaya Hill (30.27439°S: 27.21902°E), ~1860 m, in soil amongst boulders in narrow, shaded cleft above sandstone cliff, st'n 08-059, D. Herbert & L. Davis, 22/xi/2008 (W6573/T3907, three specimens). E. CAPE: Witteberge, Balloch farm, north of Barkly East (30.71255°S: 27.69507°E), Lesotho highland grassland, under rock, D. Stuart-Fox, 1/iv/2005 (W4836/T3914, one adult and two juvenile specimens).

Additional material examined: See Appendix 4.

Identification. Differs from *Nata vernicosa* in that the apical surface is almost completely devoid of regular, close-set, axial riblets; although axial sculpture remains, it is present only in the form of weak, irregularly spaced growth-lines. More similar to *Nata watsoni* **sp. nov.**, but that species has very different radula morphology and occurs in a different region and biome (Albany Thicket).

Shell (Fig. 30): Lenticular, occasionally discoidal; whorls comparatively shallow and spire often low; largest specimens comprising 3.25–3.5 teleoconch whorls; periphery at or more usually slightly below mid-whorl; suture above periphery, at most weakly descendant prior to aperture. Protoconch diameter 1.0–1.9 mm, comprising ±1.0 whorl, smooth and glossy, junction with teleoconch usually rather weakly defined. Apical surface of teleoconch smooth and glossy, lacking regular axial riblets and sculptured only by weak growth irregularities; these strongest below suture, weakest at periphery and on base; no significant spiral sculpture, but some specimens with faint traces of vermiform wrinkles in places. Base and umbilical margin evenly rounded; umbilicus of moderate width, steep-sided; growth-lines slightly stronger within umbilicus. Aperture roundly or distinctly ovate, often obliquely descendant (Fig. 30J); peristome interrupted by bulging parietal region; outer lip thin with membranous periostracal fringe (commonly lost); outer lip shallowly sinuous when undamaged; upper part of columella lip extending forward and slightly reflected.

Shell translucent milky-white when fresh; periostracum glossy, pale yellowish-brown to honey-gold, commonly with some axial variation in intensity, producing unevenly spaced, slightly darker axial banding, but this generally weak.

Dimensions: Holotype, diameter 15.5 mm, height 8.1 mm; largest specimen, diameter 21.0 mm, height 11.4 mm; H:D of adults 0.46–0.60 [N=34].

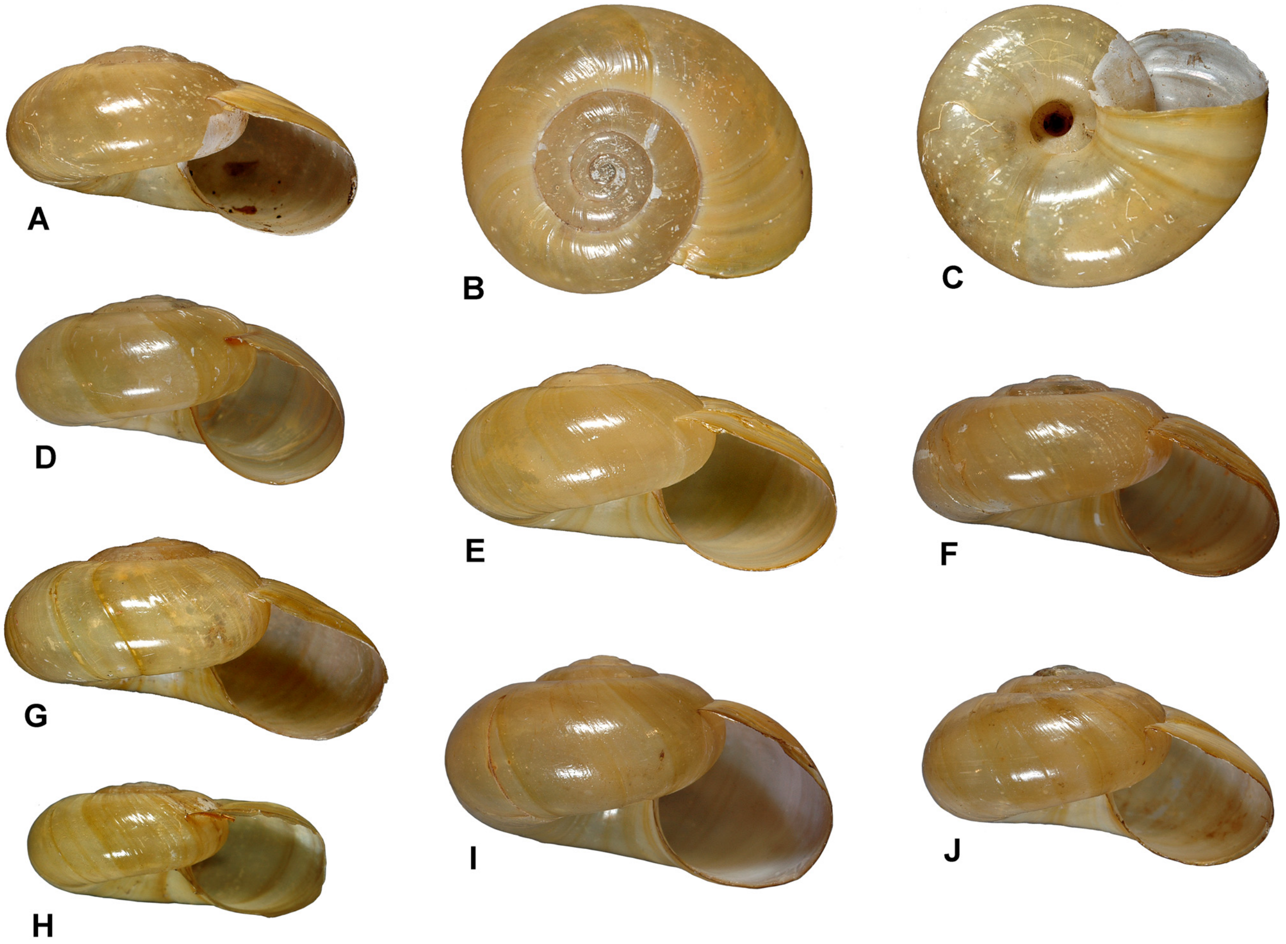

FIGURE 30. *Nata erugata* **sp. nov. A–C,** holotype, Monk's Cowl Forest, KwaZulu-Natal, diameter 15.5 mm (NMSA W5599/T3906). **D–J,** additional specimens from throughout the range of the species [**D,** Majuba, KwaZulu-Natal, diameter 14.5 mm (paratype, NMSA V5932/T3909). **E,** Pongola Bush, KwaZulu-Natal, diameter 17.0 mm (paratype, NMSA V776/T3915). **F,** Phinda Game Reserve, KwaZulu-Natal, diameter 16.2 mm (W1334). **G,** Balloch, Barkly East, E. Cape, diameter 16.8 mm (paratype, NMSA W4836/T3914). **H,** Mapaya Hill, Zastron, Free State, diameter 13.2 mm (paratype, W6573/T3907). **I,** Mariepskop, Mpumalanga, diameter 17.1 mm (W9364). **J,** Sand River area, Kruger National Park, diameter 15.6 mm (A9759)].

Living animal (Figs 4C, 31): Body generally pale; head and neck greyish-white to cream, dorsal region of neck sometimes pale grey or pale bluish-grey; optic tentacles a slightly darker shade of grey; foot paler beneath shell; posterior portion of foot relatively short; some individuals with microscopic orange pigment granules in skin, particularly on hind end of foot; skin texture moderately well defined; mantle edge pale, also with minute orange granules in some individuals; lining of mantle cavity with little or no dark pigmentation, except for a diffuse blackish mark just inside pneumostome, visible through shell; kidney trigonal, pale buff, not conspicuous through shell.

Radula (Figs 6C, 32): Very similar to that of *Nata vernicosa*, but usually with fewer lateral teeth. Formula 0+(7–8)+(3–4); length up to 12.0 mm, with 24–33 V-shaped rows of teeth; teeth progressively larger from anterior to posterior of radula; rachidian absent; largest tooth (number 7 or 8) taken to be outermost lateral. Tooth morphology as in *N. vernicosa*.

Distal genitalia: As in *Nata vernicosa*. Epiphallus enters penis between one-third and two-thirds length of the latter from its base; internally, lining of penis forms a raised rim around epiphallus pore; basal portion of bursa copulatrix duct swollen (particularly so in specimens from Hogsback), tapering to mid region and evenly slender thereafter, but constricted prior to bursa copulatrix which is small, subovate to reniform and thin walled.

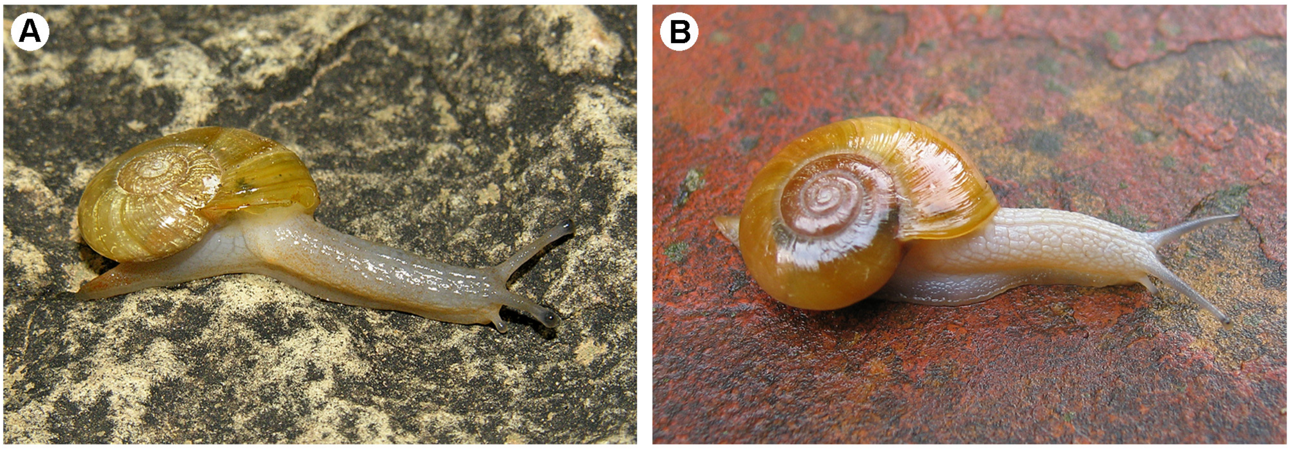

FIGURE 31. *Nata erugata* **sp. nov.**, living animals. **A,** Mapaya Hill, Zastron, Free State, shell diameter 13.2 mm (paratype, NMSA W6573/T3907). **B,** Tullach-Mohr, Nelspruit area, Mpumalanga, shell diameter 20 mm (MV, ex NMSA W3301).

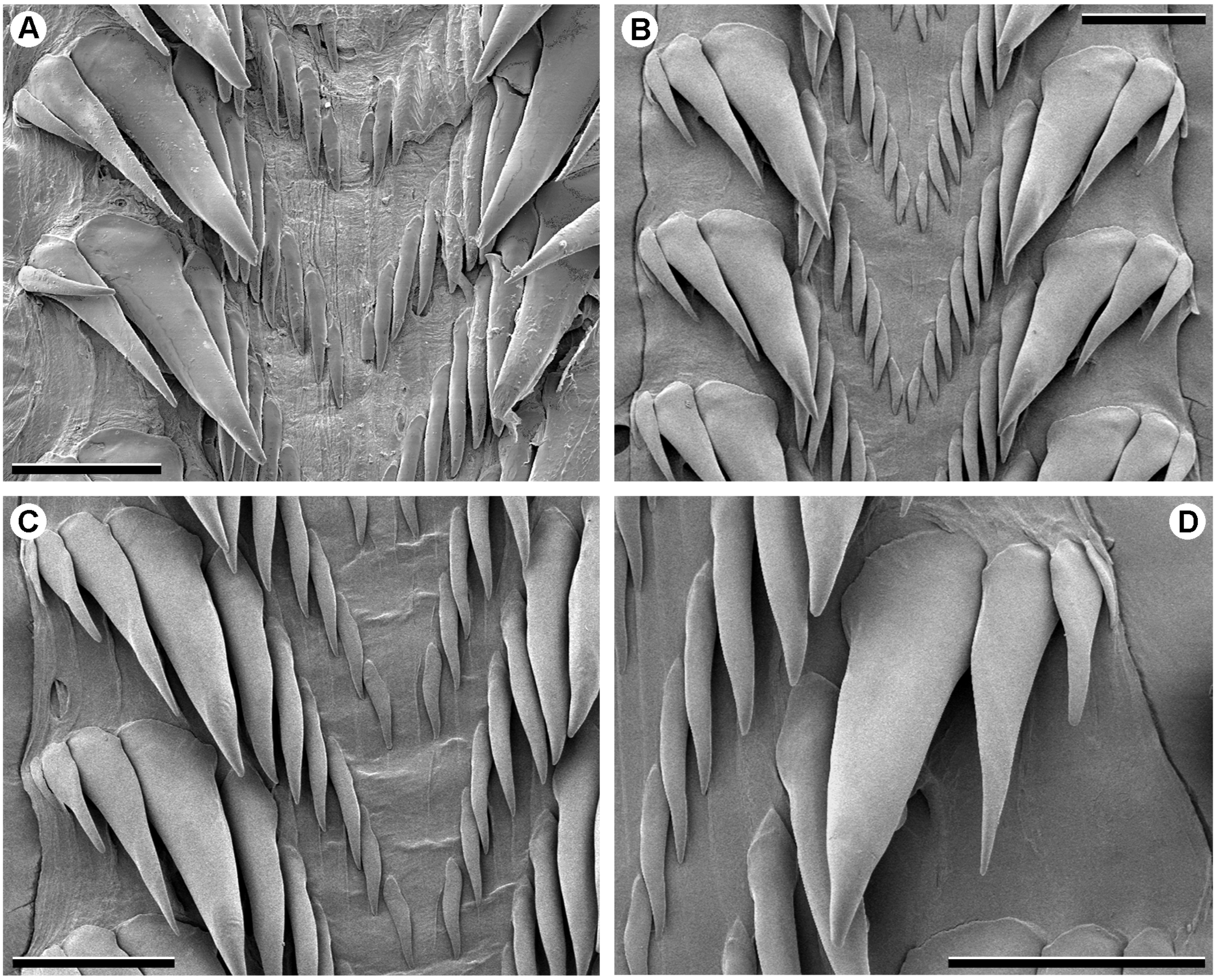

FIGURE 32. *Nata erugata* **sp. nov.**, radula. **A,** Sudwala, Mpumalanga (NMSA W4473). **B,** Hogsback E. Cape (NMSA W6654). **C, D,** Mapaya Hill, Zastron, Free State (paratype, NMSA W6573/T3907). Scale bars = 250 µm.

Distribution (Fig. 29): Endemic to eastern South Africa and southern Mozambique, but relatively widely distributed within this region, ranging from Hogsback in the south west, through western Lesotho, eastern Free State and Gauteng, into western and northern KwaZulu-Natal, the Lowveld of Mpumalanga and southern

Mozambique. Throughout the southern and western parts of its range the species is largely restricted to altitudes over 1000 m and extending to 2200 m along the KwaZulu-Natal escarpment edge. However, the populations in north-eastern KwaZulu-Natal (Zululand), the Mpumalanga Lowveld (southern Kruger National Park) and Mozambique occur at much lower altitudes (30–300 m).

Habitat. At altitudes above 1000 m the species occurs primarily in afrotemperate forest and more thickly vegetated habitats such as *Leucosidea* scrub. However, specimens have also been found in sheltering microhabitats in more open vegetation, even montane grassland. At lower altitudes in Zululand and the Kruger National Park it occurs in a variety of vegetation types within the Savannah Biome.

Remarks. When discussing Pfeiffer's 'var. *minor*', Connolly (1939) noted that although Pfeiffer's description '*costulis superficiei obsoletioribus*' (Pfeiffer 1853: 95) may apply to an immature example of *Nata liparoxantha*, '…there extends from the Cape Province to Delagoa a hitherto undetermined race, which may represent his variety. It differs from *vernicosa* solely in being very much smoother, the sculpture consisting of fine growth striolae instead of costulae' (Connolly 1939: 100). We have likewise been able to discern such a 'race', but we do not consider that it can be considered conspecific with Pfeiffer's var. *minor*. Examination of the lectotype of the latter at the SMNH (see above regarding its authenticity) reveals that although the axial sculpture is weak, distinct and regularly spaced axial riblets are nonetheless present on the adapical surface and the specimen is simply a weakly sculptured example of the variable *N. vernicosa*. Since all the other names currently considered to be junior synonyms of *N. vernicosa* likewise relate to material with distinct axial riblets, we are therefore obliged to propose a new name for the present material.

Throughout much of its distribution *Nata erugata* **sp. nov.** is the only species of *Nata* to be found, but at the lower limits of its altitudinal range, particularly in E. Cape and KwaZulu-Natal, there is some geographical overlap with *Nata vernicosa* (Fig. 29). However, further studies are needed to establish whether and to what extent the two species co-occur. There is certainly evidence that this may be the case at some localities (Hogsback, Umthatha area, Karkloof and Pilgrim's Rest area).

The occurrence of populations of what is largely a higher altitude species in the hotter more low-lying regions of northern KwaZulu-Natal, the Kruger National Park and southern Mozambique (Fig. 29), at altitudes of well below 1000 m, is anomalous and hard to explain. It is certainly suggestive of there being a further cryptic lineage in what we group under one species. For this reason, we have not included any specimens from these localities in the type material for this species. This is an issue needing to be studied in more detail using molecular data.

Conservation. As interpreted here, *Nata erugata* **sp. nov.** is a widespread and moderately common species occurring in a range of habitat types. As such, its conservation is not at present a matter of concern.

Nata watsoni sp. nov.

Figures 4E, F, 6E, 8C, 33–36

Etymology. Named after Hugh Watson (1885–1959), who first drew attention to the unusual radula of this species in 1934 (obituaries: Salisbury 1959; Verdcourt 1960).

Type material. Holotype (Fig. 25A–C): SOUTH AFRICA: E. CAPE: Somerset East, Glen Avon Falls, immediately upstream of waterfall (32.6804°S: 25.63437°E), 1130 m, found in crevice on shaded (northern) cliffs beside river, D. Herbert, M. Bursey & G. Redman, 20/i/2002 (NMSA W6266/T2299).

Paratypes: SOUTH AFRICA: E. CAPE: same data as holotype (NMSA V9819/T2273, one specimen); Graaff-Reinet, Camdeboo National Park, Valley of Desolation view site (32.26585°S: 24.49203°E), 1350 m, in deep shaded gulley between dolerite cliffs, found feeding on *Sheldonia asthenes* (Melvill & Ponsonby, 1907), D. Herbert, L. Davis & M. Cole, 14/iii/2008 (NMSA W6091/T2303, one specimen); Hankey, Sarah Bartmann municipal grounds (33.83834°S: 24.88594°E), 75 m, thicket, in leaf-litter and under fallen aloes, D. Herbert, L. Davis & M. Cole, st'n 08-050, 21/ix/2008 (W6524/T3921, three specimens); Somerset East, environs of Glen Avon Falls, *ca*. 0.5 km upstream of waterfall (32.67735°S: 25.6277°E), riverine woodland, in leaf-litter, D. Herbert, M. Bursey & G. Redman, 20/i/2002 (NMSA V9821/T2274, one specimen); Somerset East, Glen Avon, 'The Gorge' (32.67733°S: 25.62767), M. Bursey, 22/ix/2002 (ELM D13640, one specimen); Somerset East, slopes of Bosberg (32.70257°S: 25.57605°E), indigenous woodland, in leaf-litter, D. Herbert, M. Bursey & G. Redman, 22/i/2002 (NMSA V9789/T2297, one specimen); Kuzuko Game Res. (33.198°S: 25.487°E), thicket beside small dry water course, D. Herbert, L. Davis & M. Cole, 08/iii/2008 (NMSA W6022/T2296, one specimen); Kuzuko Game Res. (33.16804°S: 25.46650°E), *Acacia karoo* thicket beside water course, D. Herbert, L. Davis & M. Cole, 09/iii/2008 (NMSA W6029/T2298, 16 specimens); Grahamstown area, Riebeek East, Teafontein Farm (33.22975°S: 26.25088°E), *Aloe ferox* veld with bush clumps, in leaf-litter and under fallen aloes, D. Herbert, L. Davis & M. Bursey, 10/iii/2007 (ELM D15163, two specimens; NHMUK 20080531, one specimen; NMSA W5189/T2272, three specimens; NMW.Z.2008.039.00001, one specimen; RMNH.MOL.109.752, one specimen); Grahamstown, Mountain Drive (33.32834°S: 26.50260°E), indigenous forest, under log, A. Moussalli & D. Stuart-Fox, 3/xii/2005 (NMSA W4199/T2275, one specimen); Alexandria Forest (33.7213°S: 26.415°E), R.F. Lawrence, i/1964 (NMSA V5204/T2305, one specimen).

Additional material examined: See Appendix 5.

Identification. The shell of *N. watsoni* **sp. nov.** closely resembles that of *N. erugata* **sp. nov.** and *N. vernicosa*. The latter differs in possessing fine, close-set axial riblets on the adapical surface, but both *N. watsoni* **sp. nov.** and *N. erugata* **sp. nov.** share the same almost smooth, highly glossy shell, sculptured solely by growth-lines. Compared to *N. erugata* **sp. nov.**, the shell of *N. watsoni* **sp. nov.** is smaller (max. diameter 16 mm vs. 21 mm), its spire usually less prominent and the umbilicus somewhat narrower, but definitive separation of the two requires examination of the radula, which has finer, much more numerous teeth in *N. watsoni* **sp. nov.** The distributions of the two species do not overlap, which aids in determining the likely identity of empty shells.

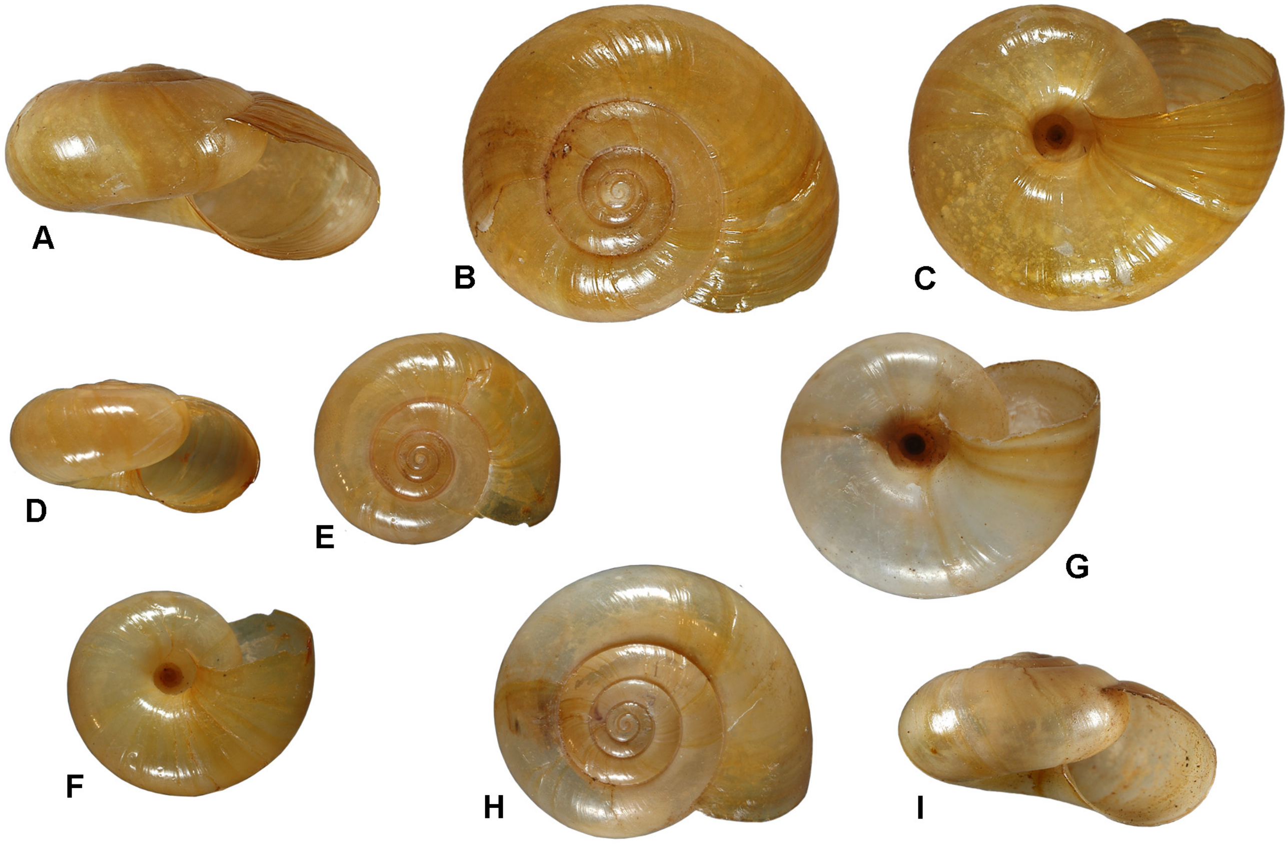

FIGURE 33. *Nata watsoni* **sp. nov. A–C,** holotype, Glen Avon Falls, Somerset East, E. Cape, diameter 16.0 mm (NMSA W6266/T2299). **D–F,** low-spired juvenile, Riebeek East, Grahamstown, diameter 10.5 mm (paratype, NMSA W5189/T2272). G–I, Hankey, diameter 13.6 mm (paratype, NMSA W6524/T3921).

Shell (Fig. 33): Lenticular to discoidal; spire very low; with up to 3.0 teleoconch whorls, exceptionally up to 3.75 whorls (holotype); suture well above periphery, last adult whorl descending slightly prior to aperture only in the largest specimens and even then remaining well above periphery. Protoconch small, diameter 1.03–1.42 mm, comprising ± 1.25 whorls, but junction with teleoconch often not clear; smooth and glossy. Teleoconch weakly sculptured, lacking axial riblets, but with faint, relatively widely spaced subsutural pleats and occasional stronger growth-lines or scars; surface glossy. Aperture subcircular when young, becoming more oblique with growth;

peristome interrupted by parietal region which bulges into aperture; outer lip thin with membranous periostracal fringe when undamaged; base and umbilical margin evenly rounded; umbilicus relatively narrow, steep-sided; columella lip scarcely if at all reflected.

Shell glossy, periostracum relatively uniform pale yellowish-brown, but with occasional indistinct, slightly darker, golden-brown axial bands.

Dimensions: Holotype (=largest specimen) diameter 16.0 mm, height 8.25 mm; H:D 0.49–0.59; few specimens with diameter >11.0 mm.

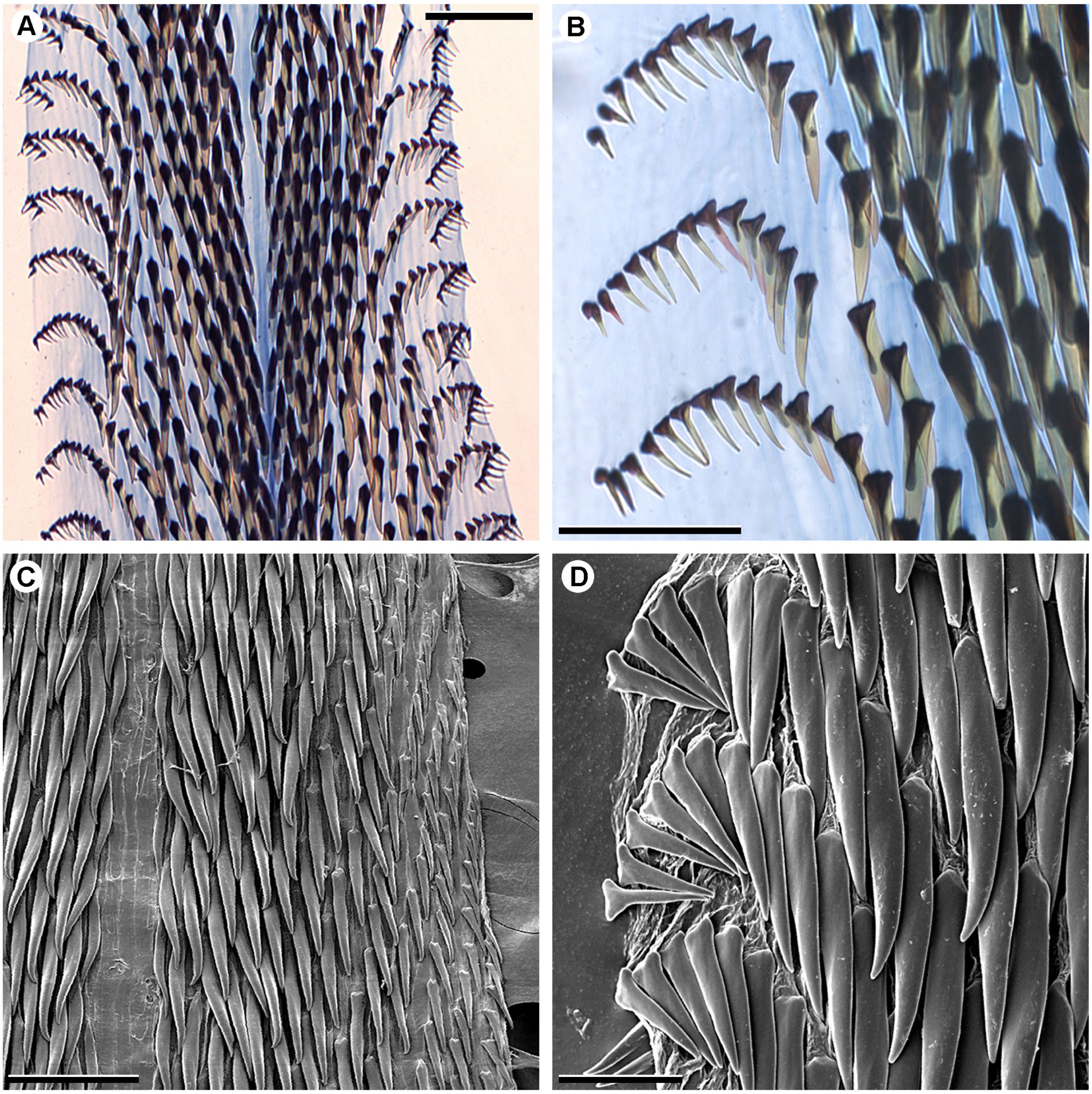

FIGURE 34. *Nata watsoni* **sp. nov.**, radula. **A,** entire width of radula. **B,** recurved rows of teeth at radula margin. **C,** middle and right side of radula. **D,** recurved rows of teeth at radula margin. A, B, D, Camdeboo National Park, paratype NMSA W6091/T2303; C, Somerset East, holotype. A, B, stained radula slides; C, D, scanning electron micrographs. Scale bars: A, D = 100 µm; B = 50 µm; C = 250 µm.

Living animal (Fig. 4E, F): Coloration of head foot variable; head and neck commonly orange-brown to brown (Fig. 4E), darker dorsally, paler and more greyish beneath shell and posteriorly, pedal margin sometimes deeper orange, tentacles grey to dark grey; one specimen more uniformly pale cream-buff with greyish tentacles (Fig. 4F). Neck region capable of great elongation; skin in this region relatively strongly textured; in occasional specimens skin tubercles may be darker than intervening grooves. Lung wall variously flecked with conspicuous black spots and blotches, sometimes heavily so (Fig. 4E); mantle edge with pinkish or orange tinge, no blue coloration evident in vicinity of pneumostome; lower left mantle lobe with a narrow base and alate extensions on both sides.

Radula (Figs 6E, 34): Highly distinctive; formula 0+(20–33); length up to 13 mm, with 42–60 transverse rows of teeth; rows acutely V-shaped in central area with a distinct mid-line diastema (perhaps an artefact of preparation), rows broadening laterally and sometimes recurved at margin; number of transverse rows and number of teeth per row related to size of animal, 4–6 rows/mm in large individuals (shell diameter >12 mm), over 10 rows/mm in smaller ones. Rachidian absent; no one tooth in each half-row is clearly the largest and thus a cut-off between lateral and marginal series cannot be identified; inner series of teeth well developed, elongate and aculeate, sometimes weakly curved or sinuous (Fig. 34C); increasing slightly in size from first to 6–8; outer series decreasing in size somewhat more noticeably, but still gradually; teeth at radula margin considerably smaller, with a trigonal base-plate and very slender, sharply pointed cusp (Fig. 34B, D).

Distal genitalia (Fig. 35): Genital pore ventral to pneumostome; right optic tentacle retractor passing to left of penis. Penis relatively long and slender (length 5.5–8.0 mm), somewhat constricted at its junction with genital atrium and in mid region; retractor muscle attached apically; epiphallus inserts laterally, approximately one-quarter length of penis from its apex; penis lumen lined by very fine, close-set papillae; epiphallus pore surrounded by an oval-shaped complex of ridges (considerable individual variation evident in pattern), this more extensive basal to pore; 1–2 well-developed longitudinal ridges present on lumen wall opposite epiphallus pore. Epiphallus short, its lumen lined with longitudinal rows of papillae, somewhat coarser than those in penis; vas deferens narrow, passing down penis (sometimes sinuously so), reflexing around angle between penis and vagina, and then running alongside free oviduct to join base of spermoviduct.

Genital atrium simple, cylindrical; vagina short, base of bursa duct connected to body wall by muscle fibres; free oviduct short, basal part of spermoviduct comprising oviductal tissue only, prostatic portion present only in upper half to two-thirds, vas deferens continuing thereafter on oviduct surface; spermoviduct sinuous and with superficial folds in oviductal portion. Bursa copulatrix duct somewhat broader basally, narrowing at about one-third its length then broadening during the mid and upper portion before narrowing again prior to the bursa itself (thus reminiscent of the penis shape); bursa pyriform to elongate ovate.

Distribution (Fig. 36): Endemic to E. Cape, South Africa; primarily in the lower catchments of the Gamtoos, Sundays and Great Fish rivers, but extending inland to Graaff-Reinet; from the coastal hinterland to 1350 m.

Habitat. Largely restricted to areas falling within the broader confines of the Albany Thicket Biome (Mucina & Rutherford 2006), but occurring in a relatively wide variety of habitats within this, from southern coastal forest to fragments of southern mistbelt forest in shaded gorges and gullies, as well as low, open thicket. Lives in leaf-litter beneath bushes, under logs, stones and fallen aloes, and in rocky crevices.

Remarks. Two existing names are available for moderately sized *Nata* specimens from the Albany Thicket, *N. caenotera* (Melvill & Ponsonby, 1892) and *N. chaplini* (Melvill & Ponsonby, 1894). However, the types of both of these taxa (Fig. 24G–I and J–L, respectively) have distinct axial riblets and they are thus not applicable to the present material. We treat both as junior synonyms of *N. vernicosa*.

As discussed in the above identification section, *N. watsoni* **sp. nov.** is chiefly comparable with *N. erugata* **sp. nov.** and *N. vernicosa*. Although its shell exhibits no truly characteristic features, its radula is highly distinctive, having finer and much more numerous teeth. In addition to the differences in its radula morphology, *N. watsoni* **sp. nov.** also possesses features of the distal genitalia that distinguish it from *N. erugata* **sp. nov.** and *N. vernicosa*. These include the dumbbell shape of the penis, the more elaborate pattern of ridges on the inner penis wall associated with the epiphallus pore and the finer papillae lining the lumen. The bursa copulatrix duct is also not as obviously swollen basally and there is a constriction at approximately one-third of its length, mirroring the constriction in the penis. In addition, the prostatic portion of the spermoviduct is distinctly shorter than the oviductal portion, and the vas deferens initially passes over the folded lobes of the oviduct.

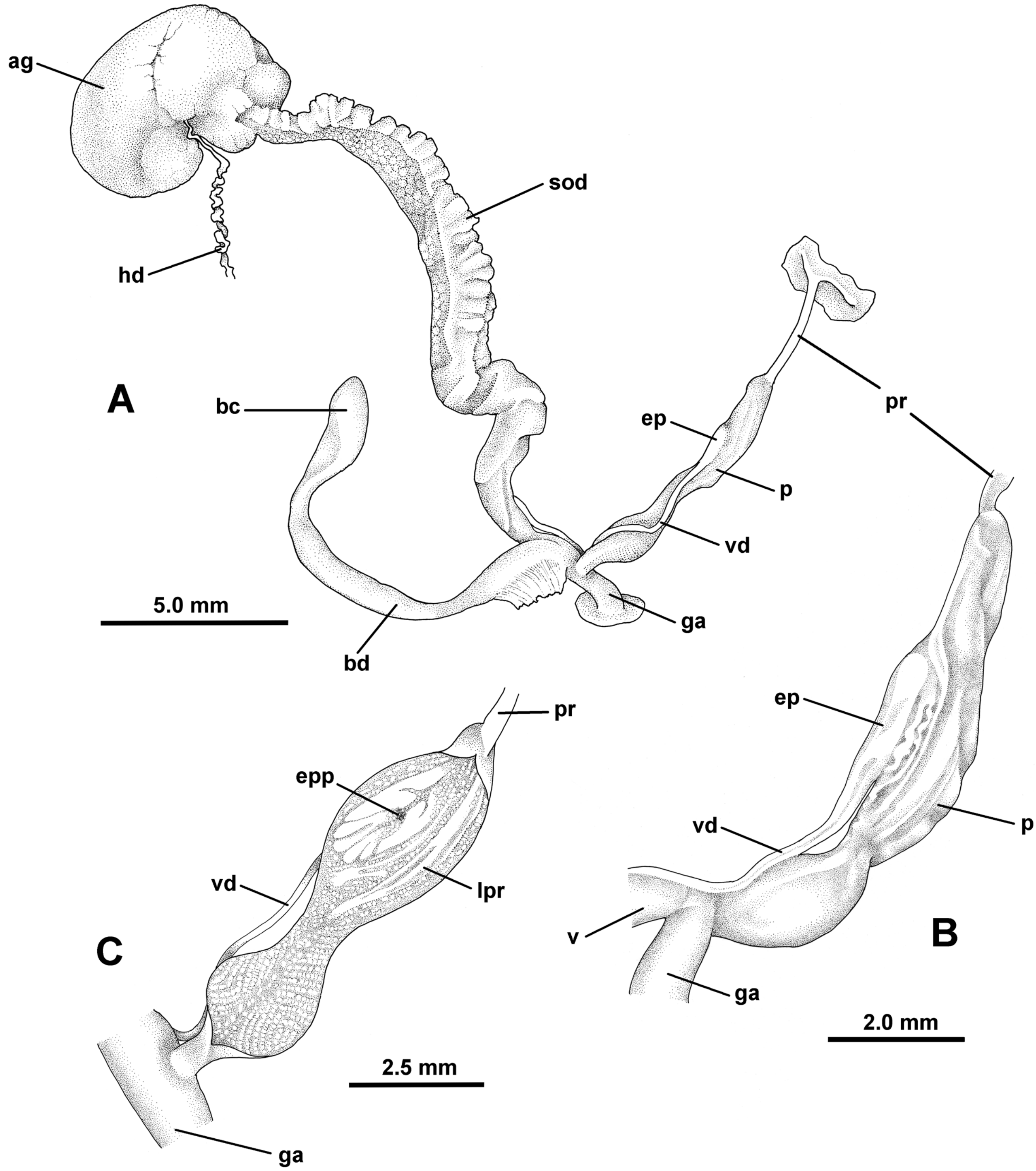

FIGURE 35. *Nata watsoni* **sp. nov.**, genitalia. **A,** entire genital tract, minus ovotestis, holotype (NMSA W6266/T2299). **B,** penial complex, paratype (NMSA W5189/T2272). **C,** longitudinal dissection of penis to show internal structure, holotype. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; ep, epiphallus; epp, epiphallus pore; ga, genital atrium; hd, hermaphrodite duct; lpr, longitudinal penis ridge; p, penis; pr, penial retractor muscle; sod, spermoviduct; v, vagina; vd, vas deferens.

The marked variation in body colour exhibited by this species is surprising (Fig. 4E, F), but the specimens concerned consistently show the same distinctive features of radula and genital morphology. The distribution of *N. vernicosa* overlaps extensively with that of *N. watsoni* **sp. nov.**, particularly near the coast, and in places the two have been found at the same locality. A specimen from Graaff-Reinet was found feeding on the urocyclid *Sheldonia asthenes* (Melvill & Ponsonby, 1907), indicating that despite its unusual radula morphology, the species still feeds on other molluscs.

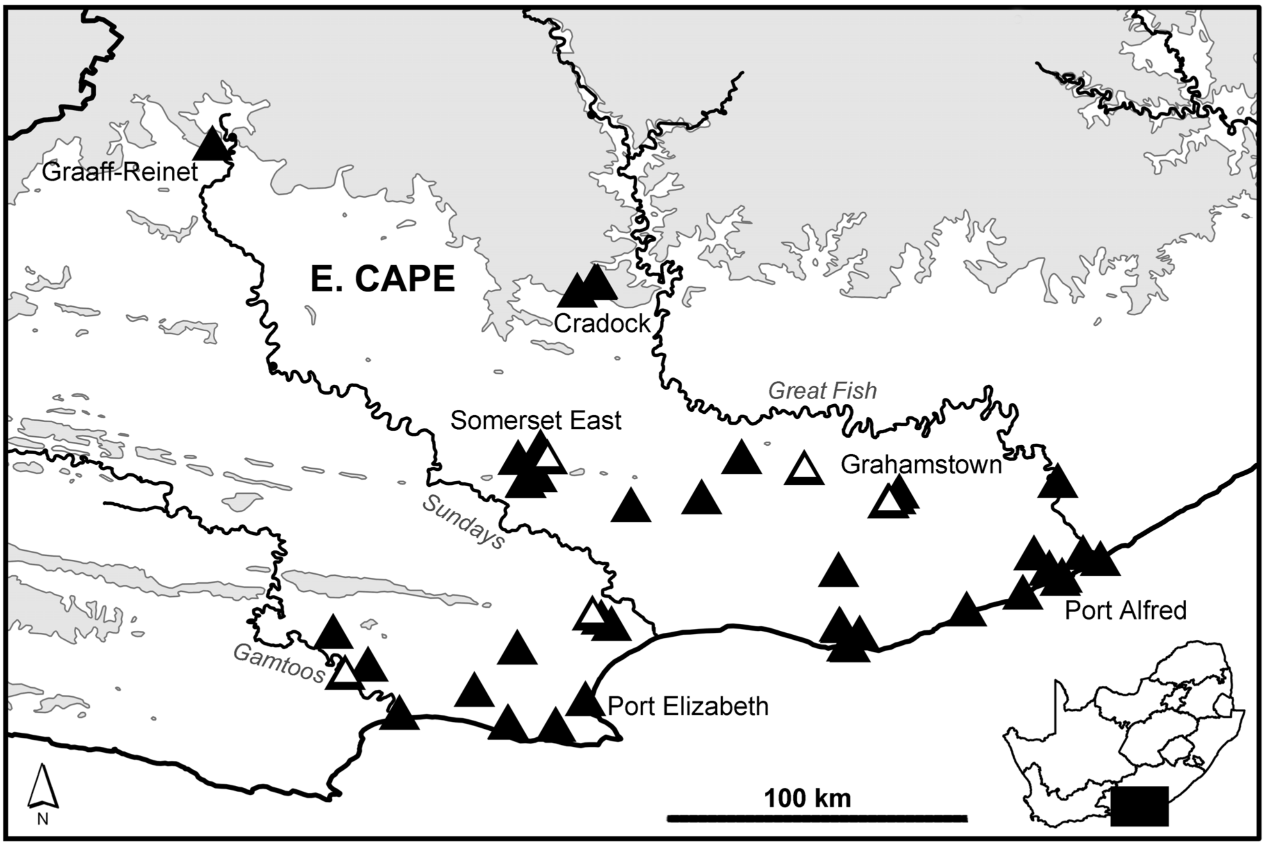

FIGURE 36. Distribution of *Nata watsoni* **sp. nov.** Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli & Herbert 2016); contour at 1000 m.

Conservation. Although endemic to E. Cape and the Albany Thicket Biome, *Nata watsoni* **sp. nov.** is not a rare species and it has relatively broad habitat preferences. In places it may be locally common and it is recorded from a number of sites within the Greater Addo Elephant National Park, as well as the Camdeboo National Park and various municipal and local authority conservation areas. Its conservation is thus currently not an issue of concern, though its status as a provincial endemic is noteworthy.

Genus *Natella* Watson, 1934

Natella Watson, 1934: 160. Type species (by original designation): *Helix* (*Patula*) *viridescens* Melvill & Ponsonby, 1891.

Diagnosis. Shell small (adult diameter *ca* 5.0 mm), thin, discoidal, broadly umbilicate, glossy, pale yellowish; axial sculpture weak, spiral sculpture lacking; protoconch smooth. Radula beloglossan; labial palps not evident; penis stout, epiphallus absent, vas deferens short and not reflexed, inserting apically into penis; penis lumen not papillate, apical verge present; retractor muscle of right optic tentacle passes to left of penis; vagina broad, no atrial diverticulum or oviduct caecum present; kidney ovate to bean-shaped, primary ureter reflexed around anterior of kidney; suprapedal mucus gland not convoluted, the posterior portion lacking glandular tissue.

Remarks. Watson's separation of '*Nata*' *viridescens* in to a distinct, monotypic section [=subgenus] *Natella* (Watson 1934), is strongly supported by both the morphological data presented here and by molecular data (Moussalli & Herbert 2016). Furthermore, since the latter data show *Nata s.l.* to be a deeply divergent and quite possibly non-monophyletic taxon (*Natella* is not sister to *Nata s.s.*), we consider *Natella* should be treated as a full genus.

In addition to the characters given in the above diagnosis, Watson also listed the presence of a rachidian tooth in the radula as a feature distinctive of *Natella.* While we can confirm that a rachidian tooth is present in *Natella*, this can no longer be considered a distinctive character of the genus since such a tooth is also present in *Nata aequiplicata* **sp. nov.**, which genital morphology and molecular data show to belong to *Nata*. (It is also present in some unusual specimens tentatively identified with *Nata tarachodes*.) As stated in the Introduction, the presence of a rachidian tooth may represent an ancestral character state retained in juveniles and small-shelled species. The presence/absence of a rachidian tooth may thus not be phylogenetically informative. Watson also noted that the bursa copulatrix duct (as 'spermatheca duct') of *Natella* was longer than in species of *Nata s.s.*, but he provided no illustration of this and we do not find this to be the case.

A further unusual and possibly distinctive feature of the buccal apparatus of *Natella* is its possession of a proboscis. First observed in a drowning individual as an extended oral tube with the radula near its tip (Fig. 2A), this structure is visible when retracted as a tube linking the mouth to the anterior end of the buccal mass, in the vicinity of the cerebral ganglia and anterior nerve ring. A similar structure has not been seen in species of *Nata* and observations of the feeding behaviour of *Nata vernicosa* suggest that there is very limited protrusion of the buccal tube beyond the mouth during feeding.

Natella is monotypic and is endemic to southern Africa. To date it has been recorded only from north-eastern South Africa, though its range may well extend into Swaziland.

Natella viridescens **(Melvill & Ponsonby, 1891)**

Figures 2A, 3D, 4H, 5C, 6F, 9C, 37–40

Helix (*Patula*) *viridescens* Melvill & Ponsonby, 1891: 238. Melvill & Ponsonby, 1892a, pl. 4, fig. 1. Type loc.: Pretoria.
Patula viridescens—Pilsbry, 1892 in 1892–1893: 78, pl. 30, fig. 32.
Natalina viridescens—Melvill & Ponsonby, 1898b: 171. Connolly, 1912: 98.
Rhytida (*Macrocycloides*) *viridescens*—Möllendorff & Kobelt, 1903, in 1903–1905: 61, pl. 10, fig. 26. Kobelt, 1909: 53.
Nata (*Natella*) *viridescens*—Watson, 1934: 160. Connolly, 1939: 103, text fig. 7 (radula). Zilch, 1959–60: 554, fig. 1937. Schileyko, 2000: 748, fig. 974.
Nata viridescens—Bruggen, 1967: 28, 29. Richardson, 1989: 46. Herbert & Kilburn, 2004: 219.

Etymology. From *viridescens* (L.)–greenish; presumably in reference to the 'olivaceous epidermis' (periostracum) noted by the original authors.

Type material. Holotype of *Helix* (*Patula*) *viridescens* Melvill & Ponsonby, 1891 in NHMUK (1905.1.26.24), diameter 4.5 mm (in poor condition).

Additional material examined and literature records: See Appendix 6.

Identification. Shell characterised by its small size, low-discoidal profile, weak sculpture and wide umbilicus. Distinctive anatomical features are given in generic diagnosis.

Shell (Fig. 37): Discoidal, spire low to almost flat; largest specimens with approx. 2.0 teleoconch whorls; suture above periphery, not noticeably descendant prior to aperture; periphery usually slightly below mid-whorl; surface glossy throughout. Protoconch very small, diameter 0.7–1.0 mm, comprising ±1.0 whorl, smooth and glossy; junction with teleoconch usually weakly defined. Teleoconch initially sculptured only by faint growth-lines, but last adult whorl with traces of weak pliculae below suture and with occasional stronger, irregularly spaced growth-lines; sculpture weaker on base. Aperture roundly ovate; peristome interrupted by bulging parietal region; outer lip thin with membranous periostracal fringe when undamaged; base and umbilical margin evenly rounded; umbilicus broad, patent to apex; columella lip not reflected.

Translucent, periostracum more or less uniformly pale golden-yellow to pale olive-yellow; little or no darker axial banding.

Dimensions: Largest specimen, diameter 5.3 mm, height 2.4 mm (Ithala Game Res., NMSA V2530); H:D of adults 0.42–0.47 (N=21).

Living animal (Fig. 4H): Few specimens examined alive; head and neck grey to dark grey, with scattered microscopic orange pigment granules, tentacles and retractor muscles often somewhat darker; foot paler ventrally, particularly the tail and beneath shell; ventro-lateral margins of foot with more numerous orange pigment granules; skin texture relatively smooth; mantle edge pale, often densely speckled with orange pigment granules; lining of mantle cavity lacking dark makings, whitish kidney sometimes conspicuous.

Radula (Figs 6F, 38): Formula 1+7 +(3–4); length up to 1.9 mm, with 27–32 broadly V-shaped rows of teeth; rachidian present, narrow with a short, curved cusp; no clear distinction between lateral and marginal series, largest tooth taken to be outermost lateral; inner lateral teeth slender, the cusp down-curved; teeth progressively increasing in length from first to sixth; seventh tooth considerably larger (fang tooth), and much broader and blade-like; 3–4 teeth (marginals) beyond largest lateral, the first also flattened, but somewhat smaller and rather more narrowly acuminate, remaining marginals decreasing rapidly in size, a minute fourth marginal sometimes evident.

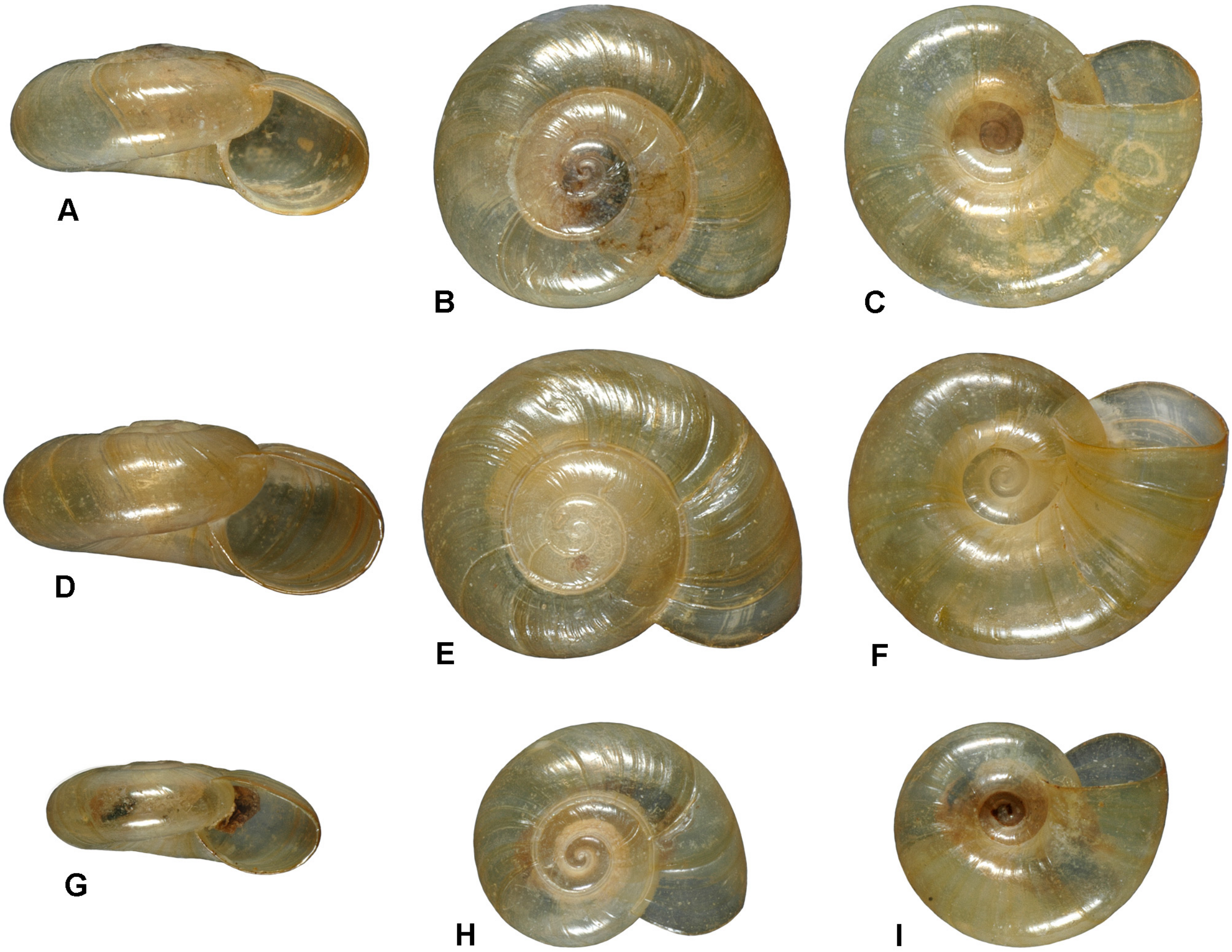

FIGURE 37. *Natella viridescens* (Melvill & Ponsonby, 1891). **A–C,** Weenen, KwaZulu-Natal, diameter 4.7 mm (NMSA A7126). **D–F,** Ithala Game Reserve, KwaZulu-Natal, diameter 5.0 mm (NMSA V3177). G–I, Pretoria, Gauteng, diameter 3.6 mm (NMSA A7122).

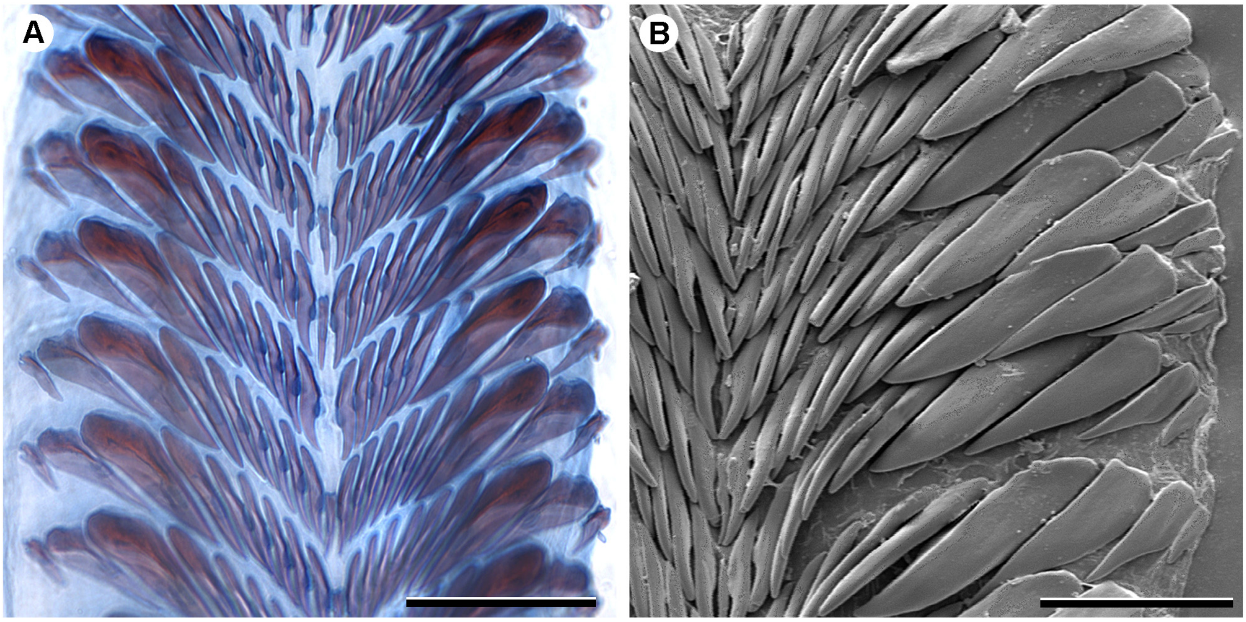

FIGURE 38. *Natella viridescens* (Melvill & Ponsonby, 1891), radula. **A,** whole width of radula, showing small rachidian tooth, stained with Shirlastain A, Ithala Game Reserve, KwaZulu-Natal (NMSA V2530). **B,** SEM of half row, Soutpansberg, Limpopo (NMSA V5664). Scale bars: A = 100 µm; B = 50 µm.

Distal genitalia (Fig. 39): Genital pore below pneumostome. Penis short and stout (length ±0.7 mm), not obviously narrowing basally, bluntly rounded at its apex, from which the vas deferens and penial retractor muscle arise. Interior of penis with a broad verge extending for half its length from apex, basal section lined with low longitudinal folds, lacking papillation. No evidence of a swollen epiphallic region prior to insertion of vas deferens; the latter not reflexed and adnate to side of penis, but runs directly backward to its origin at base of spermoviduct. Genital atrium simple and vagina short with thickened wall. Bursa copulatrix and its duct about one-third length of spermoviduct, slender basally, but apical portion slightly swollen; the whole adnate to free oviduct and lower spermoviduct. A concentration of muscle fibres arises close to base of bursa copulatrix duct, connecting with adjacent body wall.

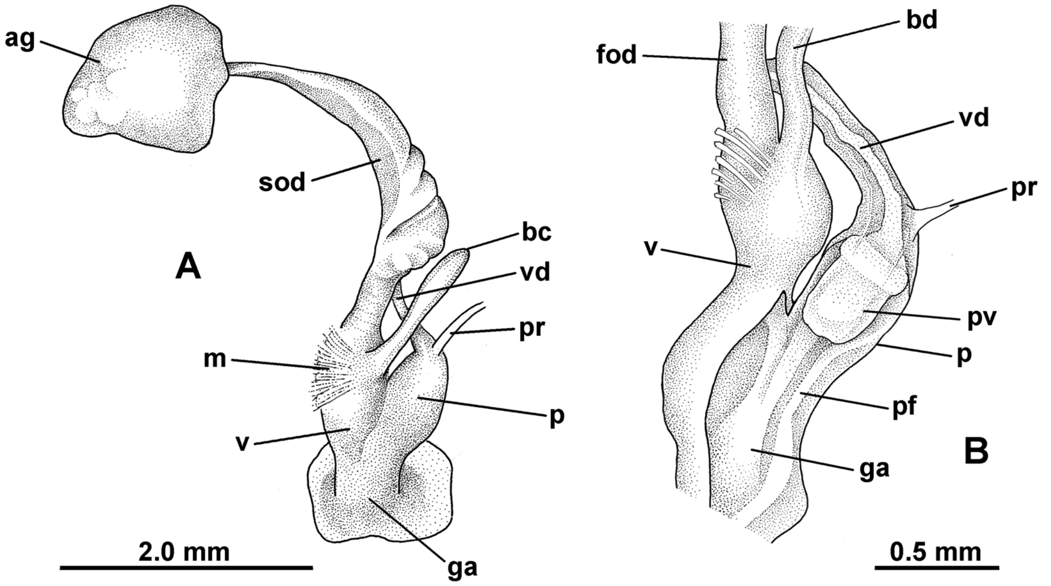

FIGURE 39. *Natella viridescens* (Melvill & Ponsonby, 1891), genitalia (NMSA V3177). **A,** middle and lower portion of genital tract. **B,** internal structure of penis. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bd, bursa copulatrix duct; fod, free oviduct; ga, genital atrium; m, muscle fibres; p, penis; pf, folds inside penis base; pr, penial retractor muscle; pv, penial verge; sod, spermoviduct; v, vagina; vd, vas deferens.

Distribution (Fig. 40): Endemic to north-eastern South Africa; from the Soutpansberg (Limpopo), south through N.W. Province, Gauteng and Mpumalanga, to the KwaZulu-Natal Midlands (Howick–Dargle area); mostly at altitudes over 500 m and commonly over 1000 m.

Habitat. Evidently catholic in habitat preferences. Most records from the northern part of the Great Escarpment are from forested habitats, but some of the localities in Gauteng, N.W. Province and KwaZulu-Natal indicate that the species also inhabits somewhat drier, thicket-type vegetation. Primarily in leaf-litter and under logs, but will climb walls and probably tree trunks.

Remarks. *Natella viridescens* is the smallest southern African rhytidid. *Nata erugata* **sp. nov.** and *Nata vernicosa*, with which it is known to co-occur, are substantially larger species and lack such a wide umbilicus. Juvenile specimens of both have deeper, fewer whorled shells with a much narrower umbilicus. The smaller *Nata* species, *N. aequiplicata* **sp. nov.** and *N. tarachodes* have stronger sculpture and occur only in the southern and western Cape respectively. Specimens of *Natella viridescens* from northern KwaZulu-Natal are often somewhat larger than those from other localities.

Conservation. With its wide distribution and broad habitat tolerance, *Natella viridescens* is not currently a species of conservation concern.

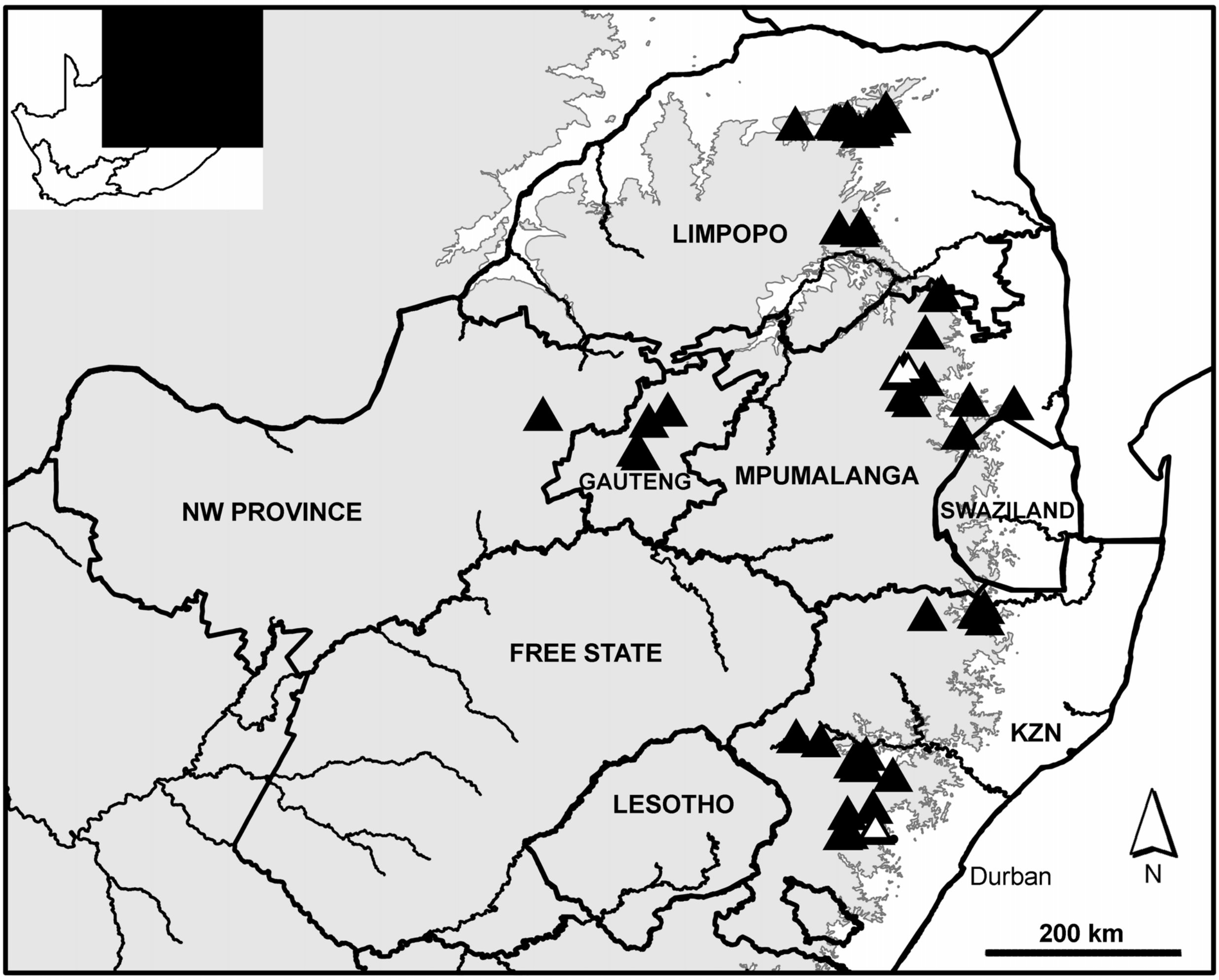

FIGURE 40. Distribution of *Natella viridescens* (Melvill & Ponsonby, 1891). Triangles with a white centre indicate localities for specimens used in DNA analyses (Moussalli & Herbert 2016); contour at 1000 m.

Biogeographic discussion

General remarks regarding the biogeography of the Rhytididae in southern Africa were provided in our earlier revision of the larger cannibal snails of the region (Herbert & Moussalli 2010) and need not be repeated. It must be noted, however, that observations therein concerning the Chlamydephoridae must now be subsumed within the Rhytididae as molecular data have since demonstrated that the former are simply a limaciform radiation of rhytidids (Herbert *et al*. 2015; Moussalli & Herbert 2016).

In many ways the distribution of the dwarf cannibal snail radiation closely matches that of the larger species and that of *Chlamydephorus*, in being mostly limited to the region south and east of the Great Escarpment (compare Figs 41A–C). This, however, is a common, rainfall-related distribution pattern exhibited by other land snail genera endemic to southern Africa that have primarily mesic habitat preferences (e.g. *Afrodonta*, *Chondrocyclus* and *Sheldonia*). Compared to their larger-shelled relatives, the overall range of the dwarf species is somewhat more extensive. In the west they range onto the Atlantic seaboard, reaching the St Helena Bay area and perhaps even Namaqualand. In the north-east, they reach the Soutpansberg (±23°S), on the southern side of the low-lying Limpopo Valley, a recognised biogeographic barrier (Stuckenberg 1962) and have only managed to cross this river in coastal Mozambique, reaching Inhambane (±24°S) (although records from Mozambique are few). The dwarf species also range further into the interior of southern Africa, reaching the Highveld of western Lesotho and neighbouring regions of the Free State and northern E. Cape, as well as Gauteng and the eastern part of N.W. Province. In contrast, the larger cannibal snail radiation does not reach the Atlantic seaboard, extends north only as far as the Drakensberg of Mpumalanga, and does not occur in the interior of the Highveld (Fig. 41A).

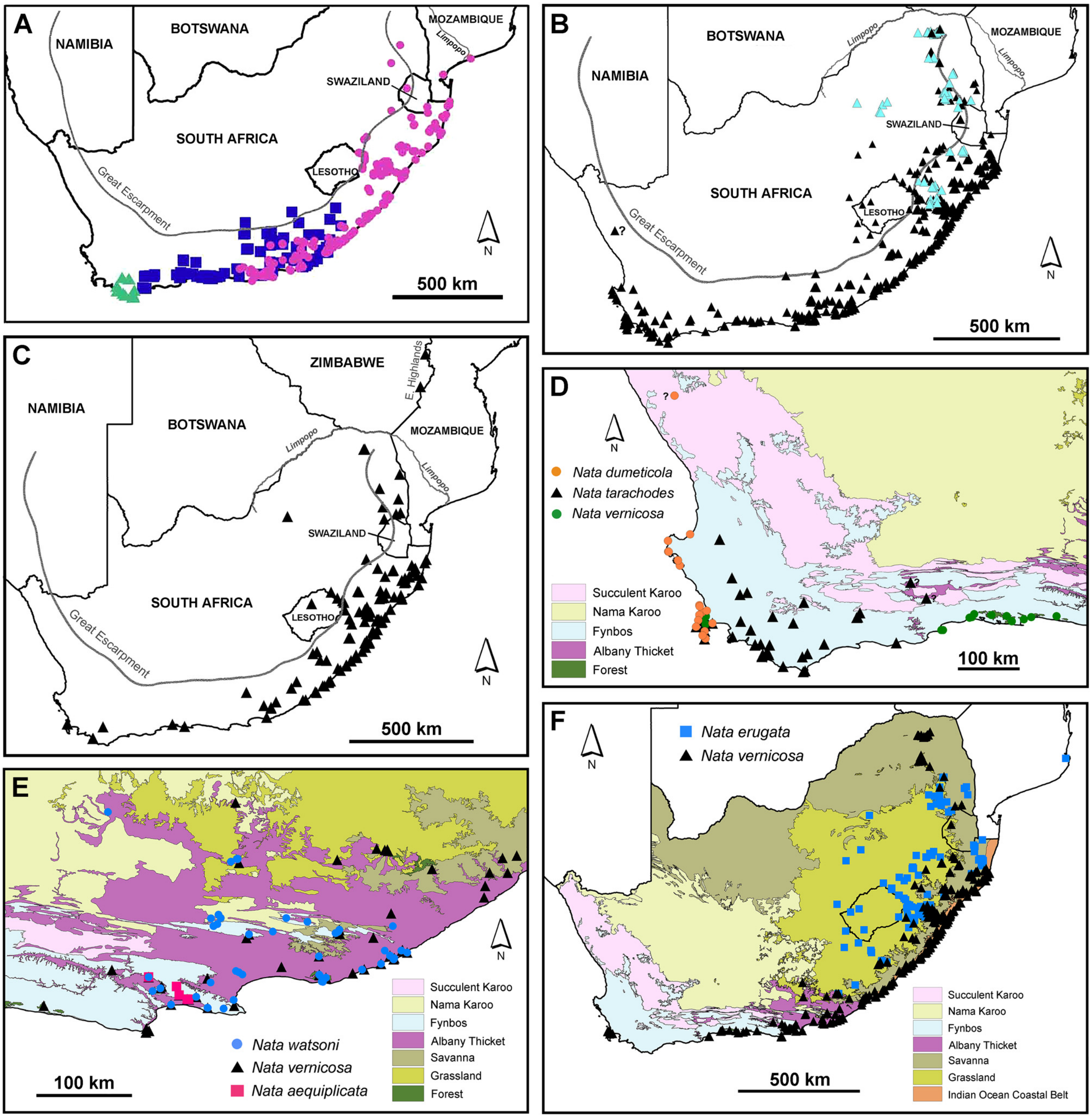

FIGURE 41. Maps showing the distribution southern African rhytidid taxa. **A,** *Natalina s.l.* (green triangles = *Capitina*; blue squares = *Afrorhytida*; pink circles = *Natalina s.s.*), from Herbert & Moussalli (2010). **B,** dwarf cannibal snails, *Nata s.l.* (black triangles = *Nata s.s.*; blue triangles = *Natella*). **C,** *Chlamydephorus* slugs. **D,** *Nata* spp. in W. Cape in relation to biomes. **E,** *Nata* spp. in E. Cape in relation to biomes. **F,** *Nata vernicosa* and *Nata erugata* **sp. nov.** in relation to biomes.

The western distribution limit of *Chlamydephorus* also extends to the Atlantic seaboard, but so far as is known, only to the Cape Peninsula. Like the dwarf cannibal snails, they also extend into the Highveld and to the Soutpansberg. In contrast to their cannibal snail relatives, however, species of *Chlamydephorus* range north into Zimbabwe, reaching the Vumba Mountains in the Eastern Highlands (Fig. 41C).

As stated in the introduction, molecular evidence indicates that the dwarf cannibal snail radiation may not be monophyletic and that *Natella* is a deeply divergent lineage occupying a basal position within the Rhytididae (Moussalli & Herbert 2016). It is now found only in the north-eastern parts of South Africa and is sympatric with species of *Nata* over much of its range (Fig. 41B). In contrast, *Nata s.s.* is a well-supported monophyletic entity and one that spans considerable evolutionary depth. Assuming an East–West Gondwana split calibration at the base of the Rhytididae, we estimated that early cladogenesis may have occurred as far back as the Late Cretaceous or Early Paleogene. Hence, despite the morphological conservatism observed within *Nata*, the genus comprises highly divergent lineages, with deep evolutionary history concordant with broad biogeographic subdivision. To the south-west, *N. tarachodes* is a species restricted to the Fynbos Biome (Fig. 41D), a distribution similar to that of the larger cannibal snail genus *Capitina* (Moussalli *et al*. 2009; Herbert & Moussalli 2010). In the south-western parts of E. Cape, the two previously undescribed species, *N. aequiplicata* **sp. nov.** and *N. watsoni* **sp. nov.** are associated with the Albany Thicket Biome (Mucina & Rutherford 2006). Although neither is confined to thicket habitats *per se*, their distributions, particularly that of *N. watsoni* **sp. nov.**, are conspicuously associated with the envelope of this biome (Fig. 41E). Comparison may be drawn here with the distribution of *Natalina cafra cafra* and two *Afrorhytida* species, *A. knysnaensis* (Pfeiffer, 1846) and *A. trimeni* (Melvill & Ponsonby, 1892) (Herbert & Moussalli 2010: figs 83, 84). *N. cafra cafra* and *A. knysnaensis* are ecologically tolerant species ranging widely within the Albany Thicket (cf. *Nata watsoni* **sp. nov.**), whereas *A. trimeni* is a forest-dependent species confined to the coastal hinterland of the biome (cf. *Nata aequiplicata* **sp. nov.**). This biome also includes the Albany Centre of plant endemism (Van Wyk & Smith 2001), suggesting that the evolutionary processes that underpin the floral characteristics of this region also result in these concordant patterns of land snail endemism.

Nata vernicosa s.l. was not further subdivided in our initial molecular analysis (Moussalli & Herbert 2016) due to limited sampling, but on morphological grounds, we have here split it into two species, both of which range widely over much of eastern South Africa. They are essentially parapatric (Fig. 41F) with *N. vernicosa s.s.* primarily occurring at altitudes of <1000 m and *N. erugata* **sp. nov.** at altitudes >1000 m, but in places there is clearly a zone of overlap at around 1000 m where the two co-occur. Such localities include the environs of Hogsback and Umthatha in E. Cape, the KwaZulu-Natal Midlands and the Mpumalanga Drakensberg. However, the situation is not entirely straight-forward and both species exhibit anomalies that run counter to the above pattern. In the case of *N. erugata* **sp. nov.** the populations in the northeast occur at very much lower altitudes in the coastal plain of Zululand and the Lowveld of Mpumalanga. Conversely, in *N. vernicosa* the populations in Limpopo and the Mpumalanga Drakensberg occur at unusually high altitudes, mostly over 1000 m, often considerably so. In neither of these instances have we been able to identify any clear conchological or anatomical differences that might serve to differentiate these populations as separate species. Nonetheless, such biogeographical anomalies are almost certainly not without significance and they point to the need for additional, finer-scale molecular studies to empirically test whether or not these species are in fact composite entities. In this regard it is pertinent to note that the distribution of *N. vernicosa* is broadly congruous with that of *Natalina* (Fig. 41A), yet within this range *Natalina* has diversified in to three distinct clades, two of which comprise several morphologically distinct species or subspecies. *Nata vernicosa* is clearly far more conservative morphologically, but Moussalli & Herbert (2016) have pointed to the considerable intraspecific genetic diversity evident in this taxon and this may signal as yet undiscovered cryptic diversity. Cryptic speciation has also been discovered in the velvet worm *Peripatopsis moseleyi*, once considered to be a single species widespread in the mesic south-eastern parts of South Africa (Daniels & Ruhberg 2010; Ruhberg & Daniels 2013) and seems to be a commonly occurring phenomenon in southern African Onychophora (Daniels *et al*. 2009).

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APPENDIX 1. *Nata dumeticola* (Benson, 1851).

Additional material examined (all NMSA, unless otherwise indicated): SOUTH AFRICA: N. CAPE: Namaqualand, Garies (30.55°S: 17.98°E), (SAMC A7719). W. CAPE: St Helena Bay area, Dwarskersbos (32.70027°S: 18.22233°E), coastal scrub, in leaf-litter, A. Moussalli & D. Stuart-Fox, 01/ii/2005 (Moussalli coll'n); north of Paternoster (32.8°S: 17.88°E), A. Moussalli & D. Stuart-Fox, 05/ii/2005 (W5971); Saldanha Bay area, Jacobsbaai (32.967°S: 17.883°E), Imke Cordes, Univ. Stellenbosch, 1994, don. W. Sirgel (V7760); Langebaan Lagoon area (33.1°S: 18.033°E), on sand next to lagoon, J.P. Marais, xi/1997 (V5741); Langebaan (33.10336°S: 18.0342°E), sparse coastal heath, in leaf-litter, A. Moussalli & D. Stuart-Fox, 05/ii/2005 (W3210 (living), W9569); West Coast Nat. Park (33.18364°S: 18.06377°E), 30 m, sparse coastal scrub, in leaf-litter, A. Moussalli & D. Stuart-Fox, 05/ii/2005 (W3224); ditto, in hollow trunk of dead shrub, A. Moussalli & D. Stuart-Fox, 05/ii/2005 (W9572); Robben Island (33.8167°S: 18.372°E), in scrubland around village, under log, D. Herbert, 30/v/2000 (V8258); Kommetjie (34.133°S: 18.317°E), M. Connolly, H.C. Burnup coll'n (2767); Cape Peninsula, W. Falcon, *ex* M. Connolly, pre-1956 (B7022); Buffels Bay, beach slopes (34.316°S: 18.463°E), 01/ii/1968, C. Connolly coll'n, don. 2009 (W7524); Cape Peninsula, M. Connolly (NHMUK 1937.12.30.1360–66); False Bay, Strandfontein dunes (34.0788°S: 18.5717°E), C. Connolly coll'n, don. 2009 (W7522).

Additional literature records (material not seen): SOUTH AFRICA: W. CAPE: Robben Island (33.80°S: 18.367°E), Fisk (Connolly 1912); Cape Town, Milnerton (33.883°S: 18.483°E) (Connolly 1912); Cape Town, Green Point (33.908°S: 18.408°E), W. Benson (Connolly 1912); Cape Town, Camps Bay (33.95°S: 18.367°E), E. Layard (Connolly 1912); Hout Bay (34.033°S: 18.35°E) (Connolly 1912); Kommetjie (34.133°S: 18.317°E) (Connolly 1912); Simonstown (34.2°S: 18.45°E), W. Benson (Connolly 1912).

APPENDIX 2. *Nata tarachodes* (Connolly, 1912)

Additional material examined (all NMSA, unless otherwise indicated): SOUTH AFRICA: W. CAPE: CAPE PENINSULA: 'Cape Peninsula', W. Falcon, *ex* M. Connolly, H.C. Burnup coll'n (W5498); Kirstenbosch, Nursery Ravine (33.983°S: 18.425°E), indigenous forest, amongst litter lying on rocks, D. Herbert, 13/ii/2000 (V7814); Kirstenbosch (33.98422°S: 18.424556°E), 330 m, afrotemperate forest, in leaf-litter, C. Uys, 12/ix/2008 (W7092); Table Mountain, Orangekloof (33.98948°S: 18.38934°E), indigenous forest beside stream on western side of catchment, under logs, D. Herbert & L. Davis, 01/x/2007 (W5957); ditto (33.99302°S: 18.40327°E), riverine fynbos beside 'original *Disa* stream', in leaf-litter, D. Herbert & L. Davis, 01/x/2007 (W5715); ditto (34.00342°S: 18.3905°E), 130 m, afrotemperate forest, sugar-baited ant trap, C. Uys, 28/i/2009 (W7171); ditto, Cecilia plantation, Rooikat Ravine (33.99382°S: 18.41989°E), afrotemperate forest, in decayed logs and leaf-litter, C. Uys, 23/v/2008 (W6436); Tokai north (34.038056°S: 18.39558°E), 370 m, afrotemperate forest, in leaf-litter, C. Uys, 21/xi/2008 (W7088); St James, Spes Bona Bush (34.1165°S: 18.442°E), in leaf-litter, A. Moussalli, 16/ix/2004 (W2471, W3111); ditto (34.11653°S: 18.44418°E), forested gully (indigenous), in leaf-litter, D. Herbert, 31/xii/2001 (V9848); Kalk Bay

Mountain [top] F. Purcell (SAMC 8299); Kommetjie (34.133°S: 18.317°E), M. Connolly, H.C. Burnup coll'n (2770); Simonstown (34.2°S: 18.45°E), M. Connolly, H.C. Burnup coll'n (2769). Swartland – Haweqwas – Hottentots Holland – Overberge: Piketberg mountains (32.77803°S: 18.68302°E), 450 m, S. Daniels, 14/vi/2006 (P0029); Bainskloof Pass (33.601154°S: 19.11035°E), 560 m, montane fynbos, under vegetation and rocks beside rock outcrops, D. Herbert, L. Davis & M. Cole, Toyota Enviro Outreach, 20/iv/2012 (W8888); Hottentots Holland Nat. Res., Landroskop (34.04929°S: 19.01029°E), 1060 m, fynbos, in vegetation beside rock outcrops near cottage, D. Herbert & L. Davis, 04/x/2007 (W5686); Hermanus (34.417°S: 19.233°E), M. Picker, 20/vi/2006 (W4873); ditto, hills behind town, scenic drive (34.40843°S: 19.23420°E), fynbos, in vegetation beside rock outcrops, D. Herbert & L. Davis, 06/x/2007 (W5688); Vogelgat Nat. Res. (34.40085°S: 19.3219°E), afrotemperate forest, under rocks in creek line, A. Moussalli & D. Stuart-Fox, 13/ii/2005 (W5404); Stanford, hills behind Weltevrede farm (34.417°S: 19.46°E), beside rocks in fynbos, D. Herbert & L. Davis, 06/x/2007 (W5678). Agulhas Plain: Grootbos Private Nat. Res. (34.54063°S: 19.41318°E), milkwood forest, in leaf-litter and under logs, A. Moussalli & D. Stuart-Fox, 13/ii/2005 (W5982); ditto (34.54135°S: 19.43871°E), afrotemperate forest, in leaf-litter and under logs, D. Herbert & L. Davis, 08/x/2007 (W5916); ditto (34.54165°S: 19.41356°E), 200 m, afrotemperate forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 13/ii/2005 (W3200); ditto (34.54205°S: 19.41529°E), milkwood forest, in leaf-litter, D. Herbert & L. Davis, 07/x/2007 (W5658); Gansbaai area, Platbos Nat. Res. (34.56654°S: 19.44933°E), 110 m, *Celtis* forest, under logs and in leaf-litter, D. Herbert, L. Davis & M. Cole, Toyota Enviro Outreach, 18/iv/2012 (W8977 [DNA barcode voucher, HVDB_T_026-028], W8846); ditto (34.56770°S: 19.44474°E), 150 m forest-fynbos margin, in leaf-litter under shrubs, D. Herbert, L. Davis & M. Cole, Toyota Enviro Outreach, 18/iv/2012 (W8853); Gansbaai (34.57946°S: 19.34421°E), coastal dune scrub, in sandy leaf-litter under vegetation, A. Moussalli & D. Stuart-Fox, 13/ii/2005 (W3541, W6947); ditto (34.59393°S: 19.34007°E), 33 m coastal scrub, in sandy leaf-litter under shrubs and prostrate plants, D. Herbert, L. Davis & M. Cole, Toyota Enviro Outreach, 18/iv/2012 (W8807); Die Dam region (34.74874°S: 19.67084°E), coastal fynbos, in sandy soil, A. Moussalli & D. Stuart-Fox, 14/ii/2005 (W5482); Cape Agulhas Nat. Res. (34.813°S: 20.012°E), limestone fynbos, D. Herbert, 10/ii/2000 (V7842); Cape Agulhas (34.82935°S: 19.98548°E), coastal dune scrub, buried deep in sand, A. Moussalli & D. Stuart-Fox, 14/ii/2005 (W4740 (living), W9561); Bredasdorp (34.55°S: 20.05°E), dry bush on hillside, J. Rennie, *ex* Albany Mus. 1980 (E7915). Riviersonderendberge – Langeberge: Riviersonderendberge, Jonaskop (33.97256°S: 19.50883°E), 1500 m, near summit, 23/viii/1997, don. W. Sirgel, 29/vii/2012 (W9118); Riviersonderendberge, Oubos (Oudebosch) (34.07702°S: 19.82884°E), afrotemperate forest, in leaf-litter and under logs, D. Herbert & L. Davis, 11/x/2007 (W5671); Robertson area, Pat Busch Nat. Res., Karin Trail (33.75513°S: 19.99471°E), 450 m, riverine fynbos, in leaf-litter beneath bushes, D. Herbert & L. Davis, 10/x/2007 (W5769); Grootvadersbosch Nat. Res. (33.98994°S: 20.816575°E), afrotemperate forest, in leaf-litter and under logs, D. Herbert & L. Davis, 13/x/2007 (W5897); Langeberge, Lemoens Hoek Mts [Grootberg] (33.917°S: 20.867°E), Connolly, 1939 (SAMC A7245).

Additional literature records (material not seen): W. CAPE: Riebeek-Kasteel Mts (33.375°S: 18.875°E), 850 m (Connolly 1939); Wellington Mts (33.633°S: 19.00°E), 430 m, K.H. Barnard (Connolly 1939); Hout Bay, Skoorsteenkop (34.033°S: 18.367°E), indigenous forest, Lund University Expedition, 28/i/1951 (Bruggen 1970a); Cape Point Nat. Res., sieved from wet leaves, common, Lund University Expedition, 10/xii/1950 (Bruggen 1970a); Kogelberg Nat. Res. (34.28719°S: 18.88291°E), 305 m, feeding on a much larger *Trachycystis* sp., 19/x/1985 (Sirgel in lit. 2012); Houw Hoek [Houhoek] (34.183°S: 19.167°E), M. Connolly (Connolly 1939); Bredasdorp, 7 miles SW of (34.6°S: 19.97°E), Lund University Expedition, 30/xii/1950 (Bruggen 1970a).

Dubious records: LESOTHO: Masite (29.567°S: 27.4°E), J. Hewitt (Connolly 1939). SOUTH AFRICA: E. Cape: Katberg, north of Fort Beaufort (32.533°S: 26.683°E), F. Cruden (Connolly 1939); Port Alfred area, Kasouga (33.6489°S: 26.745°E), J. Hewitt (Connolly 1939).

APPENDIX 3. *Nata vernicosa* (Krauss, 1848)

Selected locality data for material examined (from over 400 samples, all NMSA, unless otherwise indicated): SWAZILAND: Mbabane (26.317°S: 31.133°E), 915 m, in ravine on mountain slopes, R.F. Lawrence, 1964 (V5202). SOUTH AFRICA: LIMPOPO: Soutpansberg: Goedehoop Forest (23.0833°S: 30.1117°E), 950 m, indigenous forest, under logs, D. Herbert, xi/1997 (V5564); Ratombo Forest (23.067°S: 30.167°E), indigenous forest, J. Swaye, iii/2001 (V9490); Roodewal Forest Nat. Res. (23.025°S: 30.033°E), in leaf-litter, C. Symes, 10/x/2000 (V8711); Clouds End Hotel (23.007°S: 29.9283°E), 1100 m, mixed bush/woodland, in leaf-litter, D. Herbert, xi/1997 (V5531); Hanglip Forest (23.00002°S: 29.88789°E), 1360 m, mist-belt forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 16/xii/2006 (W5638); ditto (22.99951°S: 29.88643°E), northern mist-belt forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, 29/xi/2014 (P0208); Entabeni Forest (22.983°S: 30.250°E), 1100–1150 m, A.C. & W.H. van Bruggen, 1965 (A7129); Thathe Vondho Forest (22.876°S: 30.349°E), 1430 m, indigenous forest, in leaf-litter, C. Symes, 04/xi/1999 (V7616). Wolkberg: Forest Glens (23.97330°S: 29.91682°E), indigenous forest, J. Swaye, iii/2001 (W91); New Agatha Forest (23.96213°S: 30.11664°E), indigenous forest, J. Swaye, iii/2001 (W86); Baccarat Forest (23.88680°S: 30.01633°E), 1485 m, northern mist-belt forest, D. Herbert, L. Davis & M. Cole, 26/xi/2014 (P0155); Swartbos Forest (23.88190°S: 29.994113°E), 1430 m, northern mist-belt forest, D. Herbert, L. Davis & M. Cole, 26/xi/2014 (P0158); Woodbush Forest (23.83713°S: 29.99088°E), 1550 m, northern mist-belt forest, D. Herbert, L. Davis & M. Cole, 26/xi/2014 (P0166); Grootbosch Forest (23.84462°S: 29.99949°E), indigenous forest, J. Swaye, iii/2001 (V9491); Magoebaskloof, vicinity of forestry station (23.80734°S: 29.98374°E), mist-belt forest, in leaf-litter, A. Moussalli & D. Stuart-

Fox, 27/ii/2004 (W3337); De Hoek Forest Res. (23.82°S: 30.05°E), indigenous forest, B. Stuckenberg & J. Londt, 17/ix/1986 (V5273). Northern Drakensberg: Lekgalameetse Nat. Res. (24.1600°S: 30.3367°E), 900 m, under logs and stones in thick mixed bushveld, D. Herbert, xi/1997 (V5544). MPUMALANGA: Mariepskop Forest Res., NE Nat. Res. (24.533°S: 30.867°E), 1170 m, A.C. & W.H. van Bruggen, 1966 (A7093); Mount Sheba Nat. Res.(24.93122°S: 30.70965°E), 1760 m (estimate), afrotemperate forest, under log, A. Moussalli & D. Stuart-Fox, 25/ii/2004 (W3344); Malelane area, 10 km South, Sherlock farm, 'isolated forest' (25.590117°S: 31.525867°E), 740 m, indigenous forest, in leaf-litter, J. Horn, 26/i/2006 (W3908); Louw's Creek, near Barberton (25.63°S: 31.28°E), C.P.F. van Dam, 15/iii/1920 (V4975). KWAZULU-NATAL: Zululand: Ithala Game Res. (27.58316°S: 31.26463°E), 1433 m, northern mist-belt grassland, under rock amongst low shrubs, A. Armstrong *et al*., 04/xi/2002 (W1981); Ithala Game Res., Serendipity (27.5042°S: 31.1850°E), 580 m, riverine bushveld, in crevice on tree trunk at 1m, D. Herbert, iii/1996 (V2900); Vryheid Nat. Res. (27.753°S: 30.788°E), 1250 m, woodland/forest on slopes of mountain, in leaf-litter, D. Herbert, 02/xii/1999 (V7606); Ngome Forest (27.8370°S: 31.3917°E), 1200 m, mist-belt *Podocarpus* forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 02/xii/1998 (V8549); Gluckstadt area, Inhlanhla Ranch (28.09764°S: 31.08936°E), 1110 m, mixed broad-leafed and *Acacia* thicket with aloes, in leaf-litter and under fallen aloes, D. Herbert & L. Davis, 25/xi/2004 (W2491); Nkandla Forest (28.7421°S: 31.15151°E), mist-belt *Podocarpus* forest, A. Armstrong & P. Ngwenya, 10/iv/2001 (V9141); Nkandla Forest (28.72239°S: 31.12373°E), mist-belt forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 3/i/2004 (W4957); Entumeni Nat. Res. (28.88836°S: 31.38007°E), mist-belt forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 24/xii/2003 (W3316); St Lucia, Nibela Peninsula, SE point (27.95°S: 32.43°E), in leaf-litter on rocky slope, R.H. Taylor & S. McLean, 04/ix/1987 (E2150); Greater St Lucia Wetland Park, Charters Creek (28.20998°S: 32.41525°E), under dead wood on forest floor, A. Armstrong, B. Kasseepursad & P. Ngwenya, 07/iii/2001 (V8966); Cape Vidal, ~5km south near bird hide (28.25844°S: 32.48196°E), coastal dune forest, under small log, A. Moussalli & D. Stuart-Fox, 23/v/2003 (W3319); Cape Vidal, Bhangazi Hill (28.130°S: 32.547°E), 60–80 m, dune forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 27/xi/1998 (V7940); Dukuduku Forest (28.3670°S: 32.2917°E), 30 m, coastal lowland forest, in leaf-litter, D. Herbert, 01/i/1996 (V2182); Maphelane (28.4050°S: 32.4217°E), 0–60 m, dune forest, in leaf-litter, D. Herbert, 30/xii/1995 (V2271); Enseleni Nat. Res. (28.6917°S: 32.0070°E), under logs, P. Reavell, 1976 (V3883); Hluhluwe Game Res. (28.077°S: 32.045°E), 460 m, scarp forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 29/xi/1998 (V7680); Hluhluwe Game Res. (28.04°S: 32.10°E), 170 m, forest patches in bushveld, D. Herbert, 02/01/1996 (V2359); Hlabisa (28.145°S: 31.882°E), *ca* 540 m, H.C. Burnup, 1908 (A7106); uMfolozi Game Res. (28.2623667°S: 31.8231546°E), 120 m, woodland, A. Armstrong, C. Beattie & G. Peavey, 18/ii/2008 (W7303); uMfolozi Game Res., Mbhuzane Field Station (28.22278°S: 31.79535°E), open mixed woodland, in litter at base of trees and shrubs, D. Herbert, 08/v/2000 (V8176); Qudeni Forest (28.64882°S: 30.90391°E), mist-belt forest, dormant under log, A. Moussalli & D. Stuart-Fox, 21/v/2003 (W3313); Mfongosi (28.713 30.805°E), W.E. Jones (B0047); Empangeni (28.74°S: 31.89°E), in garden, P. Reavell, 1991 (S3450); Richards Bay (28.80778°S: 32.06528°E), disturbed coastal forest, O. Bourquin, 29/x/2000 (V8690); Eshowe (28.885°S: 31.468°E), 500 m, amongst garden debris, R. Miller, 01/iv/1996 (V2908); Nkwalini, near Eshowe (28.733°S: 31.567°E), forest, T. Murray, 1995 (V1915); Ngoye Forest (28.84170°S: 31.68700°E), mist-belt forest, on large logs, A. Moussalli & D. Stuart-Fox, 22/xii/2003 (W3321); Mtunzini, Twin Streams (28.9816°S: 31.74053°E), disturbed dune forest, in leaf-litter, UND field course, ix/2002 (W240). North Coast: Thukela Mouth, Harold Johnson Nat. Res. (29.2117°S: 31.4250°E), coastal mosaic, mixed woodland and thicket, in leaf-litter, D. Herbert, 18/xii/1996 (V4064); Blythedale Beach (29.34758°S: 31.36023°E), 2 m, under decaying log on forest floor, A. Armstrong & A. Gomez, 01/xi/2012 (W9754); Zimbali resort area, near Tongaat River mouth (29.55077°S: 31.20530°E), 20 m, coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 13/xi/2006 (W4711); La Mercy, proposed site for new airport (29.62849°S: 31.11202°E), *Ficus* thicket around old buildings in cane field, infested with *Chromolaena*, in leaf-litter, D. Herbert, 06/xii/2006 (W4905); Umdloti Beach (29.645°S: 31.100°E), W.G. Rump, 1924 (A7078); Inanda Mountain (29.64625°S: 30.84335°E), 474 m, tall forest, dense *Isoglossa* under-storey, moist, in leaf-litter, H. Payne, 10/iii/2012 (W8831); Umhlanga Lagoon Nat Res. (29.7083°S: 31.0950°E), coastal bush, in leaf-litter, D. Herbert & L. Davis, 04/xii/1995 (V2131); Hawaan Forest (29.7117°S: 31.0883°E), 60 m, coastal lowland forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, 12/x/1998 (V8105); La Lucia, north of Durban (29.750°S: 31.067°E), coastal forest, found among dead foliage, xi/1979 (D2112). Midlands and interior: Karkloof Falls, indigenous forest on east side of valley, near top of gorge (29.40882°S: 30.28404°E), 1000 m, mist-belt *Podocarpus* forest, in leaf-litter, M. Cole, L. Davis & D. Herbert, 22/i/2010 (W7150); Karkloof, Leopard's Bush (29.315°S: 30.250°E), mist-belt *Podocarpus* forest, R. Miller and students, 23/iii/2002 (W6679); Balgowan area, Kingdom Weavers (29.383°S: 30.100°E), 1400 m, small patch of mist-belt *Podocarpus* forest, in leaf-litter, Dept of Mollusca, 09/vii/1999 (V7234); Underberg area, Drakensberg Gardens road, Pennygum Cottages (29.7614°S: 29.45558°E), 1550 m, rural garden, under bedding plants and around tree trunks, D. Herbert, 16/vi/2003 (W892); Ladysmith (28.555°S: 29.782°E), H.C. Burnup, pre-1930 (1493); Ladysmith area, Gannahoek farm (28.667°S: 30.021°E), 780 m, shaded edge of stream at base of steep slope, under stones, O. Bourquin, 22/xi/1999 (V7540); Dundee area, Mooidoorn Hoek (27.98153°S: 30.19340°E), 1315 m, slope with numerous small *Acacia* trees and bush clumps, on melanic soil with calcrete granules, D. Herbert, xi/2013 (W9590); Kranskop, Ntunjambili (28.950°S: 30.967°E), 900 m, mist-belt *Podocarpus* forest, in leaf-litter, D. Herbert, viii/1997 (V5013). Pietermaritzburg area: Howick, Umgeni River Nat. Res. (29.4930°S: 30.2483°E), *ca* 850 m, woodland in valley bushveld, in leaf-litter, D. Herbert, i/1998 (V6282); Pietermaritzburg area, Otto's Bluff (29.508°S: 30.358°E), (A7134); Pietermaritzburg area, Umgeni River Valley above Table Mountain, 'Cumberland' conservancy (29.51338°S: 30.51464°E), forested kloof, in leaf-litter, D. Herbert & L. Davis, 17/iv/2004 (W1783); Hilton Vlei area (29.54342°S: 30.29033°E), 1100 m, mixed age re-growth *Eucalyptus* plantation, in leaf-litter and under logs, D. Herbert & L. Davis, 20/ix/2009 (W7073); Hilton, Celtis Rd (29.555°S: 30.297°E), mist-belt *Podocarpus* forest, in leaf-litter, D. Herbert, R. Kilburn & L. Davis, 08/xi/1995 (V2364); Pietermaritzburg, Winterskloof (29.583°S: 30.305°E), M. Arbuckle, 1995 (V825); Pietermaritzburg, World's View area (29.58°S: 30.33°E), *Eucalyptus* plantation, under log, D. Herbert & L. Davis, 27/xi/2005 (W3754); Pietermaritzburg, Town Bush (29.565°S: 30.345°E), mist-belt *Podocarpus* forest, A.C. van Bruggen, 07/x/1965

(W3910); Pietermaritzburg, 42 Hosking Road (29.5891°S: 30.3539°E), suburban garden, under pot plants, D. Herbert & L. Davis, 13/xi/2005 (W3656); Pietermaritzburg, Botanical Gardens (29.606°S: 30.347°E), (A7075); Pietermaritzburg, Alexandra Park (29.612°S: 30.383°E), W.G. Rump, 1926 (A7066); Pietermaritzburg, Scottsville (29.6230°S: 30.3967°E), suburban garden of 17, Oribi Rd, D. Herbert, 1989 (V4017); Pietermaritzburg, Bisley Valley Nat. Res. (29.6670°S: 30.3967°E), 730–830 m, mixed thorny bushveld, under logs and in leaf-litter, L. Davis & D. Herbert, ii/1996 (V2538); Pietermaritzburg, Ashburton (29.670°S: 30.453°E), 670 m, in thornveld garden, R. Miller, x/1997 (V5418); Mid-Ilovo area, Gwahumbe Res. (29.96218°S: 30.55602°E), riverine woodland, in *Clivia* patch, in leaf-litter, D. Herbert & L. Davis, 29/iv/2007 (W5499); Mid-Illovo, Ntimbankulu (29.930°S: 30.467°E), (B0052); Baynesfield, near Maybole farm (29.750°S: 30.267°E), mist-belt *Podocarpus* forest, O. Bourquin, 1964 (V5206). Durban area: Durban, Burman Bush (29.815°S: 31.017°E), coastal lowland forest, on under-storey vegetation, D. Herbert, i/1998 (V5811); Durban, Pigeon Valley Nat. Res. (29.86403°S: 30.98506°E), coastal forest, in leaf-litter A. Moussalli & D. Stuart-Fox, 25/ii/2006 (W4358); Durban Bluff, Treasure Beach Nat. Res. (29.945283°S: 30.998242°E), forest, J. Harvey, iv/2013 (W9322); Kenneth Stainbank Nat. Res. (29.91387°S: 30.93273°E), coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 10/xii/2003 (W3318); Durban area, North Park Nat. Res. (29.87618°S: 30.88000°E), coastal lowland forest, under dead wood on forest floor, A. Armstrong & P. Ngwenya, 23/ii/2001 (V8843); Palmiet Nat. Res. (29.8217°S: 30.9300°E) 180 m, moist riverine woodland, in leaf-litter and under logs, D. Herbert, i/1988 (V5787); Pinetown (29.820°S: 30.892°E), H.C. Burnup, pre-1930 (E7927); Shongweni Resource Res. (29.855°S: 30.730°E), 400 m, thick valley bushveld and woodland, in leaf-litter, Dept Mollusca, i/1997 (V4076); Hillcrest, Clifton Canyon (29.808°S: 30.760°E), 600 m, scarp forest, in leaf-litter, D. Herbert, R. Kilburn & L. Davis, 24/i/1996 (V2492); Krantzkloof Nat. Res. (29.7717°S: 30.8350°E), *ca* 360 m scarp forest, in leaf-litter, D. Herbert, M. Seddon & P. Tattersfield, st'n 1, 24/xi/1998 (V8452); Winston Park, vicinity of Mhlatuzana River (29.82812°S: 30.78215°E), riparian scarp forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 14/v/2005 (W4372). Southern interior: Hlabeni Forest (29.975°S: 29.742°E), 1350 m, mist-belt *Podocarpus* forest, in leaf-litter, C. Symes, vii/1997 (V4861); Kokstad area, near Crystal Spring, north of Mt Currie Nat. Res. (30.47855°S: 29.37968°E), patch of mist-belt forest in ravine, dominated by *Olinia emarginata*, in leaf-litter, D. Herbert, 03/v/2000 (V8182); Ngele Forest (30.525°S: 29.692°E), 1300 m, mist-belt *Podocarpus* forest, in leaf-litter, L. Davis & D. Herbert, 11/1995 (V2077); Harding, Redlands farm (30.583°S: 29.833°E), under log in grassland, O. Bourquin, ii/1963 (V5203). South Coast: Isipingo (30.003°S: 30.942°E), coastal bush, L. Davis & D. Herbert, 14/iii/1995 (V2046); Umbongintwini, Umbogavango Nat. Res. (30.03155°S: 30.89476°E), 50 m, degraded coastal lowland forest, in leaf-litter, L. Davis & D. Herbert, st'n 08-062, 08/xii/2008 (W6621); Umkomaas, Empisini Nat. Res. (30.20162°S: 30.78923°E), 10 m, coastal lowland forest, in leaf-litter, D. Herbert, L. Davis, D. Stuart-Fox & A. Moussalli, 18/vi/2006 (W4399); Vernon Crookes Nat. Res. (30.272834°S: 30.605200°E), 410 m, scarp forest, leaf-litter, D. Herbert, M. Cole, R. Daniels & L. Davis, st'n 11-14, 15/iv/2011 (W8020); Umzinto, Nkwifa [Equeefa] (30.325°S: 30.600°E),(B0018); Kelso Junction, beside station (30.362366°S: 30.713246°E), 20 m, degraded coastal bush, in leaf-litter, D. Herbert, L. Davis, M. Cole & R. Daniels, st'n 11-16, 15/iv/2011 (W7940); Pennington (30.383°S: 30.697°E), dune forest leaf-litter, R. Miller, 1996 (V3947); Ifafa (30.458°S: 30.653°E), W.G. Rump, 1931 (B88); Hibberdene (30.575°S: 30.575°E), dune bush, M. Hamer, 1996 (V3283); Umzumbe area, Highbury farm (30.610732°S: 30.507487°E), 110 m, coastal forest patch in cane and banana plantations, in leaf-litter, D. Herbert, L. Davis, M. Cole & D. Kinsler, st'n 12-02, 09/i/2012 (W9037); Port Shepstone area, Natal Portland Cement Nat. Res.(30.6743°S: 30.3383°E), riverine woodland, not on limestone, in leaf-litter, D. Herbert *et al*., 06/xii/2001 (W9989); Port Shepstone area, Marble Delta, north side Mzimkulwana River, base of Simuma Hill (30.6728°S: 30.3427°E), dense riverine thicket/woodland, heavily invaded with *Lantana* and *Chromolaena*, in leaf-litter, D. Herbert *et al*. 04/xi/2001 (W9850); Port Shepstone (30.742°S: 30.453°E), H.C. Burnup, 1908 (A7109); Oribi Gorge Nat. Res., Hoopoe Falls trail (30.70765°S: 30.26992°E), scarp forest, in leaf-litter, D. Herbert, 06/x/2001 (V9433); Ramsgate, Mvutshini Valley (30.891592°S: 30.345197°E), 31 m, valley forest, A. Armstrong (E W 323493), 25/xi/2003 (W7216); Trafalgar area, Mpenjati Nat. Res., Yengele Trail (30.9691°S: 30.28197°E), dune forest, in leaf-litter, D. Herbert, 28/xii/2002 (W388); Umtamvuna Gorge Nat. Res., Loerie Trail (31.056297°S: 30.168879°E), 40 m, riverine scarp forest, in leaf-litter D. Herbert, M. Cole, R. Daniels & L. Davis, st'n 11-08, 13/iv/2011 (W7901). E. CAPE: Transkei: Mtentu River mouth, forest at foot of cliffs along north side of estuary (31.23800°S: 30.03057°E), 10–20 m, coastal forest, in leaf-litter, D. Herbert, 25/vii/1999 (V7253); Mkambati Nat. Res., 'Super Bowl' forest at junction of Msikaba and KwaDlambu Rivers (31.2955°S: 29.9292°E), 200 m, indigenous forest, in leaf-litter, D. Herbert, 05/iii/2001 (V8959); 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 (W590); Mbotyi Forest (31.43107°S: 29.72656°E), 305 m, indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 3/xi/2005 (W4119); Manteku area (31.52037°S: 29.67262°E), coastal scarp forest, in leaf-litter, D. Herbert & M. Bursey, 30/iv/2004 (W1865); Mntafufu, southern side of river (31.5618°S: 29.62883°E), coastal forest, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 23/iv/2005 (W3001); Umthatha area, Nqadu Forest (31.417°S: 28.767°E), 1250 m, afromontane forest, in leaf-litter, C. Symes, 26/iv/1998 (V6884); Langeni area, Nocu Forest (31.41547°S: 28.49983°E), *ca* 1190 m, large block of indigenous forest, in leaf-litter, D. Herbert & L. Davis, 18/ii/2006 (W3924); Langeni area, Baziya Forest (31.5208°S: 28.4123°E), large block of indigenous forest, in leaf-litter, D. Herbert & L. Davis, 19/ii/2006 (W3960); Port St Johns area, crater-like travertine deposit on southern side of Umzimvubu River valley (31.52053°S: 29.45662°E), valley thicket, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 22/iv/2005 (W2924); Port St Johns, Isinuka sulphur springs and travertine deposit (31.60953°S: 29.47989°E), woodland/forest, in leaf-litter, D. Herbert, 04/iii/2003 (W537); Port St Johns, 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 (W3033); Port St Johns, Second Beach (31.6417°S: 29.5170°E), coastal forest, under log, D. Herbert, vi/1996 (V3642); Port St Johns, Silaka Nat. Res. (31.65130°S: 29.50918°E), coastal forest, in leaf-litter, D. Herbert, 05/iii/2003 (W565); Nothinsila, *ca* 20 km NW of Hluleka (31.74733°S: 29.20008°E), indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 14/xi/2005 (W5458); Mpande, coastal forest north of Sinangwana River (31.74738°S: 29.37078°E), 27 m, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 21/iv/2005 (W2856); Hluleka Nat. Res. (31.82333°S: 29.30550°E), coastal forest, in leaf-litter,

D. Herbert, L. Davis & M. Bursey, 20/iv/2005 (W3046); Xora, Kumqolo Forest, small patch of coastal forest on west bank of river (32.159°S: 28.985°E), 50 m, in leaf-litter, M. Bursey, 14/ix/2005 (W5394); Haven Nat. Res., vicinity of camp ground (32.24435°S: 28.90600°E), 15 m, coastal dune forest, at base of *Dracaena*, A. Moussalli & D. Stuart-Fox, 16/xi/2005 (W4151); Dwesa Nat. Res. (32.304°S: 28.828°E), coastal forest, in leaf-litter, D. Herbert, 05/iii/2000 (V7884); 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 (W4015); Mazeppa Bay area, Manubi Forest (32.44433°S: 28.59837°E), coastal forest, in leaf-litter, D. Herbert & L. Davis, 22/ii/2006 (W3991); Kentani (32.5°S: 28.3°E), under dry leaves, B. Smailes, xi/1969 (V7290). SOUTH COAST: Kei Mouth area, Morgan Bay, northern side of Inchara River (32.70667°S: 28.35333°E), coastal bush, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 03/iii/2007 (W5172); Kei Mouth area, 'Ocean View' [Mpetu Hill] (32.64898°S: 28.09741°E), forest, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 03/iii/2007 (W5216); Gonubie River Crossing, ~25km NW of East London (32.79805°S: 27.85776°E), 262 m, wet valley thicket, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Bursey, 29/xi/2005 (W4187); East London area, Phumalanga farm (32.80°S: 28.02°E), M.J. Wigley, 10/viii/2005 (W3544); East London, Umtiza Nat. Res. (33.01600°S: 27.80900°E), 70 m, coastal indigenous forest, under log, A. Moussalli & D. Stuart-Fox, 26/xi/2005 (W4181); Kap River Nat. Res. (33.47921°S: 27.08996°E), 25 m, riverine forest, D. Herbert & L. Davis, 22/xi/2012 (W9130); Great Fish Point area, Tharfield farm, east bank of Riet River, approx. 6 km upstream of mouth (33.527217°S: 26.97917°E), riverine forest, on rotten log, M. Bursey, 30/i/2008 (W5995); Kleinmonde (33.55927°S: 27.01146°E), coastal dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox & M. Bursey, 09/xii/2005 (W5436); Port Alfred (33.6°S: 26.9°E), R.H. Ivy (W7174); Essendene (33.62635°S: 26.02207°E), 205 m, thicket near limestone quarry, D. Herbert & L. Davis, 20/xi/2012 (W9143): Kasouga (33.64759°S: 26.75219°E), 20 m, coast dune forest, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Bursey, 10/xii/2005 (W4214); Alexandria Forest, around Bailey's Kop (33.69520°S: 26.35468°E) 350 m, indigenous forest, D. Herbert & L. Davis, 20/xi/2012 (W9174); Port Elizabeth area, Island Forest Res. (33.98668°S: 25.37151°E), low coastal forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, 18/ix/2008 (W6404); Van Stadens Wild Flower Res. (33.91200°S: 25.20507°E), 175 m, gorge forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, 22/ix/2008 (W6484); Lady's Slipper Res., Kouga grassy sandstone fynbos (33.889010°S: 25.270470°E), amongst rocky outcrops after fire, A. Moussalli & D. Stuart-Fox, xii/2005 (W6479); Gamtoos River mouth (33.95760°S: 25.04755°E), 35 m, dune forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, 28/ix/2011(W8451); Cape St Francis, Irma Booysen Res. (34.20200°S: 24.82758°E), 25 m, dune fynbos, under shrubs, D. Herbert, L. Davis, M. Cole & R. Cowling, 20/ix/2008 (W6569); Tsitsikamma Forest, near Paul Sauer Bridge (Storms River) (33.9682°S: 23.92634°E), sorted from leaf-litter, D. Herbert, iv/1997 (V4743); Nature's Valley, Salt River area (33.9833°S: 23.5330°E), under log in indigenous forest, D. Herbert, 19/ix/2003 (W986). INTERIOR: Hogsback, environs 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 (V9901); Hogsback (32.58711°S: 26.86171°E), 1506 m, grassland, under rock, A. Moussalli, D. Stuart-Fox & M. Bursey, 1/xii/2005 (W4197); Fort Beaufort area, Fort Fordyce (32.68694°S: 26.514444°E), 950 m indigenous forest, M. & K. Cole, 29/xii/2008 (W6704); Grahamstown, Longford Grange (33.5333°S: 26.3525°E), J. Hewitt, ix/1935 (W3474); Grahamstown, Mountain Drive (33.325°S: 26.517°E), J. Farquhar (A7090); Grahamstown, Botanical Gardens (33.31728°S: 26.52250°E), 576 m, indigenous forest gardens, in leaf-litter, A. Moussalli & D. Stuart-Fox, 3/xii/2005 (W4198); Zuurberg, Addo Elephant Park, Camp Fig Tree (33.37163°S: 25.71389°E); 260 m, indigenous forest/valley thicket, under log, A. Moussalli & D. Stuart-Fox, 12/xii/2005 (W4221); Zuurberg (33.34042°S: 25.73592°E), 475 m, indigenous forest, D. Herbert & L. Davis,19/xi/2012 (W9193); Somerset East, Glen Avon farm (32.71388°S: 25.64777°E), garden of farmhouse, D. Herbert, M. Bursey & G. Redman, 21/i/2002 (V9804); Cradock (32.183°S: 25.617°E), (V5277); Thornhill area, Berg River valley (33.87457°S: 25.11965°E), 155 m, indigenous forest, D. Herbert & L. Davis, 17/xi/2012 (W9200); Loerie, land adjacent to PPC quarry (33.79821°S: 24.96718°E), 130 m, riverine thicket (not on limestone), in leaf-litter, D. Herbert, M. Cole & L. Davis, 22/ix/2008 (W6507); Hankey area, Kleinrivier road (33.81429°S: 24.95415°E), 255 m thicket, in leaf-litter and under fallen aloes, D. Herbert, L. Davis & M. Cole, 21/ix/2008 (W6514); Ferndale, near Patensie (33.71642°S: 24.85030°E), 160 m, riverine woodland, in leaf-litter, D. Herbert, L. Davis & M. Cole, 28/ix/2011 (W8435/6); Baviaanskloof, Poortjies area (33.6537°S: 24.5270°E), riverine thicket, in leaf-litter, D. Herbert, 09/x/2000 (V8573). W. CAPE: OUTENIEKWA: Harkerville Nat. Res., Kranshoek Trail (34.04759°S: 23.23081°E), afrotemperate forest, in leaf-litter, A. Moussalli, 21/viii/2006 (W4665); Knysna, Prince Alfred's Pass, Diepwalle Forest St'n (33.967°S: 23.150°E), indigenous forest, D. Herbert, iv/1995 (V3615); Knysna area, 4km west of Keurhoek (33.9519°S: 22.9122°E), indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 12/iii/2005 (W5967, W3245); Wilderness Nat. Park, Big Tree (33.93652°S: 22.64403°E), indigenous forest, under log, A. Moussalli & D. Stuart-Fox, 6/iii/2005 (W3277); Wilderness Nat. Park, Touws River (33.98348°S: 22.60949°E), indigenous forest, under log, A. Moussalli & D. Stuart-Fox, 13/iii/2005 (W3278); Mossel Bay (34.18456°S: 22.15824°E), 23 m, coastal succulent karoo, under dead aloe, A. Moussalli & D. Stuart-Fox, 5/iii/2005 (W3285). CAPE TOWN AREA: Strandfontein dunes (34.0788°S: 18.5717°E), (W7523); Lakeside (34.092945°S: 18.463305°E), 4 m, suburban garden, K. Tolley, 02/x/2007 (W5832); Table Mtn, Orangekloof (34.00342°S: 18.3905°E), 130 m, afrotemperate forest, sugar-baited ant trap, C. Uys, 28/i/2009 (W7170); Cape Town, Newlands, 28 Upper Angelina Ave (33.975°S: 18.467°E), suburban garden, under stone in flower bed, L. Miszczak, Snailiens Project, xii/2000 (V8775); Cape Town, Rondebosch, 36 Malcolm Rd. (33.967°S: 18.467°E), suburban garden, abundant, P. Raine, Snailiens Project, iii/2001 (V9205).

APPENDIX 4. *Nata erugata* sp. nov.

Additional material examined (all NMSA, unless otherwise indicated): MOZAMBIQUE: Inhambane (23.865°S: 35.383°E), Mrs Ford, v/1975 (ELM D05282). SOUTH AFRICA: KRUGER NATIONAL PARK: Sand River area, Block C155 (24.922°S:

31.7°E), A.C. van Bruggen, 22/x/1962 (A9759, A9762); Sabi River area, Block C162 (24.98°S: 31.62°E), R.F. Lawrence, 22/xi/1962 (A9761); Ship Mountain, Block S51 (25.217°S: 31.75°E), A.C. & W.H. van Bruggen, 04/xii/1962 (A9760). Mpumalanga: Mariepskop Forest Res., NE of reserve (24.533°S: 30.867°E), 1170 m, A.C. & W.H. van Bruggen, 30/i/1966 (A7093); ditto (24.56374°S: 30.86293°E), 1640 m, northern mist-belt forest, in leaf-litter, D. Herbert, L. Davis, & M. Cole, 03/xii/2014 (P0259, P0321); ditto (24.5633°S: 30.8633°E), indigenous afromontane forest, B.R. Stuckenberg, 04/x/1956 (W3882); ditto, Bushpig Trail (24.56694°S: 30.86270°E), 1491 m, mist-belt forest, A. Moussalli & D. Stuart-Fox, 15/xii/2006 (W5743); ditto (24.59563°S: 30.826°E), 790 m, indigenous riverine forest, in leaf-litter on forest floor, J. Horn, 25/v/2006 (W4415); Sabie area, Mt Sheba Nat. Res. (24.93122°S: 30.70965°E), afrotemperate forest, under log, A. Moussalli & D. Stuart-Fox, 25/ii/2004 (W3343); ditto (24.939°S: 30.71057°E), 1690 m, indigenous forest, in leaf-litter, J. Horn, 12/xii/2006 (W5563); Sabie, Lone Creek Falls (25.108°S: 30.7°E), indigenous forest, in leaf-litter, D. Herbert, 23/xi/1997 (V5515); Lydenburg, ~20 SW (25.22006°S: 30.29888°E), 1581 m, grassland, gully thicket, under log, A. Moussalli & D. Stuart-Fox, 13/xii/2006 (W5633); Buffelskloof Nat. Res. (25.26670°S: 30.51873°E), afrotemperate forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 17/ii/2004 (W3339); ditto (25.268633°S: 30.518983°E), 1750 m, indigenous forest, in leaf-litter, J. Horn, 16/iii/2006 (W4471, W4507); Lydenburg area, 20 km SSE, Uitsoek Forest (25.27307°S: 30.5533°E), 1200 m, indigenous forest, in leaf-litter, J. Horn, 03/ii/2006 (W4459); Sudwala Rainforest (25.36713°S: 30.70343°E), 1080 m, indigenous forest, in leaf-litter, J. Horn, 29/i/2006 (W4473); Nelspruit area, 10 km east near road to Malelane (25.483°S: 30.967°E), small swamp with indigenous bush, moist soil, D. Plisko & T. Liversage, 15/xii/1995 (W2456); Tullach-Mohr Game Res., Fairy Glen (25.55957°S: 30.58325°E), afrotemperate forest, under rock, A. Moussalli & D. Stuart-Fox, 15/ii/2004 (W3301); Malelane area, 10 km south, Sherlock farm 'isolated forest' (25.58668°S: 31.526°E), 800 m, indigenous forest, in leaf-litter, J. Horn, 24/i/2006 (W5649); Kaapsehoop forest, ~20 km SW of Nelspruit (25.61479°S: 30.76619°E), afrotemperate forest, under logs, A. Moussalli & D. Stuart-Fox, 12/ii/2004 (W3300); Waterval Boven area, Rocky Drift Private Nat. Res. (25.65345°S: 30.37585°E), 1250 m, riverine thicket/scrub with *Aloe ferox*, D. Herbert, L. Davis, & M. Cole, 25/xi/2014 (P0171); Barberton Nat. Res., Peglar's Bush (25.79679°S: 31.14400°E), afrotemperate forest, under small logs, A. Moussalli & D. Stuart-Fox, 9/ii/2004 (W3302); Barberton Nat. Res. (25.8594°S: 31.0366°E), afromontane forest in gully between pine plantations, in leaf-litter, A. Moussalli & D. Stuart-Fox, 07/ii/2004 (W2117). Free State: Koppies Dam Nat. Res. (27.25746°S: 27.78134°E), 1400 m, riverine thicket, under rotting log, G. Redman & R. Seagram, 9/i/2001 (V8940); Kroonstad (27.667°S: 27.233°E) (A7095); Platberg Nat. Res. (28.27636°S: 29.20544°E), 2200 m, montane shrubland, seepage area at base of south facing rocky slopes, A. Moussalli, D. Stuart-Fox & K. Cunningham, 11/xii/2006 (W5623); Thaba N'chu (29.27915°S: 26.89974°E), 1581 m, gully thicket/grassland, A. Moussalli & D. Stuart-Fox, 27/xii/2005 (W4727). KwaZulu-Natal – north-eastern region: Ndumo Game Res., beside Nyamithi Pan (26.888°S: 32.275°E), A.C. & W.H. van Bruggen, 14/i/1964 (A7102); Ingwavuma Rd beacon (27.133°S: 32.0167°E), 760 m, A.C. & W.H. van Bruggen, 08/i/1964 (B0095); Lebombo Mts, Gwaliweni Forest, near conservation office (27.3125°S: 31.9967°E), in leaf-litter on forest floor, G. Davies, 13/xii/2002 (W1312); ditto, Hlatikulu Forest Reserve (27.32466°S: 31.98981°E), 647 m, scarp-forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 29/xii/2006 (W5727); Ithala Game Res. (27.503°S: 31.2°E), 570 m, riverine woodland, under stone, O. Bourquin, 21/ii/1996 (V2542); ditto, Serendipity (27.5042°S: 31.185°E), 580 m, riverine bushveld, in crevice on tree trunk at 1 m, D. Herbert, 28/iii/1996 (V2900); ditto (27.58316°S: 31.26463°E), 1433 m, northern mist-belt grassland, under rock amongst low shrubs, A. Armstrong *et a*l., 04/xi/2002 (W1981); Mkhuze Game Res. (27.58590°S: 32.236772°E), 91 m, mixed *Spirostachys*, *Grewia*, *Combretum*, *Balanites* woodland, in leaf-litter, under logs and in soil around tree trunks, M54B, Earthwatch Team 3, 24/i/2003 (W605); ditto (27.59493°S: 32.20737°E), dense *Acacia nigrescens*, *Croton*, *Dichrostachys* and *Aloe* thicket on Cretaceous limestone, under logs and fallen aloes, and amongst plant debris around tree trunks, Earthwatch Team 4, 04/ii/2003 (W1082); ditto, Nhlonhlela Pan area (27.598°S: 32.203°E), A.C. & W.H. van Bruggen, 06/i/1964 (A7132); ditto (27.60051°S: 32.28966°E), *Dichrostachys* thicket, under logs and in soil/litter around tree trunks, M47A, Earthwatch Team 2, 18/xii/2002 (W1050); ditto (27.63727°S: 32.15345°E), open bushveld with aloes on rocky hillside, under fallen aloe, Earthwatch Team 11, 24/iii/2005 (W2801); ditto (27.65714°S: 32.31064°E), open *Acacia tortilis* woodland/savannah, in leaf-litter, under logs and soil around tree trunks, M42A, Earthwatch Team 1, 08/xi/2002 (W353); ditto, fig forest walk (27.667°S: 32.325°E), *Ficus sycamorus* forest, in leaf-litter, Earthwatch Team 2, 2/xi/2002 (W331); ditto (27.66962°S: 32.25135°E), *Acacia nigrescens*, *Ziziphus*, *Combretum* savannah, under logs and in soil around tree trunks, M22B, Earthwatch Team 4, 02/ii/2003 (W952); ditto (27.74692°S: 32.29112°E), *Acacia xanthophloea* grove beside Msunduzi River, in leaf-litter, under logs and amongst plant debris around tree trunks, Earthwatch Team 1, 10/xi/2002 (W1009); Phinda Game Res. (27.790318°S: 32.25412°E), open *Acacia nilotica*, *Euclea* veld, soil earthy rather than sandy, Site P2, Earthwatch Team 5, 25/xi/2003 (W1328); ditto (27.79468°S: 32.32374°E), palm veld, under bush clumps and grass tussocks, P9C, Earthwatch Team 5, 21/xi/2003 (W1334). KwaZulu-Natal – north-western region: Utrecht, Groenvlei, Guquka Hill, Ararat farm (27.39°S: 30.34°E), 1700 m, montane forest, in leaf-litter, D. Herbert, 28/i/1998 (V5925); Bivane River catchment, Elandsnek, east of Pivans waterfall farm (27.460°S: 30.421°E), 1850 m , small patch of montane *Podocarpus* forest, in leaf-litter, D. Herbert, 1/xii/1999 (V7563); ditto (27.462°S: 30.418°E), 1850 m, *Leucosidea* woodland/scrub, in leaf-litter, D. Herbert, 1/xii/1999 (V7635); ditto, Pandana Forest, north of Klipplaatdrift farm (27.460°S: 30.399°E), 1750 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, 30/xi/1999 (V7545); Utrecht, Balelesberg (27.523°S: 30.198°E), 1800 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, 27/i/1998 (V5868); ditto (27.523°S: 30.2233°E), 1900 m, *Leucosidea* thicket on dolerite, in leaf-litter, D. Herbert, 27/i/1998 (V5878); Vryheid Nat. Res. (27.749°S: 30.799°E), 1300 m, woodland/forest on slopes of mountain, in leaf-litter, D. Herbert, 2/xii/1999 (V7594); ditto (27.7491743°S: 30.7970702°E), forest, extracted from leaf-litter sample, A. Armstrong & J. Craigie, 31/i/2007 (W5199); Ncandu Forest Nat. Res. (27.89786°S: 29.704585°E), montane *Podocarpus* forest, under dead wood on forest floor, A. Armstrong & P. Ngwenya, 23/x/2001 (W70); Normandien, Buffelshoek farm (27.945°S: 29.735°E), 1600 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, 20/x/1998 (V7122, V8487); Normandien, just north of pass, near summit (27.96°S: 29.6867°E), 1950 m, montane *Podocarpus* forest, in leaf-litter, Herbert, Seddon & Tattersfield, 4/xii/1998 (V8498); Biggarsberg, Kwaggasberg (28.2°S:

29.917°E), 1500 m, in leaf-litter from small patch of indigenous forest, D. Herbert, vii/1997 (V4941). KwaZulu-Natal – Central Drakensberg: Mont Aux Sources (28.6967°S: 28.92°E), H.C. Burnup coll'n (B85); Royal Natal Nat. Park, Thukela Gorge (28.72995°S: 28.92081°E), montane *Podocarpus* forest, F83, D. Herbert (Earthwatch), 18/iii/2006 (W4282); Cathedral Peak Hotel area (28.945°S: 29.205°E), 1340 m, under log, A.C. & W.H. van Bruggen, 02/iv/1962 (V5201); Injasuthi (29.11°S: 29.4417°E), 1700 m, montane *Podocarpus* forest patch, in leaf-litter, Herbert, Seddon & Tattersfield, 8/xii/1998 (V8014); Highmoor (29.30714°S: 29.5945°E), 1915 m, indigenous forest, ground searching, F60, M. Hamer *et al*., 17/i/2006 (W5062); Kamberg, Game Pass (29.375°S: 29.65°E), H.C. Burnup coll'n, 1912 (B84); Kamberg area (29.37619°S: 29.66837°E), 1745 m, grassland, M. Hamer *et al*., 14/xi/2005 (W5051); Lotheni Nat. Res., near Yellow-Wood Cave (29.415°S: 29.48°E), 1800 m, montane *Podocarpus* forest, in leaf-litter, large specimen found eating the smaller one, D. Herbert, 25/x/1997 (V5378, V5757); Garden Castle Res., Mashai valley (29.753°S: 29.1852°E), 2020 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, 21/iii/1998 (V6384); Underberg area, Drakensberg Gardens road, Pennygum Cottages (29.7614°S: 29.45558°E), 1550 m, rural garden, under bedding plants and around tree trunks, D. Herbert, 16/vi6/2003 (W892). E. Cape: Langeni area, Jenca Valley (31.36593°S: 28.55727°E), 1420 m, small piece of indigenous forest in rocky valley, above escarpment under leaves, st'n 06-005, D. Herbert & L. Davis, 18/ii/2006 (W3935); Langeni Forest, West of Umtata (31.398°S: 28.555°E), 1200 m, afromontane forest, in leaf-litter, D. Herbert, 24/iv/1999 (V7055); Langeni area, Nocu Forest (31.41547°S: 28.49983°E), 840 m, large block of indigenous forest, in leaf-litter, st'n 06-004, D. Herbert & L. Davis, 18/ii/2006 (W3924); Nqadu Forest, North of Umtata (31.4267°S: 28.7517°E), 1250 m , afromontane forest, in leaf-litter, D. Herbert, 24/iv/1999 (V7193); Kambi Forest, West of Umtata (31.468°S: 28.590°E), 1200 m , afromontane forest, under leaves at forest margin, D. Herbert, 24/iv/1999 (V7083, V7084, V7174); Langeni Forest Station, sawmill village (31.48293°S: 28.47707°E), unkempt garden, st'n 06-003, D. Herbert & L. Davis, 17/ii/2006 (W4024); Langeni area, Baziya Forest (31.5208°S: 28.4123°E), large block of indigenous forest, in leaf-litter, st'n 06-007, D. Herbert & L. Davis, 19/ii/2006 (W3960); Witteberge, Balloch farm, north of Barkly East (30.71226°S: 27.69136°E), 1890 m, in vegetation beside large rocks in camp site, disturbed habitat, st'n 09-018, D. Herbert, L. Davis, M. Cole & J. Fearon, 04/iv/2009 (W6761); Kei River Valley, NNE of Stutterheim, Moonstone farm, 'Colin’s forest camp' (32.27756°S: 27.57184°E), indigenous forest in kloof, in leaf-litter, st'n 07-009, D. Herbert, L. Davis & M. Bursey, 05/iii/2007 (W5305); Hogsback, Rattray, Taylor & Hewitt (V5597, V2730, W9077); ditto (32.58935°S: 26.93563°E), 1221 m, indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 21/i/2005 (W3326); ditto, environs of Madonna & Child waterfall (32.60703°S: 26.96268°E), indigenous forest, in leaf-litter, D. Herbert, M. Bursey & G. Redman, 25/i/2002 (V9901); ditto, forest above Hobbiton, path to Kettlespout (32.59610°S: 26.96194°E), indigenous forest, M. & K. Cole, 31/xii/2008 (W6654).

APPENDIX 5. *Nata watsoni* sp. nov.

Additional material examined (all NMSA, unless otherwise indicated): SOUTH AFRICA: E. Cape: Ferndale, near Patensie (33.71642°S: 24.85030°E), 160 m, riverine woodland, in leaf-litter, D. Herbert, L. Davis & M. Cole, st’n 11-25, 28/ix/2011 (W8324); Hankey area, Kleinrivier road (33.81429°S: 24.95415°E), 255 m, thicket, in leaf-litter and under fallen aloes, D. Herbert, L. Davis & M. Cole, st’n 08-053, 21/ix/2008 (W6510); Gamtoos River mouth (33.95760°S: 25.04755°E), 35 m, dune forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, st’n 11-26, 28/ix/2011 (W8446); Van Stadens River gorge (33.90937°S 25.19090°E), 130 m, indigenous forest, D. Herbert & L. Davis, st’n 12-42, 16/xi/2012 (W9233); Vanstadensberg, Lady’s Slipper Reserve (33.88901°S: 25.27047°E), Kasouga grassy sandstone fynbos, amongst rocky outcrops after fire, leg. A. Moussalli & D. Stuart-Fox, xii/2005 (W9803); Kaboega game farm (33.26890°S: 25.42366°E), mixed woody vegetation beside watercourse, D. Herbert, L. Davis & M. Cole, 10/iii/2008 (W6041); Kaboega game farm (33.26719°S: 25.42147°E), mixed woody vegetation in blind-ending kloof with stream and pools, in leaf-litter, D. Herbert, L. Davis & M. Cole, 10/iii/2008 (W6042); Kuzuko Game Res. (33.25091°S: 25.45660°E), open valley thicket with scattered bush clumps, D. Herbert, L. Davis & M. Cole, 09/iii/2008 (W6021); Kuzuko Game Res. (33.2°S: 25.4°E), M. Bursey, 09/iii/06 (ELM D15017); Port Elizabeth area, Island Forest Res. (33.98668°S: 25.37151°E), low coastal forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, st’n 08-040, 18/ix/2008 (W6405); ditto (33.98514°S: 25.36998°E), coastal forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 14/xii/2005 (W7453); Uitenhage (33.76373°S: 25.39764°E), valley thicket, in leaf-litter and under fallen aloes, A. Moussalli & D. Stuart-Fox, 22/xii/2005 (W5489); Port Elizabeth, Lovemore Heights (33.99267°S: 25.51210°E), 280 m, indigenous forest, D. Herbert & L. Davis, st’n 12-46, 18/xi/2012 (W9215); Port Elizabeth (33.917°S: 25.6°E), *ex* J. H. Ponsonby, don. H. C. Burnup, 1904 (1484); Port Elizabeth, N.E. bush, Crawford (NHMUK 1937.12.30.1367, labelled as *Nata minor*); Port Elizabeth area, Grassridge, PPC mining concession (33.6744°S: 25.64731°E), bontveld, under fallen aloes, D. Herbert, L. Davis & M. Cole, st’n 08-044, 19/ix/2008 (W6374); ditto (33.66244°S: 25.62116°E), bontveld, under fallen aloes and in grass clumps, D. Herbert, L. Davis & M. Cole, st’n 08-042, 19/ix/2008 (W6409); ditto (33.69370°S: 25.67761°E), bontveld, under bush clumps and fallen aloes, D. Herbert, L. Davis & M. Cole, 08-043, 19/ix/2008 (W6421); Somerset East, Glen Avon Falls "The Gorge" (32.677°S: 25.63681°E) (A7099); Zuurberg (33.3404°S: 25.73592°E), 475 m, indigenous forest, D. Herbert & L. Davis, st’n 12-47, 19/xi/2012 (W9192); Olifantskop, north of Paterson (33.31700°S: 25.94570°E), 800 m, indigenous forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, st’n 11-28, 29/ix/2011 (W8305); Riebeek East, Waterkloof farm (33.19752°S: 26.06469°E), succulent thicket with aloes, in leaf-litter and under fallen aloes, D. Herbert, L. Davis & M. Bursey, 09/iii/2007 (W5328; ELM D15156); Alexandria Forest, Langebos, in vicinity of hiking huts (33.69963°S: 26.35882°E), 210 m, indigenous forest, D. Herbert & L. Davis, st’n 12-52, 21/xi/2012 (W9182); Alexandria Forest, around Bailey’s Kop (33.69520°S: 26.35468°E), 350 m, indigenous forest, D. Herbert & L. Davis, st’n 12-51, 20/xi/2012 (W9173); Alexandria, coast, M. Cole, 02/ii/2009 (W6827); Woody Cape Nat. Res. (Addo) (33.75442°S: 26.37708°E), 70 m, dune scrub, D. Herbert & L. Davis, st’n 12-54, 21/xi/2012 (W9153); ditto (33.75708°S: 26.38742°E), 40 m, dune forest, D. Herbert & L. Davis, st’n 12-53, 21/xi/2012 (W9162); Grahamstown, McKean Coll’n (NHMUK 20090081, labelled as *Nata vernicosa*); Grahamstown, Botanical Gardens

(33.31728°S: 26.52250°E), indigenous forest gardens, in leaf-litter A. Moussalli & D. Stuart-Fox, 03/xii/2005 (W6966): ditto, Mountain Drive, Dassie Krantz trail (33.32915°S: 26.49911°E), indigenous forest in south facing kloof, in leaf-litter, D. Herbert, L. Davis & M. Bursey, 10/iii/2007 (W5348); ditto, Longford Range, J. Hewitt, ix/1935, *ex* Albany Museum (W5496); Kasouga (33.65°S: 26.733°E), J. Hewitt, i/1927, *ex* Albany Museum (W3551); Port Alfred (33.6°S: 26.9°E), R. H. Ivy, *ex* Transvaal Mus. (W7175); Riet River, Pig Island farm, 'The Glen' (33.4833°S: 26.9333°E), M. Bursey, 12/i/2007 (ELM D15391/2); Kleinmonde (33.55927°S: 27.01146°E), coastal dune forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 09/xii/2005 (W7067); Great Fish Point area, Tharfield farm (33.55°S: 27.0167°E), Miss M. L. Bowker, *ex* Albany and Transvaal Museums (W6153/5); ditto, near coast, M. Bursey, 30/i/2008 (W6137); ditto, riverine forest (33.52944°S: 26.97972°E), M. Bursey, 30/xii/2002 (W5378); ditto, east bank of Riet River, approx. 6 km upstream of mouth (33.52722°: 26.97917°E), riverine forest, on rotten log, M. Bursey, 30/i/2008 (W6136); Great Fish River valley, near NoBumba village, east side of river (33.268309°S: 27.003942°E), 145 m, steep south-facing slope, Great Fish thicket, M. Cole, 27/ii/2013 (W9378); Kap River Nat. Res. (33.48222°S: 27.07889°E), north bank of river, leg. M. Cole, 9/iv/2012 (W9369); Great Fish River mouth (33.49975°S: 27.13064°E), 16 m, coastal dune forest, in leaf-litter, A. Moussalli, D. Stuart-Fox & M. Bursey, 09/xii/2005 (W7039).

APPENDIX 6. *Natella viridescens* (Melvill & Ponsonby, 1891)

Additional material examined (all NMSA, unless otherwise indicated): SOUTH AFRICA: Limpopo – Soutpansberg: Entabeni Forest, ±40km NE of Louis Trichardt (22.99103°S: 30.25873°E), 1300 m, indigenous Afromontane forest, in leaf-litter J. Horn, 01/iii/2006 (W7720); summit west of Hanglip (22.99858°S: 29.86959), 1520 m, rocky mist-belt fynbos/thicket, in leaf-litter, D. Herbert, L. Davis & M. Cole, 29/xi/2014 (P0283); Hanglip Forest (23.00°S: 29.89°E), indigenous forest, J. Swaye, ii–iii/2001 (W0097); ditto (23.02°S: 29.90°E), 1370 m, A.C. & W.H. van Bruggen, 8–9/ii/1965 (A7128); Hanglip Forest area (23.0050°S: 29.9045°E), thicket/dry indigenous forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 02/iii/2004 (W2237); Clouds End Hotel (23.007°S: 29.928°E), 1100 m, mixed bush/woodland, in leaf-litter, D. Herbert, 21/xi/1997 (V5532); Entabeni East (23.04597°S: 30.23638°E), 800 m, C. Symes, 16/vii/1999 (V8505); Levubu area (23.067°S: 30.233°E), secondary growth forest and encroaching bush, previously grassland, in leaf-litter, C. Symes, 10/x/2000 (V8703); Goedehoop Forest (23.0833°S: 30.1117°E), 950 m, indigenous forest, under logs and stones, and in leaf-litter, D. Herbert, 20/xi/1997 (V5555, V5664); Roodewal Forest (23.02322°S: 30.03956°E), indigenous forest, J. Swaye, iii/2001 (W0084); Thathe Vondho Forest (22.876°S: 30.349°E), 1430 m, indigenous forest, in leaf-litter, C. Symes, 04/xi/1999 (V7647); Studholm (22.963°S: 29.994°E), 1460 m, open grassland with woodland patches, *Syzigium legatii* dominant, in leaf-litter, C. Symes, xii/1999 (V7622). Limpopo – Wolkberg: Forest Glens (23.96951°S: 29.91860°E), indigenous forest, J. Swaye, ii–iii/2001 (W0093); ditto (23.97330°S: 29.91682°E), indigenous forest, J. Swaye, iii/2001 (W0092). Mpumalanga: Mariepskop Forest, Bushpig Trail (24.56795°S: 30.86138°E), 1520 m, northern mist-belt forest, in leaf-litter, D. Herbert, L. Davis & M. Cole, 03/xii/2014 (P0266); Mariepskop Forest (24.5936°S: 30.8265°E), 790 m, indigenous riverine forest, in leaf-litter, J. Horn, 22/xi/2005 (W4419, W4422); Sabie area, Mt Sheba (24.9391°S: 30.7118°E), afromontane forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 25/ii/2004 (W2049); Lydenburg area, 20 km SSE, Uitsoek Forest (25.27685°S: 30.5516°E), 1220 m, indigenous forest, in leaf-litter, J. Horn, 01/ii/2006 (W4461); ditto, Buffelskloof Forest Res., middle of gorge (25.3134°S: 30.4724°E), afromontane forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 17/02/2004 (W2103); ditto, Buffelskloof Forest Res., highest part of gorge (25.2667°S: 30.5187°E), afromontane forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 17/ii/2004 (W1991); ditto, Buffelskloof Nat. Res. (25.30067°S: 30.50968°E), 1530 m, indigenous forest, in leaf-litter, J. Horn, 13/iii/2006 (W4442); ditto, 38 km SE, Sudwala Rainforest, 25.36723°S: 30.70323°E); 1080 m, indigenous forest, in leaf-litter, J. Horn, 29/i/2006 (W4457); Nelspruit, Krokodilpoortberge, Witkop (25.55620°S: 31.11957°E), 1057 m, low dry *Commiphora* dominated deciduous woodland on side of large granite basolith, N. Crouch & T. Edwards, ii/2008 (W6124); Waterval Boven area, Tullach-Mohr, Fairy Glen (25.5596°S: 30.5833°E), afromontane forest, gully, rocky slate substratum, in leaf-litter, A. Moussalli & D. Stuart-Fox, 15/ii/2004 (W2001, W2104); Malelane area, 10 km South, Sherlock farm, 'isolated forest' (25.58780°S: 31.52725°E), 750 m, indigenous forest, in leaf-litter, J. Horn, 24/i/2006 (W4578); Barberton Nat. Res. (25.8594°S: 31.0366°E), afromontane forest in gully between pine plantations, in leaf-litter, A. Moussalli & D. Stuart-Fox, 07/ii/2004 (W2116). N.W. Province: Rustenburg Kloof, path to waterfall (25.68732°S: 27.19328°E), 1468 m, thicket/woodland/forest in gorge, steep slope, in leaf-litter, R. Slotow, i/2000 (V7812). GAUTENG: Roodeplat Dam (25.64850°S: 28.34248°E), 1278 m, forest/woodland slope down to dam, R. Slotow, 17/i/2000 (V7786); Pretoria (25.75°S: 28.17°E) (1497, A7122, E7928); Johannesburg, Kyalami, Barbeque Downs (26.017°S: 28.050°E), on banks of Jukskei River, in debris under trees, M. Evans, 01/iv/2005 (W6935); ditto, Woodmead, Khyber Rock (26.05°S: 28.09167°E), in loose soil/leaf debris amongst rocks, residential property, M. Evans, 01/v/2007 (W6940). KwaZulu-Natal: Ithala Game Res., Dakaneni loop road (27.4630°S: 31.2583°E), *ca.* 480 m, beside Pongola River, riverine bush, in leaf-litter, D. Herbert, 06/i/1997 (V6807); ditto, Serendipity (27.5042°S: 31.1850°E), 580 m, on wall of building in riverine bushveld, D. Herbert, 28/iii/1996 (V3177); ditto, Serendipity (27.50795°S: 31.20319°E), 590 m, riverine bush, in leaf-litter, M. Cole, 20/i/2010 (W7263); ditto, Ngubhu loop road (27.5670°S: 31.2583°E), 1000 m, thicket beside stream, in leaf-litter, D. Herbert, 06/i/1997 (V4906); Paulpietersburg (27.52736°S: 30.72763°E), 1256 m, indigenous forest, sorted from leaf-litter sample, A. Ndaba, B. Mkhize & G. Zamisa, 13/xii/2012. (W9296); Spioenkop Nat. Res. (28.6500°S: 29.5217°E), in leaf-litter and under stones, R. Miller, 07/ix/1988 (V6069); Colenso, Hilltop farm (28.689°S: 29.750°E), 1200 m, dense bushveld, south facing, sorted from leaf-litter, C. Symes, 17/vii/2003 (W1301); Weenen, Mkolombe Mtn (28.905°S: 30.1383°E), H.P. Thomasset, 1927 (A7121); ditto, Umngwenya River valley (28.917°S: 30.1°E), 950 m, iii/1922 (A7120); ditto, Umsobotsheni, H.P. Thomasset, iv/1922 (A7126); ditto, Bushman's River Falls (28.8133°S: 30.167°E), 7 miles below Weenen, 700 m, H.P. Thomasset, iv/1922 (A7125); ditto, Tiger

Kloof (28.85°S: 30.083°E), H.P. Thomasset, 5/iii/1926 (A7127); Weenen Nat. Res. (28.883°S: 30.050°E), 1200 m, thick riverine bush in valley bushveld, in leaf-litter, D. Herbert, 30/iii/1997 (V4535); Muden area, Mhlopeni Nat. Res. (29.007°S: 30.413°E), riverine thicket/woodland, in leaf-litter, D. Herbert, 21/iii/2000 (V8028); Karkloof (29.3°S: 30.23°E), H.C. Burnup coll'n (B0045); Nottingham Road (29.358°S: 29.995°E) (2207); Howick, Umgeni River Nat. Res. (29.4930°S: 30.2483°E), *ca* 850 m, woodland in valley bushveld, in leaf-litter, D. Herbert, i/1998 (V6283); Dargle, near Umgeni River (29.53°S: 30.01°E), under stone near bridge, H.C. Burnup, pre-1930 (A7123).

Additional literature records (material not seen): SOUTH AFRICA: LIMPOPO: Sibasa area, Pepiti [Phiphidi] Falls (22.9483°S: 30.395°E), C. Harries (Connolly 1939). KWAZULU-NATAL: Dargle, Nhlosane (29.5417°S: 29.9533°E), H.C. Burnup (Connolly 1912, 1939).