SYSTEMATICS AND BIOGEOGRAPHY OF FOREST SNAILS, *CHONDROCYCLUS* (MOLLUSCA: GASTROPODA: CAENOGASTROPODA: CYCLOPHORIDAE) IN SOUTHERN AFRICA

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

at

RHODES UNIVERSITY

by

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December 2015

Abstract

This study presents a molecular phylogeny and systematic revision of *Chondrocyclus*, the major South African group of the large family of operculate terrestrial molluscs, the Cyclophoridae. *Chondrocyclus* snails are small gastropods found in forest and moist thicket throughout South Africa. This is the first detailed systematic treatment of a group of Cyclophoridae in mainland Africa and the first to provide molecular data. This study complements regional studies on the systematics of the family in Asia and provides comparative data for studies of higher level relationships within the Cyclophoridae. Phylogenetic reconstruction by BI and ML methods of combined and single gene datasets of 16S and CO1 all showed *Chondrocyclus* to be monophyletic and recovered five well-supported clades that corresponded to groups of populations identifiable on the basis of combinations of morphological characters. Species were diagnosed morphologically and were shown to be genetically distinct lineages. Informative morphological features include shell dimensions, protoconch, periostracum, operculum, radula and penis. Two species in Afromontane regions of Zimbabwe and Malawi respectively are excluded from *Chondrocyclus* based on morphology and tentatively placed in *Cyathopoma*. Diversity recognised within the genus more than doubled, from a previous seven South African species to seventeen. Re-descriptions of established species and descriptions of new species are provided, together with photographs of morphological characteristics. New taxon names and nomenclatural acts within it are disclaimed and are therefore not available in the sense of the International Code of Zoological Nomenclature until validly published elsewhere. Several cryptic species within previously widespread "species" and unrecorded narrowly endemic species were documented. The clade consisting of populations of *"Chondrocyclus isipingoensis"*, now considered to be a species complex, was sister to a group containing the other four clades. The "Isipingoensis" clade occurs widely in Afromontane regions, along the Great Escarpment, and on the south-east coast. The other four clades occur from Zululand to the Cape Peninsula with a pattern of east-west lineage

turnover. The biogeography of *Chondrocyclus* is interpreted by comparison with concordant patterns in other terrestrial molluscs and unrelated taxa with poor dispersal ability. This study complements other research on composition, spatial distribution and phylogenetic diversity of low-vagility invertebrates and expands the data available for biodiversity conservation in South Africa.

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Declaration

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author unless otherwise stated.

1 Introduction

Chondrocyclus are small gastropods found in forest and thicket throughout South Africa. They occupy leaf litter on the forest floor and although patchily distributed within a given forest, they may be locally abundant and are frequently the most common snails found. Details of diet are not recorded (Herbert & Kilburn, 2004) but they probably feed on detritus, bacterial films, fungi and lichens, contributing to nutrient recycling. Fresh specimens are relatively easy to distinguish by their dorso-ventrally flattened shell, circular and detached peristome, large umbilicus, elaborate periostracum and presence of an operculum.

Historically, South African Cyclophoridae were assigned to various genera (Pfeiffer, 1855; Craven, 1880; Sturany, 1898; Kobelt, 1902). Ancey (1898) created the genus *Chondrocyclus* for species "from the Cape of Good Hope, remarkable by the nature of its epiderme, its depressed shape, its thin peristome and its small size." The genus was last reviewed in 1939 (Connolly, 1939) and then contained seven species, all endemic to South Africa. Subsequently, two small cyclophorids *Chondrocyclus meredithae* Bruggen, 1983 and *C. chirindae* Bruggen, 1986 were described from Malawi and Zimbabwe respectively. Three Madagascan cyclophorids were also classified in *Chondrocyclus* (Fischer-Piette *et al.*, 1993), but these have been removed from *Chondrocyclus* and assigned to three other genera (Emberton, 2004).

Cyclophoridae is the most speciose family of operculate, terrestrial molluscs, currently containing approximately 34 genera and 810 species (Nantarat, 2014a). The family is near the base of the Caenogastropoda, a group containing the majority of molluscan taxa (Colgan *et al.*, 2007; Hayes *et al.*, 2009). The higher level relationships between Cyclophoridae and other families and within the Cyclophoridae are largely unknown. The family is extremely morphologically diverse both in size range and shape, and is mainly tropical, distributed throughout south-east Asia, the Philippines, India, Madagascar and mainland Africa, with a few species reaching the western Pacific and northern Australia (Stanisic, 1998). In mainland Africa cyclophorids are widely distributed in East, Central, West and South Africa, but the known species are all very small and diversity appears to be comparatively low, with only 19 described species placed in three genera: *Chondrocyclus* (9 species), *Cyathopoma* (9 species) (Fig. 1) and *Elgonocyclus* (1 species). Until recently three of these species were placed in the African genus *Afroditropis* Bequaert & Clench, 1936 (revised by

Bruggen (1986)) but subsequently this genus was synonymised with *Cyathopoma* W. & H. Blanford, 1861 (de Winter, 2002). Hence, recently described African cyclophorids have been assigned to *Cyathopoma* (de Winter, 2002; Bruggen, 2008; Rowson *et al.*, 2010) but the genus is in much need of revision (Emberton, 2003). The other African genus, *Elgonocyclus* Verdcourt, 1982, contains one described species, *E. koptaweliensis* (Germain, 1934), common in montane areas of East Africa, and a minute undescribed cyclophorid from north-eastern South Africa (D. Herbert, pers. comm.).
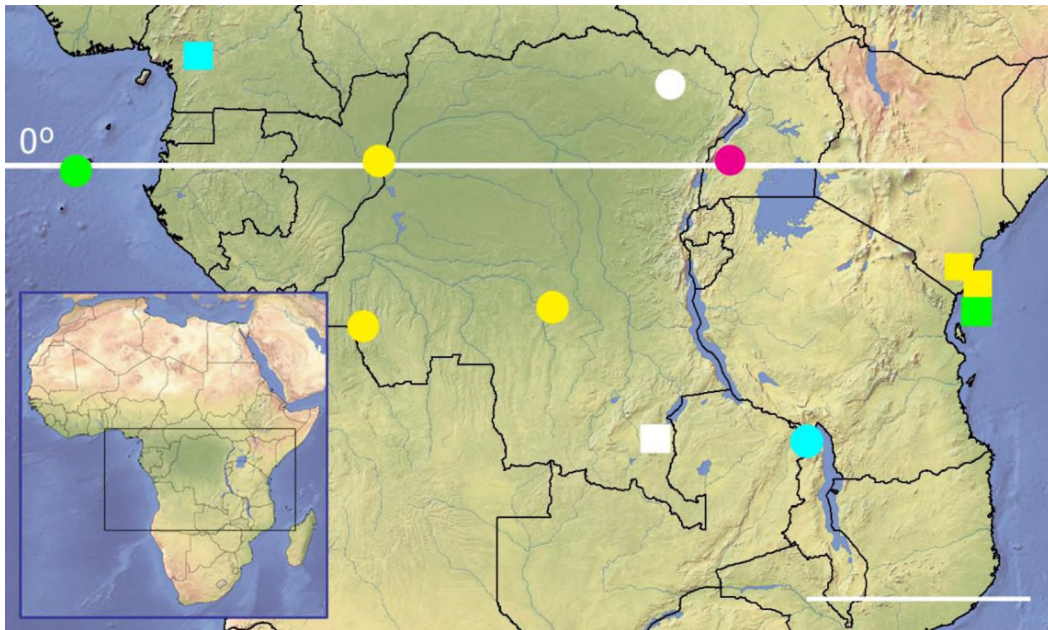
Figure 1.1 Distribution of *Cyathopoma* species in mainland Africa. Key: *C. africanum* white circle; *C. stralaeni* white square; *C. strongi* yellow circles, *C. azaniense* yellow squares; *C. papillaris* pink circle; *C. molleri* green circle, *C. pembense* green square; *C. tres* turquoise circle; *C. camerunense* turquoise square. Scale bar = 1000 km.

Cyclophoridae is a very large family and a comprehensive global phylogeny has not been attempted. Detailed anatomical studies on various genera have been undertaken (e.g. Tielecke, 1940; Morton, 1952; Kasinathan, 1975; Jonges, 1980). Emberton has done island-wide work in Madagascar, revising several cyclophorid genera and describing numerous species (Emberton & Pearce, 1999; Emberton 2002a, 2002b, 2003, 2004, 2009, 2010). Several regional phylogenetic studies on Cyclophoridae and closely related families in the Cyclophoroidea have been done in Asia (Lee *et al.*, 2008a,b; Webster *et al.*, 2012; Liew *et al.*, 2014; Nantarat *et al.*, 2014b; Sutcharit *et al.*, 2014; Pall-Gergely *et al.*, 2015), New Zealand (Marshall & Barker, 2007) and Micronesia (Rundell, 2008). Phylogenetic studies on freshwater gastropods in the Viviparidae and

Ampullariidae (the families most closely related to the Cyclophoridae) have been undertaken in lakes in the Rift Valley area in Africa (Jørgensen *et al.*, 2008; Sengupta *et al.*, 2009). The present study is the first detailed systematic treatment of a group of Cyclophoridae in mainland Africa and the first to provide molecular data. This study will complement other research on the systematics of this large family.

Considerable progress has been made in taxonomy and systematics of South African terrestrial molluscs in the past few decades (e.g. Bruggen, 1965, 1966, 2006; Sirgel, 1985; Herbert, 1997, 2006, 2007; Bursey & Herbert, 2004; Cole & Herbert, 2009; Herbert & Mitchell, 2009; Moussalli *et al.*, 2009; Herbert & Moussalli, 2010) but many families still require revision. At the time of Connolly's (1939) revision of *Chondrocyclus*, several species were known from relatively little material and/or worn examples without periostracum or operculum and, other than radulae of a few species, no anatomical details were known. Since then, South African Cyclophoridae have not received further attention and the current knowledge of species occurring in the eastern parts of the country was synthesised in 2004 (Herbert & Kilburn, 2004). The worn specimens on which certain descriptions and records were based are indistinguishable morphologically, creating taxonomic confusion. The aim of this study is to present a molecular phylogeny and systematic revision of *Chondrocyclus* using museum specimens and fresh material collected throughout South Africa.

The unified species concept recognises the underlying unity of different species concepts and equates species with separately evolving metapopulation lineages, or more specifically, segments of such lineages (de Queiroz, 2007). Different species concepts are regarded as different lines of evidence (operational criteria) relevant to assessing lineage separation, e.g. reproductive isolation, monophyly, diagnosability, etc. A highly corroborated hypothesis of lineage separation requires multiple line of evidence and this is what is attempted here. Species delimitation, the process by which species boundaries are determined and new species discovered (Wiens, 2007), will be informed by morphology of the shell, protoconch, periostracum, operculum, radula and penis, and molecular data based on regions of 16S and CO1. Sequence divergences at CO1 regularly enable discrimination of closely allied species in all animal phyla (Hebert *et al.*, 2003). In cases where there is mismatch between mitochondrial DNA phylogenies and morphology-based species delimitation (e.g. Kohler *et al.*, 2010; Kohler, 2016) or incongruence in topology of mtDNA and nDNA trees (e.g. Nekola *et al.*, 2015) further independent sources of evidence should be sought for species-level assignment.

3

The shell of *Chondrocyclus* species is up to 7 mm in diameter, but usually smaller, lenticular or discoidal and bears an elaborate periostracum with lamellate axial costae, expanded into bristles, triangular or rounded flanges, these extensions arranged in a series of spiral rows. The function of such costly structures is suggested to increase adhesion to wet surfaces during foraging (Pfenniger, *et al.*, 2005) and *Chondrocyclus* is only active during humid conditions. The shell is smooth once the periostracum is removed and there are no spiral keels on the shell, but spiral grooves may occur. The protoconch may be flat or mammillate and tilted. The thin, circular peristome is detached from the last whorl in adult specimens and droops downwards. The operculum is chitinous (corneous), with no calcification, and duplex, consisting of a translucent, thin, smooth inner portion, and a shallow to deeply concave outer portion, formed by an erect spiral lamella which is elevated towards the outer whorls and bears a fringe reflexed over the peristome. The radula is taenioglossate (central tooth flanked on either side by three laterals in each row), all with well-developed, sharp cusps. The penis lies dorsally on the neck immediately behind the right tentacle, and consists of a muscular cylindrical or flattened shaft with annular rugae and a shorter, tapering intromittant organ without flagellum.

This study will complement other research on composition, spatial distribution and phylogenetic diversity of low-vagility forest-dwelling invertebrates and expand the scientific evidence available for biodiversity conservation in South Africa. Forests cover only 0.1% of the country's land surface and are highly fragmented (Mucina & Geldenhuys, 2006). There is a growing body of information on various taxa in these habitats (e.g. Huber, 2003; Daniels *et al.*, 2009; Tilbury & Tolley, 2009; Daniels & Ruhberg, 2010; de Bivort & Giribet, 2010; McDonald & Daniels, 2012). These studies highlight the existence of cryptic species and reveal marked levels of endemism previously undetected. Information on systematics, distribution patterns and the processes that contribute to diversity and areas of endemism are essential for biodiversity conservation. This study will provide comparative material on a widespread molluscan group.

2 Materials and Methods

2.1 Molecular phylogenetics

For molecular analysis whole specimens were collected into 100% ethanol. Shells were first cracked to ensure penetration of ethanol to all tissues. One species of Cyclophoridae from Madagascar, five species from south-east Asia and one species belonging to a closely related family (latter six from Genbank) were included as outgroups. Specimens were dissected to separate shell, operculum and gut contents from the animal's body, which was macerated and incubated at 52°C for several hours or overnight. Total genomic DNA was extracted from several randomly selected specimens from each sampling locality using an Invitek Invisorb MSB Spin Tissue kit (Invitek, Germany) according to the manufacturer's instructions. Concentration and quality of DNA was tested with a Thermo Scientific NanoDrop 2000 spectrophotometer. Very small specimens yielded low concentration and the volume of extract used in PCR amplifications was adjusted accordingly to 100 ng DNA per reaction.

Portions of two mitochondrial genes were sequenced from each sample: the small subunit ribosomal 16S RNA (16S) and the Cytochrome Oxidase subunit I (COI). Primers used for amplification and sequencing reactions were: 16S - either 16Sar (Palumbi *et al.*, 1991) or 16Sar-chondro (5' GCCTGTTTAWCAAAAACAT, designed for this study) with 16Sbr (Palumbi *et al.*, 1991); COI - LCO-1490 with HCO-2198 (Folmer *et al.*, 1994). Polymerase Chain Reactions (PCR) were done on a GeneAmp 2720 Thermal Cycler or an Applied Biosystems Veriti 96 Well Thermal Cycler. PCR conditions were guided by the manufacturer's instructions of Bioline MyTaq^{TM}HS Mix and followed an initial denaturation of 3 minutes, 30 to 38 cycles of denaturation at 95°C for 15 seconds, annealing for 15 seconds and extension at 72°C for 30 seconds. In order to yield PCR products the number of cycles of denaturation, the annealing temperature and concentrations of primer and $MgCl_2$ were varied between samples. PCR products were confirmed by electrophoresis of 5µl PCR product and 5µl syber green tracking dye in a 1% agarose gel. Supernumery bands were obtained for samples from a few localities and then 10µl PCR product was run in the gel and the band of the correct size was excised under ultraviolet light. Successful amplification was not achieved in a small minority of cases.

PCR products were purified using the Invitek Invisorb MSB Spin PCRapace Purification kit and sequenced in both directions, or sent to Macrogen or to the University of Stellenbosch for purification and sequencing. Sequence trace files were checked for base ambiguities and edited

using BioEdit v7.2.5 (Hall, 1999) or Sequencher v4.5 (Gene Codes Corporation, Ann Arbor, MI, USA). The CO1 sequence data were imported into MEGA v6 (Tamura *et al.*, 2013), aligned using the Clustal W algorithm (Thompson *et al.*, 1994) and the alignments were checked against translated amino acid sequences. The 16S sequences were aligned using the online MAFFT v7 server (Katoh *et al.*, 2002) with the Q-INS-i Strategy Iterative Refinement method (Katoh & Toh, 2008). Sections with multiple gaps were deleted. Locality information of samples used for molecular analyses is given in Appendix 1.

A phylogeny was inferred using Maximum Likelihood (ML) and Bayesian Inference (BI) methods on four datasets using the computational resources of the CIPRES portal (hppt://www.phylo.org). The CO1 and 16S datasets were analysed separately and two concatenated datasets were analysed: one with 100% coverage of both genes, referred to as the Combined Conserved dataset (92 taxa) and one with partial coverage of each gene, referred to as the Combined Expanded dataset (133 taxa). Both datasets had a total of 1200 base pairs, 672 from CO1 and 528 from 16S.

The Combined concatenated datasets were submitted to partitioning analyses using Partitionfinder v1.1.0 (Lanfear *et al.*, 2012) to establish what partitions to use for the Maximum Likelihood analysis with the GTR+G model, and what nucleotide substitution models and data partitions would be needed for the Bayesian analysis (Table 1).

The 16S dataset was tested for the most appropriate model for the BI analyses using the BIC criteria in jModelTest2 (Guindon & Gascuel, 2003; Darriba, *et al.*, 2012) and the HKY+I+G was selected for 16S. Since the 16S gene is affected by indels that make alignment very difficult, the 16S dataset was also analysed with POY v4.1.2 (Phylogenetic tree inference using dynamic homologies), which uses unaligned sequences as characters (Varón *et al.*, 2010). ML analyses were performed using RAxML v8.2.3 and the GTR+G model was implemented in analyses of all datasets as recommended (Stamatakis, 2014) with four partitions (1st, 2nd and 3rd codon positions of CO1 and 16S) and 1000 bootstrap repetitions. BI analyses were performed using MrBayes v3.2.2 (Ronquist *et al.*, 2012). Bayesian posterior probability support was estimated by running four Markov chains (8 million generations each, with trees sampled each thousand generations). The first 25% of trees were rejected as burn-in. Stationarity was confirmed by examining the two runs on Tracer (Rambaut *et al.*, 2014) and the diagnostics in the log file (potential scale reduction factor data, plots of generation versus log likelihood values and average standard deviation of split frequencies).

Trees were visualised using FigTree v1.4.2 (available from http://tree.bio.ed.ac.uk/software/figtree) and rooted using the outgroups. Nodes with Bayesian posterior probabilities ≥0.95 and ML bootstrap support ≥80% were considered to be well-supported.

Table 2.1 Data partitions and model choice for Bayesian analysis of concatenated datasets generated by Partitionfinder.

Partition	No. of sites	Model
CO1_1	224	GTR+I+G
CO1_2	224	GTR+I
CO1_3	224	GTR+G
16S	528	GTR+I+G

2.2 Morphology

Material examined is housed mainly in the East London Museum (ELM) and the KwaZulu-Natal Museum (NMSA). Most of this material has been accumulated by recent field surveys undertaken since the mid-1990s by D. Herbert and the author, assisted by staff of the ELM and NMSA. The specimens thus acquired have accurate and detailed provenance and habitat data. Importantly, fresh specimens with intact periostracum and operculum were collected throughout South Africa. Much of the past confusion surrounding the taxonomy of *Chondrocyclus*, including synonyms and failure to discriminate between species, arose because worn specimens do not display characters important for identification. Types in The Natural History Museum, London (NHMUK) and specimens in the National Museum of Natural History, Leiden (RMNH) were also examined. Fresh specimens were donated to the NHMUK, RMHN and the National Museum of Wales, Cardiff (NMW).

For anatomical study, living adult specimens were drowned in sealed containers and preserved in 70% ethanol for dissection. Cleaning and dissections were performed under a Euromex dissecting microscope. Shells and opercula were cleaned in an ultrasonic bath and then manually under the dissecting microscope to remove caked soil from within the delicate ornamentation of both structures. Radulae were extracted by maceration of the front end of the body in dilute NaOH and the radula teased out from the surrounding tissue, and rinsed in distilled water. The radula was then placed in a drop of ethanol on a stub with double-sided carbon tape and manouvered into position as the ethanol dried. The teeth at the outer edge of each row were folded outwards to expose the seven teeth per row. Penes were prepared for

examination by cutting away the mantle tissue to expose the penis where it lies on the neck behind the right tentacle. Samples were dehydrated by placing in a series of ethanol of increasing concentration, and dried in a Polaron Critical Point Drier.

Shells, opercula, radulae and penes for Scanning Electron Microscope examination were coated with gold-palladium and examined at 5-20 kv accelerating voltage in a Tescan Vega SEM. Colour photographs were taken using an Olympus SZX 16 microscope with the AnalySIS programme.

Shell diameter (W) and height (H) measurements (Fig. 2.1) were made using an eyepiece graticule. The number of lamellate axial costae on the last whorl were counted. Immature shells (peristome not detached from last whorl) were excluded from the data used to calculate W:H ratios and densities of lamellate costae. The number of protoconch whorls were counted as shown in Fig. 2.1.
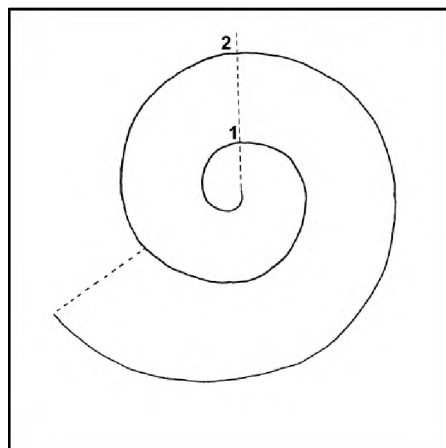
Figure 2.1 Diagram illustrating method for measuring protoconch whorls.

Systematic descriptions are provided for all taxa identified during this study. Materials examined have been summarised, but full details are provided in a supplementary file.

The following acronyms and abbreviations are used:

ELM	-	East London Museum, East London, South Africa
NMSA	-	KwaZulu-Natal Museum, Pietermaritzburg, South Africa
NHMUK	-	The Natural History Museum, London, United Kingdom
NMW	-	National Museum of Wales, Cardiff, Wales

RMNH	-	National Museum of Natural History, Leiden, The Netherlands
SA	-	South Africa
E. Cape	-	Eastern Cape
W. Cape	-	Western Cape
KZN	-	KwaZulu-Natal

2.3 Evaluation of threatened species status

Extent of Occurrence (EOO) was calculated using ArcGIS 10.2.2 from polygons of projected geographic range of each species, guided by latitude and longitude co-ordinates of all *Chondrocyclus* records in the collections of the East London Museum and KwaZulu-Natal Museum and field knowledge. Area of Occupancy (AOO) was calculated within these polygons using a compilation of different datasets including the Department of Agriculture, Forestry and Fisheries' National Forest Inventory which contains the areas of all mapped patches of forest in the country. Unmapped patches within polygons were mapped and these areas were included.

3 Results

3.1 Molecular phylogenetics

Sequence alignment for CO1 was unambiguous as no length variation or premature stop codons were observed.

Molecular analyses found strong support for monophyly of *Chondrocyclus*. Phylogenetic reconstruction by BI and ML methods of combined and single gene datasets all produced phylograms containing five well-supported clades (Fig. 3.1). The relationships between the clades were usually congruent and any differences are mentioned below. The support for deeper nodes improved with the inclusion of all four outgroups. All analyses, except the single gene CO1 BI and ML analyses, recovered the Isipingoensis clade, consisting of populations of what is known as *Chondrocyclus isipingoensis*, as sister to a clade containing all the other major clades. Within the latter assemblage there was strong geographic structure with a division into an Eastern Clade and a Western group of clades in the vicinity of Port Elizabeth (Fig. 3.2). In all analyses the Western group of clades contained three monophyletic clades: two in the western half of the Western Cape (the Southwestern Cape and Overberg clades) and one eastwards of this in the Southern Cape and western half of the Eastern Cape (Southern – Eastern Cape clade abbreviated as the S + E Cape clade) (Fig. 3.1 and 3.2). There was moderate support for a combined Western Cape clade in the "Combined Expanded" analysis, but not in the "Combined Conserved" or in the single gene analyses. There was a geographical division within the S + E Cape clade into a western and an eastern assemblage in the region of the Gamtoos River, although missing CO1 data for several populations in the S + E Cape clade probably led to lack of resolution of the relationships within this clade. All analyses produced identical topologies of the terminal branches, representing populations of species, except for two species, *C. exsertus* and *C. "kevincolei"* (discussed below). (Note: names of taxa recognized herein as undescribed species appear in quotation marks to distinguish them from described species.)

All analyses recovered four well-supported groups within the Isipingoensis clade and the group at the western end of the mountain range in the Bedford and Somerset East area formed a monophyletic subclade, denoted herein as *Chondrocyclus "oxygala"* (Fig. 3.3). The position of *Chondrocyclus exsertus* was not resolved in the BI and ML analyses. The two populations of *C. exsertus* formed a moderately well-supported cluster (69%) in the "Combined Expanded" ML analysis but not in the Bayesian analysis (Fig. 3.3). CO1 data for *C. exsertus* were not obtained,

but in the 16S analyses *C. exsertus* formed a moderately to well-supported cluster with the Ongoye sample.

The POY analysis of the 16S dataset recovered the same five clades, with populations of *C. isipingoensis* forming a clade and all other populations forming a separate clade, and within the latter, a division into an Eastern Clade and a western group of clades.

The Isipingoensis clade is sympatric with the Eastern Clade and the S + E Cape clade (Fig. 3.2). None of the other clades are sympatric with one another. Within the two Western Cape clades (Fig. 3.4) and the S + E Cape clade (Fig. 3.5) the species are all allopatric, and the majority of populations occur in isolated forests with unsuitable intervening habitat. The Eastern clade occupies the strip of forest along the south-east coast and contains several instances of sympatric species (Fig. 3.6).

3.2 Morphology

Morphological scrutiny identified groups of populations based on combinations of characters, corresponding to the five clades identified in the molecular analyses (Table 3.1). A glossary of anatomical terms appears in Appendix 2. Certain morphological characters used to identify the major clades appear to closely resemble those features described in other cyclophorids or species in closely related families in Africa, Asia and New Zealand (e.g. see Morton, 1952; Bruggen 1983, 1985, 1986; Emberton, 2003; Marshall & Barker, 2007; Lee *et al.*, 2008a; Rowson *et al.*, 2010). These include multiple spiral rows of hairs on the periostracum, radular structure, mammillation of the protoconch, and penis shape.

Features of the periostracum distinguishing these clades were the type of expansions of the axial lamellate costae (hairs/bristles, pointed or rounded flanges (Fig. 3.7)) and whether there was a single spiral row of these structures around the periphery of the shell or multiple rows.

Table 3.1 Congruence of molecular and derived morphological data (in bold) in delineating five major clades.

Molecular Clade	Morphological characteristics			
	Periostracal flanges	**Radula, 2nd lateral tooth**	**Protoconch**	**Penis**
Isipingoensis	Hairs, multiple rows	2 large cusps	Mammillate	Cylindrical
Eastern	**Rounded "paddles"**, multiple rows	**3 large cusps**	**Flat**	**Flattened**
Southwestern Cape	**Pointed spines, single row round periphery**	**3 large cusps**	Mammillate	Cylindrical
Overberg	Hairs, multiple rows	**3 large cusps**	Mammillate	Cylindrical
S + E Cape	**Pointed or rounded, single row, periphery**	2 large cusps	Mammillate	Cylindrical

The radula was taenioglossate, i.e. each row contained seven teeth and each tooth had cusps. The major difference between the clades lay in the second lateral tooth, which had either two or three large cusps (Fig. 3.8). The rachidian (central) tooth in the Isipingoensis clade had a serrated upper edge (Fig. 3.8A). The protoconch was mammillate in the majority of clades except in the Eastern Clade where it was flat (Fig. 3.9) and the degree of malleation varied (Fig. 3.10). The penis was situated on the neck immediately behind the right tentacle (Fig. 3.11A) and consisted of a muscular shaft with annular rugae and a shorter, tapering intromittant organ. The shaft was more-or-less cylindrical in the majority of clades; in the Eastern Clade it was dorso-ventrally flattened and laterally expanded towards the distal end (Fig. 3.11B).

3.3 Systematics

The placement of the Isipingoensis clade as sister to all other clades (Fig. 3.1) together with morphological distinctiveness were considered as evidence for separation of *Chondrocyclus* into two genera. However, diagnosis of the two genera was hampered by lack of consistently exclusive, diagnostic morphological features within species belonging to each assemblage, so it was decided to retain one genus.

A combination of molecular and morphological data also proved useful in delimitation of the species within the major clades, but relationships between the clades were not consistent in all analyses. There were no incongruencies between the mtDNA-based trees and morphology-based species delimitations and biogeography and hence these three types of data were considered independent sources of evidence for species-level assignments. Effort was directed at gathering

nuclear ITS2 sequences but an adequate data set was not assembled and it was decided to exclude these unsatisfactory data. The inferred molecular phylogenies guided observations of morphological similarities or differences to inform species delimitation, particularly when morphological differences were subtle. Many populations of *Chondrocyclus* are allopatric and application of phylogenetic data assisted with evaluation of species boundaries when compared to divergence between sympatric species. Species discrimination within the major clades depended on the number of spiral rows of expansions of the periostracum, differences in their shape (spine-tipped, pointed or rounded), the density of axial costae, and the form of the operculum (Fig. 3.12). The latter character was useful for discriminating species in combination with periostracal details; if these appeared to be similar, the operculum sufficed on its own.

All analyses within the Isipingoensis clade produced consistent groupings of populations (a group at the western limit of the range of the clade in the Bedford and Somerset East area was sister to all other sampled populations; a group in mainly coastal regions of the Eastern Cape; a group in central Transkei interior and Kei River valley; a group in eastern Transkei interior) (Fig. 3.3). *Chondrocyclus exsertus* has unique morphological features within the genus (Fig. 4.24). It has a single row of slightly expanded flanges on the axial costae around the periphery and the protoconch not mammillate. The radula conforms to that of the Isipingoensis clade. Observations of morphological variation between the groups identified above, and the nesting of *C. exsertus* within this clade, led to the conclusion that *C. "isipingoensis"* is a species complex. The clade in the Bedford and Somerset East area is described as a new species in this study (*C. "oxygala"*) while other groups of populations are not investigated here.

Consistent and clearly recognizable morphological differences are apparent between certain populations within the Eastern Clade, whereas other populations display subtle differences. The operculum is a useful character for discriminating species. The molecular analyses helped to inform decisions regarding interspecific variation between existing species and potentially undescribed species as opposed to cases of intraspecific variation. Based on the operculum, it would appear that two lineages overlap in central to northern Transkei, one with a relatively flat operculum and the other with a deeper and more elaborately ornamented operculum (Fig. 3.12), but the molecular analyses did not resolve this deeper division.

All data were consistent in delineating two distinct clades in the south-west of the Western Cape, containing at least three species, but the relationship between the two clades is unresolved. The clade in the Agulhas – Langeberg Mountains contains a well-supported clade in the Langeberge, while the populations on the Agulhas Plain (*C. "kevincolei"*) also form a well-

supported monophyletic group in certain analyses, but not in others; the populations sampled display morphological differences and large genetic divergence.

The 5th major clade, the S + E Cape clade, contains two well-supported clades in the majority of molecular analyses, each with two groups of populations (species) structured geographically from west to east. *Chondrocyclus "amathole"* sp. n. has rounded, paddle-like flanges resembling those of the Eastern clade, but other features conform to those of the S + E Cape clade.

Seventeen species are recognized here and described or redescribed; all are endemic to South Africa. Ten are new species, some were cryptic species known previously under other names but were overlooked as being distinctive due to lack of fresh material for examination, while others are newly discovered. Taxa described in this thesis are named accordingly throughout, although not yet formally published. Species were diagnosed on recognizable morphological characters and are distinct genetic lineages. The phylogenies consistently inferred several other distinct genetic lineages but these are not described pending further investigation based on more extensive geographic coverage of samples. *Chondrocyclus meredithae* and *C. chirindae* recorded in Malawi and Zimbabwe respectively are removed from the genus based on morphology of shell and operculum and placed in *Cyathopoma*.
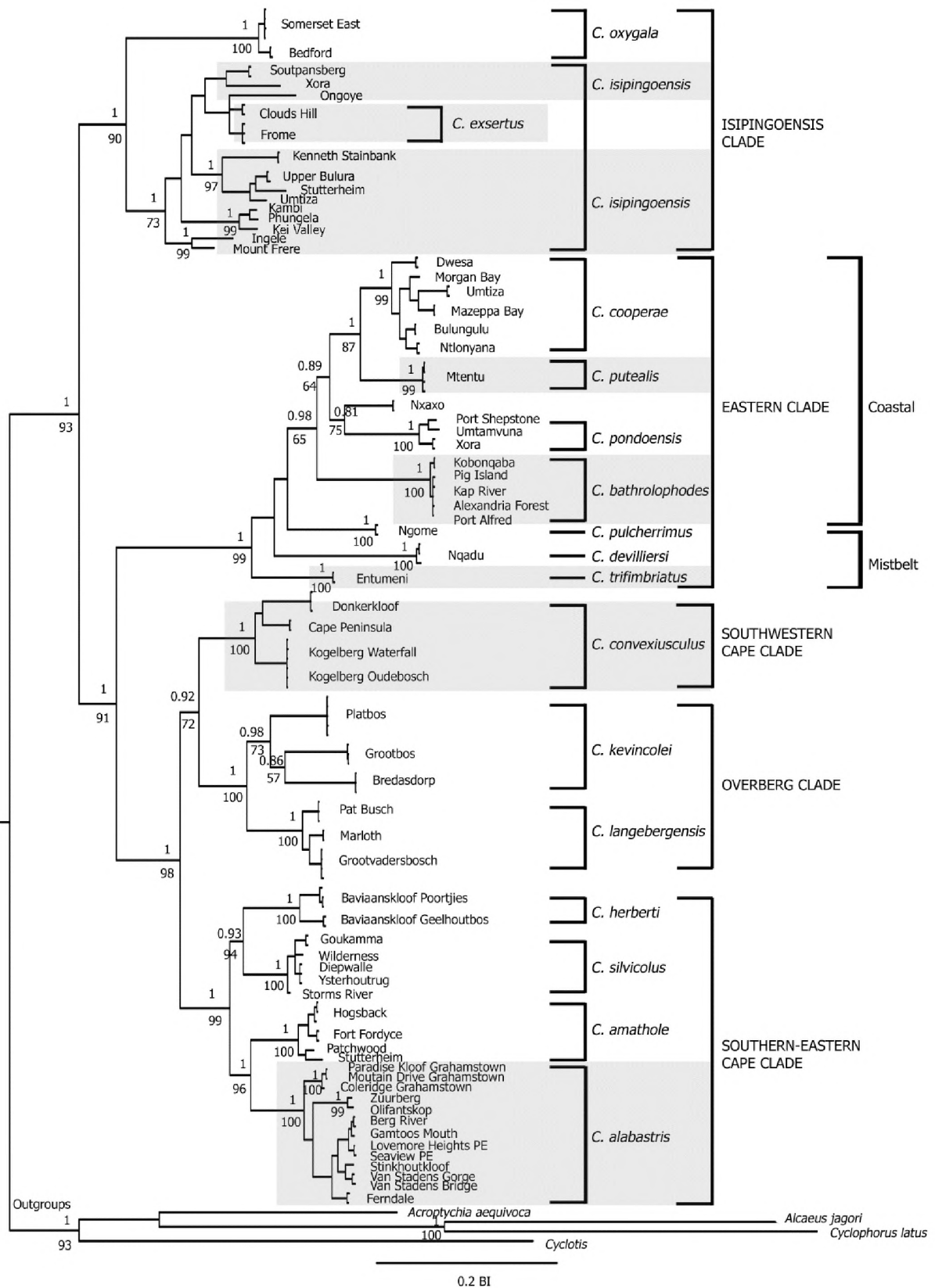
Figure 3.1 Bayesian Inference phylogram based on partial sequences of CO1 and 16S RNA genes, indicating major clades. Numbers above nodes indicate posterior probabilities and below nodes indicate ML bootstrap support. Described species are highlighted in grey; other taxa are potentially new species for which descriptions are provided in this thesis.
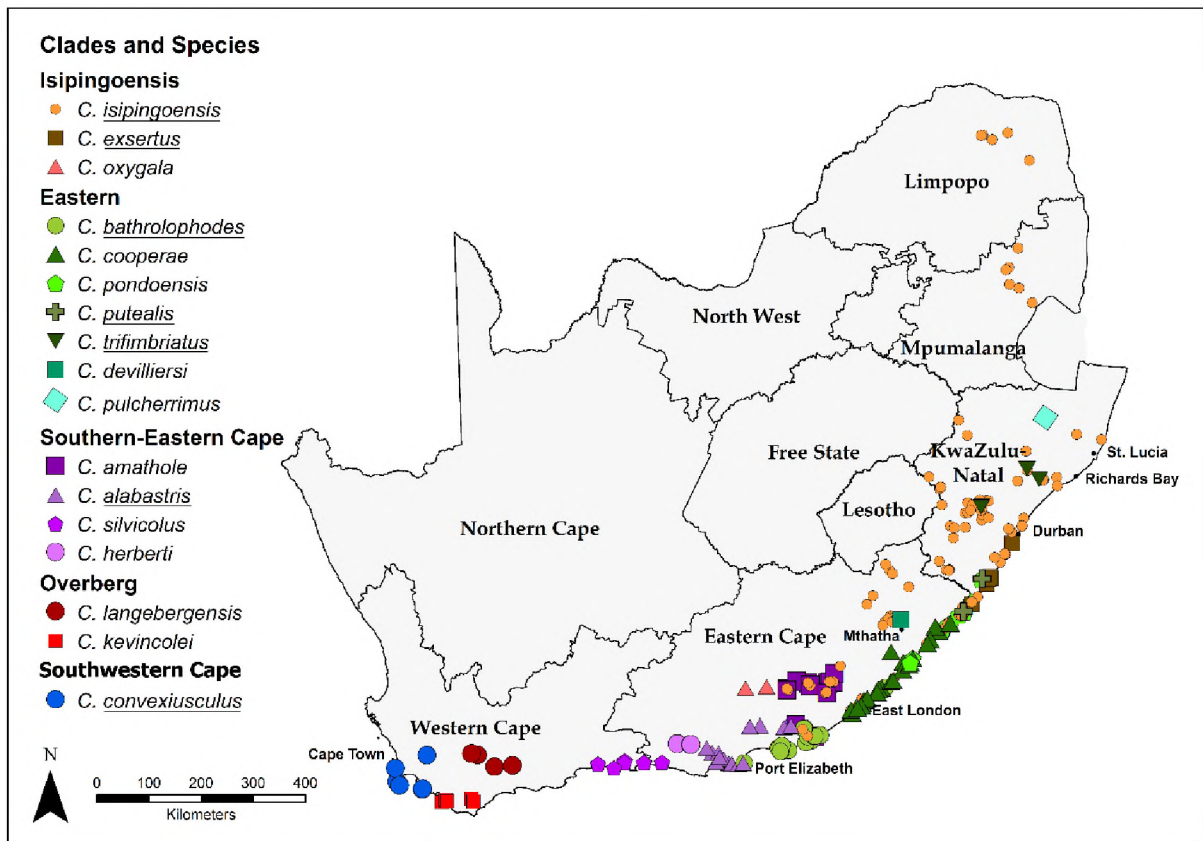
Figure 3.2 Map of distribution of the five major clades corresponding to Fig. 3.1. Described species are underlined; others are potentially new species.
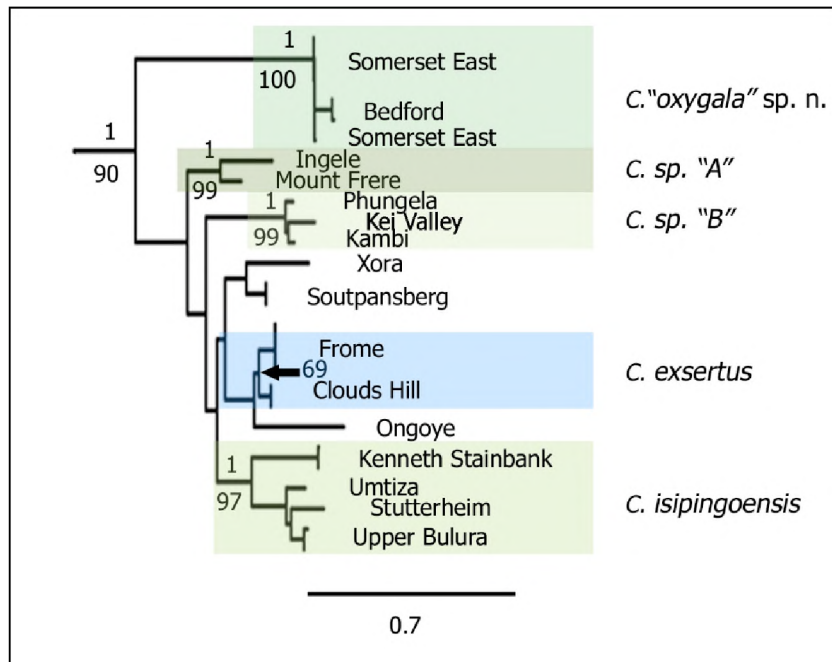
Figure 3.3 Maximum Likelihood phylogram of the Isipingoensis clade based on partial sequences of CO1 and 16S RNA genes. BI posterior probabilities are indicated above nodes and ML bootstrap support values below nodes for each of the well-supported groups of populations of *Chondrocyclus isipingoensis* (highlighted in shades of green). These are potentially new species; one, *C. "oxygala"*, is described herein. The two populations of *C. exsertus* do not form a well-supported cluster (highlighted in blue).
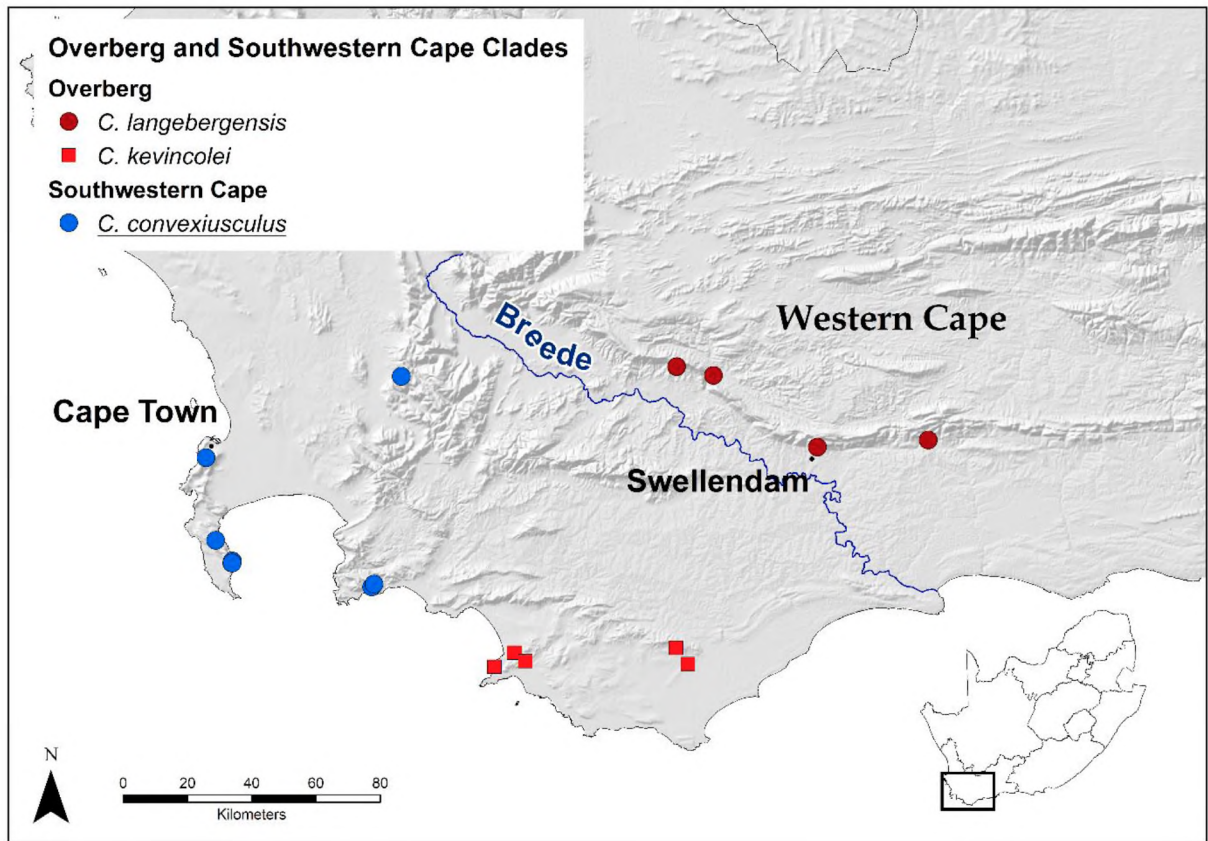
Figure 3.4 Map of distribution of the two major clades in the Western Cape, the Overberg clade and the Southwestern Cape clade. The described species is underlined; others are potentially new species.
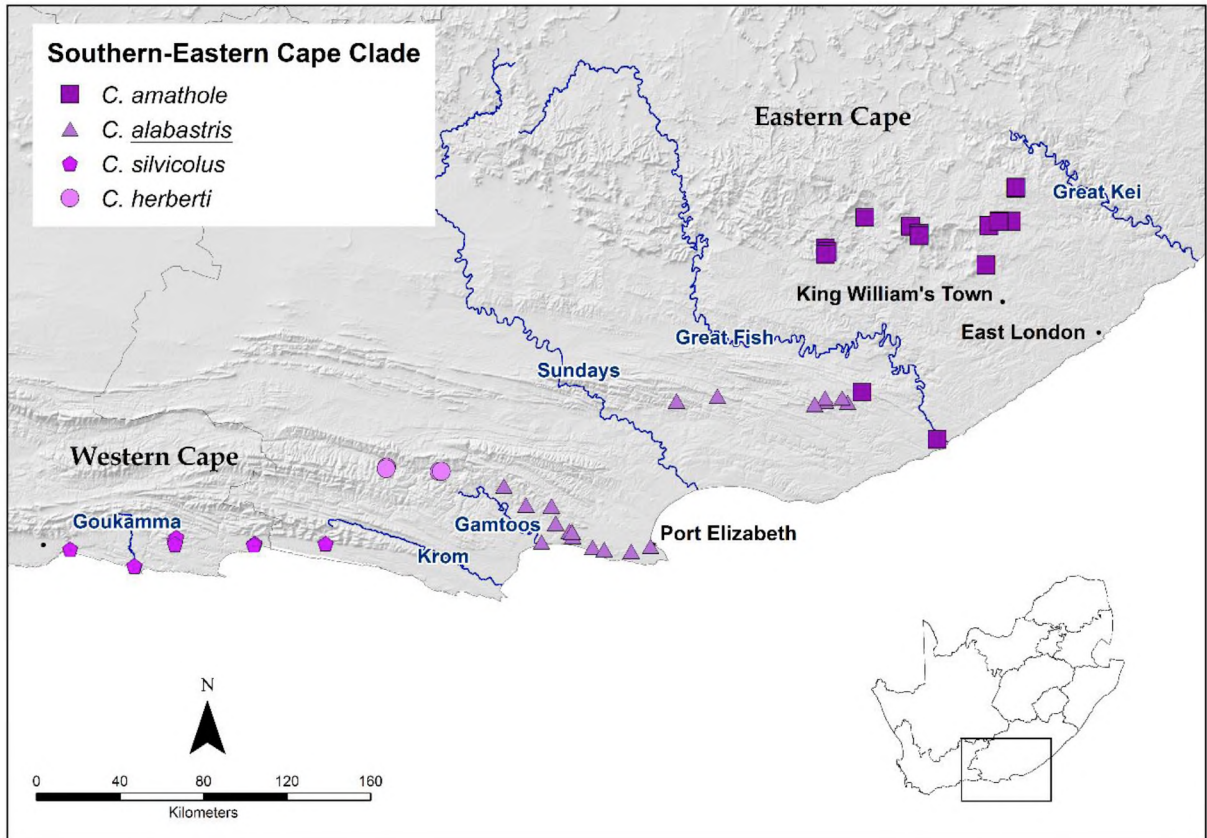
Figure 3.5 Map of distribution of species in the Southern-Eastern Cape clade in the southern Cape and western half of the Eastern Cape. The described species is underlined; others are potentially new species.
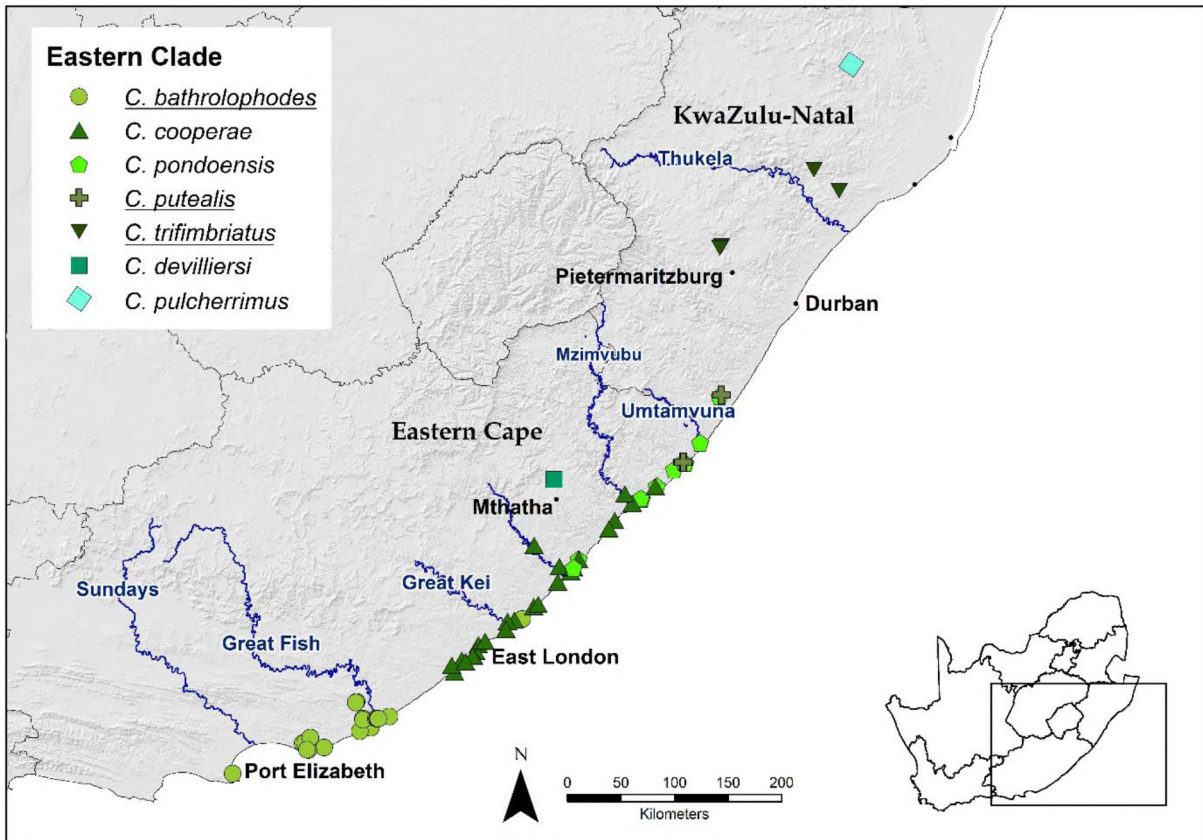
Figure 3.6 Map of distribution of species in the Eastern clade, on the coast of the Eastern Cape and KwaZulu-Natal and extending inland. Described species are underlined; others are potentially new species.
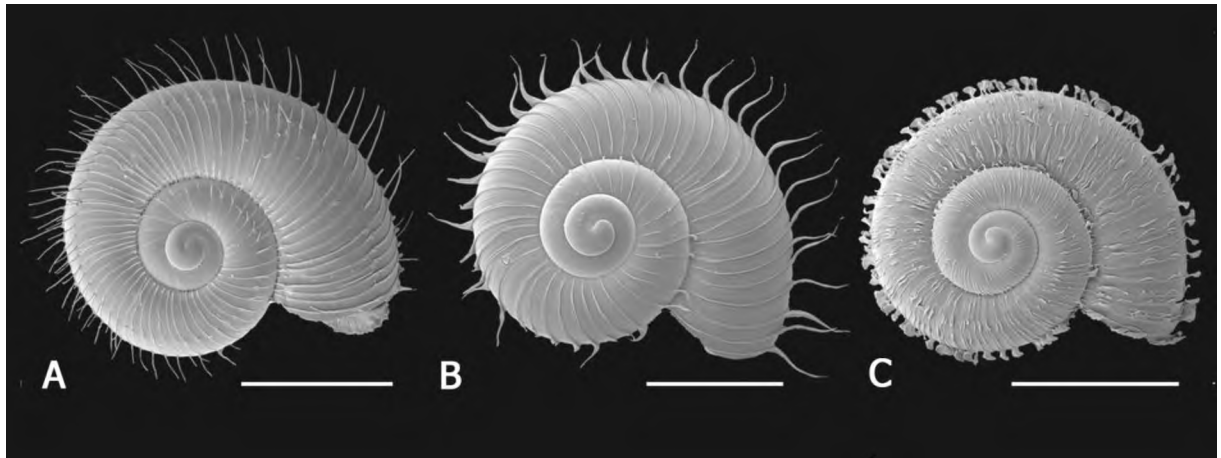
Figure 3.7 Shells of juveniles showing periostracum. (A) Spiral rows of hairs, *Chondrocyclus isipingoensis*, scale bar = 1 mm; (B) single row of flanges round periphery, *C. convexiusculus*, scale bar = 1 mm; (C) multiple spiral rows of rounded flanges, *C. "cooperae"*, scale bar = 2 mm.
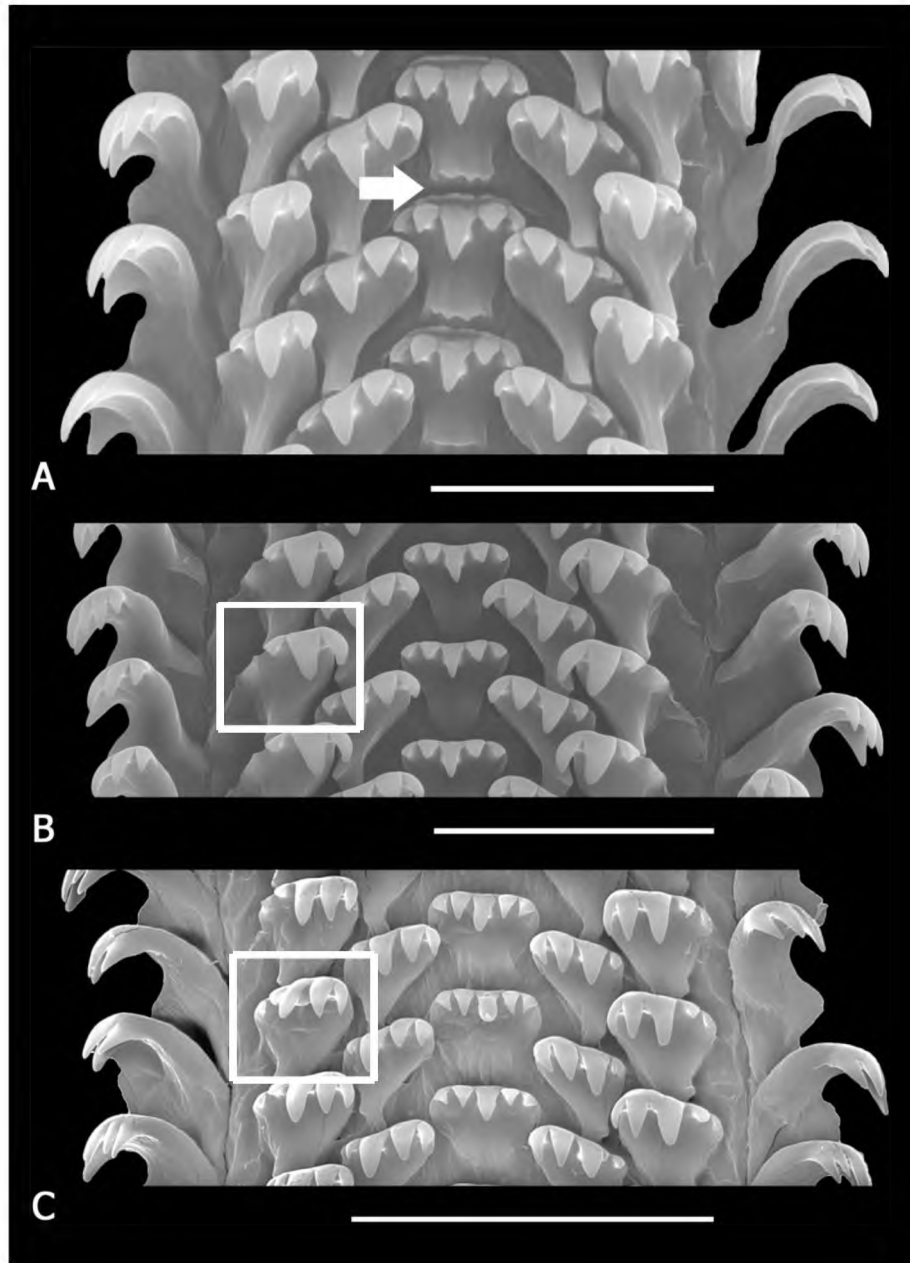
Figure 3.8 Close-up of segments of radulae to show distinguishing features. (A) *Chondrocyclus isipingoensis*, arrow indicates serrated upper edge of rachidian (central) tooth, scale bar = 20 µm; (B) second lateral tooth with two large cusps, *C. "silvicolus"*, scale bar = 50 µm; (C) second lateral tooth with three large cusps, *C. bathrolophodes*, scale bar = 50 µm.
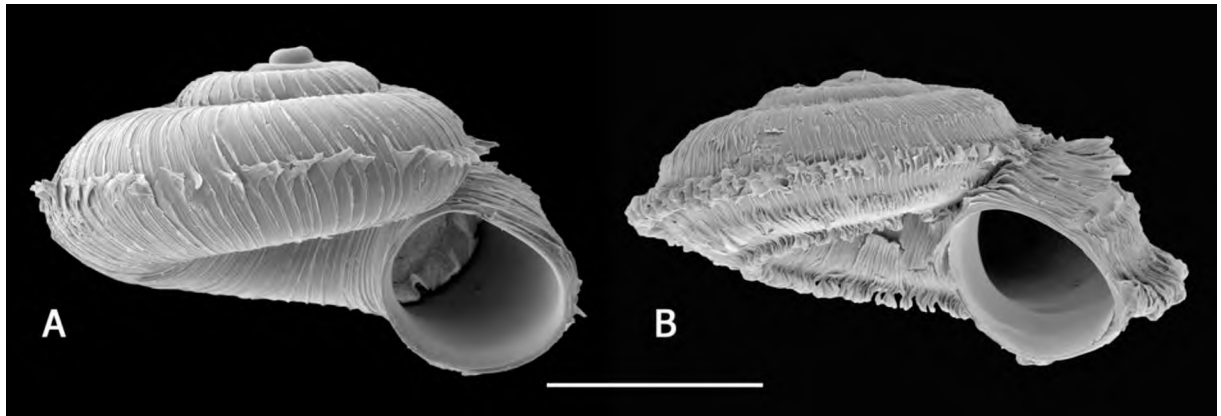
Figure 3.9 Examples of protoconch shape: (A) mammillate protoconch of *Chondrocyclus* *"silvicolus"*, (B) flat protoconch of *C. "pondoensis"*, scale bar = 2 mm.
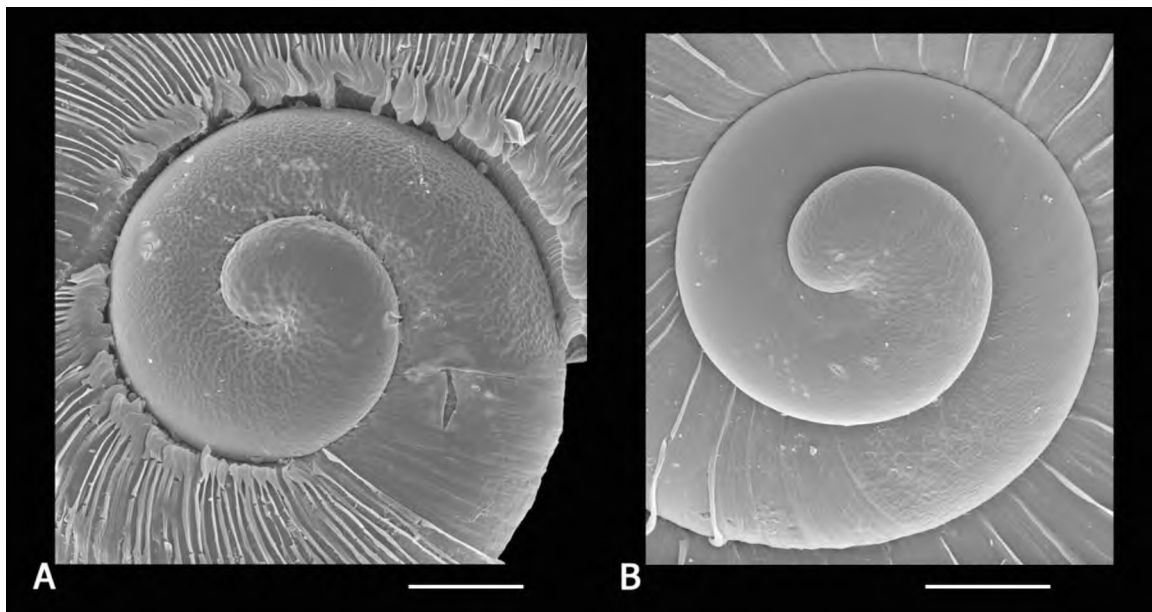
Figure 3.10 Protoconch detail: (A) malleated protoconch of *Chondrocyclus* *"pulcherrimus"*, scale bar = 200 μm, (B) relatively smooth protoconch of *C. convexiusculus*, scale bar = 500 μm.
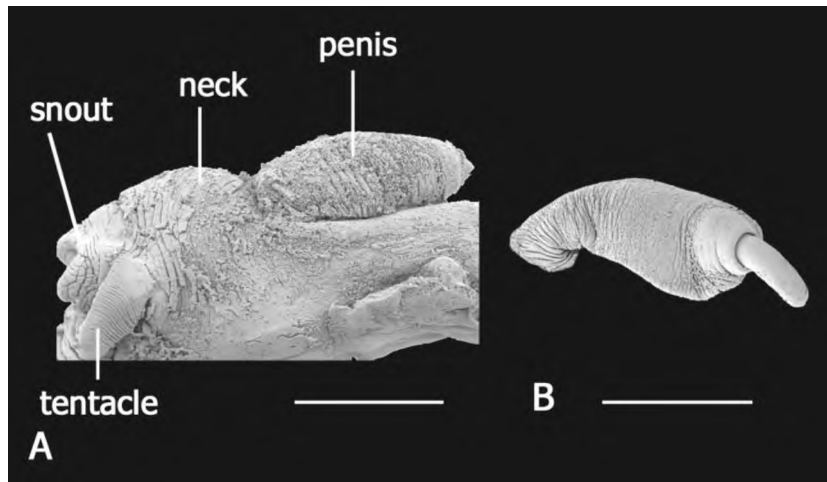
Figure 3.11 Penis: (A) position on neck; (B) example of dorso-ventrally flattened penis of *Chondrocyclus "cooperae"*; scale bars = 1mm.
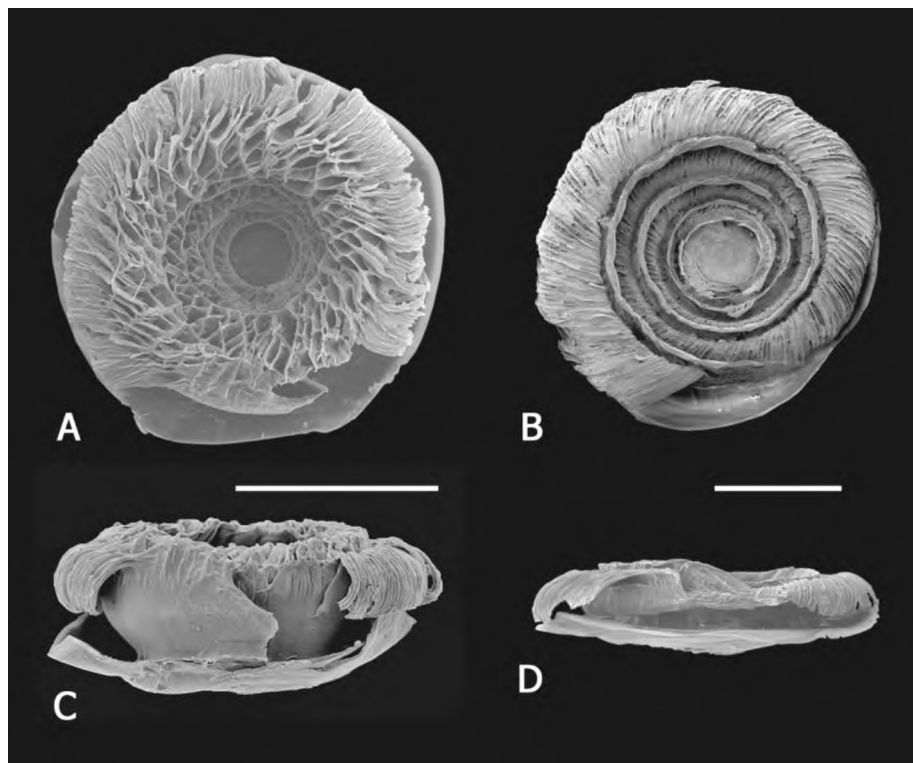
Figure 3.12 Opercular variation in the Eastern Clade: (A,C) *Chondrocyclus putealis,* scale bar = 500 μm; (B,D) *C. "pulcherrimus"*, scale bar = 1mm.

4 Taxonomy

4.1 Nomenclatural disclaimer

This thesis or copies of it are not to be considered published works for the purposes of the International Code of Zoological Nomenclature (ICZN, 2000, Arts. 8.2, 9.12). New taxon names and nomenclatural acts within it are disclaimed and are therefore not available in the sense of the Code (ICZN, 2000, Art. 8.3) until validly published elsewhere. Names of taxa recognized herein as undescribed species are used throughout and appear in quotation marks, and descriptions are written in the form of a manuscript. Type material is listed with redescriptions and descriptions; other material examined is listed in Appendix 3.

4.2 Taxonomy

Class Gastropoda
Superfamily Cyclophoroidea Gray, 1847
Family Cyclophoridae Gray, 1847
Genus *Chondrocyclus* Ancey, 1898

Chondrocyclus: Ancey 1898: 136. Type species: *Cyclostoma convexiusculum* Pfeiffer, 1855, by original designation; Kobelt, 1902: 230; Connolly, 1929: 239; Connolly, 1939: 536; Herbert & Kilburn, 2004: 90.

Diagnosis. – Shell dextral, small, depressed, lenticular or discoidal; aperture circular, last whorl descending near aperture, peristome not thickened, continuous and free; umbilicus wide and deep, extending to summit and exposing all the whorls; periostracum glossy and lacquer-like with lamellate axial costae at regular intervals, expanded into hairs or flanges around the periphery; operculum duplex, corneous; inner portion consists of a thin disc which grows outwards in a tight spiral, smooth on inside where it attaches to foot; fused to disc on its outer surface is a multispiral, elevated horny blade-like lamella formed by fused bristles; height of lamella increases as it spirals outwards forming a concave exterior element; lamella not vertical, but stepped or flared, so that diameter of each whorl larger at proximal edge of lamellar blade; a fringe of fused bristles emanates from outer surface of each lamellar whorl; fringe reflexed over peristome but operculum can be withdrawn into aperture; radula taenioglossate (central tooth flanked on either side by three laterals in each row); penis lies dorsally on neck immediately behind right tentacle and consists of a stout, muscular shaft, cylindrical or dorsoventrally flattened and wrinkled along most of its length due to annular rugae, and a terminal, tapering intromittant organ without flagellum; seminal tube completely enclosed without seminal groove.

Key to species of *Chondrocyclus*

1   Periostracum bears spiral rows of hairs arising from axial lamellae...........................2

-    Axial lamellae of periostracum expanded into pointed or rounded flanges......................5

2   Operculum flat, very fragile and pale corneous honey-brown; radula with 2 large cusps on second lateral tooth..3

-    Operculum slightly concave, robust and dark brown; second lateral tooth of radula with 3 large cusps; Western Cape only...4

3   Three spiral rows of hairs around periphery; upper edge of rachidian smooth........*"oxygala"*

-    More than three spiral rows of hairs on body whorl; upper edge of rachidian tooth serrated..*"isipingoensis"*

4   Distinct spiral grooves on shell corresponding to rows hairs........................*"kevincolei"*

-    Spiral grooves weak if present..*"langebergensis"*

5   Protoconch mammillate and tilted..6

-    Protoconch not mammillate or tilted..10

6   Axial lamellae expanded into broadly rounded flanges around periphery; lamellae with numerous ridges perpendicular to shell surface...*"amathole"*

-    Periostracal flanges taper towards their proximal ends..7

7   Flanges taper to rounded point..8

-    Flanges taper to spine tip..9

8   Axial lamellae widely spaced; approx. 45 on body whorl..............................*"herberti"*

-    Axial lamellae less widely space, approx. 70 on body whorl..........................*"silvicolus"*

9   Flanges taper from broad base into a long spine; second lateral tooth of radula with 3 large cusps; Western Cape ....*convexiusculus*

-    Flanges taper gradually towards tips; if spine-tipped, spine short; second lateral tooth of radula with 2 large cusps; Eastern Cape...*alabastris*

10   Axial lamellae slightly expanded around periphery, but not produced into flanges; second lateral tooth of radula with 2 large cusps..*exsertus*

-    Axial lamellae expanded round periphery into raised broadly rounded or quadrangular flanges second lateral tooth of radula with 3 large cusps; penis shaft dorsoventrally flattened and expanded laterally towards distal end...11

11   Operculum deeply or shallowly cup-shaped in side view 12

-    Operculum more or less flattened in side view with outer portion parallel to disc surface and appears attached to disc by pedestal..14

12   Body whorl with at least 6 spiral rows of broadly rounded flanges..................*"cooperae"*

-    Body whorl with 3 spiral rows of broadly rounded flanges.......................................13

13   Operculum deeply cup-shaped; southern Kwazulu-Natal and northern Transkei ....*putealis*

-    Operculum cup-shaped; Albany area and southern Transkei ....*bathrolophodes*

14	Operculum with spiral lamella of outer portion raised above level of fringe in side view; southern KwaZulu-Natal and Transkei ....”*pondoensis*”
-	Operculum with spiral lamella not raised above fringe...15
15	Body whorl with only one row of broadly rounded flanges around periphery......”*devilliersi*”
-	Body whorl with multiple spiral rows of rounded or paddle-shaped flanges 16
16	Body whorl with 12 spiral rows of flanges; spire almost flat ....”*pulcherrimus*”
	Body whorl with 5 spiral rows of flanges ....*trifimbriatus*

Chondrocyclus convexiusculus (Pfeiffer, 1855)

Fig. 4.1

Cyclostoma (Cyclophorus) convexiusculum Pfeiffer, 1855: 104. Type loc.: Simonstown [Macgillivray]
Cyclophorus convexiusculus var. minor Benson, 1856: 438. Type loc.: Table Mountain [Layard]
Chondrocyclus convexiusculus Kobelt, 1902: 230; Connolly, 1939: 536; Herbert & Kilburn, 2004: 92.

Diagnosis. – Shell small, depressed, lenticular; protoconch mammillate and tilted; periostracum with axial costae developing at the periphery broad triangular flanges each terminating in a long, hair-like spine; operculum flattened, exterior portion shallowly concave, with step-shaped multispiral lamella terminating in a long solid fringe; radula with three large cusps on second lateral tooth.

Description (Fig. 4.1A-K). – Shell small, depressed, lenticular, adult width 3.97-5.18 mm, height 2.29-3.20 mm, width:height 1.59-1.88 (n = 21). Spire little exserted, each whorl rising just above the next, apex mammillate and tilted (Fig. 4.1A,C). Embryonic shell (Fig. 4.1E) approx. 2.25 whorls, microscopically malleate, sculpture strongest on earliest part, junction between embryonic shell and teleoconch evident with development of axial costae and threads. Teleoconch comprising 2.25 whorls, convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus broad and deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with lamellate axial costae at regular intervals, 44-61 (n = 16) on last whorl, developing at periphery broad triangular flanges terminating in a long, hair-like spine (Fig. 3.7B, 4.1F); intervals between costae with about 3-5 indistinct microscopic axial threads. Shell translucent glossy honey-brown or creamy-white when fresh. Living animal: head, tentacles and snout dark grey; underside of foot white. Operculum (Fig. 4.1H-I): duplex, outer portion concave, consists of multispiral lamella with almost 5 whorls, each step-shaped; the growing edge of the lamellar blade angular and is more or less perpendicular to disc where it is attached; long fringe of fused bristles emanates from outer side of lamellar blade and curves

upwards and outwards forming a furrow between fringe and lamellar blade partially covered by top edge of lamellar blade which curves outwards; top edge of lamella projects above fringe; fringe of each whorl fused to lamella of following whorl. Radula (Fig. 4.1G): rachidian with 5 cusps, central cusp approx. twice as long as two on either side of it; first and second lateral tooth each with four cusps and a swelling representing the fifth cusp, first three cusps (from centre) increasing in size and fourth considerably smaller. Penis (Fig. 4.1J-K): shaft more-or-less cyclindrical with slightly swollen distal end and a short intromittant organ.

Type material: Syntypes of *Cyclostoma (Cyclophorus) convexiusculum* Pfeiffer, 1855 in NHMUK (20120231) (Fig. 4.1A).

Distribution (Fig. 3.4). – Western Cape, mountains of the Cape Peninsula and north-south running mountains to the east of the Cape Flats.

Habitat. – Western Cape Afrotemperate forest patches in sheltered ravines; in leaf-litter.

Notes. – *Chondrocyclus convexiusculus* resembles populations of *C. alabastris* from the Grahamstown area which also have spine-tipped flanges around the periphery. However, the spines are longer in *C. convexiusculus*, emanating from a relatively short, broad triangular proximal portion while in *C. alabastris* the triangular flanges taper gradually into the short spine tip (Fig. 4.4). Connolly (1929) distinguished this species from *C. alabastris* on the basis of the second lateral tooth of the radula, that of *C. convexiusculus* having three large cusps and *C. alabastris* two. This is confirmed by comparing Fig. 4.1G and Fig. 4.3F. There are also differences in the operculum discussed under *C. alabastris*. The molecular analyses placed *C. convexiusculus* and *C. alabastris* in different clades.

Chondrocyclus alabastris (Craven, 1880)

Figs. 4.2-4.3

Cyclotus alabastris Craven, 1880: 619. Type loc.: Cape Receife, Algoa Bay [Craven]
Cyclophorus (Maizania) alabastris Kobelt, 1902: 149.
Chondrocyclus alabastris Connolly, 1929: 238; 1939: 539.

Diagnosis. – Shell small, very depressed, lenticular; protoconch mammillate and tilted; periostracum with axial costae developing at the periphery elongated triangular flanges usually with serrated edges; operculum flattened, exterior portion shallowly concave, with step-shaped multispiral lamella terminating in solid fringe reflexed over peristome; radula with two large cusps on second lateral tooth.

Description (Fig. 4.2-4.3). – Shell small, usually very depressed, lenticular, adult width 3.7-5.32 mm, height 1.92-2.86 mm, width:height 1.79-2.28 (n = 20) (from The Island Nature Reserve, Port Elizabeth, close to type locality). Variation in dimensions between populations is given in Table 4.1. Spire little exserted, each whorl rising just above the next, protoconch acutely mammillate and tilted. Embryonic shell (Fig. 4.3A) approx. 2.25 whorls, microscopically malleate, sculpture strongest on earliest part, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising 2.5 whorls, convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus deep, extending to apex and exposing all the whorls.

Table 4.1 Measurements of *Chondrocyclus alabastris* showing variation between populations (W = shell width/diameter, H = height).

Site	W (max)	W (min)	Avg	H (max)	H (min)	Avg	W/H (max)	W/H (min)	Avg	n	Costae	Avg	n
Grahamstown	6.31	5.13	5.88	3.45	2.66	3.09	2.09	1.76	1.91	21	75-97	84	10
van Stadens	7.59	5.82	6.46	3.85	2.76	3.19	2.36	1.79	2.04	14	71-90	81	7
Olifantskop	6.9	5.92	6.55	3.75	3.01	3.40	2.26	1.75	1.93	20	70-94	82	9
Ferndale	7.1	5.72	6.32	3.35	2.56	2.95	2.38	2	2.15	12	77-81	79	6
Island	5.32	3.7	4.48	2.86	1.92	2.96	2.28	1.79	1.96	20	74-82	81	6
Maitland	6.56	4.44	5.36	3.55	2.17	2.74	2.26	1.8	1.97	13	77-87	82	3
Gamtoos	5.05	4.17	6.78	2.96	2.36	3.88	1.88	1.63	1.75	20	67-83	73	6

Periostracum glossy, honey-brown and lacquer-like with lamellate axial costae at regular intervals, 67-97 on last whorl (average 80; n = 47), their edges scalloped or serrated in the majority of populations (Fig. 4.4A) and expanded into elongated flanges around periphery, flanges smooth with a spine-tip in populations from around Grahamstown (Fig. 4.4B), intervals between costae with 3 – 6 microscopic axial threads. Shell translucent honey brown when fresh. Living animal dark grey. Operculum (Fig. 4.3C-E): duplex outer portion shallowly concave, and consisting of multispiral lamella with 5 whorls, at growing edge the top edge of lamellar blade sloping, becoming perpendicular to disc where it is attached; fringe of fused bristles emanates near top of vertical portion of lamellar blade on its outer surface and curves upwards and outwards forming a shallow furrow between fringe and lamellar blade, a second very short fringe emanates from lower down on lamellar blade; top edge of lamella does not project above level of fringe; fringe of each whorl fused to lamella of following whorl. Fringe overlaps disc slightly, but operculum can be withdrawn into aperture. Radula (Fig. 4.3F): rachidian with 5

cusps, central approximately twice as long as two on either side of it; first lateral tooth with four cusps and sometimes a vestigial fifth, first three cusps (from centre) gradually increasing in size and fourth considerably smaller; second lateral tooth with two large cusps and two small cusps towards outside. Penis (Fig. 4.3G-H): shaft more or less straight-sided and slightly flattened, with numerous annular rugae, intromittant organ short.

Type material: Syntypes of *Cyclotus alabastris* Craven, 1880 in NHMUK (1891.3.7.42-47) (Fig. 4.2A).

Distribution (Fig. 3.5). – Endemic to Eastern Cape, centered around Port Elizabeth and including the Albany district.

Habitat. – A variety of forest and Albany subtropical thicket types (Algoa Dune Strandveld, Albany Coastal Forest, Southern Mistbelt Forest, Great Fish Thicket); in leaf-litter.

Notes. – There is variation in size of shells between populations (Table 4.1), an observation also recorded by Connolly (1939). Shells in some populations are among the largest recorded in the genus (the only other species attaining a similar size is *C. "amathole"*). However, the types (Fig. 4.2A) from Cape Receife, populations at The Island Nature Reserve (40 km west of type locality) and at Gamtoos River mouth are smaller on average and the population at Gamtoos mouth has a distinctly less depressed shape than is typical for the species. Its width/height proportions resemble those of relatively less depressed species, e.g. *C. convexiusculus, C. "herberti"* and *C. exsertus*. Another variation between populations lies in the peripheral extensions of the axial lamellae: the edges are not serrated and each flange tapers gradually into a short spine tip in populations around Grahamstown (Fig. 4.4B). The latter populations superficially resemble *C. convexiusculus* (Fig. 4.4C), but the radulae clearly distinguish the species. The lamellar blade of the outer portion of the operculum of *C. alabastris* is relatively lower and hence the operculum is less concave and there is a very short fringe below the long fringe, absent in *C. convexiusculus*.

Chondrocyclus "herberti" sp. n.

Fig. 4.5

Diagnosis. – Shell very small, moderately depressed; periostracum with widely spaced axial costae developing at the periphery broad flanges, rounded distally; operculum duplex, exterior portion shallowly concave, with step-shaped multispiral lamella terminating in a long solid fringe reflexed over peristome; radula with two large cusps on second lateral tooth.

Description (Fig. 4.5). – Shell very small, moderately depressed, adult width 3.43-4.31 mm, height 2.09-2.69 mm, width:height 1.46-1.94 (n = 20). Spire moderately exserted, protoconch acutely mammillate and tilted. Embryonic shell (Fig. 4.5D) approx. 2.25 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising approximately 2.5 whorls, very convex, rapidly increasing, suture impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus deep, extending to summit and exposing all the whorls. Periostracum glossy, light yellowish-brown and lacquer-like with relatively widely spaced lamellate axial costae at regular intervals, 39-51 (n = 22) on last whorl (Fig. 4.5A-C), which produce broad flanges with rounded apices around periphery (Fig. 4.4D, 4.5E); intervals between costae with six to nine distinct microscopic axial threads. Shell translucent and corneous when fresh. Living animal very dark grey. Operculum (Fig. 4.5G-H): duplex, outer portion shallowly concave and consisting of multispiral lamella with 4.5 whorls, each step-shaped and increasing in height towards outside, sloping at growing edge; very long fringe of fused bristles emanates near top of lamellar blade with a slight groove between fringe and lamellar blade; lamellar blade does not project above level of fringe; fringe of each whorl fused to lamella of following whorl. Radula (Fig. 4.5F): rachidian with five cusps, central one approximately twice length of outer two on each side; first lateral tooth with four cusps and a vestigial fifth, third cusp (from centre) the largest; second lateral tooth with two very large cusps and two small ones on the outer side (outermost sometimes vestigial). Penis (Fig. 4.5I): shaft more or less cylindrical, distal half slightly expanded on left, intromittant organ short.

Holotype: SOUTH AFRICA: *E. Cape*: Baviaanskloof, Poortjies area (-33.65370°S: 24.527°E) riverine thicket on rocky bank adjacent to Witte River, 258 m a.s.l., in leaf litter, M. Cole, V. Ndibo & R. Daniels 26/i/2011 (NMSA W9279/T3077).

Paratypes: SOUTH AFRICA: *E. Cape*: same data as holotype (ELM D16891/T41, ELM W3691/T42; NHMUK 2012028, 2 specimens; NMW.Z.2012.065.00012, 3 specimens; RMNH MOL.330501, 3 specimens); Baviaanskloof, Western Poortjies area (-33.653667°S:24.516100°E), riverine thicket, in leaf-litter, D. Herbert, 9/x/2000 (NMSA V8632/T4127); Baviaanskloof, Poortjies area (-33.653685°S: 24.527176°E), riverine thicket, in leaf-litter, D. Herbert, 9/x/2000 (NMSA V8576/T4129); Baviaanskloof, Geelhoutbos (-33.633517°S:24.244917°E), forest in narrow kloof, in leaf-litter, D. Herbert, 11/x/2000 (NMSA V8763/T4130); Baviaanskloof, Geelhoutbos (-33.643001°S:24.242637°E), near pool and weir, forest in narrow kloof, 468 m, in leaf-litter, M. Cole 9/iii/2015 (ELMD 17990/T43); Baviaanskloof, Geelhoutbos (-33.635662°S:24.245741°E), near Hikers' hut, forest in narrow kloof, 373 m, in leaf-litter, M. Cole 9/iii/2015 (ELMD 17986/T44); Baviaanskloof wilderness area, Grassnek (-33.643001°S:24.242637°E), thicket/fynbos transition, under stones and amongst leaf litter, D. Herbert, 11/x/2000 (NMSA V8648/T4128).

Other material examined: Baviaanskloof, Western Poortjies area (-33.654181°S:24.515988°E), riverine thicket on rocky bank adjacent to Witte River, in leaf litter, M. Cole 8/iii/2015 (ELMD 17995).

Distribution (Fig. 3.5). – Eastern Cape, Baviaanskloof Mountains.

Habitat. – Indigenous forest patches in narrow ravines and Albany subtropical thicket (Groot Thicket group), in leaf-litter; also in subtropical thicket/fynbos transition, under stones and amongst leaf litter.

Notes. – Shell less depressed than in the majority of other species of *Chondrocyclus*. The periostracum of *C*. *"herberti"* is distinctive; the flanges have broadly rounded apices and an unserrated margin. *C*. *convexiusculus* has similar proportions and widely spaced costae, but shape of flanges as well as the radulae, distinguish the species. The population of *C*. *alabastris* at Gamtoos River mouth has similar proportions but the periostracal flanges are serrated. The operculum of *C*. *"herberti"* is more concave than in the other two species and lacks the furrow between the vertical portion of lamellar blade and fringe. *C*. *exsertus* also has a relatively high spire, but its periostracum and operculum are totally different.

When the animals were killed by drowning, they survived for weeks fully submerged with head and foot extended, which although not quantified, was noticeably longer than any other species. *C*. *"herberti"* can be very abundant; Herbert (pers. comm.) who first collected the species at Poortjies, found in excess of 1000 shells per m^2 in a leaf litter sample.

Etymology. – Named for Dai Herbert, Malacologist at the KwaZulu-Natal Museum, in recognition of his expertise in South African terrestrial molluscs and in acknowledgement of his mentorship.

Chondrocyclus "silvicolus" sp. n.

Fig. 4.6

Diagnosis. – Shell small, moderately depressed; protoconch mammillate and tilted; periostracum with widely spaced axial costae developing at the periphery broad flanges with pointed tips, tips are rounded not spine-tipped; operculum duplex, exterior portion shallowly concave, with step-shaped multispiral lamella terminating in a long solid fringe reflexed over peristome; radula with two large cusps on second lateral tooth.

Description (Fig. 4.6). – Shell small, moderately depressed, adult width 3.76-6.10 mm, height 2.09-3.84 mm, width:height 1.5-1.97 (n = 49). Spire moderately exserted, protoconch mammillate and tilted. Embryonic shell (Fig. 4.6D) approx. 2.5 whorls, microscopically

malleate, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising approximately 2.5 whorls, very convex, rapidly increasing, suture impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus deep, extending to summit and exposing all the whorls. Periostracum glossy, light yellowish-brown and lacquer-like with relatively widely spaced lamellate axial costae at regular intervals, 59-79 (n = 13) on last whorl (Fig. 4.6A-C), which produce broad, pointed flanges with rounded tips around periphery (Fig. 4.6E); intervals between costae with six to nine distinct microscopic axial threads. Shell translucent golden brown or creamy white when fresh. Living animal with head, tentacles and snout pigmented with grey; underside of foot creamy white. Operculum (Fig. 4.6G-H): duplex, outer portion shallowly concave and consisting of multispiral lamella with 4.75 whorls, each step-shaped and increasing in height towards outside, sloping at growing edge; long fringe of fused bristles emanates near top of lamellar blade with a slight groove between fringe and lamellar blade; lamellar blade does not project above level of fringe; fringe of each whorl fused to lamella of following whorl. Radula (Fig. 4.6F): rachidian with five cusps, central one approximately twice length of outer two on each side; first lateral tooth with three large cusps, one small and a vestigial fifth, third cusp (from centre) the largest; second lateral tooth with two very large cusps and two small ones on the outer side (outermost sometimes vestigial). Penis (Fig. 4.6I): shaft more or less cylindrical, intromittant organ short.

Holotype: SOUTH AFRICA: *W. Cape*: Knysna Forest, Garden Route National Park, Diepwalle (-33.95°S: 23.15°E), M. Cole, V. Ndibo & R. Daniels, 28/i/2011, M. Cole, V. Ndibo & R. Daniels 26/i/2011 (NMSA P0639/T4156).

Paratypes: SOUTH AFRICA: *W. Cape*: same data as holotype (ELM D16892/T45, W3644/T46,); Knysna Forest, Diepwalle, Ysterhoutrug, (-33.95056°S: 23.14957°E), M. Cole, V. Ndibo & R. Daniels, 28/i/2011 (ELM D16963/T45, NHMUK 20160073, 4 specimens; NMW.Z.2016.003.00001, 3 specimens; RMNH.MOL.338283, 4 specimens); Knysna Forest Diepwalle, Ysterhoutrug (-33.966°S: 23.150°E), sorted from leaf-litter, D. Herbert, 28/iv/1997 (NMSA V4710/T4126); Knysna Forest, Diepwalle, vicinity of King Edward VII Big Tree (-33.95623°S: 23.15211°E), M. Cole, V. Ndibo & R. Daniels, 28/i/2011 (ELM D16962/T53); Tsitsikamma Forest, near Paul Sauer Bridge (-33.950°S: 23.933°E), sorted from leaf-litter, D. Herbert, 28/iv/1997 (NMSA V4730/T4125); Tsitsikama Forest, near Paul Sauer bridge over Storms River (-33.967372°S: 23.929261°E), M. Cole, V. Ndibo & R. Daniels, 27/i/2011 (ELM D16893/T52, NHMUK 20160074, 1 dry specimen; RMNH.MOL338284, 1 specimen; W3645/T51, NHMUK 20160075, 1 specimen in ethanol); Goukamma N.R., 10 km west of Knysna, riverine forest below River Lodge, on banks of Goukamma river, 2.7 km upstream of mouth (-34.059119°S: 22.938885°E), M. Cole, 12/iii/2015 (ELM D17939/T47, ELM W 3869/T48); Wilderness National Park, trail along west bank of Touw River opposite Ebb & Flow north campsite (-33.984350°S: 22.607273°E), M. Cole, 12/iii/2015 (ELM D17946/T50, ELM W3871/T49).

Other material examined (all ELM unless otherwise indicated): SOUTH AFRICA: *W. Cape*: Tsitsikama Forest, near Paul Sauer bridge over Storms River (-33.967372°S: 23.929261°E), M. Cole, 16/viii/2014 (ELM D17972); Natures Valley, Kalanderkloof Trail (-33.971°S: 23.558°E), east-facing rocky slope opposite Devasselot Restcamp, M. Cole, V. Ndibo & R. Daniels, 27/i/2011 (ELM D16997); Natures Valley, North side of Groot River, (-33.966°S: 23.563°E), near Devasselot Restcamp, M. Cole, V. Ndibo

& R. Daniels, 27/i/2011 (ELM D16894); Knysna Forest, Diepwalle, Velsbroekdraai (-33.93822°S: 23.15742°E), M. Cole, V. Ndibo & R. Daniels, 28/i/2011 (ELM D16964); Goukamma Nature Reserve, 10 km west of Knysna, riverine forest behind Forest Lodge, on banks of Goukamma River, 2.3 km upstream of mouth (-34.061372°S: 22.939649°E), M. Cole. 12/iii/2015 (ELM D17959); Goukamma Nature Reserve, 10 km west of Knysna, riverine forest behind Forest Lodge, on banks of Goukamma River, 2.3 km upstream of mouth (-34.061372°S: 22.939649°E), M. Cole. 15/viii/2014 (ELM D17965).

Distribution (Fig. 3.5). – Western Cape, from Storms River to Wilderness (Touw River).

Habitat. – Indigenous Southern Afrotemperate Forest and Dune Strandveld; in leaf-litter.

Notes. – Shell less depressed than in the majority of other species of *Chondrocyclus*. *C. "herberti"* has similar proportions, but the costae in *C. "silvicolus"* are not as widely spaced (Table 4.2) and have more pointed ends. *C. "silvicolus"* shells are also larger on average (Table 4.2). The opercula and radulae of the two species are very similar. In the molecular analyses each species was represented by a well-supported monophyletic cluster of populations. Forest patches between populations of *C. "herberti"* in the Baviaanskloof and populations in the southern Cape Afrotemperate forests where *C. "silvicolus"* occurs have not been sampled.

C. convexiusculus has similar proportions and relatively widely spaced costae, but the ends of the flanges are produced into a narrow point. The operculum is less concave and the radula differs in having three rather than two large cusps on the second lateral tooth.

Table 4.2 Measurements of *Chondrocyclus "herberti"* and *C. "silvicolus"* showing differences between the species.

Species	W max	W min	Avg	H max	H min	Avg	W/H max	W/H min	Avg	n	Costae	Avg	n
C."herberti"	4.31	3.43	3.85	2.69	2.09	2.34	1.94	1.46	1.65	23	39-51	43	22
C."silvicolus"	6.1	3.76	5.17	3.84	2.09	3.03	1.97	1.5	1.71	49	59-79	69	13

Etymology. – From Latin *"silvicolus"* (an inhabitant of the woods) referring to the occurrence of the species in the largest forest blocks in South Africa in the Knysna area.

Chondrocyclus "amathole" sp. n.

Fig. 4.7

Diagnosis. – Shell small, very depressed, discoidal to lenticular; protoconch mammillate; periostracum with dense transverse costae developing at periphery broad quadrangular flanges; lamellate axial costae with dense axial riblets, rendering upper edge of each blade scalloped along its length; operculum duplex, exterior portion very shallowly concave to almost flat,

multispiral lamella with fringe of very long bristles, fused at their tips, below main fringe is a second shorter fringe of loose bristles; umbilicus broad and deep, extending to apex and exposing all the whorls; radula with two large cusps on second lateral tooth.

Description (Fig. 4.7). – Shell small, very depressed, discoidal to lenticular, adult width 5.09-7.4 mm, height 2.34-3.92 mm, width:height 1.52-2.54 (n = 68 measured in 3 populations spanning the Amathole Mountains). Spire little exserted, each whorl rising just above the next, apex mammillate. Embryonic shell (Fig. 4.7E) 2.25 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising 2.5 whorls, convex, very rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus broad and deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with dense lamellate costae at regular intervals, 73-167 (n = 58) on last whorl, expanded into broad quadrangular flanges at periphery (Fig. 4.7A-C); lamellar blades with dense axial riblets, rendering upper edge of each blade scalloped along its length; intervals between costae with about 6 microscopic axial threads. Shell translucent glossy honey-brown when fresh. Living animal with head, tentacles and snout dark grey, underside of foot creamy white. Operculum (Fig. 4.7D,G): duplex, very shallowly concave to almost flat; outer portion consists of multispiral lamella with 5-6 whorls; each step-shaped; height of lamellar blade very low; fringe of very long bristles, fused at their tips but not along their entire length, below main fringe is a second shorter fringe of relatively loose bristles, long outer fringe of each whorl fused to lamella of following whorl, but due to its long length, fringe forms convex curve between one whorl and next, height of fringe of each whorl exceeds height of lamellar blade, outermost lamellar fringe very long and is reflexed over peristome in life, but operculum can be withdrawn into aperture. Radula (Fig. 4.7F): rachidian with 5 cusps, central cusp approximately twice length of outer cusps; first lateral tooth usually with three large cusps, small fourth cusp and a vestigial fifth, third cusp (from centre) largest; second lateral with two large cusps, second cusp (from centre) longer and broader than first, a very small third cusp and a vestigial fourth. Penis (Fig. 4.7H-I): shaft more or less cylindrical, slightly flattened, with prominent annular rugae, distal end smooth, intromittant organ short.

Holotype: SOUTH AFRICA: *E. Cape*: Amathole Mountains: Hogsback, downstream of Madonna and Child Waterfall (-32.606802°S: 26.962248°E) 1061 m, Southern Mistbelt forest, M. Cole, D. Herbert & L. Davis, 6/iv/2014 (NMSA P0640/T4157).

Paratypes (all ELM unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Amathole Mountains: same data as holotype (ELM W3812/T59); Hogsback, downstream of Madonna and Child Waterfall (-32.606802°S: 26.962248°E) 1061 m, Southern Mistbelt forest, M. Bursey, 31/xii/2008 (D16944/T55,

W3629/T56); ditto, M. Cole, 13/ix/2012 (D17014/T57, W3665/T58; NMSA P0601/T4115; NHMUK 20120278, 2 specimens; NMW.Z.2012.065.00008, 3 specimens; RMNH MOL.33050, 3 specimens); Hogsback, forest above Hobbiton Camp (-32.595837°S: 26.961697°E) 1253 m, Southern Mistbelt forest, M. Bursey & V. Ndibo, 01/xii/2005 (W02966/T54); ditto, 13/ix/2012 (D17013/T60, W3662/T61); ditto, 10/vi/2013 (D17338/T63); ditto, 6/iv/2014 (W3811/T62); Murray's Krantz, Evelyn valley, Kologha Forest, (-32.72570°S: 27.30782°E), north side of Maden Dam, alive under a log M. Bursey & N. Smith, 25/iv/1998 (D14417/T76, W3693/T77); Stutterheim, Kologha Forest, waterfall walk from picnic site (-32.53389°S: 27.43083°E), M. Cole, 18/i/2009 (W3633/T64); ditto, M. Cole & T. Pretorius, 22/xii/2009 (D 16942/T65, W 03628/T66); ditto, M. Cole, 11/xii/2010 (W3634/T67); Fort Fordyce, south facing slope near top of pass (-32.68435°S: 26.495627°E), 1110 m, M. Cole, 29/xii/2008 (D 16946/T68; W3630/T69); ditto: M. Cole, 03/i/2010 (D16947/T70; W3632/T71); ditto, 31/xii/2011 (D 17005/T72, W3631/T73; NHMUK 20120279, 4 specimens, NMSA P0600/T4111 4 specimens); Fort Fordyce, south facing slope behind lookout (-32.695607°S: 26.485676°E), 1120 m, M. Cole, 30/xii/2008 (D 16950/T74); ditto, 17/i/2015 (D17860/T75); Kapp River, north bank (-33.483046°S: 27.080696°E) indigenous riverine forest on shady, south-facing slope, M. Bursey, 30/xii/2002 (W3694/T78); Beggars Bush, 15 km E of Grahamstown, south facing slope (33.287080°E: 26.688521°E) M. Cole, G. Godfrey & Ritcher, 25/ii/2013 (D 17289/T79); Patchwood Farm, forest at source of Quanti River (32.392392°S: 27.446963°E), 1238 m, M & K Cole, 18/xii/2012 (D 17100/T80).

Other material examined (all ELM unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Amathole Mountains: Hogsback, downstream of Madonna and Child Waterfall (-32.606802°S: 26.962248°E) 1061 m, Southern Mistbelt forest, M. Bursey, 25/i/2002 (D13627, W02834); Hogsback, forest above Hobbiton Camp (-32.595837°S: 26.961697°E) 1253 m, Southern Mistbelt forest, M. Bursey, 31/xii/2008 (D 16945); Kologha Forest, near Stutterheim (-32.53333°S: 27.36667°E) R. Scott, 27/xi/1993 (D14405); Stutterheim, Kologha Forest, forest drive near Protea Hill (-32.55583°S: 27.31750°E), M. Cole, 26/i/2010 (D 16943); Stutterheim, Kologha Forest, waterfall walk from picnic site (-32.53389°S: 27.43083°E), M. Cole, 30/xii/2012 (D17623); Fort Fordyce, kloof with watercourse, running eastwards (-32.670358°S: 26.485055°E), 1137 m, M. Cole, 29/xii/2008 (D 16949); Fort Fordyce, top of krantz near campsite (-32.681261°S: 26.480208°E), 1134 m, M. Cole, 30/xii/2011 (D 16948; W3631); Patchwood Farm, forest at source of Quanti River (32.392392°S: 27.446963°E), 1238 m, M & K Cole, 18/xii/2012 (W 03695); Patchwood Farm, forest below (north of) house (32.387515°S: 27.450092°E), 1196 m, M. Cole, 18/xii/2012 (D 17107, W 03699).

Distribution (Fig. 3.5). – Throughout Amathole Mountains; also recorded at Beggars' Bush near Grahamstown and at Kap River Nature Reserve near the mouth of the Great Fish River.

Habitat. – Amathole Mistbelt forest and Great Fish Thicket (Kap River); in leaf-litter.

Notes. - The operculum of *Chondrocyclus "amathole"* is unique in its flatness, its long terminal fringe and relatively long secondary fringe below it and the low height of the multispiral lamellar blade. *C. "amathole"* resembles *C. alabastris* in its large size, depressed proportions and mammillate apex. The radula resembles that of *C. alabastris, C. "herberti"* and *C. "silvicolus"* with two large cusps on the second lateral tooth. The axial lamellae in these three species are scalloped, but are expanded into broad quadrangular flanges in *C. "amathole"* and triangular flanges in *C. alabastris, C. "herberti"* and *C. "silvicolus". C. bathrolophodes, C. putealis* and *C. cooperae* also have quadrangularly shaped flanges, but *C. "amathole"* differs from these three species in all other diagnostic features. The molecular study confirms these

conclusions based on morphology. *C.* *"amathole"* is sister to *C.* *alabastris* and forms a well-supported clade with *C.* *"herberti"* and *C.* *"silvicolus"*.

Etymology. – Named for the Amathole Mountains, Eastern Cape, an area of natural and historic interest.

Chondrocyclus isipingoensis (Sturany, 1898)

Figs. 3.7A, 3.8A, 4.8, 4.9, 4.12A

Cyclotus isipingoensis Sturany, 1898: 161. Type loc.: Isipingo [Penther]
Cyclophorus minimus Melvill & Ponsonby, 1898: 129, pl. vii, fig. 9; Melville & Ponsonby, 1899: pl. iii, fig. 15 (operculum). Type loc.: Pietermaritzburg [Burnup]
Cyclophorus (*Maizania*) *isipingoensis* Kobelt, 1902: 149.
Chondrocyclus isipingoensis Connolly, 1939: 540; Herbert & Kilburn, 2004: 91.

Diagnosis. – Shell very small, very depressed, discoidal; periostracum with axial costae producing spiral rows of simple hairs; operculum very fragile and duplex, exterior portion very shallowly concave, with low multispiral lamella terminating in a solid fringe; rachidian tooth of radula with serrated upper edge, two large cusps on second lateral tooth.

Description (Fig. 4.8). – Specimens from Kenneth Stainbank Nature Reserve, Durban, approx. 9 km from the type locality Isipingo, are considered to represent the type in the following description. Shell very small, very depressed, discoidal, adult width 2.24-3.67 mm, height 1.09-1.67 mm, width:height 1.9-2.31 (n = 16). Spire almost flat, sometimes concave, usually with only the mammillate, tilted protoconch projecting. Embryonic shell (Fig. 4.12A) approx. 2.25 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with development of widely spaced axial costae. Teleoconch comprising just over two whorls, very rapidly increasing, convex, suture impressed. Aperture circular, last whorl descending steeply nearing aperture, peristome simple, continuous and free. Umbilicus very wide, extending to summit and exposing all the whorls. Periostracum glossy and lacquer-like with lamellate well-spaced axial costae at regular intervals, the average number on last whorl varying between 55 and 92 (Table 4.3), which produce 10-12 spiral rows of simple hairs, longest around periphery (four rows) and shortest around umbilicus; intervals between costae usually with six to nine microscopic axial threads (Fig. 4.8D). Shell translucent when fresh. Operculum (Fig. 4.8F-H): very fragile and duplex, outer portion consists of multispiral lamella with 5-6 whorls, height of lamellar blade very low thus operculum is very shallowly concave to almost flat, thickened horizontal ridge on lamellar blade just above disc surface; long fringe of fused bristles emanates from this ridge, fused to blade and then curving outwards, leaving no furrow between

fringe and vertical portion of blade, fringe of each whorl fused to lamella of following whorl, fringe of outer whorl fairly long and overlaps disc slightly; inner portion of operculum is a thin disc, in some populations side of disc facing body has a prominent tubercle or swelling in centre (Fig. 4.8F). Radula (Fig. 3.8A): rachidian with five cusps, central one very long, outermost two very small to almost vestigial, cusps set a little distance below "top" of tooth, top edge serrated; first lateral tooth with four cusps and a vestigial fifth, third cusp (from centre) largest; second lateral tooth with two large cusps, second cusp (from centre) largest, a third small cusp and a vestigial fourth. Penis (Fig. 4.8E): shaft more or less cylindrical and slightly flattened dorsoventrally.

Table 4.3 Measurements of *Chondrocyclus isipingoensis* showing variation between populations.

Site	W (max)	W (min)	Avg	H (max)	H (min)	Avg	W/H (max)	W/H (min)	Avg	n	Costae	Avg	n
Kenneth Stainbank	3.67	2.24	2.88	1.67	1.09	1.41	2.31	1.9	2.05	16	55-92	75	14
Vernon Crookes	3.26	2.39	2.89	1.71	1.07	1.46	2.24	1.84	2	13	52-66	60	12
Upper Bulura	3	2.24	2.59	1.68	1.02	1.24	2.55	1.67	2.12	21	28-40	34	8
Quanti	2.82	2.17	2.44	1.38	1.03	1.22	2.2	1.7	2.01	31	31-45	37	17
Soutpansberg	3.1	2.24	2.75	1.48	1.12	1.31	2.38	1.89	2.09	10	59-72	64	7
Lotheni	3.16	2.42	2.82	1.55	1.14	1.35	2.29	2	2.1	6	40-41	41	2
Ongoye	3.63	2.96	3.22	1.75	1.08	1.41	2.75	2.09	2.3	14	61-88	75	10
Nkandla	4.11	2.96	3.52	1.88	1.48	1.73	2.18	1.93	2.03	3	68-70	69	2

Type material: Holotype of *Cyclotus isipingoensis* Sturany, 1898 in Vienna Museum. Syntype of *Cyclophorus minimus* Melvill & Pfeiffer, 1898 in NHMUK (1902.10.1.7).

Distribution (Fig. 4.10). – Widely distributed throughout the eastern region of South Africa, from Soutpansberg mountains in Limpopo Province to the Amathole mountains in the Eastern Cape; from the coast to the Drakensberg foothills (1800 m).

Habitat. – Indigenous forest of several classification types: Southern and Northern Coastal Forest, Scarp Forest, Southern and Northern Mistbelt Forest, Northern Afrotemperate Forest, and Albany Thicket (Kowie Thicket); in leaf-litter.

Notes. – Data from the molecular analyses and morphological examination provide compelling evidence that *C. isipingoensis* is a species complex rather than one widespread species. Selected populations from across the range of this lineage were sampled for the molecular study and examined for morphology, but a more comprehensive study is required to revise this lineage.

The phylogeny inferred suggests that populations from the western end of the range (Somerset East and Bedford) belong to a distinct lineage (*C. "oxygala"* described below), and all other populations sampled form a second well-supported clade, with several well-supported groups (potentially separate species) nested within it, including the distinct species *C. exsertus* (Fig. 3.3). Examples of variations in some of the populations examined are discussed and illustrated below.

The density of axial lamellae and the number and position of spiral rows of hairs on the last whorl varies in different populations, but is consistent within a population (e.g. see Figs. 4.8A-C, 4.9A, B). In specimens from Durban (Fig. 4.8A), there is one row of very short hairs on lamellate costae below the suture, a wide gap with no hairs and four rows of very long hairs at the periphery, and approx. 5-7 rows between periphery and umbilicus, the latter becoming progressively shorter nearer the umbilicus. Specimens from coastal areas of Eastern Cape (but excluding northern Pondoland) have a similar arrangement. Specimens from the Zululand scarp forests of Ongoye and Nkandla are relatively large (Table 4.3), and also have a row of very short hairs below the suture and 3 rows of very long hairs round periphery, while those from the mistbelt Krantzkop have a fourth row of long hairs around the periphery. Populations from the Quanti district in the Kei River valley have relatively widely spaced costae (Table 4.3, Fig. 4.9B), with dense (over 20) microscopic axial threads in their intervals.

By contrast, in some populations the spiral rows of hairs are evenly distributed over the body whorl and not concentrated round periphery. Specimens from Kwazulu-Natal south coast are very small with approx. 6 rows of very narrow hairs (excluding the additions rows of shorter hairs near the umbilicus); in northern Pondoland there are approx. 9 spiral rows of robust hairs; in the southern and northern Drakensberg, Transkei mistbelt and Kei River valley there are 7-10 spiral rows of very narrow hairs (Fig. 4.9B); northernmost localities in the Soutpansberg and Mpumalanga have approx. 8 spiral rows of hairs (Fig. 4.9A).

The spire also varies from being concave to almost flat or slightly exserted and the protoconch is acutely mammillate in some populations.

The rachidian tooth of the radula is unusual in having a serrated upper edge and cusps set below this. Populations examined which showed this feature were from Karkloof, Durban, Qora on the Transkei coast, and Phumalanga Farm near East London (Fig. 3.8A). The radula of *C. exsertus* conforms to this design (Fig. 4.24).

Chondrocyclus "oxygala" sp. n.

Fig. 4.11, 4.12B

Diagnosis. – Shell very small, depressed, discoidal; periostracum with axial costae producing spiral rows of simple hairs; operculum very fragile and duplex, exterior portion very shallowly concave, with low multispiral lamella terminating in a solid fringe, radula with two large cusps on second lateral tooth and rachidian tooth without serrated upper edge.

Description (Fig. 4.11). – Shell very small, depressed, discoidal, adult width 2.19-3.0 mm, height 1.12-1.68 mm, width:height 1.61-2.12 (n = 29). Spire low, each whorl just rising above the next, apex acutely mammillate and tilted (Fig. 4.11A). Embryonic shell (Fig. 4.12B) just over 2.25 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with termination of malleation. Teleoconch comprising just over two whorls, very rapidly increasing, convex, suture impressed. Aperture circular, last whorl descending steeply nearing aperture, peristome simple, continuous and free. Umbilicus very wide, extending to summit and exposing all the whorls. Periostracum glossy and lacquer-like with lamellate well-spaced axial costae at regular intervals (Fig. 4.11D), the average number on last whorl varying between 63 and 95 (Table 4.4), which produce three spiral rows of long, simple hairs around periphery; intervals between costae usually with approx. five microscopic axial threads. Shell translucent when fresh. Operculum (Fig. 4.11E,F) very fragile and duplex, outer portion consists of multispiral lamella with 5-6 whorls, height of lamellar blade very low thus operculum is very shallowly concave to almost flat, thickened horizontal ridge on lamellar blade just above disc surface; long fringe of fused bristles emanates from this ridge, fused to blade and then curving outwards, leaving no furrow between fringe and vertical portion of blade, fringe of each whorl does not appear to be fused to lamella of following whorl, fringe of outer whorl fairly long and overlaps disc slightly; inner portion of operculum is a thin disc, without a prominent tubercle in centre. Radula (Fig. 4.11G): rachidian with five cusps, central one very long, outermost two relatively short, first lateral tooth with four cusps and a vestigial fifth, third cusp (from centre) very long; second lateral tooth with two large cusps, second cusp (from centre) larger, a third small cusp and a vestigial fourth. Penis (Fig. 4.11H,I): relatively short, shaft more or less cylindrical.

Table 4.4 Measurements of *Chondrocyclus* *"oxygala"* showing variation between populations.

Site	W (max)	W (min)	Avg	H (max)	H (min)	Avg	W/H (max)	W/H (min)	Avg	n	Costae	Avg	n
Bedford	2.8	2.19	2.53	1.43	1.12	1.27	2.12	1.87	1.99	9	63-81	69	7
Glen Avon	3	2.49	2.76	1.68	1.32	1.49	2.04	1.61	1.86	20	76-95	85	12

Holotype: SOUTH AFRICA: *E. Cape*: Bedford, Maasstrom Farm, forest in kloof (-32.68300°S: 26.08300°E), M. Cole, R. Daniels & V. Ndibo, 24/i/2011 (NMSA P0638/T4153).

Paratypes: SOUTH AFRICA: *E. Cape*: same data as holotype (ELM D16895/T151, W03646/T152, NHMUK 20160078); Bedford, Maasstrom Farm, forest in kloof (-32.68300°S: 26.08300°E), M. Bursey, 01/i/2007 (D15108/T153, W3122/T154); Bedford, Maasstrom Forest, leg. J. Farquhar (NMSA V6684/T5154); Somerset East, Glen Avon Falls, forest beside base of falls (-32.67700°S: 25.63681°E), in leaf-litter, D. Herbert, 19/i/2002 (NMSA W0754/T4155); Somerset East, Glen Avon, downstream of falls (-32.67700°S: 25.63667°E), M. Cole, V. Ndibo and R. Daniels, 25/i/2011 (D16896/T155, NHMUK 20160076, 3 specimens, RMNH.MOL.338285 3 specimens, NMW.Z.2016.003.00003 4 specimens, W03647/T156, NHMUK 20160077, 2 specimens).

Distribution (Fig. 4.10). – Eastern Cape, southern end of Great Escarpment.

Habitat. – Eastern Cape Escarpment Thicket associated with river valleys.

Notes. – The molecular phylogeny suggests that *C. "oxygala"* belongs to a distinct lineage and all other populations of *C. "isipingoensis"* sampled form a second well-supported clade (Fig. 3.3). This western lineage has diagnosable morphological characteristics.

The periostracum has three rows of long hairs round the periphery while *C. isipingoensis* has four rows. *C. "oxygala"* lacks the additional spiral rows of hairs present in *C. isipingoensis*: approx. 5-7 rows of shorter hairs between the periphery and umbilicus and one row of very short hairs on lamellate costae below the suture. *C. "oxygala"* has a higher spire (and consequently deeper, less wide umbilicus) and a more strongly sculptured protoconch (Fig. 4.12B). The operculum has a smooth inner disc without a tubercle in its centre. The radula more closely resembles those of species in the Southern-Eastern Cape clade than those of *C. isipingoensis* populations examined. The rachidian tooth of *C. isipingoensis* is unique in that the upper edge is serrated and the cusps are set a little distance below the "top" of tooth. *C. exsertus* shares this feature, but it is absent in *C. "oxygala"*. The penis of *C. "oxygala"* is relatively short compared to those of other *C. isipingoensis* populations sampled.

Etymology. – From Greek *"oxygala"* meaning sour milk, a translation of the name of the type locality, Maasstrom.

Chondrocyclus "kevincolei" sp. n.

Fig. 4.13

Diagnosis. – Shell small, depressed, lenticular; periostracum with axial costae producing spiral rows of simple hairs; spiral grooves on shell corresponding with rows of hairs; operculum duplex, exterior portion very shallowly concave, with step-shaped multispiral lamella terminating in a short fringe with uneven edge, diameter of exterior portion less than diameter of inner disc; radula with three large cusps on second lateral tooth.

Description (Fig. 4.13). – Shell small, depressed, lenticular, adult width 3.59-5.34 mm, height 1.59-2.84 mm, width:height 1.68-2.37 (n = 87 from 4 populations; variations in dimensions between populations is given in Table 4.5).

Table 4.5 Measurements of *Chondrocyclus "kevincolei"* showing variation between populations.

Site	W (max)	W (min)	Avg	H (max)	H (min)	Avg	W/H (max)	W/H (min)	Avg	n	Costae	Avg	n
Platbos	5.01	4.43	4.63	2.59	2.17	2.41	2.11	1.74	1.93	20	51-75	61	22
Grootbos	5.34	4.34	4.87	2.84	2.17	2.47	2.31	1.68	1.98	20	73-100	86	19
Gansbaai	5.32	4.44	4.87	2.83	2.36	2.56	2.2	1.73	1.91	27	81-119	98	19
Bredasdorp	4.76	3.59	4.22	2.59	1.59	2.25	2.37	1.68	1.88	20	52	52	1

Spire little exserted, each whorl rising just above the next, protoconch large and mammillate. Embryonic shell (Fig. 4.13G) approx. 2.25 whorls, almost smooth but microscopically malleate at tip, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising just over two whorls, very convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus wide and deep, extending to summit and exposing all the whorls. Periostracum glossy and lacquer-like with lamellate axial costae at regular intervals on last whorl, 51-75 (n = 22) in Platbos population, but vary between populations (Table 4.5), which produce spiral rows of simple hairs varying in different populations from approx. 4-14 on last whorl, longest around periphery and shortest around umbilicus; intervals between axial costae with approx. eight microscopic axial threads (Fig. 4.13H); shell bears spiral grooves corresponding with the rows of hairs (Fig. 4.13D-F). Shell translucent when fresh; two colour morphs present reddish brown and creamy white. Living animal varies in colour between

populations from creamy white with slight pigmentation on tentacles to very dark grey (see below). Operculum (Fig. 4.13J-K): duplex, shallowly concave; multispiral lamella of outer portion with 4.5 whorls, each step-shaped, growing edge of lamella at angle, perpendicular where it is attached to disc; fringe very short and solid, with a frayed distal edge even in fresh specimens, fringe of each whorl not fused to lamellar blade of following whorl, diameter of outer multispiral portion smaller than diameter of inner disc due to very short fringe; operculum retractile. Radula (Fig. 4.13I): rachidian with 5 cusps, middle one longer than 2 cusps on either side of it; first and second lateral teeth each with 4 cusps and a vestigial 5th, the third cusp from centre the largest. Penis (Fig. 4.13L): shaft more or less cylindrical and slightly flattened dorsoventrally, distal half slightly expanded on left side, numerous annular rugae, distal end smooth, intromittant organ short.

Holotype: SOUTH AFRICA: *W. Cape*: Platbos Forest near Gansbaai (-34.567111°S: 19.449516°E), Western Cape Milkwood Forest with large trees including *Sideroxylon inerme* and *Celtis africana*, in leaf litter, M. Cole, K. Cole, D-J. Hodgkinson & T. Pretorius, 09/ix/2009 (NMSA W9270/T3073).

Paratypes: SOUTH AFRICA: *W. Cape*: same data as holotype (ELM D16921/T81, ELM W3615/T82; NHMUK 20120282, 20 specimens; NMSA P0598/T4121, 23 specimens; NMW.Z.2012.065.00010, 18 specimens; RMNH MOL.330503, 15 specimens); ditto, M. Cole, D. Herbert & L. Davis, 18/iv/2012 (ELM D16998/T83; W3659/T84); ditto, 13/viii/2014, M. & K. Cole (ELM D18004/T85; ELM W3898/T86); Bredasdorp, about 5 miles to SW, on Elim Rd (-34.54501°S: 19.96136°E), dry bush on hillside, Ex Transvaal Museum (NMSA W575/T4123); Bredasdorp, 7 km south west on R43 to Elim (-34.591246°S: 19.999224°E), 35 m, bushy valley with dam, M. Cole, 13/viii/2014 (ELM D17983/T87; ELM W3890/T88); Grootbos Nat. Res., Gansbaai area (-34.54205°S: 19.41529°E), milkwood forest, in leaf-litter, D. Herbert & L. Davis, 07/x/2007 (NMSA W5659/T4122); Grootbos Private Nature Reserve, between Stanford & Gansbaai (-34.541949°S: 19.412233°E) 203 m, Western Cape Milkwood Forest, M. Cole, 13/viii/2014 (D18005/T89); Gansbaai (-34.57946°S: 19.34421°E), dune scrub, in leaf-litter, A. Moussalli & D. Stuart-Fox, 13/ii/2005 (NMSA W3537/T4124).

Distribution (Fig. 3.4). – Western Cape, Agulhas Plain, between Gansbaai and Bredasdorp.

Habitat. – Various forested or bushy habitats in patches of Western Cape Milkwood Forest (part of Southern Coastal forest group) with large trees, characterised by white milkwoods (*Sideroxylon inerme*), white stinkwoods (*Celtis africana*) and white pear (*Apodytes dimidiata*), including the southernmost forests in Africa (Platbos and Grootbos), dune scrub at Gansbaai and "dry bush on hillside" (south-west of Bredasdorp); in leaf-litter.

Notes. – In terms of its hairy periostracum *Chondrocyclus "kevincolei"* resembles *C. isipingoensis* (Sturany, 1898) and *C. "langebergensis"* sp. n. The distinct spiral grooves on the shell of *C. "kevincolei"* (Fig. 4.13D-F) are unique among *Chondrocyclus* species although there are sometimes faint traces of spiral grooves on shells of *C. isipingoensis* and *C. langeberg* visible only at very high magnification. Other morphological features distinguishing *C. "kevincolei"* from *C. isipingoensis* are a higher spire, distinct operculum and the second lateral

tooth of the radula has three large cusps (Fig. 4.13I) opposed to two in *C. isipinoensis* (Fig. 3.8A). The molecular analyses placed *C. "kevincolei"* in a well-supported monophyletic clade together with *C. "langebergensis"* while *C. isipingoensis* was in a separate clade. Differences between *C. "kevincolei"* and *C. "langebergensis"* are discussed under the latter species.

In the single gene analyses, *C. "kevincolei"* did not form a monophyletic cluster, but three highly divergent populations. There are morphological differences between populations (Table 4.5). The number of spiral rows of hairs is fewer in the Bredasdorp population (only 4 – 5 as opposed to 8 – 15 in the Platbos and Grootbos populations). The colour of the living animal is creamy white with only slight pigmentation of the tentacles in the Platbos population and dark grey to almost black at Bredasdorp. In the molecular study populations at Platbos, Grootbos and Bredasdorp show deep divergence (long branch lengths) based on CO1 and 16S. The degree of sequence divergence is greater than between separate species in this study and together with the morphological differences, could warrant the recognition of three separate species. It was however decided to consider these to be one species pending further sampling and including comparison of a nuclear marker.

C. "kevincolei" has not been recorded in the Cape Fold Mountains approx. 40 km to the west where *C. convexiusculus* is present.

Etymology. – Named for my husband, Kevin Cole, in acknowledgement of his indispensable assistance on fieldtrips.

Chondrocyclus "langebergensis" sp. n.

Fig. 4.14

Diagnosis. – Shell small, very depressed, discoidal; periostracum with axial costae producing spiral rows of simple, robust hairs concentrated at and on either side of periphery; operculum duplex, exterior portion very shallowly concave, with thickened ridge on multispiral lamella from which emanates a fairly long solid fringe and a very short fringe below this; radula with three large cusps on second lateral tooth.

Description (Fig. 4.14). – Shell small, very depressed, discoidal, adult width 3.63-5.76 mm, height 1.42-2.76 mm, width:height 1.79-2.85 (n = 67, measured in 4 different populations (Table 4.6)).

Table 4.6. Measurements of *Chondrocyclus* "*langebergensis*" showing variation between populations.

Site	W (max)	W (min)	Avg	H (max)	H (min)	Avg	W/H (max)	W/H (min)	Avg	n	Costae	Avg	n
Patbusch	5.76	4.68	5.17	2.76	2.21	2.48	2.33	1.79	2.09	23	71-99	81	14
Montagu	5.32	4.98	5.11	2.62	2.32	2.48	2.23	1.92	2.07	5	74	74	1
Marloth	4.24	3.63	3.92	1.95	1.51	1.79	2.57	2	2.2	20	69-85	79	5
Grootvadersbosch	5.09	3.42	4.56	2.17	1.42	1.82	2.85	2.2	2.51	19	47-63	53	14

Spire almost flat, sometimes concave, usually with only the mammillate, tilted protoconch projecting. Embryonic shell (Fig. 4.14D) approx. 2.25 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with development of widely spaced axial costae. Teleoconch comprising 2.25 whorls, very rapidly increasing, convex, suture deeply impressed. Aperture circular, last whorl descending steeply nearing aperture, peristome simple, continuous and free. Umbilicus very wide, extending to summit and exposing all the whorls. Periostracum glossy and lacquer-like with lamellate axial costae at regular intervals, 47-63 (n = 14) on last whorl in Grootvadersbosch population but varies between populations (Table 4.6), which produce 6 spiral rows of simple, very long and robust hairs around the periphery; intervals between costae with 6-8 microscopic axial threads. Shell translucent reddish brown, honey brown or yellowish-white when fresh. Living animal variable in colour between populations from creamy white with light brown pigmentation on tentacles to almost black, underside of foot creamy white. Operculum (Fig. 4.14F,I): duplex and shallowly concave; multispiral lamella of outer portion with 5 low whorls, thickened horizontal ridge near base of lamellar blade runs parallel to disc surface, a long fringe of fused bristles and a second very short fringe below it emanate from this ridge; main fringe grows upwards (i.e. parallel to lamellar blade) and then downwards, leaving a deep, wide groove between fringe and blade of lamella; lamellar blade projects above level of fringe and is very thin; fringe of each whorl fused to lamellar blade of next whorl; fringe of outermost whorl overlaps disc slightly and is reflexed over peristome in life although operculum is retractile. Radula (Fig. 4.14E): rachidian with 5 cusps, middle one longer than 2 cusps on either side of it; first and second lateral teeth with 5 cusps (5th sometimes vestigial), the third cusp from centre the largest. Penis (Fig. 4.14G-H): shaft more or less cylindrical and slightly flattened dorsoventrally, distal half slightly expanded on left side, numerous annular rugae, distal end smooth but not bulbous, intromittant organ short.

Holotype: SOUTH AFRICA: *W. Cape*: Langeberge foothills, Pat Busch Nature Reserve, Karin Trail (-33.75513°S:19.99471°E), 450 m, riverine fynbos, in leaf-litter beneath bushes, M. Cole, 7/viii/2014 (NMSA P0642/T4159).

Paratypes: same data as holotype (ELM D17981/T98; W3899/T99); Langeberg Mountains, Heidelberg area, Grootvadersbosch Nat. Res., Bushbuck Trail, Afrotemperate forest, in leaf litter (-33.98191°S: 20.83215°E), M. Cole, 19/iv/2012 (ELM D16999/T90, ELM W3660/T91; NHMUK 20120284, 1 specimen); ditto, R. Daniels, 03/iii/2012 (ELM D16918/T100, W03613/T92, NHMUK 20120283, 5 specimens, NMW.Z.2012.065.00011 5 specimens, RMNH MOL.330500, 5 specimens); Grootvadersbosch Nat. Res. Melkhoutpad, (-33.98191°S: 20.83215°E), M. Cole, 16/ix/2009 (ELM D16917/T93, W3689/T94); Grootvadersbosch Nat. Res., Redwoods area (-33.982583°S: 20.829633°E), 224 m, *Podocarpus* forest, J. Londt, 14/ix/2003 (NMSA W1043/T4117); Grootvadersbosch Nat. Res. (-33.99595°S: 20.81288°E), A.Moussalli & D. Stuart-Fox, 22/ii/2005 (NMSA W5008/T4119); Marloth Nature Reserve, Swellendam, (-33.993430°S: 20.458662°E), Duivelsbos Forest, M. Cole, 15/ix/2009 (ELM D16919/T95, W03614/T96); Marloth Nat. Res., (-33.98975°S: 20.45439°E), afrotemperate forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 23/ii/2005 (NMSA W5016/T4118); Langeberge foothills, 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 (NMSA W5768/T4120); ditto, R. Daniels, 3/iii/2012, (ELM D16920/T97); Montagu (-33.78333°S: 20.11667°E), M. Connolly (NMSA 2778/T4116).

Distribution (Fig. 3.4). – Western Cape, evidently endemic to Langeberg mountain range in Cape Fold Mountain belt, south-facing slopes and on northern side of range in Montagu area.

Habitat. – Diverse vegetation types: patches of Western Cape Afrotemperate forest and riverine fynbos, in leaf litter.

Notes. – *C. "langebergensis"* differs from *C. "kevincolei"* in its lack of prominent spiral grooves on the shell, the spiral rows of long hairs are concentrated around the periphery, the protoconch is more strongly sculptured and the opercula differ: in *C. "langebergensis"* the lamellar fringe of each spiral whorl emanates from a ridge at the base of the lamellar blade and is fused to the lamellar blade of the following whorl. The terminal fringe is long and overlaps the base when viewed from above (Fig. 4.14F). In *C. "kevincolei"* the fringe emanates from near the top of the lamellar blade and is very short and appears distinct from the following lamellar whorl; the outer saucer-shaped portion is smaller than the polished base.

In the analyses of molecular data, *C. "langebergensis"* and *C. "kevincolei"* form a monophyletic clade, with *C. "langebergensis"* consistently forming a well-supported cluster, although there are morphological differences between populations (Table 4.6). *Chondrocyclus* species have not been recorded in the Riviersonderendberge where apparently suitable habitat exists in an area more or less midway between localities of these two species.

Etymology. – Named for the Langeberg mountain range, part of the Cape Fold Mountains.

Figs. 4.15

Chondrocyclus trifimbriatus Connolly, 1929: 241, pl. xiv, f. 35-39; Connolly, 1939: 538; Herbert & Kilburn, 2004: 92. Type loc.: Karkloof, bush behind Karkloof Falls [Falcon]

Diagnosis. – Shell small, depressed, lenticular; periostracum with dense axial costae developing five rows of flanges on last whorl: at periphery, just below suture, around umbilicus and two weaker rows on either side of periphery; operculum duplex, exterior portion shallowly concave with step-shaped multispiral lamella terminating in a long solid fringe reflexed over peristome; radula with three large cusps on second lateral tooth, cusps of rachidian, first and second lateral teeth fairly uniform in size; penis flattened dorsoventrally and laterally expanded on left side from about midway down the shaft, intromittant organ relatively long.

Description (Fig. 4.15). – Shell small, depressed, lenticular, adult width 3.9-4.37 mm (4.37-5.32 mm Entumeni population), height 1.95-2.66 mm (2.39-2.86 mm Entumeni), width:height 1.65-2.0 (1.62-2.02 mm Entumeni) (n = 5 *C. trifimbriatus* from type locality; n = 6 Entumeni population). Spire not much raised, each whorl rising just above the next, protoconch sub-mammillate (Connolly, 1929). Embryonic shell 2 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising 2.75 whorls, convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus wide and deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with dense lamellate axial costae at regular intervals, approx. 150-155 (n = 4) on last whorl in specimens from the type locality, but varying between populations (see Notes below), expanded into quadrangularly-shaped flanges around periphery, immediately below the suture and around the umbilicus, the row at the periphery the strongest, and with two less prominent rows of lower-standing flanges on either side of periphery. Shell translucent, glossy, corneous yellow-brown when fresh. Living animal creamy white with slight pigmentation on tentacles. Operculum (Fig. 4.15D,F): duplex, lamella of outer multispiral portion with 4.25 whorls, step-shaped; on outer surface of lamellar blade a long, solid fringe curves upwards and then outwards forming a groove between fringe and lamellar blade, spanned by a very loose network of bristles; a very short solid horizontal fringe emanates just below main fringe; upper edge of lamella thin and projects above fringe in side view; outer surface of lamellar blade tuberculate at high magnification. Radula (Fig. 4.15E, details from Entumeni population): rachidian with five cusps, approximately equivalent length; first and second lateral teeth similar,

each with five cusps, first three cusps approximately equivalent in size, the fourth very small and the fifth (from centre) vestigial; cusps increase in size very slightly from central tooth outwards, but there is not a large difference in size between cusps. Penis (Fig. 4.15G from Entumeni population): flattened dorsoventrally and laterally expanded on left side from about midway down the shaft, with numerous annular rugae, smooth distal end narrows, intromittant organ relatively long.

Type material: Holotype in NHMUK (1928.3.16.5) (Fig. 4.15A)

Distribution (Fig. 3.6). – Originally known only from Karkloof River Valley, downstream of Karkloof Falls, but the species appears to have disappeared from the Karkloof vicinity. Specimens recently discovered at Entumeni and Nkandla forests are tentatively considered here to be *C. trifimbriatus*.

Habitat. – No habitat data available for original specimens, but indigenous Northern Mistbelt forest occurs in the Karkloof vicinity. Recently collected specimens occur in Scarp forests (Entumeni) and Mistbelt/Scarp (Nkandla) in leaf litter.

Notes. – There are morphological differences between populations from different localities. Specimens from Entumeni (Fig. 4.15B-C) lack the spiral row of flanges just below the suture and the weak row below the periphery. Specimens from Nkandla also bear fewer spiral cords than *C. trifimbriatus*: there is a spiral cord just below suture and one between periphery and umbilicus but the weak cords on either side of periphery are absent. Although not many specimens were available to measure (4 from Karkloof, 6 from Entumeni and 2 from Nkandla), W:H ratio is similar throughout but the axial costae on last whorl are more dense in Entumeni specimens (approx. 200) and less dense in Nkandla specimens (117) compared to 150-155 in Karkloof specimens. The operculum of *C. trifimbriatus* from the type locality has a groove between the lamellar blade and the fringe spanned by a loose network of bristles (Fig. 4.15D) and opercula of specimens from Entumeni and Nkandla are similar. The radulae of all populations agree with Connolly's (1929, 1939) descriptions and figure, and his observation that the cusps are smaller than on radular teeth of other *Chondrocyclus* species.

Few specimens were available for study since they seemed to be very rare in the two forests where they were found, and more sampling from these and other forests in north-central KwaZulu-Natal are required to resolve more conclusively whether *C. trifimbriatus* occurs throughout the region or whether there may be additional narrow-range species. The only

localities represented in the molecular study were Entumeni and Ngome (considered to contain a separate species, see below). Other taxa in forests of north-central Kwazulu-Natal contain species with very narrow ranges (e.g. Huber, 2003; Herbert & Kilburn, 2004; Tilbury & Tolley, 2009) suggesting that morphological differences between populations may indicate undescribed species.

Chondrocyclus "pondoensis" sp. n.

Fig. 4.16

Diagnosis. – Shell small, depressed, lenticular; protoconch not mammillate; periostracum with dense, erect, transverse costae, expanded to form five spiral rows of raised flanges: a paddle-shaped row around periphery, a row of well-developed quadrangularly-shaped flanges around umbilicus and above periphery and a row of lower semi-circular flanges below suture; operculum duplex, lamella forming outer portion of operculum step shaped and terminating in a long solid fringe, portion above fringe consists of a lattice-like network of interwoven bristles some fused to fringe, projecting well above fringe and sloping inward towards centre; umbilicus deep, extending to apex and exposing all the whorls; radula with three large cusps on second lateral tooth, cusps of rachidian, first and second lateral teeth fairly uniform in size; penis flattened dorsoventrally and laterally expanded about midway down the shaft, intromittant organ relatively long.

Description (Fig. 4.16). – Shell small, depressed, lenticular, adult width 4.59-6.18 mm, height 2.42-3.42 mm, width:height 1.59-2.00 (n = 19). Spire not much raised, each whorl rising just above the next, protoconch not mammillate. Embryonic shell just over 1.5 whorls, microscopically malleate, junction between embryonic shell and teleoconch not particularly distinct, initially costae weak, becoming well developed after about a quarter of a whorl (Fig. 4.16D). Teleoconch comprising 2.75 whorls, moderately convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with dense lamellate costae at regular intervals, approx. 154-184 (n = 14) on last whorl, expanded into five spiral rows of flanges: a paddle-shaped row around periphery, a row of well-developed quadrangularly-shaped flanges around umbilicus and above periphery and a row of lower semi-circular flanges below suture; flanges bear numerous axial riblets visible at very high magnification (Fig. 4.16E); intervals

between costae with microscopic axial threads. Shell translucent, glossy, corneous yellow-brown when fresh. Living animal creamy white with slight pigmentation on tentacles. Operculum (Fig. 4.16G-H) duplex, outer portion consists of multispiral lamella with 4.5-5 whorls; lamellar blade high, stepped, long fringe emanates near top of vertical portion of blade; blade projects high above fringe and slopes inward towards centre, upper portion of lamellar blade consists of lattice-like network of interwoven bristles, some bristles connected to main fringe so there is no groove between fringe and lamellar blade (Fig. 4.16G); at the growing edge the top portion of lamellar blade is more or less square, not sloping, becoming arrow shaped below fringe (Fig. 4.16H). Outer lamellar fringe reflexed over peristome preventing animal withdrawing into shell. Radula (Fig. 4.16F): rachidian with five cusps, central one slightly longer; first and second laterals each with three large cusps, a smaller fourth and a vestigial fifth, cusps increase in size very slightly from central tooth outwards, but there is not a large difference in size between cusps. Penis expanded towards distal end, intromittant organ relatively long (Fig. 4.16I-J).

Holotype: SOUTH AFRICA: *KwaZulu-Natal:* Port Shepstone area, Marble Delta, Hlokohloko Valley, middle section (30.661892 °S: 30.334189 °E), 175 m, riverine/scarp forest, in leaf-litter, leg. J. Harvey, ii/2012 (NMSA P0643/T4160 ex W8763).

Paratypes: SOUTH AFRICA: *KwaZulu-Natal:* same data as Holotype, (NMSA W8763/T4161, NHMUK 20160079, 2 specimens; RMNH.MOL.338286); Port Shepstone area, Marble Delta, Hlokohloko Valley, middle section (30.660786 °S: 30.332556 °E), 188 m, riverine/scarp forest, in leaf-litter, leg. J. Harvey, ii/2012 (NMSA W8733/T4162, NMW.Z.2016.003.00002); Port Shepstone area, Marble Delta, Hlokohloko Valley, middle section (30.662186 °S: 30.338608 °E), 145 m, riverine/scarp forest, in leaf-litter, leg. J. Harvey, ii/2012 (NMSA 8765/T4171, RMNH.MOL.338287); Port Shepstone, Simuma area, Hlokohloko valley (-30.66310°S: 30.33685°E), ca 150-200 m, riverine/scarp forest, in leaf-litter, Herbert & Davis, 05/iii/2011 (NMSAW7844/T4144); Umtamvuna Nature Reserve, Old Pont Road (-31.060320°S: 30.172487°E), 56 m, Port Edward, 2.5 km upstream of mouth, M. Cole, D. Herbert, L. Davies & R. Daniels, 13/iv/2011 (ELM D16940/T113, W03627/T114, NHMUK 20120271); *E. Cape* (All ELM unless otherwise indicated): Ntafufu, below lodge (-31.55139°S: 29.61750°E), west bank, 2 km upstream of mouth. D-J Hodgkinson, 24/iv/2005 (D15532/T101); Ntafufu, east bank (-31.55652°S: 29.62606°E), 1.5 km upstream of mouth, M. Bursey, 24/iv/2005 (D15531/T102); Xora, Kumqolo Forest (-32.15889°S: 28.98481°E), west bank of Xora river opposite Mangrove swamp, M. Bursey, 25/x/2005 (D15537/T103); ditto, M. Cole, 13/viii/2011(W03663/T104); Mpame forest (-32.085595°S: 29.030633°E), M. Cole, 19/ii/2009 (D16941/T105); Mbotyi, Drewes camp (-31.44317°S: 29.76861°E) east of village, dune forest at east end of beach, just before cliffs, M Bursey, 13/i/2003 (D14396/T106); Mkambati Nature Reserve, "Superbowl" forest (-31.297833°S: 29.929333°E), 5 km upstream of Msikaba mouth, east side of Msikaba river, in leaf-litter, M. Bursey, 03/v/2004 (D14256/T107); ditto, 18/x/2005 (D15585/T108); Mtentu, north bank (-31.24000°S: 30.03667°E) M. Bursey & V. Ndibo, 20/x/2005 (W03027/T109); Mtentu, north bank, 1.5 km upstream (-31.238879°S: 30.034039°E), inlet to first waterfall on east side of inlet, M. Cole, 13/i/2012 (D17406/T110, W03602/T111); Mtentu, north bank, 3 km upstream of mouth (-31.229476°S: 30.018190°E), 43 m, inlet to second waterfall, west side of inlet, M. Cole, 12/i/2012 (W03603/T112).

Distribution (Fig. 3.6). – Known primarily from near the coast between Xhora in Transkei and Umtamvuna in southern Kwazulu-Natal, and also recorded inland in the Port Shepstone area (ca 200 m a.s.l.)

Habitat. – Indigenous Scarp forest of the Pondoland Gorge and Transkei Coastal Scarp subtypes, adjacent to rivers, in leaf litter.

Notes. – Morphologically, *C. "pondoensis"* resembles *C. trifimbriatus* in features of the periostracum and radula. The position of spiral rows of flanges is equivalent in *C. "pondoensis"* and *C.trifimbriatus* specimens from the type locality. The radulae have teeth with large cusps relatively uniform in size. *C. "pondoensis"* is distinguished from other species by its unique operculum, with the outer lamellar blade projecting high above the fringe and sloping towards the centre and a well-developed lattice of interwoven bristles joining the lamellar blade to the fringe (Fig. 4.16G). Other species bearing a lattice of interwoven bristles at the top edge of lamellar blade, fused with the main fringe are *C.putealis*, *C. bathrolophodes* and *C. "cooperae"* but these three species have a relatively deep operculum.

In the molecular study, *C. "pondoensis"* did not appear related to *C. trifimbriatus* or to any other lineages. In the Maximum Likelihood analyses a distinct lineage from the Nxaxo region of southern Transkei formed a moderately well-supported cluster with *C. "pondoensis"*, but differs from *C. "pondoensis"* in all distinguishing morphological features. The identity of the lineage from Nxaxo will require further investigation.

In coastal areas of Transkei where *C. "pondoensis"* is sympatric with *C. putealis* and *C. "cooperae"*, specimens appeared to be scarce and patchily distributed, while at localities in southern KwaZulu-Natal (Umtamvuna Nature Reserve and Hlokohloko valley inland of Port Shepstone) where *C. "pondoensis"* was the only species recorded, they appeared to be common.

Etymology. – Named for the distribution of the species, centered around the Pondoland region.

Chondrocyclus "devilliersi" sp. n.

Fig. 4.17

Diagnosis. – Shell small, depressed, lenticular; protoconch not mammillate; periostracum with widely spaced axial costae developing at the periphery broad rounded flanges, semi-circular in

shape; operculum duplex, exterior portion very shallowly concave to almost flat, with step-shaped multispiral lamella terminating in a short fringe of fused bristles. (Other features still to be examined under SEM).

Description (Fig. 4.17). – Shell small, depressed, lenticular, adult width 5.01-6.01 mm, height 2.59-3.17 mm, width:height 1.70-2.16 (n = 16). Spire not much raised, each whorl rising just above the next, apex almost flat. Embryonic shell (Fig. 4.17C-D) nearly 2.25 whorls, microscopically malleate, junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising 2.75 whorls, convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus wide and deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with widely spaced lamellate axial costae at regular intervals, approx. 65 (n = 2) on last whorl, expanded into a single row of semi-circular flanges around periphery (Fig. 4.17C,E). Shell translucent, glossy, corneous yellow-brown when fresh. Operculum (Fig. 4.17F-G): duplex, outer portion slightly concave; lamella of outer multispiral portion with 4.5 whorls, step-shaped; upper edge of lamella thin and projects slightly above fringe. Penis: relatively short and broad, flattened dorsoventrally and laterally expanded on left side from about midway down the shaft, with numerous annular rugae, smooth distal end narrows, intromittant organ relatively long.

Holotype: SOUTH AFRICA: *E. Cape*: Nqadu Forest, 19 km north of Mthatha (-31.42412°S: 28.75475°E), Transkei Mistbelt Forest, in leaf litter, M. Cole, 16/iv/2015 (NMSA P0641/T4158).

Paratypes (all ELM unless otherwise indicated): *E. Cape*: same data as holotype, M & K. Cole, 16/iv/2015 (D 17922/T116, W3861/T117); Nqadu Forest, north of Mthatha (-31.4278°S: 28.7520°E), Southern Mistbelt *Podocarpus* forest, in leaf litter, D. Herbert, 12/v/2001 (NMSA V9111/T4110); Nqadu Forest, 19 km north of Mthatha (-31.42412°S: 28.75475°E), Transkei Mistbelt Forest, in leaf litter, M. Cole, V. Ndibo & T. Morgenthal, 26/i/2013 (D 17147/T115, W 3716/T167).

Distribution (Fig. 3.6). – Known only from Nqadu forest, approximately 20 km north of Mthatha.

Habitat. – Transkei Mistbelt forest, in leaf litter.

Notes. – *C. "devilliersi"* has several unique morphological features and in the molecular analyses it was not closely related to other *Chondrocyclus* species in its clade on the Transkei coast or to populations in other Transkei Mistbelt forests. Although the majority of adult specimens are worn even when collected alive and display no features of the periostracum, the fresh juveniles reveal that there is only one row of expanded flanges around the periphery of the

shell (Fig. 4.17C) and not multiple spiral rows on the body whorl, and this resembles the pattern in other clades (*C. convexiusculus, C. alabastris, C. "herberti", C. "silvicolus"* and *C. "amathole"*).

C. "devilliersi" has not been recorded in other Transkei Mistbelt forests, but there are several potential localities that have not been sampled. A full description of all the morphological characteristics and illustrations will be required before this manuscript is submitted for publication.

Etymology. – Named for Div DeVilliers whose unwaivering dedication to nature conservation in the Eastern Cape province, and the Transkei in particular, has helped preserve the remaining forests and their biota.

Chondrocyclus "pulcherrimus" sp. n.

Fig. 4.18

Diagnosis. – Shell very small, very depressed, discoidal; periostracum with very dense axial costae developing at the periphery a row of quadrangularly-shaped flanges and several spiral rows of semicircular flanges above and below this; operculum duplex, exterior saucer-shaped portion with step-shaped multispiral lamella terminating in a long solid fringe reflexed over peristome; radula with three large cusps on second lateral tooth; penis flattened dorsoventrally and laterally expanded on left side from about midway down the shaft, intromittant organ relatively long.

Description (Fig. 4.18). – Shell small, very depressed, discoidal, adult width 3.50-4.85 mm, height 1.38-2.56 mm, width:height 1.87-2.54 (n = 22). Spire almost flat with sometimes only protoconch projecting, suture deeply impressed. Embryonic shell (Fig. 4.18D) just over 2 whorls, sculptured with pock marks, junction between embryonic shell and teleoconch not particularly distinct, with weak costae at first, becoming stronger. Teleoconch comprising two whorls. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus very wide, extending to summit and exposing all the whorls. Periostracum glossy, light yellowish-brown and lacquer-like, with very dense lamellate axial costae at regular intervals, approx. 300 on last whorl (300 and 340 in Fig. 4.18B and A respectively), developing at the periphery quarangularly-shaped flanges, their expanded distal ends fused to form a solid

fringe (Fig. 4.18E); above periphery are 4-5 spiral rows of flanges and 6-7 rows below it spiraling into umbilicus, height of flanges forming spiral rows varies; row of flanges below suture forms a channel (see Fig. 4.18B,D); intervals between costae smooth. Shell pale, corneous and translucent when fresh. Operculum (Fig. 4.18G-I): duplex, outer portion consists of multispiral lamella with about 4.5 whorls, each step-shaped; at the growing edge the top of lamellar blade slopes down at an angle then curves under the step formed by the previous whorl and is thinner and more or less perpendicular where it is attached to the disc; very long fringe of fused bristles emanates from near base of vertical portion of step and curves upwards and then outwards forming a deep furrow between fringe and lamellar blade, spanned by a few bristles; a very short solid horizontal fringe emanates just below main fringe; top edge of lamella projects above level of fringe; fringe of each whorl fused to lamella of following whorl; outermost lamellar fringe very long and reflexed over peristome. Radula (Fig. 4.18F): rachidian with five cusps of approximately equivalent length; first lateral tooth with three cusps of approximately equivalent length and a very small fourth; second lateral tooth with three cusps of approximately equivalent length and two vestigial outer cusps; teeth do not differ much in size. Penis (Fig. 4.18J-K): flattened dorsoventrally and laterally expanded on left side from about midway down the shaft, with numerous annular rugae, smooth distal end occupies about one quarter of shaft, intromittant organ relatively long.

Holotype: SOUTH AFRICA: *KZN*: Ngome Forest, west of Nongoma (27.8245°S: 31.419130°E), 1136 m, Southern Mistbelt forest, in leaf litter, M & K. Cole, 19/i/2010 (NMSA W9272/T3075).

Paratypes: SOUTH AFRICA: *KZN*: same data as holotype (ELM D16939/T118, ELM W3626/T119; NHMUK 20120281, 5 specimens; RMNH MOL.330504, 4 specimens); Ngome Forest (-27.82500°S: 31.4183°E), 1200 m, mist-belt *Podocarpus* forest, in leaf-litter beneath T*richocladus grandilflorus*, Herbert, Seddon & Tattersfield, 02/xii/1998 (NMSA V7103/T4112); Ngome Forest (27.82500°S: 31.48333°E), 1100 m, mist-belt *Podocarpus* forest, in leaf-litter, Herbert, Seddon & Tattersfield, 02/xii/1998 (NMSA V8530/T4113).

Distribution (Fig. 3.6). – Known only from Ngome Forest, KwaZulu-Natal.

Habitat. – Indigenous Eastern Mistbelt forest with large trees, south-facing; in leaf-litter.

Notes. – The very dense costae of the periostracum of *C. "pulcherrimus"* and large number of spiral rows of flanges, as well as the flat spire, immediately distinguish this species from all other *Chondrocyclus* species.

C. "pulcherrimus" resembles *C. trifimbriatus* in features of the operculum, radula, penis and the rough texture of the protoconch. The operculum is similar to that of *C.trifimbriatus* but the

fringe emanates from near the bottom of the vertical portion of the stepped lamellar blade forming a deep groove while in *C. trifimbriatus* it emanates from near the top of the blade and there is a very shallow groove between the fringe and lamella. The radulae of these two species are also similar with cusps of relatively uniform size.

The Ngome Forest is 3360 ha and much of the forest is protected in the Ntendeka Wilderness Area. *C. "pulcherrimus"* is locally very common unlike *C. trifimbriatus* which appears to be rare in all populations sampled.

Etymology. – From Latin *"pulcherrimus"* (most beautiful), with reference to the ornate periostracum with very dense axial lamellae and a larger number of spiral rows of flanges than any other species.

Chondrocyclus bathrolophodes Connolly, 1929

Figs. 4.19-4.20

Chondrocyclus bathrolophodes Connolly, 1929: 239, pl. xiv, f. 30-34; Connolly, 1939: 538; Herbert & Kilburn, 2004: 92. Type loc.: Kowie East [Kincaid]

Diagnosis. – Shell small, depressed, lenticular; periostracum with dense axial costae expanded into three spiral rows of flanges on last whorl: around periphery, around umbilicus and below suture; costae and flanges bear numerous tiny vertical ridges; operculum duplex, exterior portion with cup-shaped multispiral lamella with horizontal shelf of interwoven bristles spiralling up on inside of cup, fused to a very long, loose fringe reflexed over peristome; radula with three large cusps on second lateral tooth; penis flattened dorsoventrally with lateral expansions of shaft towards distal end, more prominent on left side.

Description (Fig. 4.19-4.20). – Shell small, depressed, lenticular, adult width 5.32-6.16 mm, height 2.76-3.45 mm, width:height 1.73-2.00 (n = 25). Spire depressed, each whorl just rising above the next, apex almost flat (Fig. 4.19A-B). Embryonic shell (Fig. 4.20A) 1.75 whorls, microscopically malleate, roughest in centre, junction between embryonic shell and teleoconch evident with appearance of a few weak axial costae, but not sharply demarcated. Teleoconch comprising 2.75 whorls, moderately convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free. Umbilicus deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-

brown and lacquer-like with dense lamellate costae at regular intervals, 92-127 (n = 24) on last whorl, expanded into quadrangularly-shaped flanges around periphery, forming a distinct peripheral cord, as well as a row of shorter semicircular flanges below the suture and around umbilicus (Fig. 4.19A-D); flanges bear numerous axial riblets visible at very high magnification (Fig. 4.20B); intervals between costae with microscopic axial threads (Fig. 4.20B). Shell translucent honey-brown when fresh. Living animal with head, tentacles and snout dark grey, underside of foot creamy white. Operculum (Fig. 4.20C-E): duplex, outer multispiral portion with 5.5 whorls forming a strongly concave cup, upper edge of lamellar blade thickened, forming a horizontal shelf of interwoven bristles spiralling up the inside of the cup; in the outermost whorl the latter is loosely connected to a very long fringe reflexed over peristome and preventing operculum being withdrawn into shell; in earlier whorls this fringe is not visible and appears fused with the lamella; surface of lamella of last whorl tuberculate at high magnification. Radula (Fig. 4.20F): rachidian with five cusps, central cusp approximately twice length of outer two on each side; first and second lateral teeth similar but second is larger, each with four cusps and a vestigial fifth; first three cusps gradually increasing in size from centre outwards and fourth very small. Penis (Fig. 4.20G-H): shaft dorsoventrally flattened, with lateral expansions of shaft on both sides towards distal end but more prominent on left, with numerous annular rugae, distal end bulbous and smooth, intromittant organ exserted, but not elongated.

Type material: Holotype in NHMUK (1928.3.16.4) (Fig. 4.19A).

Distribution (Fig. 3.6). – Endemic to Eastern Cape coastal strip between Great Fish River and Port Elizabeth, recorded up to 9 km inland, with a disjunct population at the mouth of the Kobonqaba River in southern Transkei.

Habitat. – Albany Dune Strandveld on coastal dunes at Port Alfred, Southern Coastal Forest with large trees (Alexandria Forest), Albany Thicket (Kowie Thicket) and Eastern Cape dune forest; in leaf-litter.

Notes. – C. bathrolophodes is similar to C. putealis and to the population in the forests at Nxaxo in periostracal ornamentation, operculum, radula and penis. Differences are discussed under the latter species.

Specimens recorded near the mouth of the Kobonqaba river would have been difficult to identify on morphological grounds alone, but the molecular phylogeny shows unambiguously that the specimens sequenced are C. bathrolophodes. The species was previously thought to occur only in the Port Elizabeth – Albany area, but is shown to have a disjunct distribution.

Figs. 4.21-4.22

Chondrocyclus putealis Connolly, 1939: 538, pl. xvi, f. 25-27; Herbert & Kilburn, 2004: 91. Type loc.: Southport [Puzey]

Diagnosis. – Shell small, depressed, lenticular; periostracum with dense axial costae expanded into three spiral rows of flanges on last whorl: around periphery around umbilicus and below suture; operculum duplex, multispiral lamella of exterior portion deeply concave, with horizontal shelf of interwoven bristles spiralling up on inside of lamella and connected to a very long, loose fringe reflexed over peristome; radula with three large cusps on second lateral tooth; penis flattened dorsoventrally with lateral expansions of shaft towards distal end, more prominent on left side.

Description (Fig. 4.21-4.22). – Shell small, depressed, lenticular, adult width 4.91-5.38mm, height 2.49-3.26 mm, width:height 1.61-2.00 (n = 20). Spire not much raised, each whorl rising just above the next, apex almost flat. Embryonic shell (Fig. 4.22A) approx. 1.75 whorls, microscopically malleate, roughest in centre, junction between embryonic shell and teleoconch evident with appearance of a few weak axial costae, but not sharply demarcated. Teleoconch comprising 2.5-2.75 whorls, moderately convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending strongly near aperture, peristome simple, continuous and free. Umbilicus deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with dense lamellate costae at regular intervals, 107-150 (n = 15) on last whorl, expanded into paddle-shaped flanges around periphery and umbilicus, as well as a row of shorter broadly rounded lamellae below suture (Fig. 4.21); flanges bear axial riblets visible at very high magnification (Fig. 4.22B); intervals between costae with microscopic axial threads. Operculum (Fig. 4.22D-E,G-H): duplex, outer multispiral portion with approx. 5 whorls; lamellar blade high and steep sided, resulting in a deeply concave outer portion with more-or-less perpendicular sides towards the top and curving inwards towards the bottom; upper edge of lamellar blade thickened, forming a horizontal shelf of interwoven bristles which forms a spiral staircase on the inside of the lamellar blade; in the outermost whorl the latter is connected to a very long fringe reflexed over peristome and preventing operculum being withdrawn into shell. In earlier whorls this fringe is not visible and appears fused with the lamella; surface of lamella of last whorl tuberculate at high magnification (Fig. 4.22H). Shell translucent, glossy, honey-brown when fresh. Radula (Fig. 4.22C): rachidian with five cusps,

central one approximately twice length of outer two on each side, the latter four approximately equivalent length; first and second lateral teeth each with three large cusps, a smaller fourth and a vestigial fifth, second lateral tooth is larger. Penis (Fig. 4.22F,I): shaft dorsoventrally flattened, with lateral expansions towards the distal end on both sides but more prominent on left, with numerous annular rugae, distal end bulbous and smooth, intromittant organ moderately elongated.

Type material: Syntypes in NHMUK (1937.12.30.5087-5090) (Fig. 4.21A).

Distribution (Fig. 3.6). – Endemic to a narrow range primarily near the coast, between Mtentu in northern Transkei and Southport in southern Kwazulu-Natal, but also recorded inland in the Port Shepstone area (ca. 200 m a.s.l.)

Habitat. –Indigenous scarp forest on banks of rivers, in leaf litter.

Notes. – The shell of *C. putealis* resembles *C.bathrolophodes* in shape but attains slightly smaller size. The position of spiral rows of flanges is similar in the two species, but costae are slightly more dense on average in *C. putealis* and the peripheral and umbilical cords stronger than those of *C. bathrolophodes*. The opercula of the two species are very similar although the operculum of *C. putealis* is deeper with perpendicular sides near the top and curving inward near the disc, while the lamellar blade of *C. bathrolophodes* widens evenly towards the top. Both species occupy a relatively narrow range, separated geographically by a wide intervening distance in which *C. "cooperae"* sp. n. (below) occurs. On morphological grounds alone, it was not clear whether *C. putealis* and *C. bathrolophodes* should indeed be considered distinct species, in spite of subtle differences. In the molecular analyses *C. "pondoensis"* is nested within this group, adding weight to the decision to treat these lineages as distinct species.

C. putealis appears to be a very rare species and there are only a few localities where recent specimens could be found and it was patchily distributed at these localities. At Mtentu River mouth, five sites were sampled on both sides of the river, up to about 4.5 km upstream. It was common at only one site, present at one other site, but could not be found at the other three sites. At the latter sites, *C. trifimbriatus* was collected, but not common.

Chondrocyclus "cooperae" sp. n.

Fig. 4.23

Diagnosis. – Shell small, depressed, lenticular; periostracum with dense axial costae expanded into seven spiral rows of flanges on last whorl: one around periphery, and three each between periphery and suture and between periphery and umbilicus; costae and flanges bear numerous tiny vertical ridges; operculum duplex, exterior concave portion shaped like a wide cup or bowl, multispiral lamella with horizontal shelf of interwoven bristles spiralling up on inside of bowl, fused to a very long, loose fringe reflexed over peristome; radula with three large cusps on second lateral tooth; penis flattened dorsoventrally with prominent lateral expansion on left of shaft towards distal end, and with a characteristic long intromittant organ.

Description (Fig. 4.23). – Shell small, depressed, lenticular, adult width 4.51-6.51 mm, height 2.25-4.01 mm, width:height 1.44-2.32 (n = 66, measured in several populations throughout the range). Spire not much raised, each whorl rising just above the next, apex almost flat. Embryonic shell (Fig. 4.23D) just under 1.75 whorls, microscopically malleate, roughest in centre, junction between embryonic shell and teleoconch evident with appearance of a few weak costae, but not sharply demarcated. Teleoconch comprising 2.75 whorls, moderately convex, rapidly increasing, suture deeply impressed. Aperture circular, last whorl descending strongly near aperture, peristome simple, continuous and free. Umbilicus deep, extending to apex and exposing all the whorls. Periostracum glossy, honey-brown and lacquer-like with dense lamellate axial costae at regular intervals, density varying between populations, 105-179 (n = 27, counted in three separate populations), expanded into tall quadrangularly-shaped flanges around periphery, and six additional spiral rows of lower-standing flanges on body whorl, three between suture and periphery and three rows between periphery and umbilicus, the row closest to umbilicus weaker than other rows (Fig. 4.23A-C); flanges and portion of costae near umbilicus bear axial ridges visible at very high magnification (Fig. 4.23E); intervals between costae with microscopic axial threads. Shell translucent, glossy, honey-brown when fresh. Living animal with head, tentacles and snout dark grey, underside of foot creamy white. Operculum (Fig. 4.23G-H): duplex, outer multispiral portion with 5.5 whorls forming a widely cupolaeform cup or bowl, upper edge of lamellar blade thickened, forming a horizontal shelf of interwoven bristles in a lattice-like pattern; in the outermost whorl the latter is continuous with a very long fringe reflexed over peristome and preventing operculum being withdrawn into shell; in earlier whorls this fringe is not visible and appears fused with the lamella; growing edge of

lamella arrow shaped. Surface of lamella of last whorl tuberculate at high magnification. Radula (Fig. 4.23F): rachidian with five cusps, central one approximately twice length of outer two on each side; first and second lateral teeth similar but second is larger, each with four cusps and a vestigial fifth; first three cusps gradually increasing in size from centre outwards and fourth very small. Penis (Fig. 4.23I-J): shaft dorsoventrally flattened, with large lateral expansion on left side, with numerous annular rugae, distal end smooth and not bulbous, intromittant organ very long.

Holotype: SOUTH AFRICA: *E. Cape*: Umtiza Nature Reserve, east side of Buffalo Pass (-33.01444°S: 27.80806°E), indigenous scarp forest, in leaf litter, M. Cole, V. Ndibo & D-J Hodgkinson, 18/iii/2011 (NMSA W9271/T3074).

Paratypes (all ELM unless otherwise indicated): SOUTH AFRICA: *E. Cape*: same data as holotype (ELM D16936/T120, W3623/T121; NHMUK 20120280, 4 specimens; NMSA W9275/T3076, 2 specimens; NMW.Z.2012.065.00009, 1 specimen; RMNH MOL.330502, 3 specimens); ditto, M. Bursey, 21/iv/2006 (D14918/T122); ditto, M. Cole, 20/v/2011 (D17008/T123); Hickmans River, dune forest west of lagoon (-33.07000°S: 27.83639°E), M. Bursey, 15/iii/2003 (D16934/T124); East London, Nahoon estuary east bank (-32.98039°S: 27.94333°E), 1 km upstream of mouth, M. Bursey, 2/vi/2003 (D15533/T126, W3681/T125); ditto, M. Cole, 08/xii/2009 (D16931/T127, W03621/T128); ditto, M. Cole & D-J. Hodgkinson, 30/iii/2011 (W03622/T129); Gqunube Green, east bank of Gonubie River, (-32.93294°S: 28.02350°E), 1 km upstream of mouth, forest on steep slope, M. Bursey, 9/iv/2003 (W03028/T130); Gqunube Green, Wilderness Valley (-32.93028°S: 28.01278°E), tributary of Gonubie River on east bank 2.5 km upstream of mouth, M. Cole, 11/iv/2002 (D17009/T131); Kwelera, Monrepos, Schults Farm (-32.88833°S: 28.04167°E), M. Cole, 13/xi/2007 (D15603/T132); Viskop, east bank of Cefane River (-32.80472°S: 28.13194°E), M. Bursey, 20/xi/2006 (D15121/T133, W03112/T134); ditto, M. Cole, 30/xii/2009 (D16929/T135, W03620/T136); Mazeppa Bay, east bank of Sihlontlweni estuary near mouth (-32.478317°S: 28.646002°E), 28 m, M. Cole, 23/iv/2015 (D17931/T137, W03867/T138); Colleywobbles, south facing slope above vulture colony (-31.98333°S: 28.58333°E), sparse thicket invaded with *Lantana*, M. Bursey, 20/ii/2006 (D14968/T139); Dwesa Nature Reserve, forest along roadside east of camp (-32.15282°S: 28.84167°E), M. Bursey, 7/iii/2000 (W03212/T140); ditto, R. Daniels, 20/ii/2011 (D16935/T141); Xora, Nxeni Forest, east bank of Ntlonyane River (-32.193325°S: 28.957403°E), M. & K. Cole, 8/xi/2012 (D17499/T142, W03813/T143); Mpame forest (-32.085595°S: 29.030633°E), M. Cole, 20/ii/2009 (D16937/T144, W03624/T145); Hluleka Nature Reserve (-31.81956°S: 29.31553°E), forest on north bank of river, steeply sloping, after second bridge along forest road, M. Bursey, 20/iv/2005 (D15529/T146); Port St. Johns, east bank of Umzimvubu River (-31.59722°S: 29.53500°E), 3 km upstream, alive in leaf-litter, M. Bursey & V. Ndibo, 6/vii/2006 (D15227/T147); Port St. Johns, travertine deposit area (-31.52111°S: 29.45694°E), 26 km upstream on Umzimvubu River, M. Bursey & V. Ndibo, 22/iv/2005 (D15311/T148); Mbotyi, forest near Mkozi River (-31.44586°S: 29.75486°E), south-facing forest on steep slope on east bank of Mkozi River, M. Bursey, 02/iii/2003 (D14394/T149, W2836/T150).

Other material examined (all ELM unless otherwise indicated): SOUTH AFRICA: *E. Cape*: Umtiza Nature Reserve, east side of Buffalo Pass (-33.01444°S: 27.80806°E), indigenous scarp forest, C. J. Vernon, xi/1993 (D13141); East London, Nahoon estuary east bank (-32.98039°S: 27.94333°E), 1 km upstream of mouth, M. Cole & D-J. Hodgkinson, 30/iii/2011 (D16932); East London, forest below casino (-32.969190°S: 27.905955°E), west bank of Nahoon River near Abbotsford causeway, 4.5 km upstream of mouth, M. Cole, 28/i/2008 (D16959); Gqunube Green, east bank of Gonubie River, (-32.93294°S: 28.02350°E), 1 km upstream of mouth, forest on steep slope, M. Bursey, 9/iv/2003 (D13644); Inkwenkwezi Private Game Reserve, inland of Cintsa, (-32.83333°S: 28.06667°E), M. Bursey, 22/xi/2006 (D15186); Viskop, east bank of Cefane River (-32.80472°S: 28.13194°E), M. Bursey, 8/iv/2000 (D16930); ditto, 15/vi/2000 (D15536); Morgan's Bay, Yellowood Park (-32.69667°S: 28.33472°E), 2 km upstream of mouth, riverine forest on south-west facing slope, predominantly

Strelitzia nicolai, M. Bursey, 14/iii/2005 (D15338); ditto, R. Daniels, 06/iii/2011 (D16968); Kei River, tributary on west bank 6 km upstream of mouth (-32.63000°S: 28.34833°E), forest on steep slope, south facing, M. Bursey, 11/ii/2006 (D14990); Mcelwana, south of Mazeppa Bay, east bank of estuary (-32.49741000°S: 28.60362000°E), 15/iv/2005, M. Bursey; Dwesa Nature Reserve, forest along roadside east of camp (-32.15282°S: 28.84167°E), M. Bursey, 5/iii/2000 (W03261); Xora, Nxeni Forest, east bank of Ntlonyane River (-32.193325°S: 28.957403°E), M. Cole, 11/viii/2011 (D16938, W03625); Sinangwana, Sigxeni Forest, (-31.74738°S: 29.37078°E), east bank of Sinangwana River, M. Bursey, 21/iv/2005 (D15427); Port St. Johns, east side of Umzimvubu River in valley north of Mount Sullivan (-31.589887°S: 29.545133°E), alive in leaf-litter, M. Bursey & V. Ndibo, 6/vii/2006 (D15235).

Distribution (Fig. 3.6). – Endemic to Eastern Cape from East London to Mbotyi, primarily near the coast.

Habitat. – Indigenous scarp forest and dune forest, in leaf litter.

Notes. - *C. "cooperae"* resembles *C. bathrolophodes* and *C. putealis* in general shape, operculum and radula, but differs consistently in the larger number of spiral rows of periostracal flanges. The very long intromittant organ of the penis is unmistakable and immediately distinguishes the species.

Etymology. – Named for Janna Cooper who helped collect specimens of this species and in recognition of her intimate knowledge of the Transkei coast.

Chondrocyclus exsertus (Melvill & Ponsonby, 1903)

Fig. 4.24

Chondrocyclus exsertus Melvill & Ponsonby, 1903: 608, pl. xxxii, f. 11; Connolly, 1939: 540; Herbert & Kilburn, 2004: 92. Type loc.: Umkomaas

Diagnosis. – Shell very small, moderately despressed; periostracum with dense axial costae increasing slightly in height around periphery but not expanded into spines or flanges; operculum duplex, almost flat, multispiral lamellar blade low, loose fringe of bunches of bristles, fringe of each whorl with free ends not fused to lamella of following whorl; umbilicus deep and widely open exposing all the whorls; radula with two large cusps on second lateral tooth.

Description (Fig. 4.24). – Shell very small, adult width 2.96-4.64 mm, height 1.82-2.86 mm, width:height 1.39-1.86 (n = 25). Spire moderately exserted, protoconch not mammillate. Embryonic shell (Fig. 4.24E) just over 2.5 whorls, microscopically malleate, roughest in centre;

junction between embryonic shell and teleoconch evident with development of costae. Teleoconch comprising just under two whorls, very convex, rapidly increasing, suture impressed. Aperture circular, last whorl descending near aperture, peristome simple, continuous and free (Fig. 4.24A-B). Umbilicus wide and deep, extending to summit and exposing all the whorls. Periostracum pale yellowish-brown with lamellate axial costae at regular intervals, 84-110 (n = 14) on last whorl, each lamellar blade has numerous tiny vertical ridges visible at very high magnification; lamellar blades increase in height around periphery but not expanded into flanges or hairs (Fig. 4.24B-D,F); intervals between costae with microscopic axial threads. Shell translucent and corneous when fresh. Operculum (Fig. 4.24H-I): duplex, almost flat, multispiral outer portion with a broad, thin nucleus and 6 whorls, height of lamellar blade low and not stepped, thickened horizontal ridge near bottom of blade just above disc surface, loose fringe of bristles emanates from ridge, fringe consists of bunches of short bristles, with free ends not fused to lamella of following whorl, fringe of outer whorl overlaps disc slightly. Radula (Fig. 4.24G): rachidian with 5 cusps, central cusp approximately twice length of outer cusps, outermost cusps relatively weak, cusps of rachidian set a little distance below "top" of tooth, top edge serrated; first lateral tooth usually with three large cusps, third cusp (from centre) largest, a small fourth cusp and a vestigial fifth; second lateral tooth with two large cusps, second cusp (from centre) longer and broader than first, a very small third cusp and a vestigial fourth. Penis (Fig. 4.24J-K): shaft short, broad and more or less cylindrical, intromittant organ very short.

Type material: Holotype of *Chondrocyclus exsertus* Melville & Ponsonbyi, 1903 in NHMUK (1904.4.29.28) (Fig. 4.24A).

Distribution (Fig. 4.10). – Endemic to the coastal belt of southern Kwazulu-Natal and possibly extending into northern Pondoland. Recent specimens found in a few small patches of remaining indigenous forest inland of Umtentwini and Umzumbe.

Habitat. – Indigenous Scarp forest, on steep, rocky slopes, in leaf litter.

Notes. – Spire more elevated than in the majority of other species of *Chondrocyclus* barring *C. "herberti"* sp. n., with similar shell proportions to the latter. Periostracum has simpler axial lamellae than other species, lacking flanges or hairs. The operculum is unique in that the fringe consists of bunches of bristles with free ends which are not fused to the lamellar blade of the following whorl; fringe has a looser arrangement with fewer bristles than in all other species. The radula resembles that of *C. isipingoensis*, including the unusual serrated top edge of the rachidian.

The molecular phylogeny shows *C. exsertus* to be nested within the *C. isipingoensis* clade. Morphologically it does not resemble specimens of *C. isipingoensis*, except for features of the radula.

C. exsertus is very rare and patchily distributed. Despite searching, it has not been found recently at any of the localities recorded by Connolly (1939) or in several other patches of forest on the Kwazulu-Natal south coast, excepting three very small patches among sugarcane fields, where it was presumably too steep for clearing of original forest. The vegetation on the Kwazulu-Natal south coast has undergone extensive modification since 1939.

4.3 *Chondrocyclus meredithae* Bruggen, 1983 and *C. chirindae* Bruggen, 1986

Chondrocyclus meredithae Bruggen, 1983 and *C. chirindae* Bruggen, 1986 resemble one another in general shape, possession of periostracal hairs at junctions between axial and spiral sculpture (Fig. 4.25), and in appearance of operculum, but the latter has more dense axial lamellae and spiral keels (Fig. 4.25B). Each species has a reticulate surface sculpture with spiral keels and axial lamellae more or less equal in density, with dark brown bristles on the points where the axial and spiral sculpture meet. In both species the periostracum is described as "corneous" (Bruggen 1983, 1986). However, the periostracum of *C. chirindae* (NM L4904) (Fig. 4.25B) does not appear to be "corneous", but is white and matt, suggesting a degree of calcification and this is also apparent to a lesser degree in *C. meredithae*. The descriptions of their opercula are also identical: duplex with exterior portion in the form of a large, concave, shallow saucer with 6-8 spiral whorls (Bruggen, 1983, 1986). Bruggen does not mention whether the opercula are corneous or calcareous. Examination of the operculum of *C. chirindae* (NM L4904) and the photograph of the operculum of *C. meredithae* (Fig. 4.25A) shows that both species have a calcareous operculum.

Chondrocyclus meredithae and *C. chirindae* are removed from genus *Chondrocyclus* for three reasons, based on morphology of shell and operculum: i) Opercula are calcareous, while those of *Chondrocyclus* are corneous, ii) shells have spiral keels while those of *Chondrocyclus* are smooth once periostracum removed, iii) periostracum is not glossy and lacquer-like as in all *Chondrocyclus* species, but is white and matt, suggesting a degree of calcification. Bruggen (1986) erroneously refers to major spiral sculpture in the form of keels, ridges or cords being a feature of the Cyclophoridae in Africa. Shells of *Chondrocyclus* species have spiral rows of periostracal projections, but are usually smooth once the periostracum is removed with only

traces of axial sculpture. (*C*. *"kevincolei"* and to a lesser extent *C*. *"langebergensis"* from the Western Cape have spiral engraving).

Attempts to assign the above two species to other genera are complicated by the fact that all other genera of operculate snails in Africa and Madagascar are in great need of revision (Emberton, 2009). Until recently, three of the African cyclophorids were placed in *Afroditropis* Bequaert & Clench, 1936, a genus characterized by widely spaced spiral keels on the shell, a thin peristome, not reflexed nor flaring, and a thin, corneous, simple operculum. *Afroditropis* was synonymised with *Cyathopoma* by de Winter (2002), based on conchological similarity as well as similarities between the opercula of two specimens identified as *A. strongi*, and the opercular structure of *Cyathopoma africanum* Pilsbry, 1919, *C. straeleni* Adam, 1987 and *C. camerunense* de Winter, 2002. Whether these genera should be synonymised remains inconclusive since de Winter (2002) did not examine the operculum of the type specimen of *A. strongi* and he acknowledged that the two specimens on which he based his synonymy may actually represent an as yet undescribed species due to various differences between each of them and *A. strongi*. The other African genus of Cyclophoridae is *Elgonocyclus* Verdcourt, 1982 with two species, *E. koptawaliensis* (Germain, 1934), and an undescribed species from Ongoye forest, Zululand, both minute species with marked axial costulation and simple, corneous opercula.

It is suggested that *Chondrocyclus meredithae* and *C. chirindae* could be placed in either *Cyathopoma* or *Cyclotus* and since other recently described African cyclophorids have been placed in *Cyathopoma* (e.g. *C. camerunense* de Winter, 2002; *C. tres* Bruggen, 2008 and *C. pembense* Rowson *et al.*, 2010) they are tentatively placed in *Cyathopoma* W. & H. Blanford, 1861. Blanford's (1868) diagnosis of *Cyathopoma* relies chiefly on features of the operculum which is usually truncate-conoid, with the concave exterior portion formed by a calcareous, spiral lamella which usually curves inwards towards the centre and is sometimes beautifully sculpted and elevated. The only African cyclophorid with an operculum conforming to this pattern is *Cyathopoma tres* Bruggen, 2008, from Malawi, whereas in all the other African species, including *"Cyathopoma" meredithae* and *C. chirindae*, the operculum is concave since the erect spiral lamella is higher towards the periphery (Fig. 4.25, 4.26A-B). There is considerable variation in the opercula of the 60 Malagasy species currently assigned to *Cyathopoma s.l.* so a future revision may lead to amendment of Blanford's diagnosis (Emberton, 2003). At the time of the descriptions of *"Cyathopoma" meredithae* and *C. chirindae* the opercula of African *Cyathopoma* (except *C. africanum* Pilsbry 1919) were not known because

many of the current species had not yet been described (e.g. *Cyathopoma straeleni* Adam, 1987, *C. camerunense* de Winter 2002, *C. pembense* Rowson *et al.*, 2010) or the operculum was not known (*C. azaniense* Verdcourt, 1978). The opercula of both *Chondrocyclus* and *Cyathopoma* are duplex, with an erect spiral lamella forming the whorls of the exterior portion, but that of *Chondrocyclus* is uncalcified (Kobelt, 1902) while that of *Cyathopoma* is calcareous (Blanford, 1868).

The reticulate surface sculpture of *"Cyathopoma" meredithae* and *C. chirindae* is unlike that of all other African *Cyathopoma* which have prominent spiral keels and numerous closely set axial riblets. As far as is known, no other African cyclophorids (except *Chondrocyclus*) have periostracal bristles. In some species the axial striae grow out into long processes of the periostracum, adhering in groups to the keels, e.g. *Cyathopoma africanum* Pilsbry, 1919 and *C. pembense* Rowson *et al.*, 2010. It is not known whether such an elaborate periostracum occurs in the other African species because it is easily worn off. The type species of *Cyathopoma*, *C. filocinctum* Benson, 1851, as well as a few Malagasy species (Emberton, 2003), also have reticulate surface sculpture, and a few Malagasy species have periostracal hairs (Emberton, 2003).

The reticulate appearance of *"Cyathopoma" meredithae* and *C chirindae* also resembles several Malagasy *Cyclotus* species (Emberton, 2004) (Fig. 4.27A-B). In some Malagasy *Cyclotus* the axial lamellate costae elevate into triangular periostracal projections along the sutural edge and within the umbilicus (Emberton, 2004). In *C. chirindae* the sharp edged lamellae are raised into small triangular projections at the junctions with the spiral keels and these are particularly dense within the umbilicus (Fig. 4.25B). The operculum of *Cyclotus* is flat and bilayered, the outer surface concave, formed by an inwardly curving, spiral calcareous sheet that increases in elevation towards the periphery and without projections or appendages (Fig. 4.27C-E). Bruggen (1983) draws attention to the similarity between the opercula of *C. meredithae* and *Cyclotus mamillaris* Odhner, 1919 (which at the time of Bruggen's description was classified as *Chondrocyclus mamillaris* (Fischer-Piette *et al.*, 1993)).

"Cyathopoma" meredithae and *C chirindae* both have a thin peristome, practically free but with a limited area touching the body whorl (Fig. 4.25), but it is not certain whether the specimens examined were adult. In adult *Chondrocyclus* the peristome is detached from the last whorl and droops downwards, but in subadults it is attached in a limited area. The peristome of *C.*

filocinctum Benson, 1851 is moderately thick with a broad basal flare, and in several African and Malagasy *Cyathopoma* it is expanded and may also be thickened.

The radulae and penes of African and Malagasy *Cyathopoma* and *Cyclotus* have not been documented prior to this study and no bodies of *"Cyathopoma" meredithae* and *C. chirindae* were available for examination. These features have proved useful in diagnosis and taxonomy of *Chondrocyclus* species, so their examination in *C. meredithae* and *C. chirindae* may provide useful insights as to their affinities, even though they would probably not assist with generic placement at present. The penis of *Cyathopoma pembense* is extremely long and narrow relative to that of *Chondrocyclus* and does not appear to have an intromittant organ, but tapers to a very fine point (Fig. 4.26C). The penis of *Cyclotus* sp. from Madagascar resembles that of *C. pembense*, but has a relatively broader shaft which also narrows to a fine point and no intromittant organ (Fig. 4.27G-H). What appears to be a groove possibly corresponding to a seminal groove, runs down the ventral surface. In both these species the penis lies doubled back on itself.

The radulae of *Cyathopoma pembense* and *Cyclotus* sp. differ (Fig. 4.26D, 4.27F). *C. pembense* has a serrated upper edge to the rachidian tooth, also found in *Chondrocyclus isipingoensis* and *C. exsertus*, but the first and second lateral teeth have four large cusps (often with extras), unlike the radula of any *Chondrocyclus* species. The radula of *Cyclotus* sp. resembles the radulae of several *Chondrocyclus* species, with three large cusps on the second lateral tooth. As noted in the Results section, radulae of various Cyclophoridae look superficially alike, so similarities in the radula do not necessarily imply close relationship.
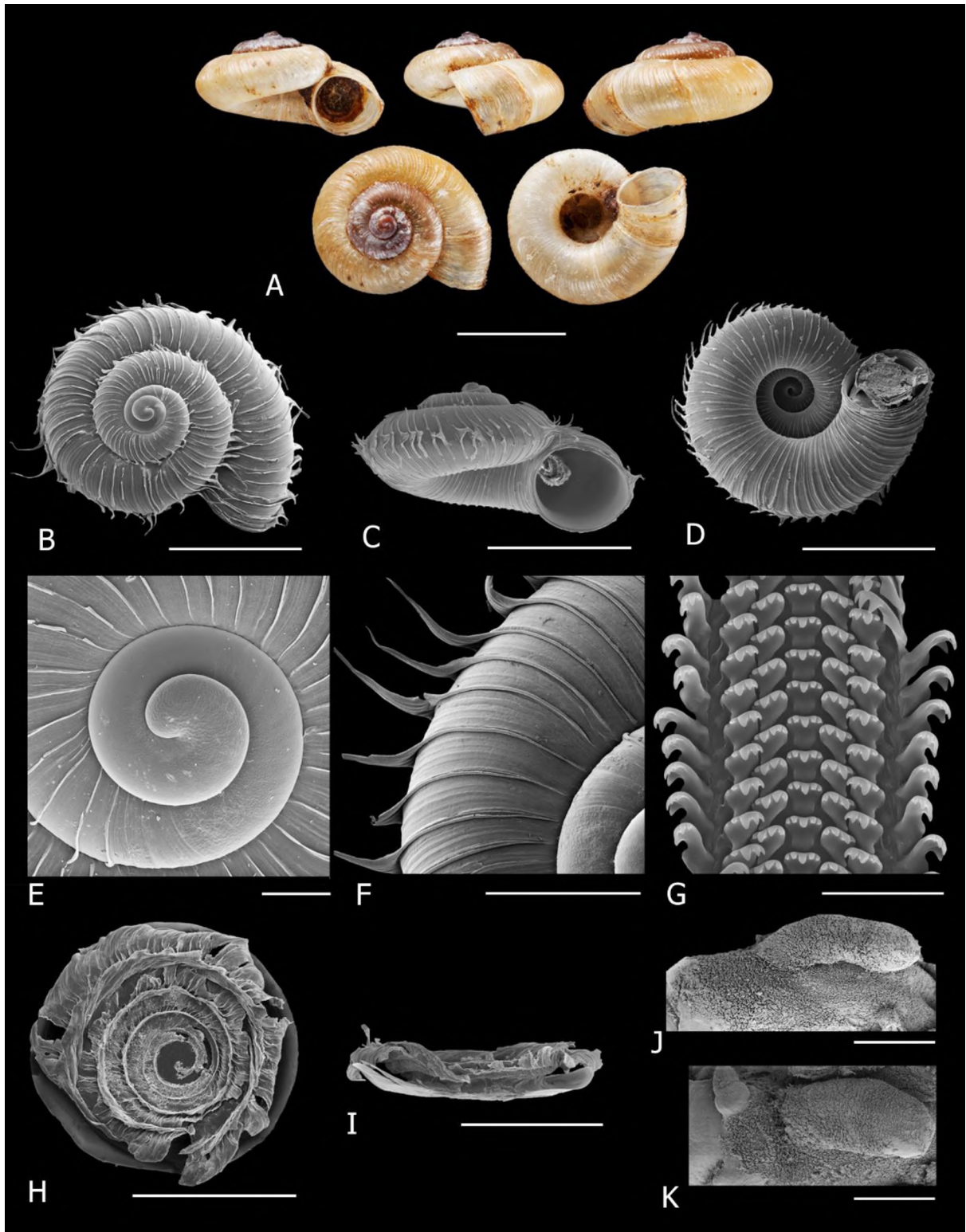
Figure 4.1 *Chondrocyclus convexiusculus* (Pfeiffer, 1855): (A) Syntype (NHMUK 20120231); all other figures ELM W3636: (B-D) aperture view, scale bar = 3 mm, dorsal and ventral view, scale bars = 2 mm; (E) protoconch, scale bar = 200 μm; (F) detail of axial lamellae of periostracum, scale bar = 500 μm; (G) portion of radula, scale bar = 50 μm; (H-I) operculum, scale bars = 1 mm; (J-K) penis lateral and dorsal view showing position on head, scale bars = 500 μm.
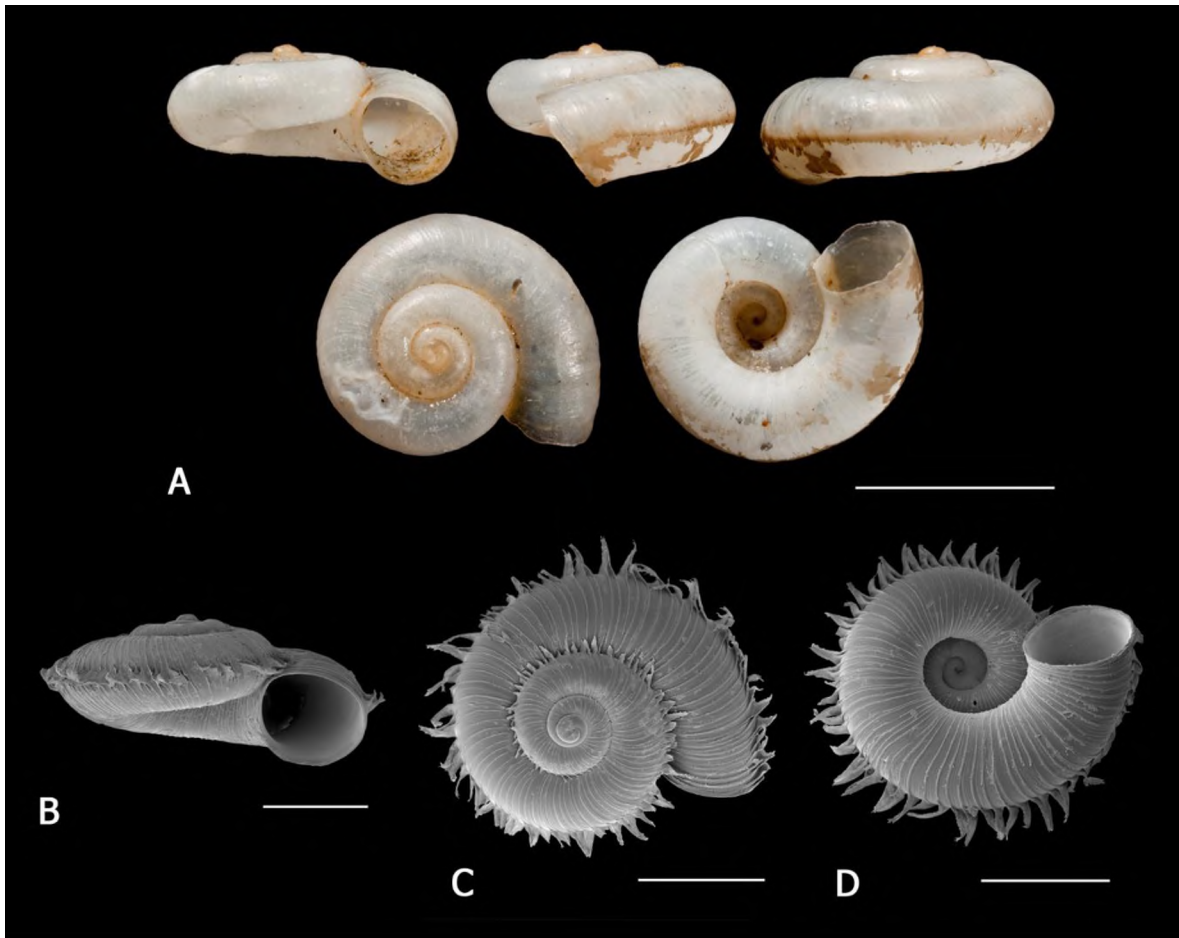
Figure 4.2 *Chondrocyclus alabastris* (Craven, 1880): (A) Syntype (NHMUK 1891.3.7.42), scale bar = 3 mm; (B-D) aperture (ELM D16882), dorsal and ventral (ELM W3640) views, scale bars = 2 mm.
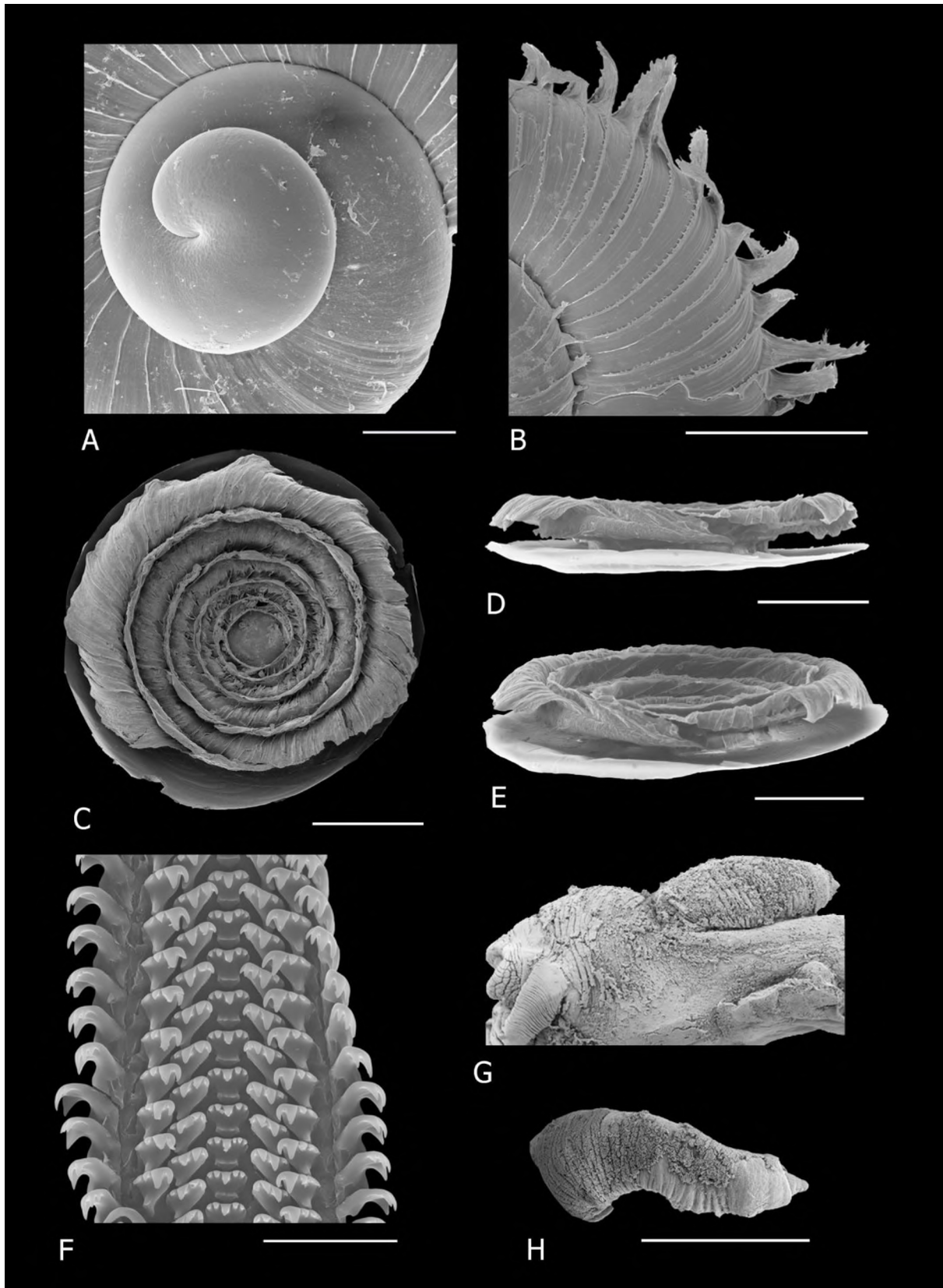
Figure 4.3 *Chondrocyclus alabastris* (Craven, 1880), all ELM: (A) protoconch (D16888), scale bar = 200 μm; (B) detail of axial lamellae of periostracum (W3639), scale bar = 1mm; (C-E) operculum (W3640), scale bars = 500 μm; (F) portion of radula (W3640), scale bar = 50 μm; (G-H) penis lateral view showing position on neck (W3638), dorsal view (W3642), scale bars = 1 mm.
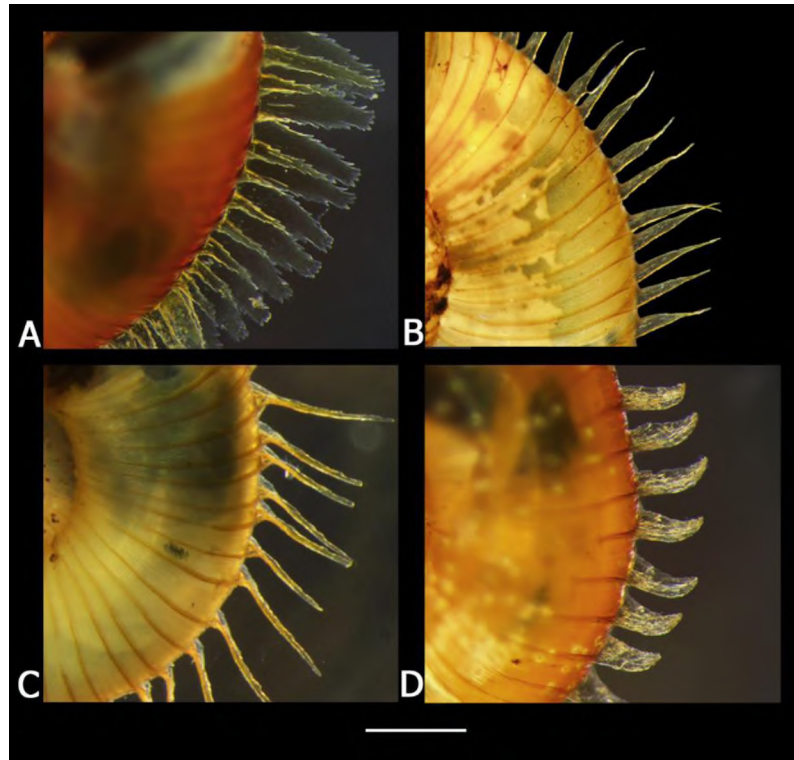
Figure 4.4 Close-up of periostracum of species of the Southern-Eastern Cape clade and *Chondrocyclus convexiusculus*, showing variation in detail of flanges around periphery (all ELM): (A) *C. alabastris* (serrated edge typical) (W3640); (B) *C. alabastris*, Grahamstown area (W3690); (C) *C. convexiusculus* (W3636); (D) *C. "herberti"* (W3691), scale bar = 500 μm.
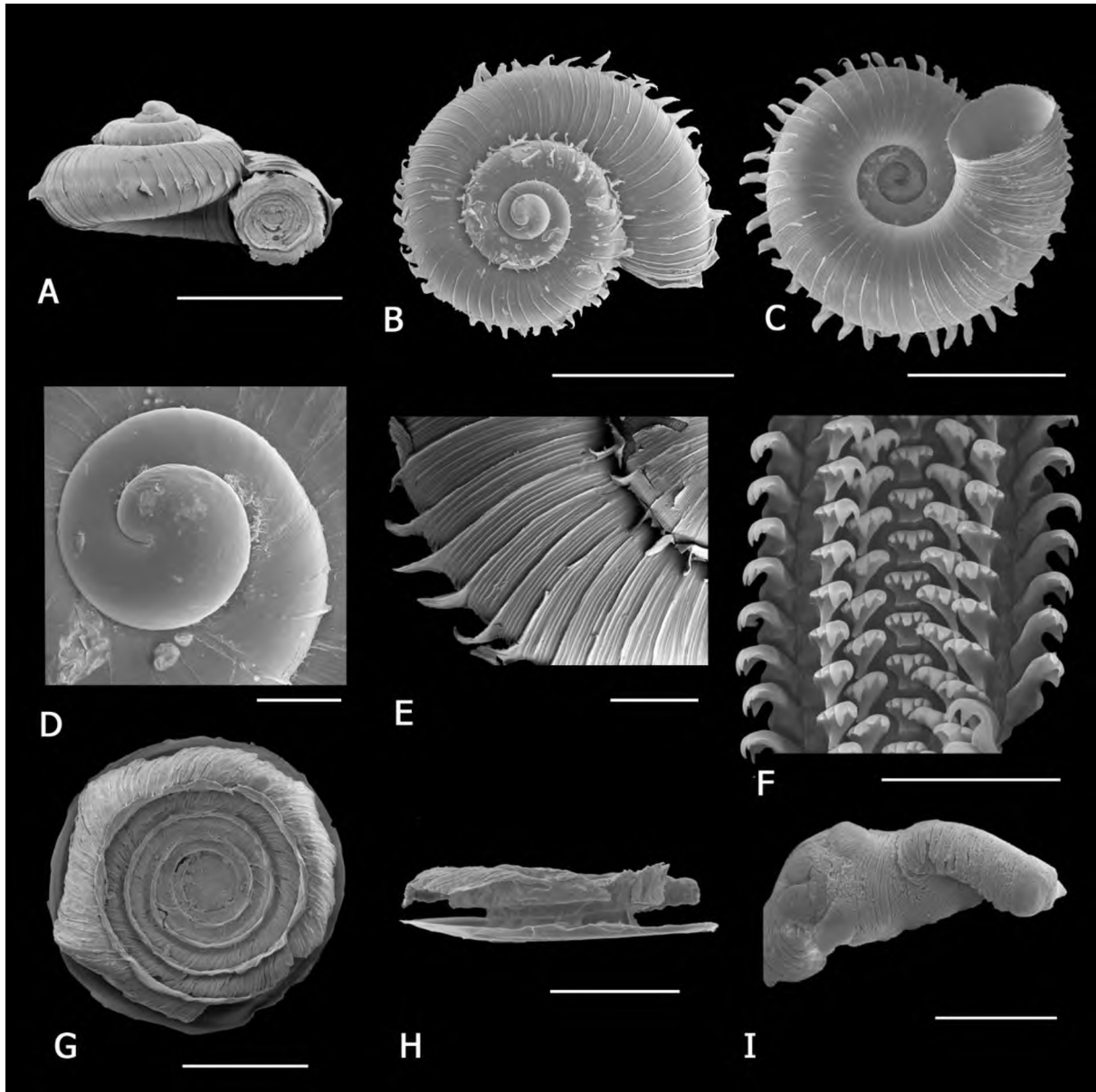
Figure 4.5 *Chondrocyclus "herberti"* sp. n.: (A-C) aperture (NMSA V8576/T4129), dorsal and ventral view (ELM W3691/T42), scale bars = 2 mm; (D) protoconch (NMSA V8632/T4127), scale bar = 200 µm; (E) detail of axial lamellae of periostracum (NMSA V8576/T4129), scale bar = 500 µm; (F) portion of radula (ELM W3691/T42), scale bar = 50 µm; (G-H) operculum (ELM W3691/T42), scale bars = 500 µm; (I) penis dorsal view showing position on neck behind right tentacle (ELM W3691/T42), scale bar = 1 mm.
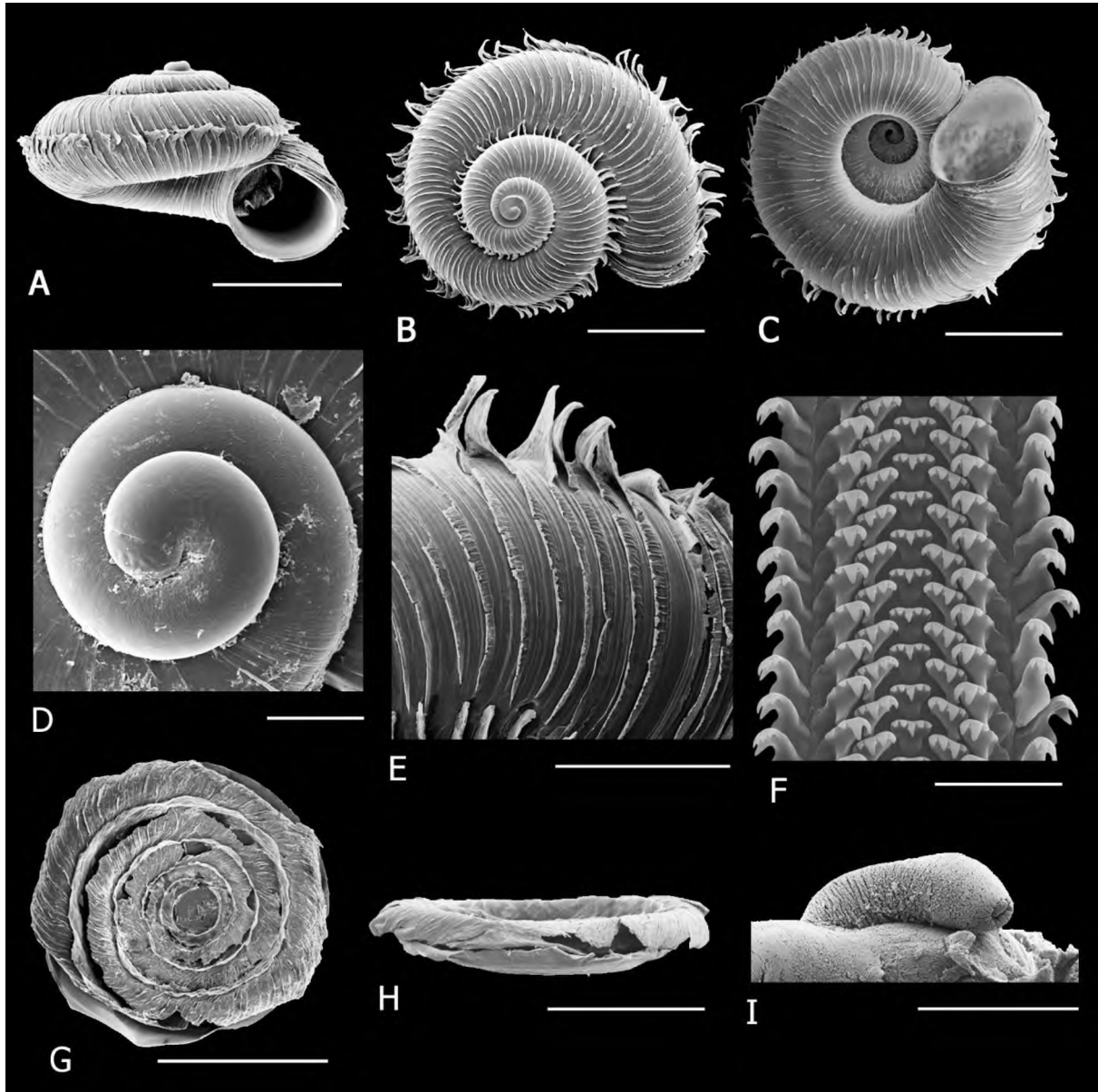
Figure 4.6 *Chondrocyclus "silvicolus"* sp. n. (all ELM): (A-C) aperture, dorsal and ventral view (D16963/T45), scale bars = 2 mm; (D) protoconch (W3644/T46), scale bar = 200 μm; (E) detail of axial lamellae of periostracum (D16963/T45), scale bar = 1mm; (F) portion of radula (D16963/T45), scale bar = 50 μm; (G-H) operculum (W3644/T46), scale bars = 1 mm; (I) penis lateral view (W3644/T46), scale bar = 1 mm.
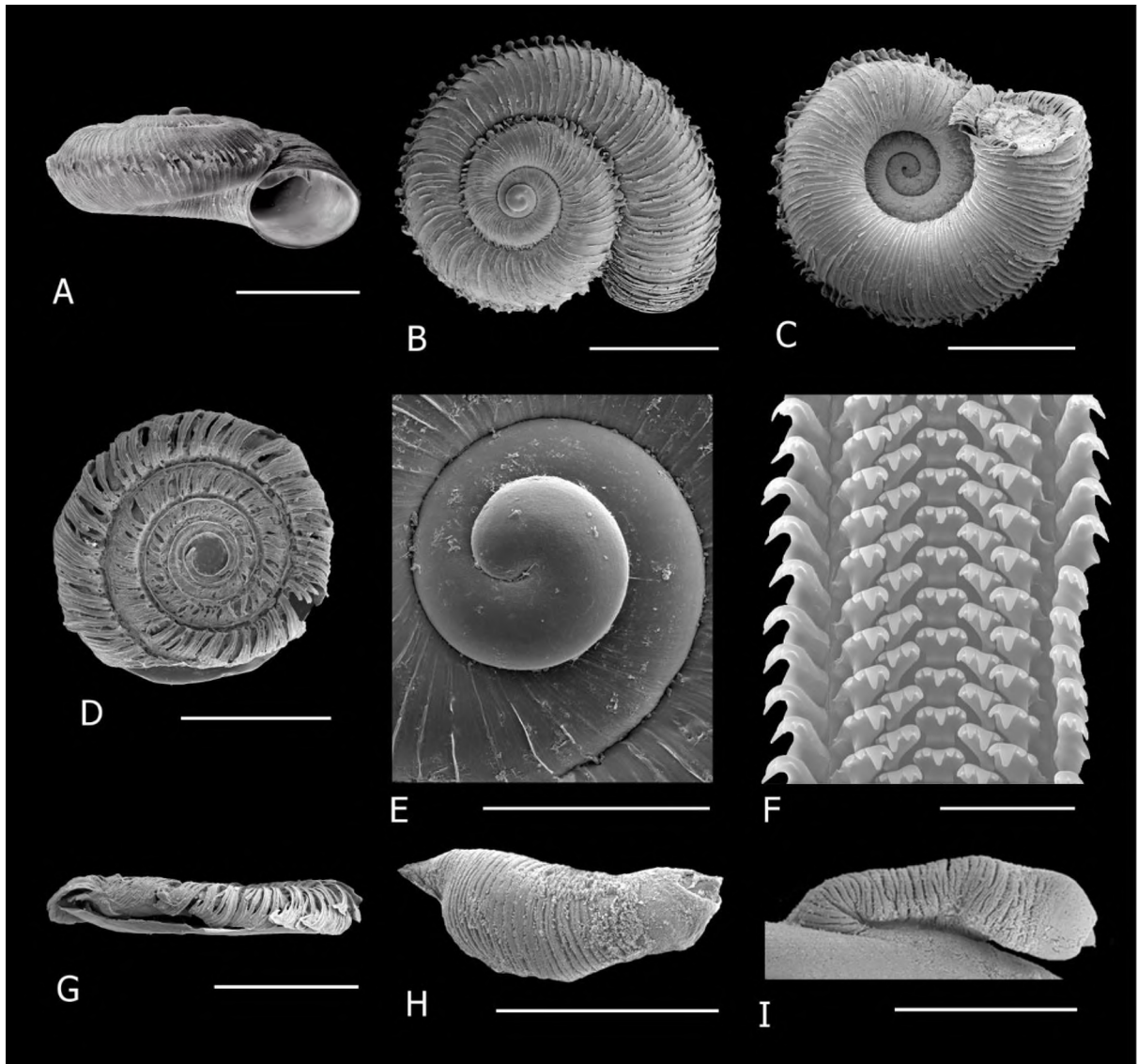
Figure 4.7 *Chondrocyclus "amathole"* sp. n. (all ELM): (A-C) aperture (W3629/T56), dorsal (W3629/T56) and ventral (W2966/T54) views, scale bars = 2 mm; (D, G) operculum (W2966/T54), scale bars = 1 mm: (E) protoconch (W3812/T59), scale bar = 500 μm; (F) portion of radula (W3628/T66), scale bar = 50 μm; (H-I) penis dorsal (W3628/T66) and lateral (W3632/T71) views, scale bars = 1 mm.
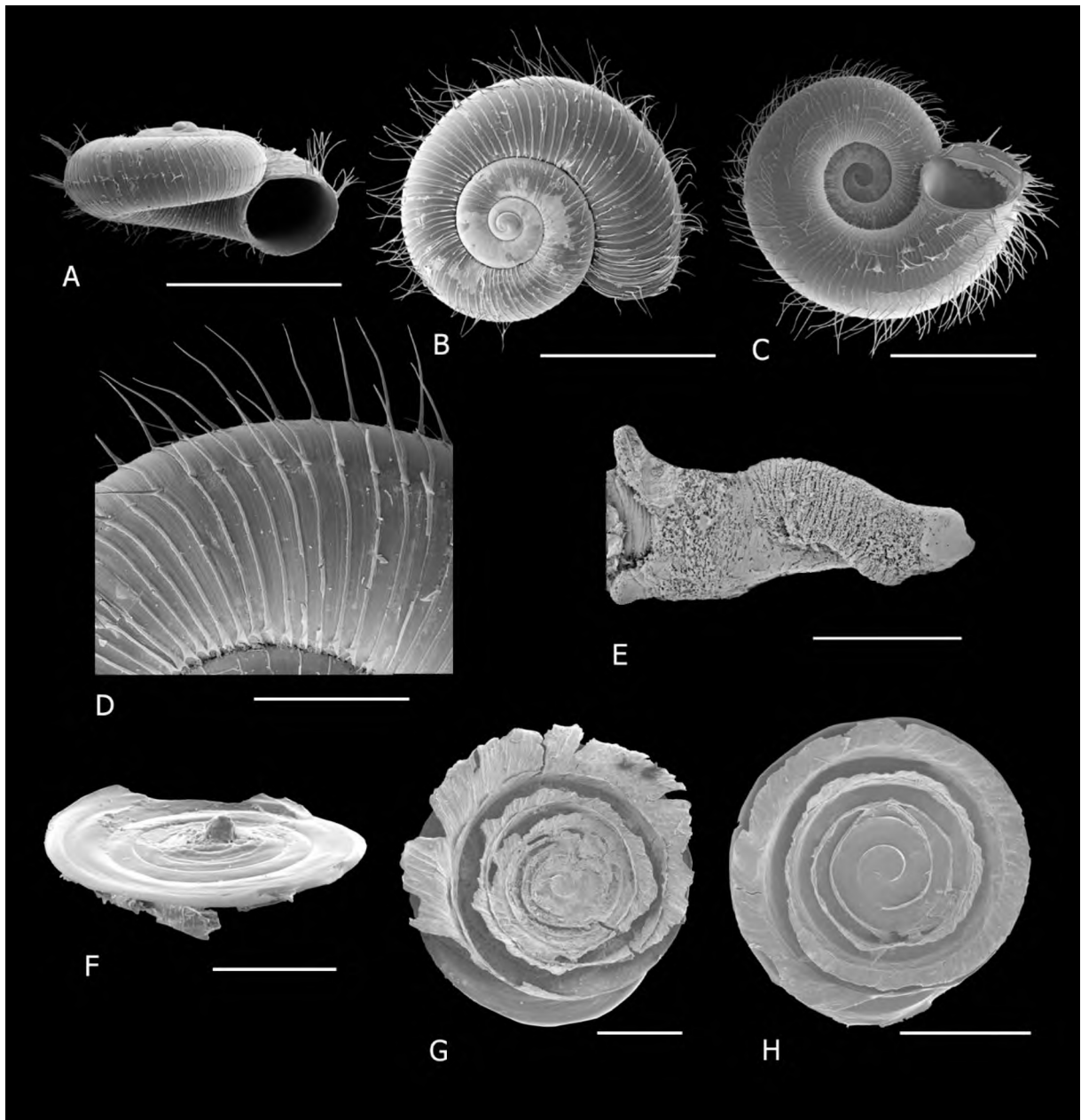
Figure 4.8 *Chondrocyclus isipingoensis* (Sturany, 1898) (all ELM unless otherwise indicated): (A-C) aperture, dorsal and ventral views (W3648), scale bars = 2 mm; (D) detail of axial lamellae of periostracum (D16897), scale bar = 500μm; (E) penis dorsal view showing position on neck behind right tentacle (W3652), scale bar = 500μm; (F-G) operculum of specimen from near type locality (W3648), (F) inner portion with tubercle, scale bars = 500μm; (H) operculum of specimen from Mpumalanga (NMSA W4486), scale bar = 200μm.
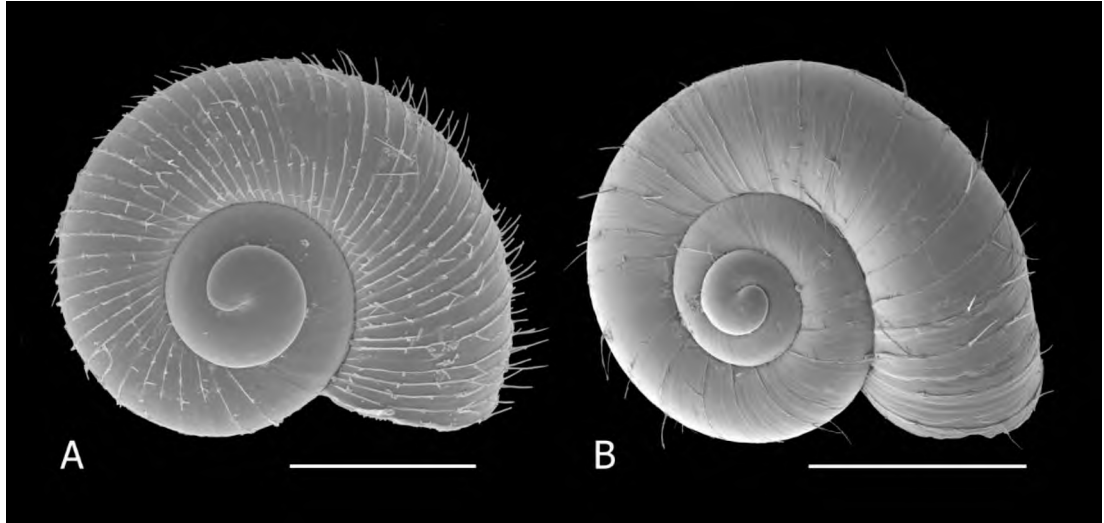
Figure 4.9 *Chondrocyclus isipingoensis* (Sturany, 1898): two juvenile shells to illustrate variation of axial lamellae between populations: (A) Soutpansberg (NMSA V5658), scale bar = 500 μm; (B) Kei River Valley (ELM D14656), scale bar = 1 mm.
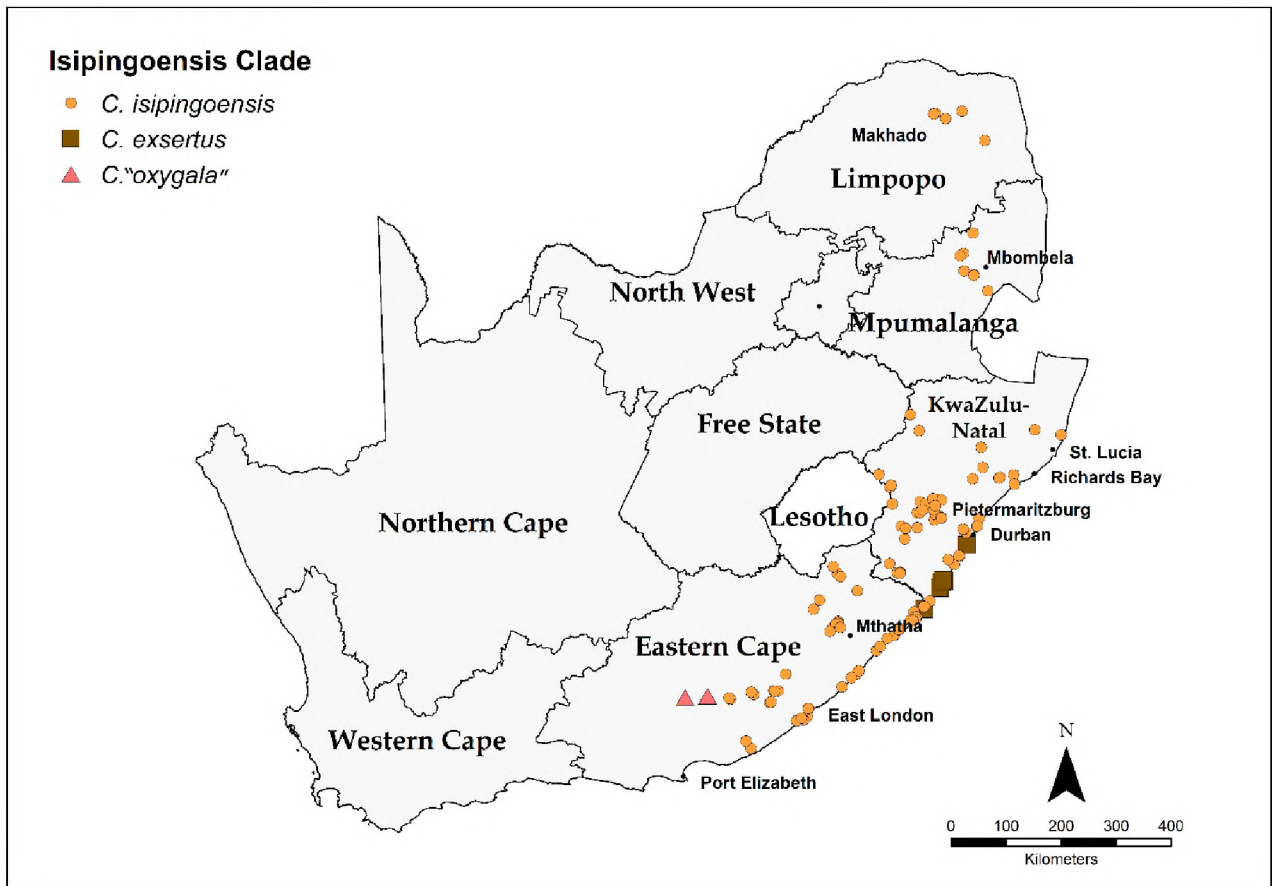
Figure 4.10 Map showing distribution of the Isipingoensis clade from the north of Limpopo Province, along the edge of the Great Escarpment as far as the Boschberg in the Eastern Cape, in montane regions coastwards of the Escarpment and along the entire south-eastern coastal belt.
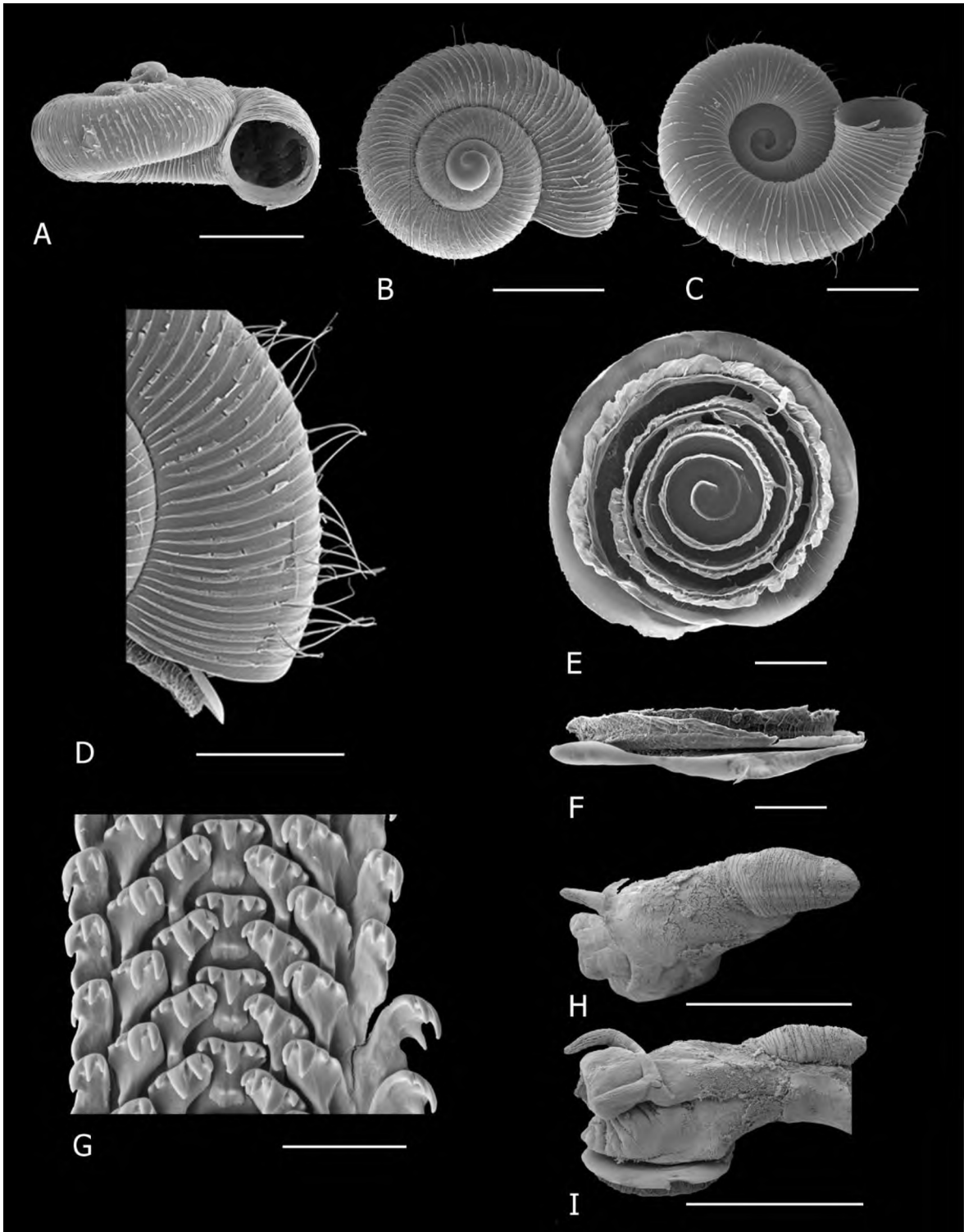
Figure 4.11 *Chondrocyclus "oxygala"* sp. n. (all ELM): (A) aperture view (D16896), (B,C) dorsal view and ventral view (W3647), scale bars = 1 mm; (D) portion of juvenile shell showing detail of periostracum (W3647), scale bar = 1 mm; (E,F) operculum dorsal and lateral view (W3647); (G) portion of radula (W3646), scale bar = 20 um; (H,I) penis showing position on neck, dorsal and lateral views (W3647), scale bars = 1 mm and 0.5 mm.
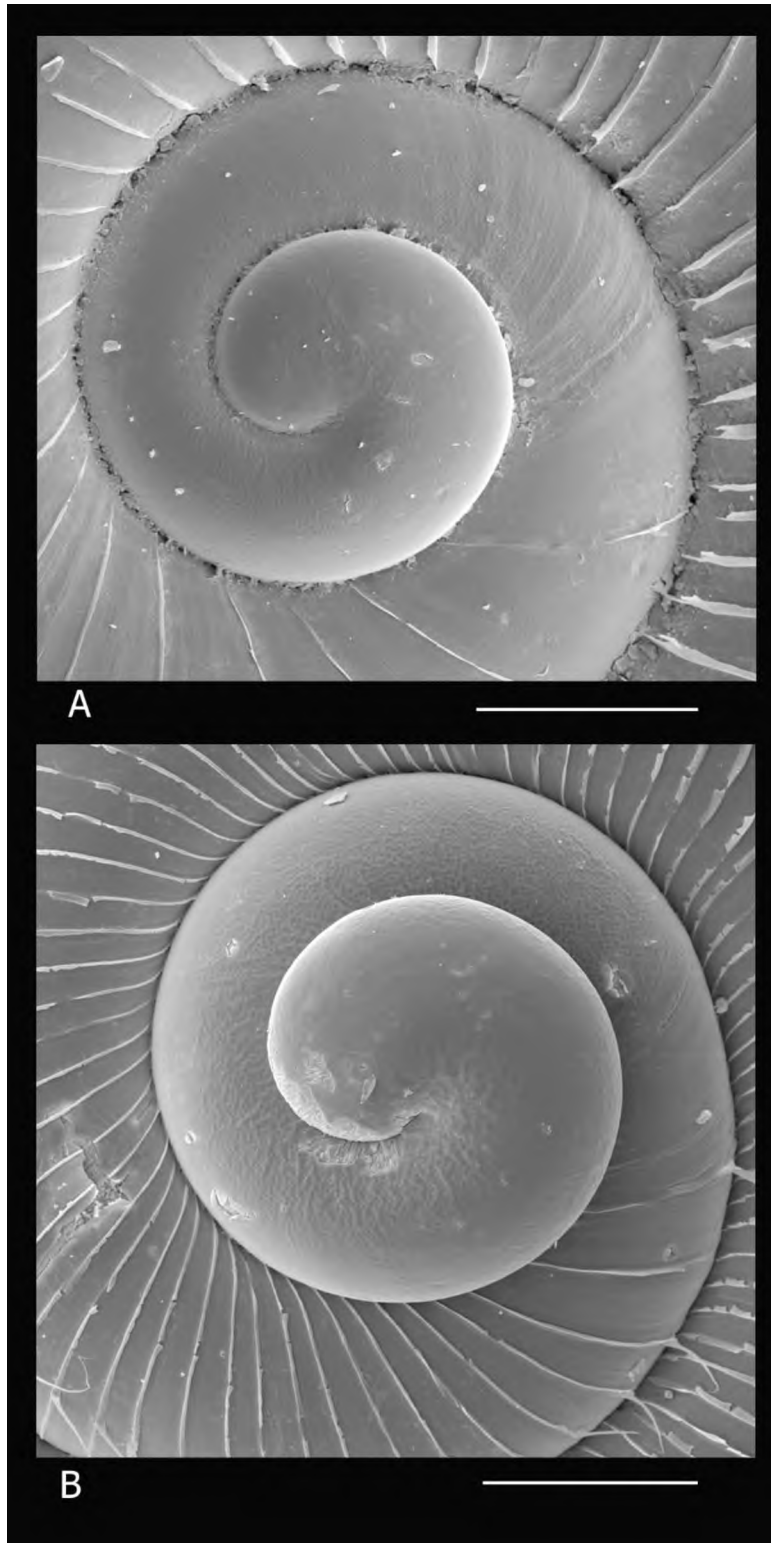
Figure 4.12 Protoconchs showing variation between (A) *Chondrocyclus isipingoensis* (Sturany, 1898) from Durban (near type locality) (ELM W3648), scale bar = 200 μm and (B) *Chondrocyclus "oxygala"* sp. n. (ELM W3647), scale bar = 200 μm.
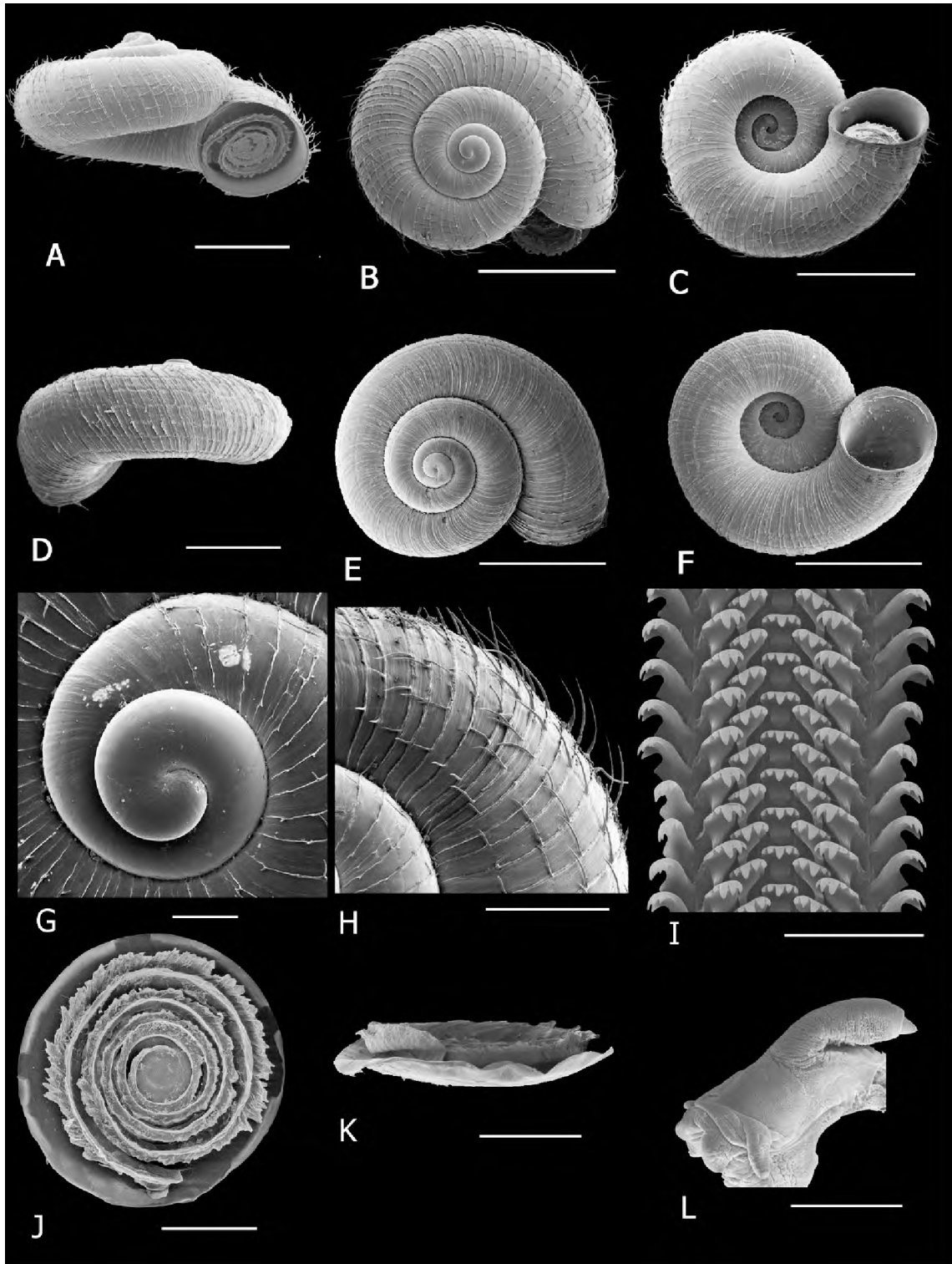
Figure 4.13 *Chondrocyclus "kevincolei"* sp. n. (all ELM W3615/T82 unless otherwise indicated): (A-C) aperture, dorsal and ventral view, scale bars = 2 mm; (D-F) shell views showing spiral grooves (NMSA W5659/T4122), scale bars = 2 mm; (G) protoconch, scale bar = 200 µm; (H) detail of axial lamellae of periostracum, scale bar = 500 µm; (F) portion of radula, scale bar = 50 µm; (J-K) operculum, scale bars = 500 µm; (L) penis lateral view, scale bars = 1 mm.
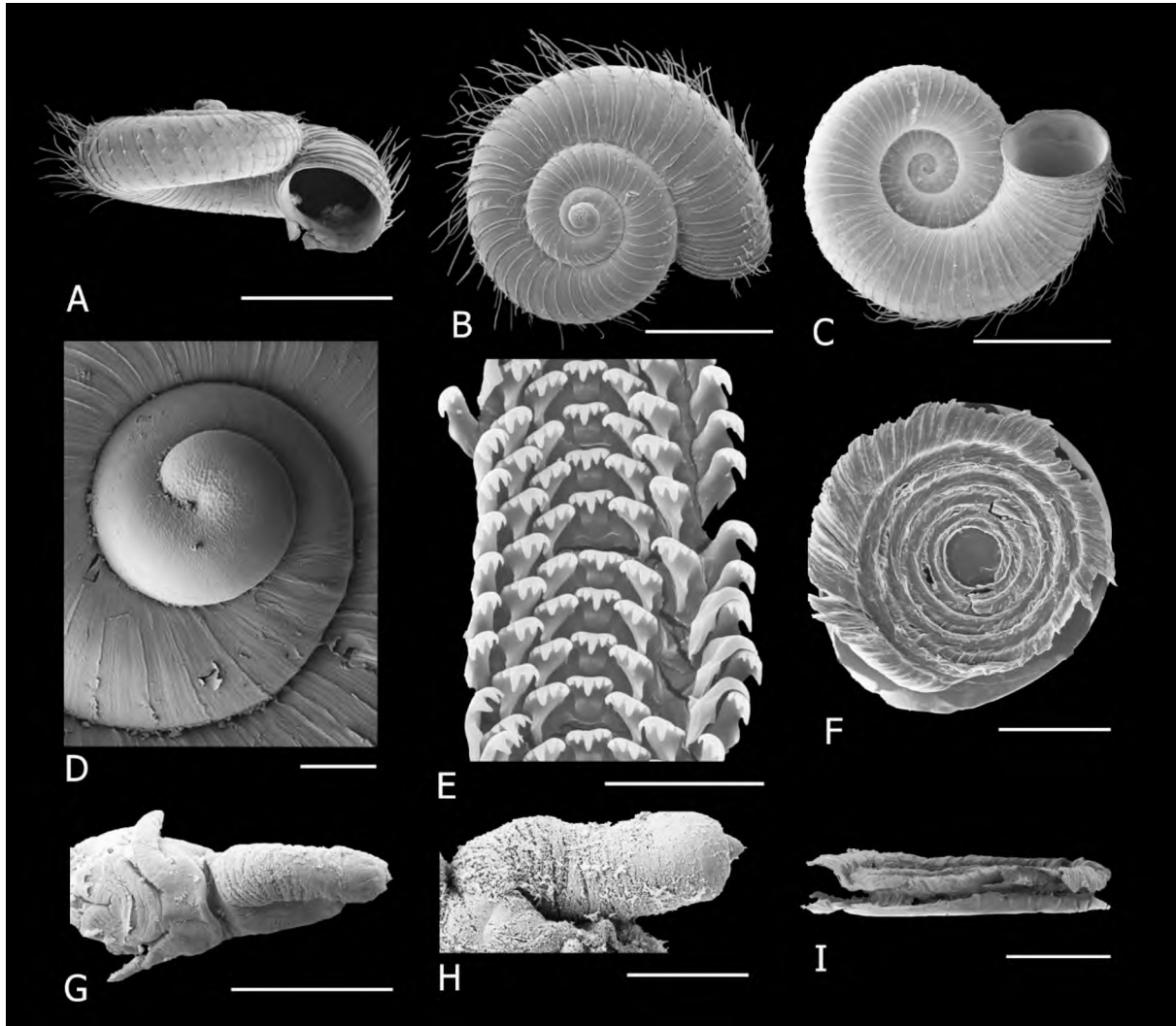
Figure 4.14 *Chondrocyclus "langebergensis"* sp. n.: (A-C) aperture (NMSA W1043/T4117), dorsal and ventral view (NMSA W5008/T4119), scale bars = 2 mm; (D) protoconch (ELM W3614/T96), scale bar = 200 μm; (E) portion of radula (NMSA W5008/T4119), scale bar = 50 μm; (F) operculum (ELM W3614/T96), scale bar = 500 μm; (G-H) penis dorsal view showing position on neck behind right tentacle (ELM W3660/T91) and lateral view (NMSA W5008/T4119), scale bars = 1 mm; (I) operculum lateral view (NMSA W5008/T4119) (scale bar = 500 μm).
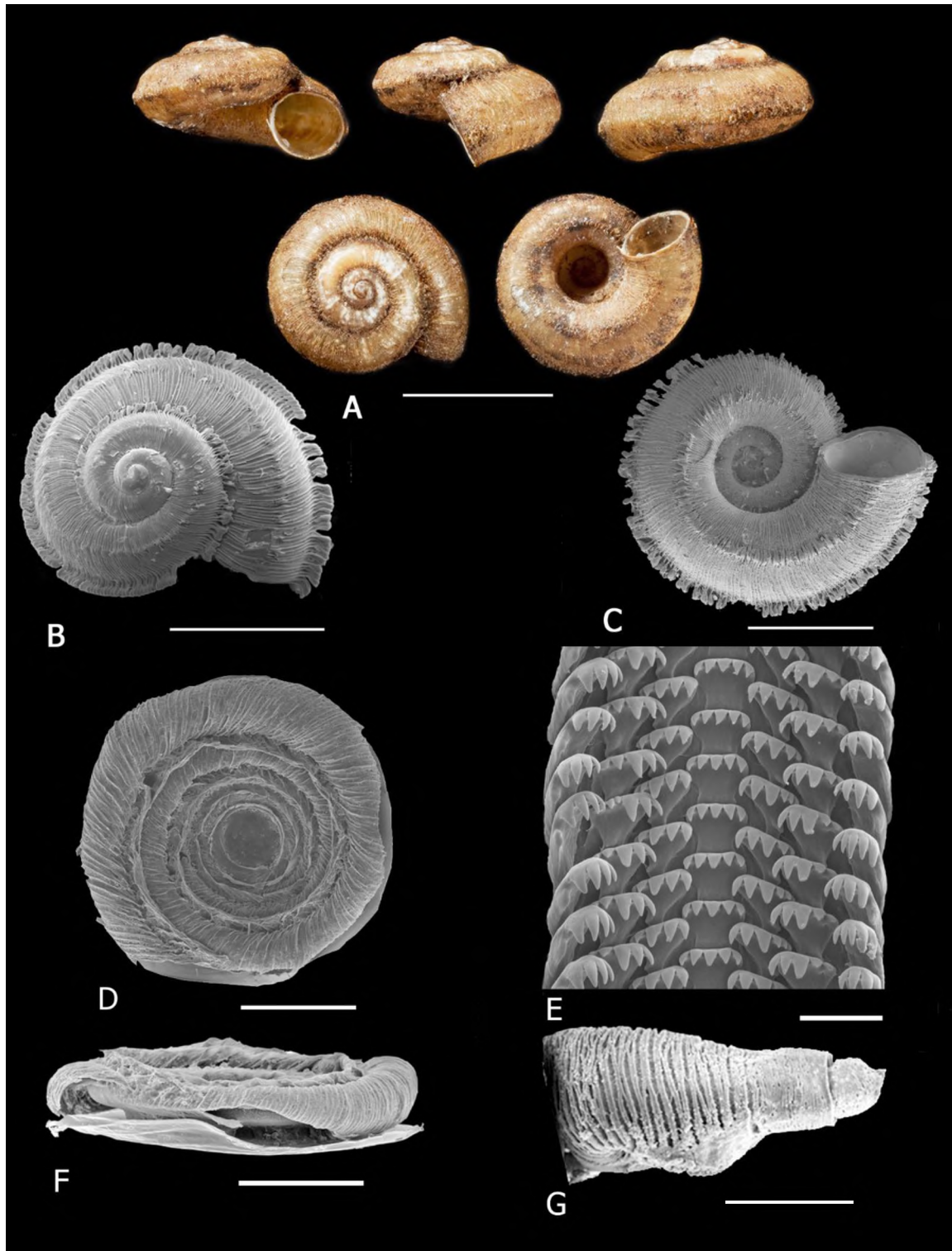
Figure 4.15 *Chondrocyclus trifimbriatus* Connolly, 1929: (A) Holotype (NHMUK 1928.3.16.5), scale bar = 3 mm; (B) dorsal and ventral view (ELM W3661), scale bars = 2 mm; (D, F) operculum (NMSA A8000), scale bars = 500 µm; (E) portion of radula (ELM W3661), scale bar = 20 µm; (G) penis dorsal view (NMSA W1115), scale bar = 500 µm.
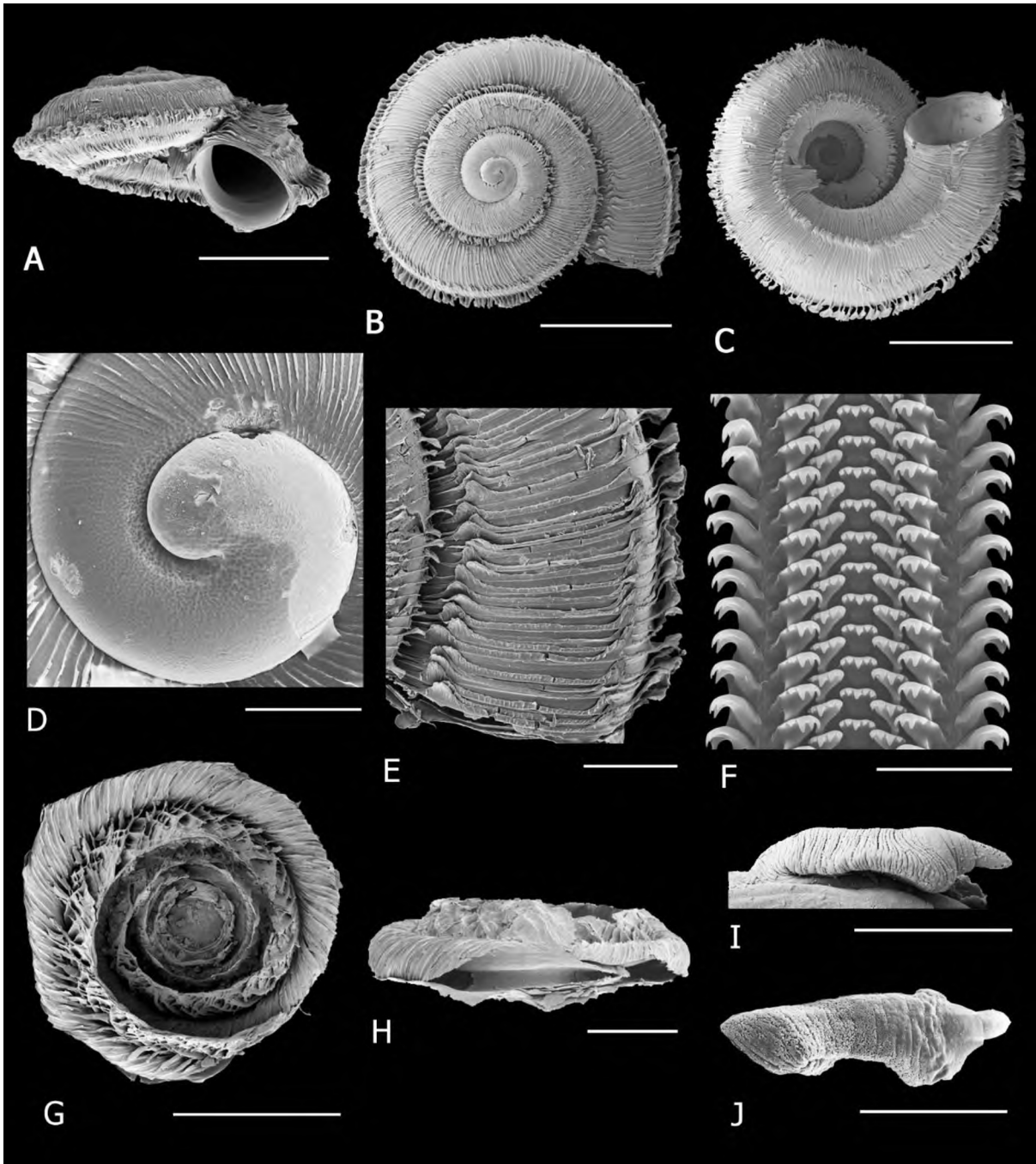
Figure 4.16 *Chondrocyclus "pondoensis"* sp. n. (all ELM unless otherwise indicated): (A-C) aperture (W3602/T111), dorsal and ventral (W3627/T114) view, scale bars = 2 mm; (D) protoconch, scale bar = 200 μm (W3627/T114); (E) detail of axial lamellae of periostracum (W3627/T114), scale bar = 500 μm; (F) portion of radula (W3627/T114), scale bar = 50 μm; (G-H) operculum (W3627/T114), scale bars = 1 mm and 500 μm; (I-J) penis lateral (NMSA W7844/T4144) and dorsal (W3627/T114) view, scale bars = 1 mm.
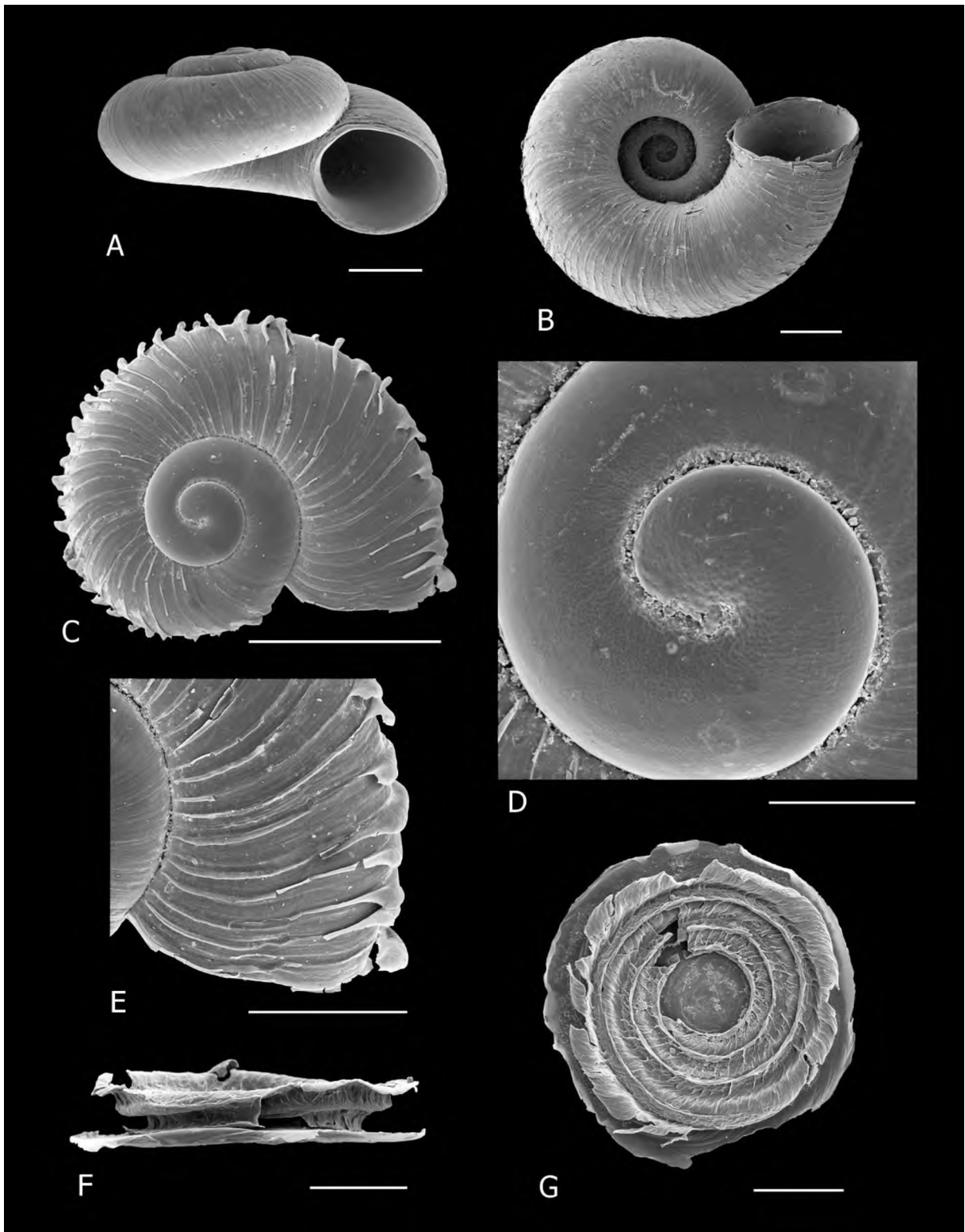
Figure 4.17 *Chondrocyclus "devillersi"* sp. n.: (A-B) aperture and ventral view (ELM D17922/T116), scale bars = 1 mm; (C) dorsal view of juvenile shell (NMSA V9111/T4110), scale bar = 1 mm; (D) protoconch (NMSA V9111/T4110), scale bar = 200 μm; (E) detail of axial lamellae of periostracum (NMSA V9111/T4110), scale bar = 500 μm; (F, G) operculum lateral (ELM W3716/T167) and dorsal view (ELM W3861/T117), scale bars = 500 μm.
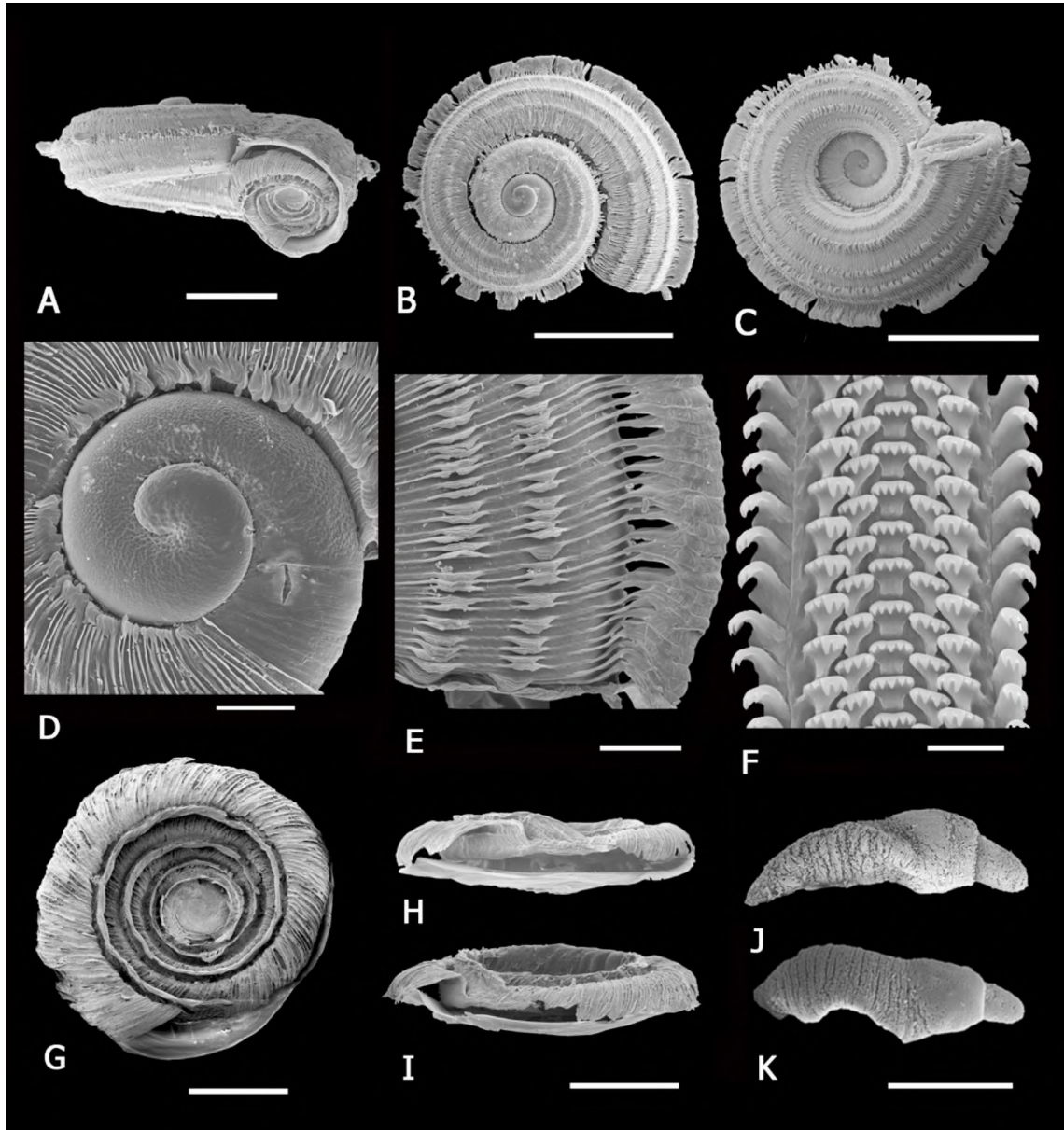
Figure 4.18 *Chondrocyclus "pulcherrimus"* sp. n.: (ELM W3626/T119): (A-C) aperture, dorsal and ventral view, scale bars = 2 mm; (D) protoconch, scale bar = 200 μm; (E) detail of axial lamellae of periostracum, scale bar = 200 μm; (F) portion of radula, scale bar = 20 μm; (G-I) operculum, scale bars = 500 μm; (J-K) penis lateral and dorsal view, scale bars = 500 μm.
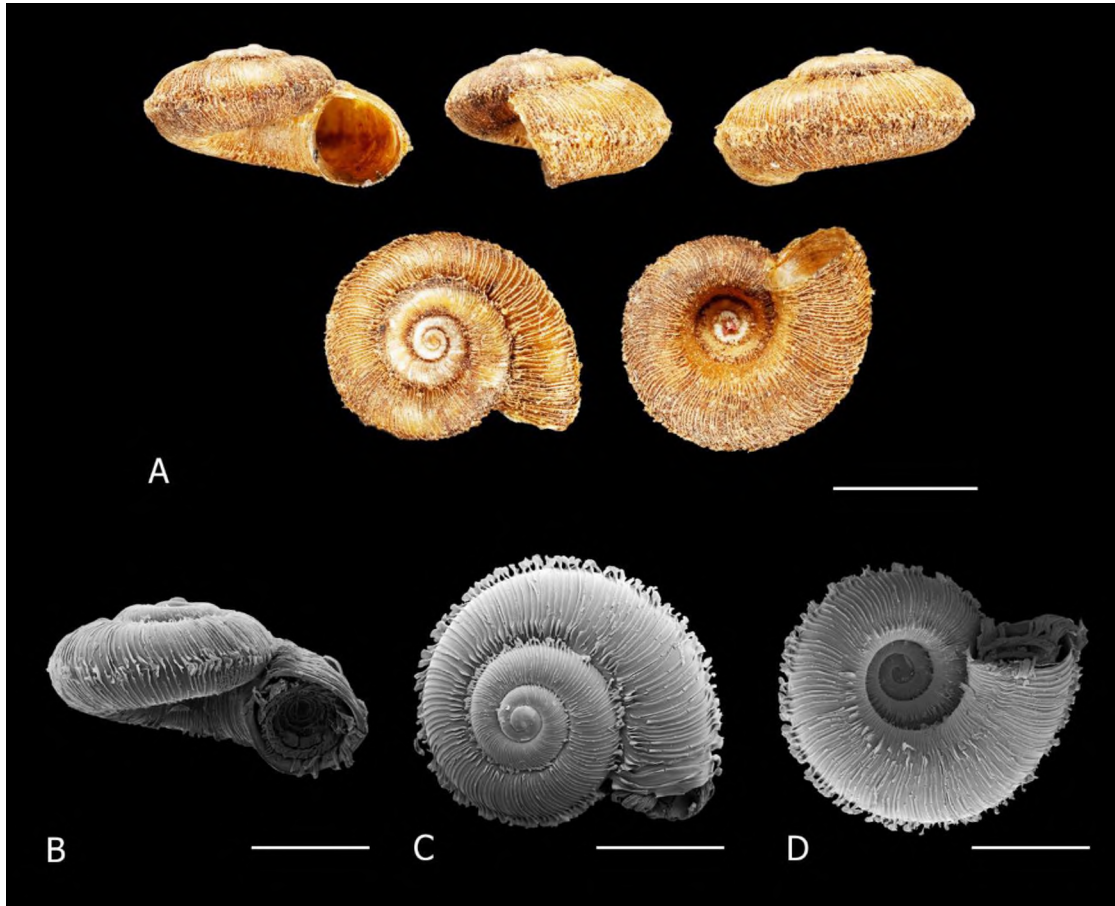
Figure 4.19 *Chondrocyclus bathrolophodes* Connolly, 1929: (A) Holotype (NHMUK 1928.3.16.4), scale bar = 3 mm; (B-D) aperture, dorsal and ventral view (ELM W3616), scale bars = 2 mm.
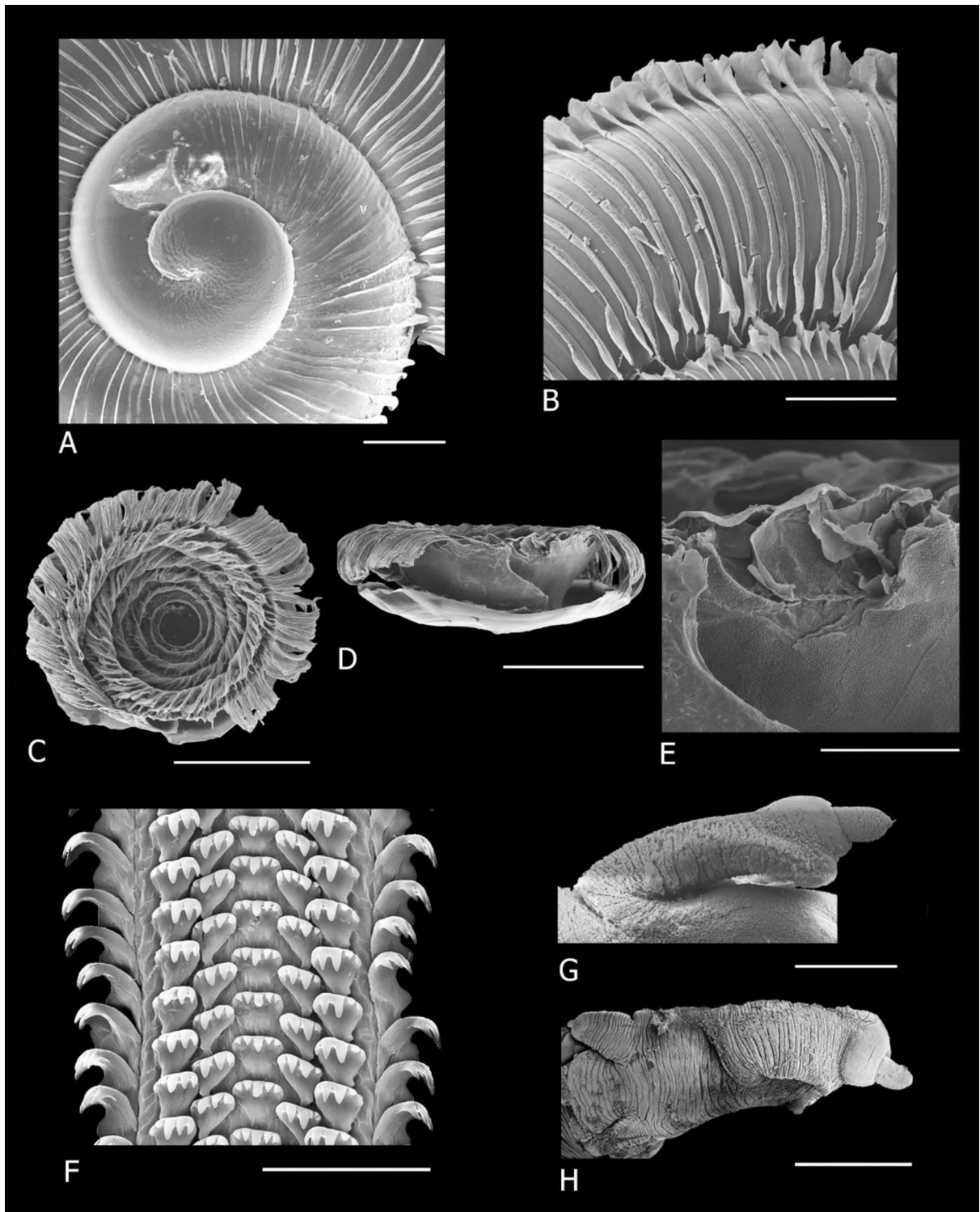
Figure 4.20 *Chondrocyclus bathrolophodes* Connolly, 1929 (all ELM): (A) protoconch (D15882), scale bar = 200 μm; (B) detail of axial lamellae of periostracum (W3616), scale bar = 500 μm; (C-D) operculum (W3616), scale bars = 1 mm; (E) detail of sculpture of wall of operculum (W3616), scale bar = 200 μm; (F) portion of radula (W3616), scale bar = 50 μm; (G-H) penis lateral (W3658) and dorsal (W3616) view, scale bars = 500 μm.
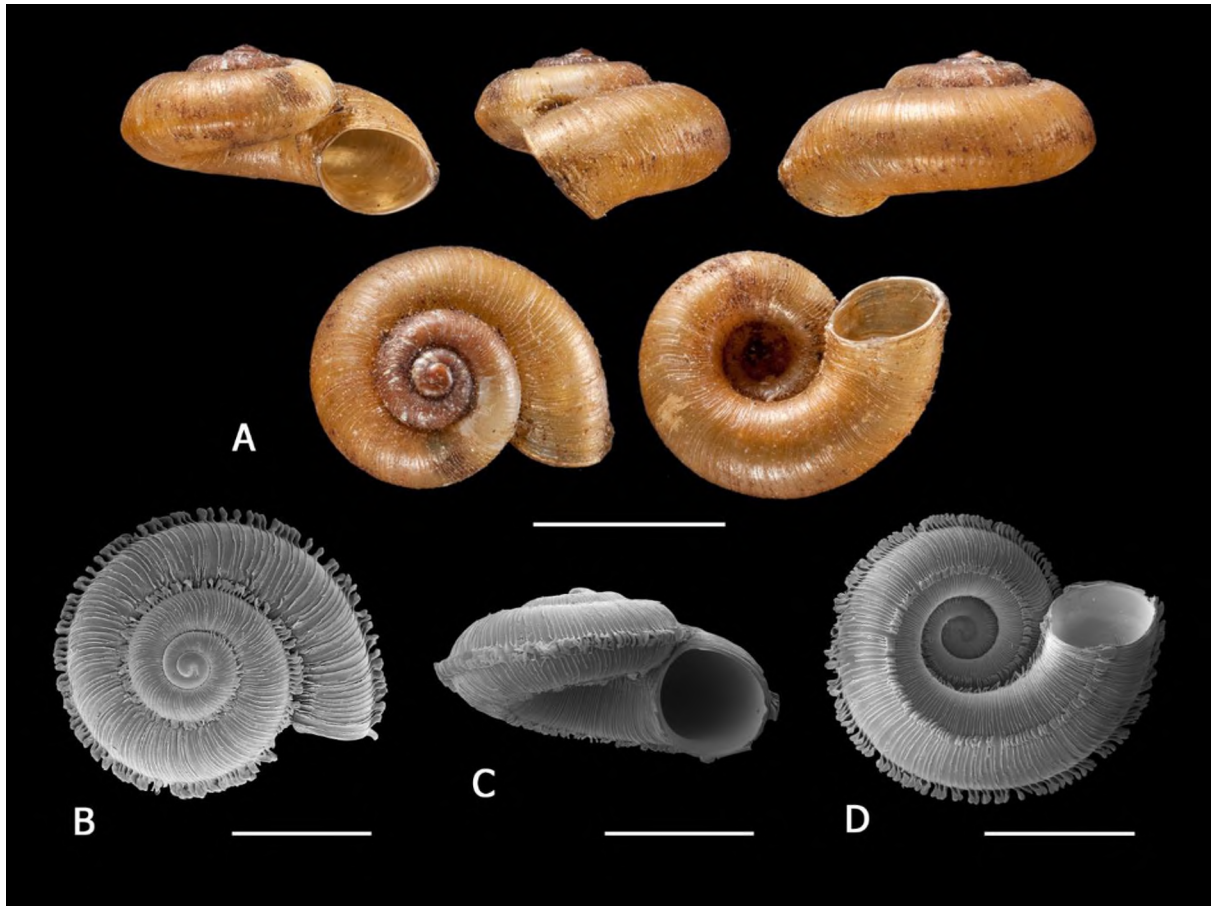
Figure 4.21 *Chondrocyclus putealis* Connolly, 1939: (A) Syntypes (NHMUK 1937.12.30.5087-5090), scale bar = 3 mm; (B-D) aperture, dorsal and ventral view (ELM W3656), scale bars = 2 mm.
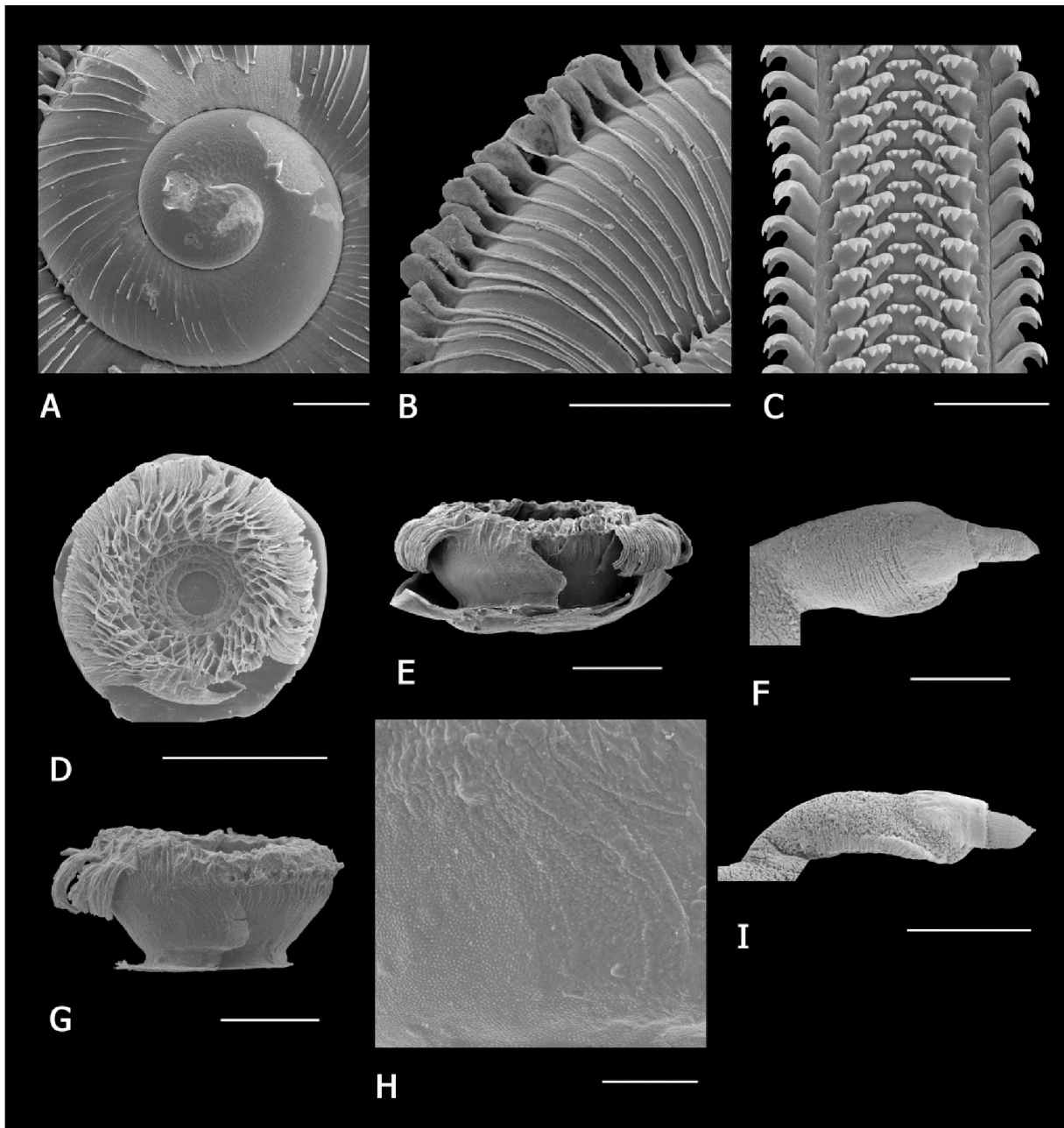
Figure 4.22 *Chondrocyclus putealis* Connolly, 1939 (all ELM unless otherwise indicated): (A) protoconch (W3656), scale bar = 200 μm; (B) detail of axial lamellae of periostracum (W3656), scale bar = 200 μm; (C) portion of radula (W3656), scale bar = 50 μm; (D) operculum (W3656), scale bar = 1 mm; (E) operculum (NMSA V9390), scale bar = 500 μm; (F) penis dorsal view (W3657), scale bar = 500 μm; (G) operculum (W3656), scale bar = 500 μm; (H) detail of sculpture of operculum wall (NMSA V9390), scale bar = 100 μm; (I) penis lateral view (W3657), scale bar = 500 μm.
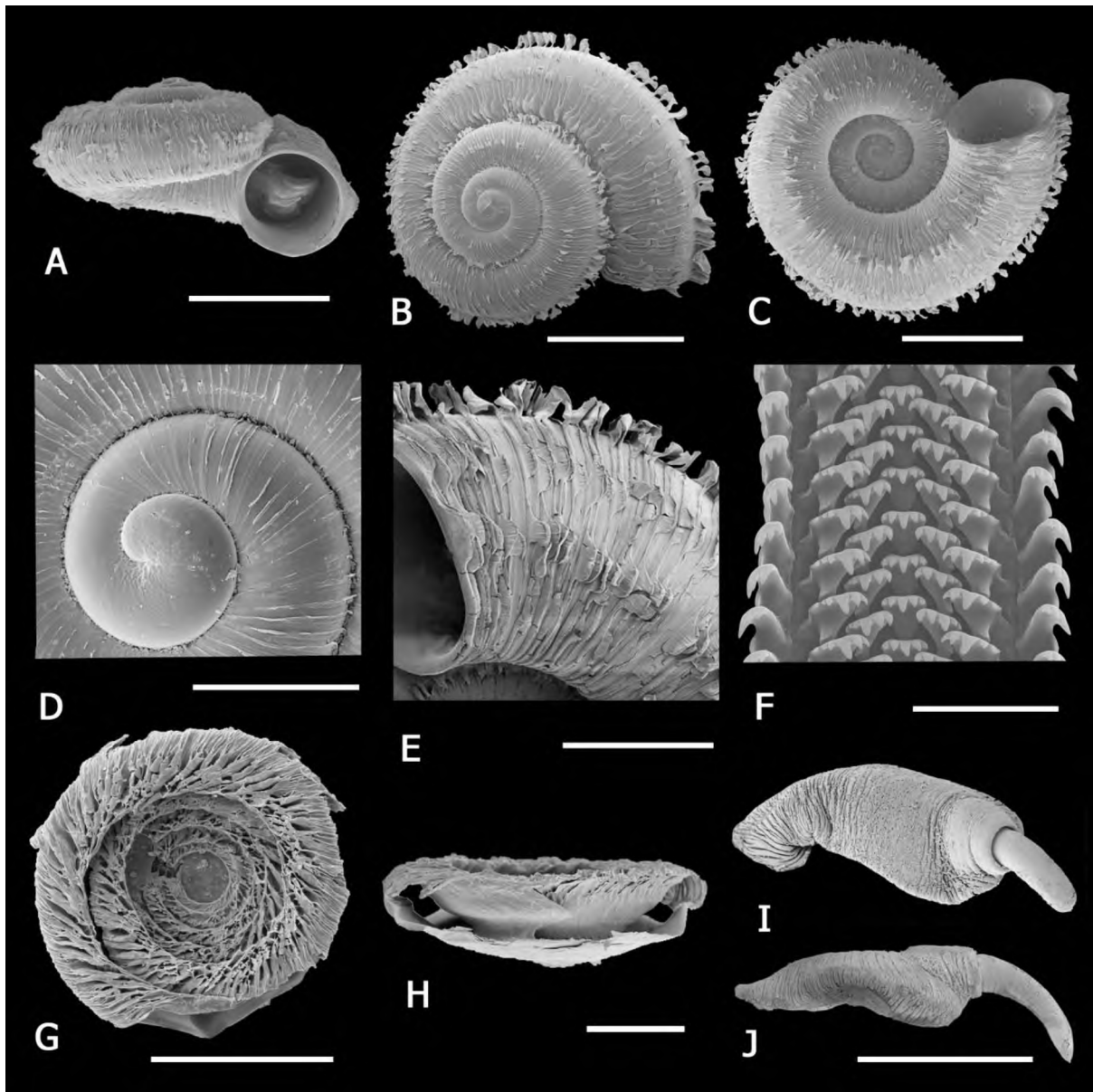
Figure 4.23 *Chondrocyclus "cooperae"* sp. n.: (all ELM): (A-C) aperture, dorsal and ventral view (W3620/T136), scale bars = 2 mm; (D) protoconch (W3620/T136), scale bar = 500 μm; (E) detail of axial lamellae of periostracum (W3620/T136), scale bar = 1 mm; (F) portion of radula (W3623/T121), scale bar = 50 μm; (G-I) operculum (W3623/T121), scale bars = 1 mm and 500 μm; (J-K) penis dorsal (W3623/T121) and lateral (W3212/T140) view, scale bar = 1 mm.
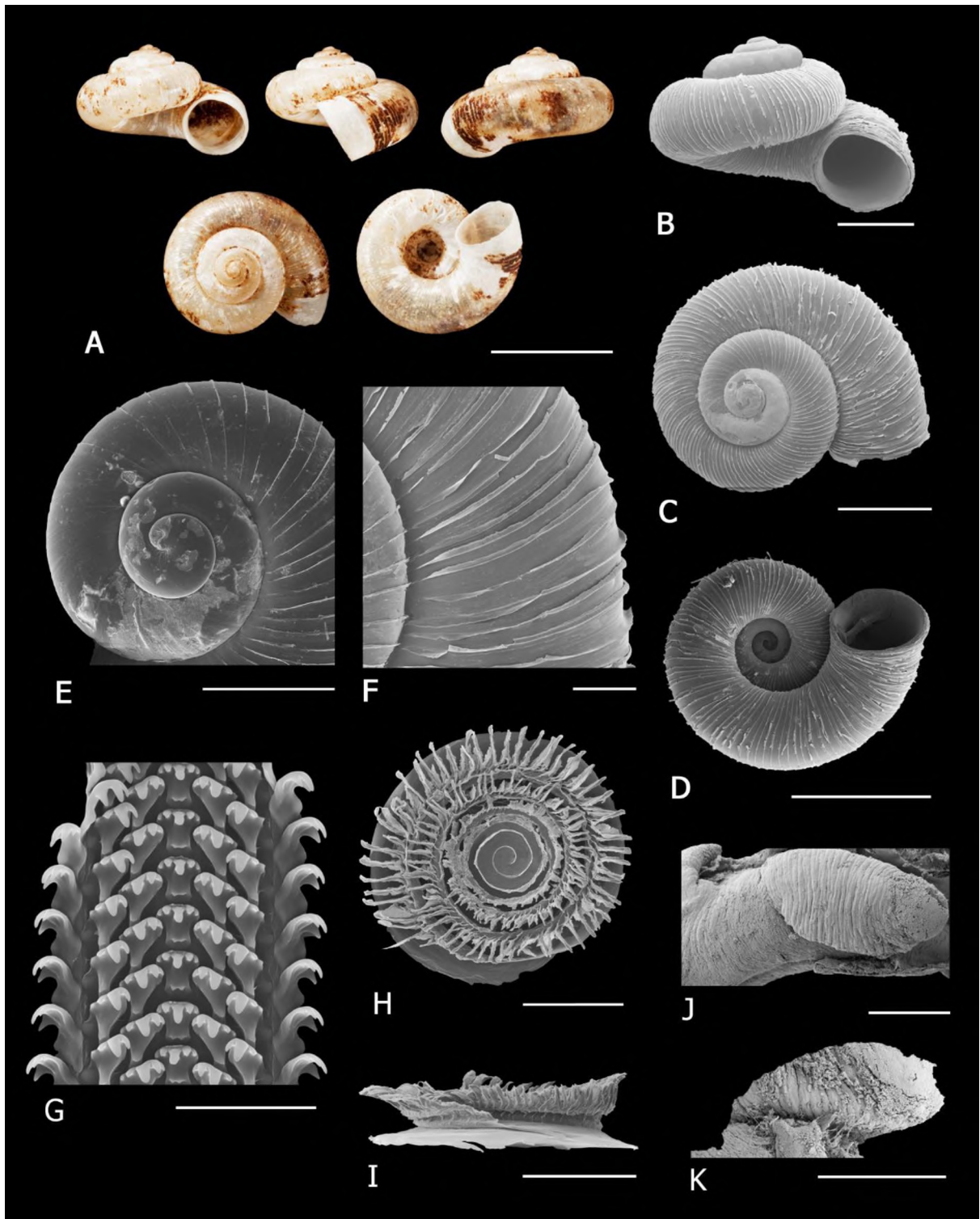
Figure 4.24 *Chondrocyclus exsertus* Melvill & Ponsonby, 1903: (A) Holotype (NHMUK 1904.4.29.28), scale bar = 3 mm; all ELM: (B-C) aperture (D16953) and dorsal (D16951) views, scale bars = 1 mm, (D) ventral view (W3654), scale bar = 2 mm; (E) protoconch (D16951), scale bar = 500 µm; (F) detail of axial lamellae of periostracum (D16951), scale bar = 200 µm; (G) portion of radula (W3654), scale bar = 50 µm; (H) operculum (W3654), scale bar = 500 µm; (I) operculum lateral view (W3655) scale bar = 500 µm; (J-K) penis on neck, dorsal view and lateral view (W3654), scale bars = 500 µm.
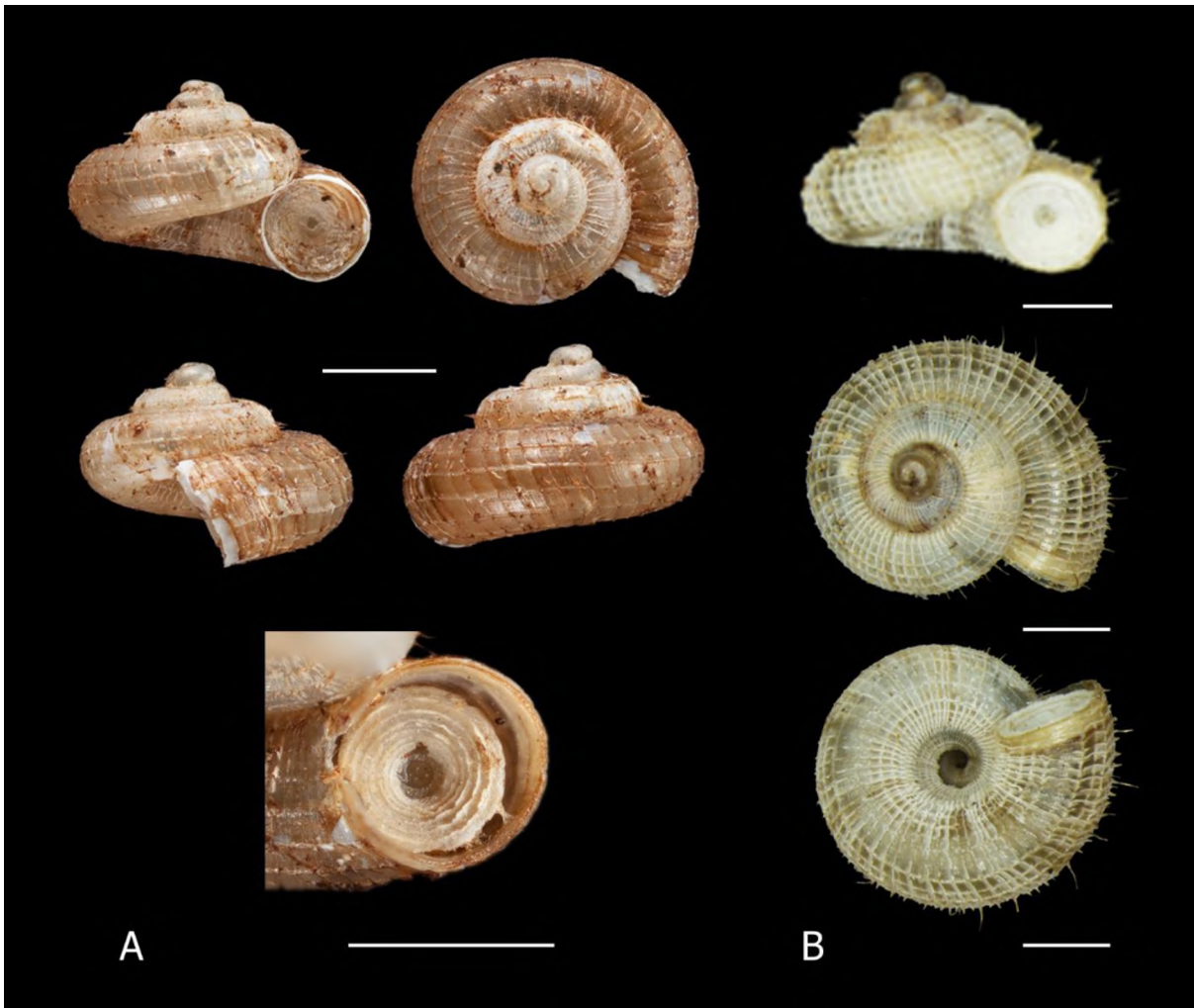
Figure 4.25 (A) *Chondrocyclus meredithae* Bruggen, 1983, paratype (NHMUK 198338), scale bar = 1 mm; close-up of operculum, scale bar = 1 mm; (B) *Chondrocyclus chirindae* Bruggen, 1986 (NMSA L4904), scale bar = 1 mm.
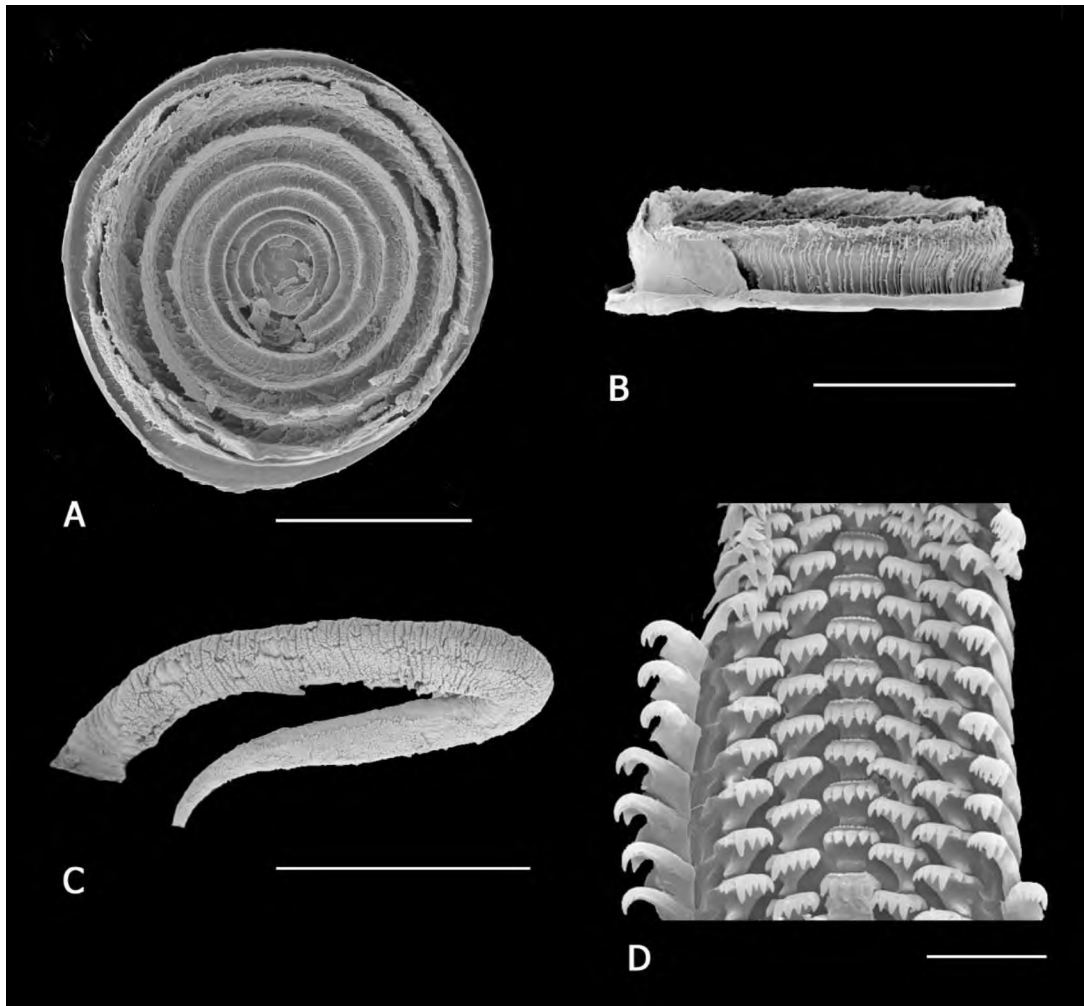
Figure 4.26 *Cyathopoma pembense* Rowson *et al.*, 2010 (NMW.Z.2009.013.00002-00032): (A-B) operculum, scale bars = 500 μm; (C) penis lateral view, scale bar = 500 μm: (D) portion of radula, scale bar = 20 μm.
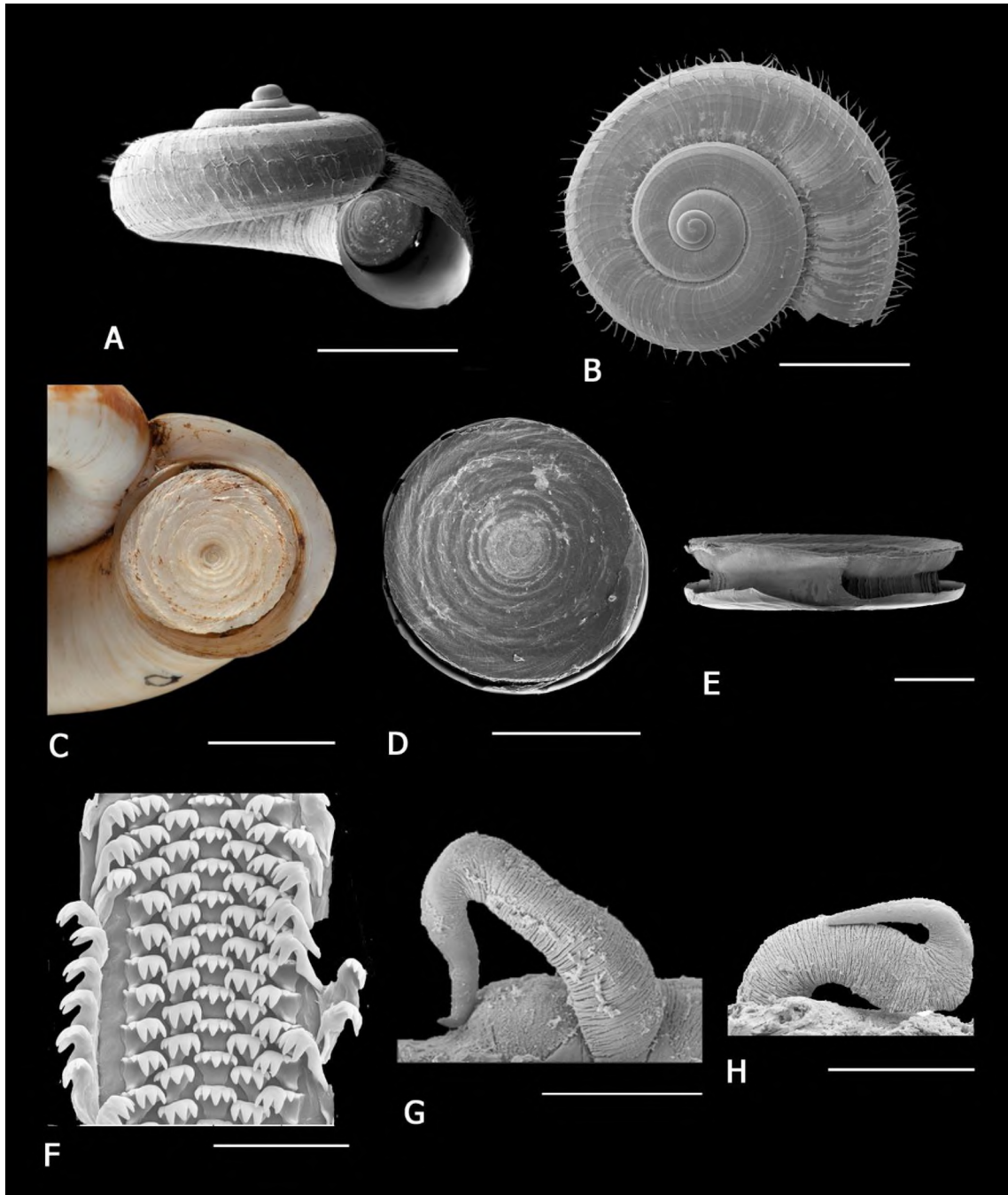
Figure 4.27 *Cyclotis* sp.: (A-B) aperture and dorsal view (NMSA L7108), scale bars = 2 mm; (C) *Cyclotis variegatus* Swainson, 1840 operculum (NHMUK1893.6.7.43-5), scale bar = 1 mm; (D-H) *Cyclotis* sp. (NMSA L7108): (D-E) operculum, scale bars = 1 mm and 500 μm; (F) portion of radula, scale bar = 50 μm; (G-H) penis dorsal and lateral view, scale bars = 500 μm.

5 Biogeography

5.1 Overview of distribution of clades

The molecular and morphological studies were congruent and provided data on which to base species discrimination. The molecular data indicated that *Chondrocyclus* is monophyletic and suggested that there were two separate radiations, one within the "Isipingoensis" clade and the other leading to the four remaining clades (Fig. 3.1). The Isipingoensis clade is sister to all other clades; the other four clades are structured geographically into an Eastern clade and a Western group of clades around Port Elizabeth (Fig. 3.2). The Western group of clades contains three clades, also structured geographically from east to west. In summary, the distribution of the major clades is as follows:

1) The Isipingoensis clade is widespread from northern Limpopo Province (Soutpansberg) to Eastern Cape, is montane and coastal and is sympatric with other clades except those in the Western Cape.

2) The "Eastern" clade occurs on the south-east coast from Port Elizabeth to northern KwaZulu-Natal; some lineages extend inland in Transkei (the area between the Kei and Umtamvuna Rivers extending inland to the first escarpment) and KwaZulu-Natal.

3) The "Southern-Eastern Cape" (S+E Cape) clade also has two subclades, both occurring at the coast and inland, one in the southern Cape and at the eastern end of Cape Fold Mountains, and the other centered in the Albany district of the Eastern Cape.

4) The "Overberg" clade in the Western Cape contains two subclades, one on the Agulhas Plain and the other in the Langeberge.

5) The "Southwestern Cape" clade occurs in the Western Cape at the western end of the Cape Fold Mountains, on the Cape Peninsula mountain chain and in the north-south running mountains to the east of the Cape Flats.

The aim of this study was to revise the species of the genus based on evidence from morphological examination and genetic sequences. Geographical distribution patterns in *Chondrocyclus* lineages showed several striking similarities to those in other taxa, which provides a platform to formulate hypotheses for future studies regarding biogeographical processes which may have influenced *Chondrocyclus*.

The genus occupies a wide geographic area, and its species are dependent on thickly vegetated habitats with high humidity, making them suitable organisms to test hypotheses about past contractions and expansions of their habitats in the light of climatic fluctuations and geomorphic evolution. A chronogram would be desirable to interpret the palaeobiogeography of *Chondrocyclus*, but there are no known fossils of *Chondrocyclus* to calibrate the phylogeny, nor any reliable estimated mutation rates. In the following section, the distribution of the major clades is discussed with reference to evidence for similar patterns in other taxa and palaeoclimatic data, but no attempt has been made to tie events to particular nodes on the phylogeny.

5.2 Dispersal

Forest covered South Africa until the formation of the Great Escarpment separated the moist coastal belt from the arid interior, and then occupied a narrow but probably continuous belt along the steps of the Great Escarpment and along the coastal belt (Mucina & Geldenhuys, 2006). Fragmentation began with the onset of cooler, drier conditions in the mid to late Miocene (between approx. 16 and 5 million years ago), and although there may have been many periods of forest expansion and contraction in response to climatic fluctuations, present distribution of forest is highly fragmented. Occurrence of *Chondrocyclus* in these modern fragmented forests throughout the country indicates that dispersal has taken place but subsequent speciation may be influenced by dispersal events and/or vicariance.

Living *Chondrocyclus* specimens are found clinging to dead vegetable matter or actively crawling over leaf surfaces during conditions of favourable humidity. Horizontal distances covered by small terrestrial snails of comparable size are difficult to quantify since they occupy multiple layers of leaves and consequently distances travelled may be larger than horizontal displacement (Bauer & Bauer, 1988). During dry conditions they withdraw into the shell and seal off the aperture with the operculum, an effective barrier to desiccation.

In addition to active crawling, passive dispersal lodged in fur or feathers of mammals, birds or even individual feathers may be possible, especially for species covered with hairs or bearing serrated spines. Wind-borne transport is regarded as an important factor for the dispersal of small species of land snails, including litter-dwellers, particularly in areas of high relief (Kirchner *et al.*, 1997). Even in larger species, passive dispersal may play a surprisingly

important role and wind and birds are suggested agents (Gittenberger *et al.*, 2006; Holland & Cowie, 2007). Strong winds are characteristic of coastal and montane areas of South Africa and it seems feasible that *Chondrocyclus* individuals could be dispersed in wind-blown debris or feathers. Passive dispersal by wind on leaves seems unlikely since animals immediately withdraw into the shell if disturbed and thus fall off leaf surfaces.

Land snails are dispersed by the ocean (Ozgo *et al.*, 2015) and *Chondrocyclus* inhabiting dune or riparian forest in close proximity to the coast could get caught up in vegetable debris, washed into the sea and deposited elsewhere. This is a potential dispersal mechanism suggested by Holland & Cowie (2007) to account for over-water dispersal between Hawaiian islands, and dispersal could have taken place in a similar manner across the many deep river valleys characteristic of the South African coastal landscape. *Chondrocyclus* tolerate relatively long periods of submergence possibly due to their operculum although live specimens sink and are unable to crawl around under water, unlike many other land snails.

5.3 Links with areas north of South Africa

The genus *Chondrocyclus* appears to be endemic to South Africa and has a wide, discontinuous distribution tied to forests seaward of the Great Escarpment, and extending westwards to the Cape Peninsula. This pattern is mirrored in several other molluscan genera endemic to South Africa (Bruggen, 1978). It is assumed that the majority of southern African terrestrial molluscs had their origin in tropical Africa, migrated southwards and radiated in the south (Bruggen, 1978) although there are no phylogenetic studies to test this hypothesis.

Family Cyclophoridae occurs mainly in the Tropics and is very well represented in south-east Asia and Madagascar, but has few representatives in tropical mainland Africa; the latter include several species of very small cyclophorids in mountainous areas of Malawi and the Eastern Highlands of Zimbabwe (Fig. 5.1). Investigating the relationship between cyclophorids from the latter regions and *Chondrocyclus* may provide clues about the origin of *Chondrocyclus*.

The Eastern Escarpment of South Africa (Drakensberg) is a floristic and faunal link between the Cape Floral Region and the remainder of the Afromontane archipelago (Stuckenberg, 1962; Galley *et al.*, 2007) and the Eastern Arc Mountain chain could have been a potential route linking *Chondrocyclus* and its relatives to the north although the dry Limpopo valley has been

a biogeographical barrier to species requiring humidity far back into the Tertiary (65 million to 2 million years ago) (Stuckenberg, 1962).

Another possible route of dispersal is along the coast and between there and the mountainous areas of northern South Africa and the Eastern Highlands of Zimbabwe. The Indian Ocean Coastal Belt came into being since the marine regression of the Last Glacial Maximum (LGM, 24 000 to 18 000 years ago) and is the southernmost outlier of East African Tropical Coastal Forest (Mucina *et al.*, 2006), but the *Chondrocyclus* ancestor could have used these routes during earlier periods of forest cover in the region. These earlier periods could be linked to prior gladiation cycles, of which there have been about 80 during the 5 My spanned by the Pliocene and Pleistocene. There is evidence of strong phytogeographic links between coastal and northern Drakensberg afromontane forests (Morgenthal & Cilliers, 2000). The presence in the Zululand scarp forest, Ongoye, of a species of the cyclophorid genus *Elgonocyclus* and the green barbet, both with closest relatives in East African coastal and montane forests, provide evidence for historic faunal links between these regions. In certain taxa, there is greater similarity between assemblages of the Mozambique coast and the Zimbabwe Eastern Highlands than between the latter area and the mountains of northern South Africa (Lawes *et al.*, 2007). There is a gap in knowledge of the terrestrial molluscs of southern Africa in Mozambique and no Cyclophoridae have been collected there, possibly due to lack of sampling effort.

5.4 Northern South Africa, Great Escarpment and east coast

The *Isipingoensis* clade is the most widely distributed, both latitudinally and altitudinally, occurring in tropical, subtropical and temperate conditions from the north of Limpopo Province, along the edge of the Great Escarpment as far as the Boschberg in the Eastern Cape (the western limit of Great Escarpment forest in South Africa (Clark *et al.*, 2010)), in montane regions coastwards of the Escarpment and along the entire south-eastern coastal belt (Fig. 4.10). This clade occupies wet and dry forests and mesic thicket. Within the *Isipingoensis* clade are two lineages: one at the western extremity of the clade's distribution (Somerset East and Bedford) is distinct (*C.* "*oxygala*" sp. n.) and all other sampled populations together form another monophyletic lineage. The long branch length of the former suggests that this lineage is older and that radiation in the latter group has been more recent. Somerset East and Bedford

are on opposite sides of the upper Great Fish River valley, but although currently considered an arid barrier for dispersal of montane taxa (Weimarck, 1941; Stuckenberg, 1962), it has not consistently been a major hindrance to connectivity along this region of the Great Escarpment (Clark *et al.*, 2010) and may have been an area of persistence of thicket during the contractions of the LGM (Potts *et al.*, 2012).

The other *Isipingoensis* lineage contains the only "Afromontane" population sequenced (from the Soutpansberg mountains in the north of South Africa) and two well-supported groups of populations in montane areas between the coast and Great Escarpment: central Transkei mistbelt and Kei River valley (Sp. "B") and north-eastern Transkei mistbelt forest (Sp. "A"). Distribution of Sp. "B" on opposite sides of the Kei Valley suggests migration across this presently arid barrier and/or up this valley from the coast, or fragmentation of a widespread group. The extent of forest cover along the inland Transkei mistbelt during the Holocene altithermal is likely to have been more extensive than at present, facilitating recent migration of *Streptocarpus rexii* from the Amatholes to central Transkei (Hughes *et al.*, 2005). The majority of analyses also showed a third well-supported group containing coastal populations from KwaZulu-Natal and the Eastern Cape (Sp. "C"). The *Isipingoensis* clade requires more thorough sampling throughout its range and more comprehensive molecular and morphological studies to unravel the taxonomy of this clade.

In four floral clades, many migration events over a wide time span (0.54 – 10 My) occurred from the Cape to Afrotropical mountains, with the Drakensberg as an important stepping stone (Galley *et al.*, 2007). The timing of migration and radiation of Cape fynbos taxa to the Drakensberg was probably co-incident with forest contraction and evolution of fire-adapted biomes (Stuckenberg, 1962; Cowling & Potts, 2015). Initial isolation of *Chondrocyclus* populations may be associated with aridification 31 Mya and 14 Mya that pushed forests from the interior to the coast and spread fire-prone C4 grasses.

5.5 Southeast coast

The Eastern clade occurs in the east of the country between Zululand and Port Elizabeth, an area known as the Maputaland-Pondoland-Albany biodiversity hotspot. In the north-east of its range the Eastern clade occurs in forest classified as mistbelt or scarp and has not been recorded in coastal forest; in the western and central areas of its range this clade is mostly in coastal and

scarp forest (Fig. 3.6). The Eastern clade is associated with the Indian Ocean Coastal Belt (IOCB) and with scarp forests, a forest type unique to the east of the country. IOCB forest is relatively recent and became established after the LGM, between 15000 and 7000 BP (Lawes, 1990; Eeley *et al.*, 1999; Mucina *et al.*, 2006; Lawes *et al.*, 2007; Mucina *et al.*, 2007). Scarp forests occur on south- and east-facing hills and gorges of the first plateau escarpment (300 – 1100 m) from Zululand to the Eastern Cape and support a high biodiversity of fauna and flora including Afrotemperate and IOCB elements, subtropical thicket elements (e.g. *Schotia* and *Umtiza*) and a large number of endemics (Lawes *et al.*, 2007; Mucina *et al.*, 2006; Mucina *et al.*, 2007). The southern boundary of the Scarp Forest group is in the vicinity of East London, but varies slightly according to forest classification system (Von Maltitz *et al.*, 2003, Mucina & Geldenhuys, 2006).

In the Eastern clade are complex distribution patterns of sympatry, disjunctions and turnover within sharp contact zones. These could be the result of dynamic changes in vegetation over time, with forest contraction and expansion due to climatic shifts and marine regressions and transgressions. These processes could have caused repeated periods of isolation of populations in shrinking refuges, followed by dispersal and contact. At the end of the Miocene and in the Pliocene, uplifts raised the escarpment and eastward-flowing rivers cut deep valleys and gorges where scarp forests remained and were important refuges after forest fragmentation commenced in the mid-Miocene (16-11 MYA). Subtropical forests in the region are thought to have expanded westwards and contracted eastwards during the glacial and interglacial cycles of the Pleistocene (i.e. the last 2 Myr) (Partridge *et al.*, 1999). During the LGM, vegetation belts were generally lowered by 1000 m with Afrotemperate forest occupying altitudes now occupied by scarp (Eeley *et al.*, 1999; Lawes *et al.*, 2007), although there is evidence that some Afrotemperate forests persisted in a few high altitude refugia (e.g. Eeley *et al.*, 1999; Herbert & Moussalli, 2010). Moreover, 24 000-18 000 yr BP during the LGM there was a SW-NE rainfall gradient and the eastern parts of the country were dry relative to the west (Partridge *et al.*, 1999; Chase & Meadows, 2007) leading to contraction of forest extent and potentially isolating species in shrinking refuges. The Zululand scarp forests were important refuges at the height of the LGM (Eeley *et al.*, 1999). During interglacials Afrotemperate forests expanded and Indian Ocean Coastal Belt forests extended all along the east and south-east coast with Scarp Forests occupying a belt between where there would have been potential for mixing of Afrotemperate and IOCB lineages (Eeley *et al.*, 1999; Hughes *et al.*, 2005; Lawes *et al.*, 2007).

In several unrelated taxa there is evidence that lineages in northern KZN date to the late Miocene or Pliocene (~5 MYA), persisted in scarp forest refugia during forest contraction in the Pliocene and Pleistocene, and the surviving relict lineages expanded and radiated as forest cover increased after the LGM (Griswold, 1985; Tolley *et al.*, 2008; Tilbury & Tolley, 2009; Herbert & Moussalli, 2010). Molecular data in the present study suggest that north-eastern lineages in the Eastern clade are basal to those in the Eastern Cape (Fig. 3.1) but further study is required to test whether phylogeography of *Chondrocyclus* can be explained by processes demonstrated in other taxa. In Ngome, Nkandla and Entumeni forests, there are separate lineages of *Chondrocyclus*, distinguished morphologically and/or with molecular data. These highly fragmented forests and others in the region contain many other examples in unrelated taxa of species with extremely narrow distributions (Hamer & Slotow, 2000; Huber, 2003; Herbert & Kilburn, 2004; Tolley *et al.*, 2008; Tilbury & Tolley, 2009) suggesting that fragmentation, isolation and extinction filtering have characterized the evolution of these lineages (Lawes *et al.*, 2007; Tolley *et al.*, 2008; Tilbury & Tolley, 2009; Herbert & Moussalli, 2010).

The ranges of *C. bathrolophodes* (Eastern clade) and *C. alabastris* (S+E Cape clade) overlap in the Albany – Port Elizabeth region, known as a biogeographical area of transition where eastern subtropical elements mix with western temperate ones. In the west *C. bathrolophodes* is common in coastal forest and Albany thicket in the valleys with an outlying population occurring at the mouth of the deeply incised Kobonqaba River in southern Transkei (Fig. 3.6). Immediately to the east of this population in the forests adjacent to the Nxaxo River, occurs a distinct lineage. The ranges of these two lineages overlap with that of *C. "cooperae"* which also has a disjunct distribution, occuring in the area between the populations of *C. bathrolophodes* and extending along the coast east of the Kobonqaba River (Fig. 3.6). During glacials the subtropical forest between Cape St. Francis and the Kei River was displaced northwards, leaving remnants in favourable enclaves such as the deeply incised valleys of the Albany forelands (Cowling & Pierce, 2009) from where expansion occurred during climatic amelioration, and in scarp forest refugia.

The region of Pondoland and southern KwaZulu-Natal spanning Ugu Sandstone geology contains the greatest diversity of *Chondrocyclus*: *C. isipingoensis, C. exsertus, C. "pondoensis", C. putealis* and *C. "cooperae"* which points to it being an area which supports persistence and radiation. This is the Pondoland Centre of botanical endemism, an area

harbouring a large number of palaeoendemics and neoendemics concentrated in scarp forests in deep gorges (van Wyk & Smith, 2001; Mucina *et al.*, 2007) and is also a focus of endemism in molluscan genera (Bursey & Herbert, 2004; Herbert & Kilburn, 2004; Cole & Herbert, 2009). The Pondoland area was an important centre of cladogenic events in rhytidid snails (Moussalli *et al.*, 2009; Herbert & Moussalli, 2010). A phylogeographic study of the mesophytic forest-floor herb, *Streptocarpus*, confirmed hypotheses of the relictual nature of scarp forest and supported a hypothesis of southerly coastal migration (Hughes *et al.*, 2005). The Port St. Johns vicinity has been able to support sizeable populations throughout recent periods of climate change and the Umtamvuna gorge also appears to have been an important refuge during the Pleistocene climate shifts (last 2 Myr) (Geldenhuys, 1992b; Hughes *et al.*, 2005) as well as a suggested dispersal corridor between the coast and the mountains of the Transkei (Geldenhuys, 1992b). By inference from concordant patterns in these taxa it is possible that the ancestral populations in the Eastern clade may have persisted in refugia in Pondoland (or southern Kwazulu-Natal) and colonized areas to the south (and north) as forest expanded but further study is required to identify basal lineages and possible directions of migration.

The *Natalina cafra* complex of rhytidid molluscs diverged into three lineages in the Eastern Cape, with foci of distributions in the Transkei, west of the Great Fish River, and in the Amathole Mountains (Moussalli *et al.*, 2009; Herbert & Moussalli, 2010). The Eastern and S+E Cape clades contain species with ranges in the same areas which suggests that common processes may have been instrumental in cladogenesis in both genera. The geographically isolated lineage in the inland Transkei mistbelt forest Nqadu (*C. "devilliersi"*) is not closely related to coastal species in the Eastern Cape (Fig. 3.1). This lineage may be the product of extinction filtering of related lineages in inland or coastal forests.

5.6 Transition from subtropical to temperate influence

The S+E Cape clade occurs in the southeastern Cape Floristic Region, from the forests in the southern Cape through the Albany Thicket biome to the mistbelt forests of the Amathole Mountains in the north-east (Fig. 3.5). There is a geographical division within the S+E Cape clade into a western and an eastern assemblage, each consisting of two species, in the region of the Gamtoos River.

The eastern reaches of the Cape Fold Mountains occur here in relatively close proximity to the south-western corner of the southern African Great Escarpment, referred to as the Cape Midlands Escarpment (Great Winterberg-Amatholes, Sneeuberg and Stormberg) (Clark *et al.*, 2011). Thicket and forest contracted and expanded during glacials and interglacials of the Pleistocene (Cowling *et al.*, 2005; Cowling & Pierce, 2009; Potts *et al.*, 2012), the complex scenery of the region providing sheltered refugia during glacials and enabling episodes of allopatry and subsequent contact for associated fauna including possibly *Chondrocyclus*. In the west, Southern Afrotemperate forests are considered ancient and have floristic links with Afrotemperate forests in the east of the country as well as with the relictual forest patches further west in the Langeberge (Geldenhuys, 1992b). Subtropical thicket is also an ancient vegetation type derived from former forest; by 40 Mya thicket prevailed throughout the subtropical and semiarid parts of the world (Cowling & Pierce, 2009). Decline in temperatures and the establishment of fire-driven ecosystems dominated by grass or fynbos during the Miocene and Pliocene resulted in its contraction, but it remained the predominant vegetation on the southeastern coastal forelands where large tracts persisted in the deeply-incised river valleys (Cowling *et al.*, 2005). These valleys may have been exposed for a few kilometres to the south of the present coastline during the late Pleistocene and early Holocene and coastal forest and mesic thicket may have had a reduced but fairly continuous range that included a shift onto the continental shelf (Geldenhuys, 1992a; Potts *et al.*, 2012).

The habitat of some populations of the S+E Cape clade may have long persisted in its current places, while other habitats are more recent. *Chondrocyclus "silvicolus"* occupies large blocks of Southern Afrotemperate Forest in the southern Cape, but also occurs in dune strandveld adjacent to the Goukamma River, an area probably inundated by marine transgressions subsequent to 7000 years BP, with forest elements spreading into the area from nearby kloof refugia since about 2000 years BP (Martin, 1968).

It appears that some populations of the S+E Cape clade are adapting to drier conditions. *C. "herberti"* appears to be restricted to the Baviaanskloof, a steep-sided, narrow valley running more-or-less in a west-east direction where it occurs in isolated patches of the relatively dry unit of Albany Thicket, Groot Thicket. In the east of its range *C. "herberti"* is found in thicket/fynbos transitional areas, and is the only *Chondrocyclus* species known to be associated with fynbos. Large tracts of fynbos and renosterveld are a barrier separating its range from the forests to the south harbouring *C. "silvicolus"*. There are currently no potential dispersal

corridors for forest species in this area (Geldenhuys, 1997). Further sampling in refugial forest patches in this interval and on the coastal plain of the Kouga region may provide insight into evolutionary processes leading to cladogenesis in the S+E Cape clade, and may reveal sympatry not previously recorded. *C. "herberti"* and *C. alabastris* have not been recorded sympatrically, although the Baviaanskloof (*C. "herberti"*) and Ferndale (*C. alabastris*) are in river valleys very close to each other as the crow flies. Both of these valleys are tributaries of the Gamtoos River, a postulated dispersal corridor between the coast and the Baviaanskloof (Geldenhuys, 1997). The valleys are steep-sided with high walls, creating barriers between them. Watersheds may have been significant barriers to gene flow for thicket plant species during glacial periods as thicket retracted downward into catchment valleys and survived in isolated refugia (Potts *et al.*, 2012). Terrestrial fauna with poor dispersal ability were also bounded by watersheds during Pleistocene climate cycling (Price *et al.*, 2010).

Chondrocyclus alabastris is found in a wider variety of vegetation types than other *Chondrocyclus* species and its range is in a convergence zone where the vegetation is a complex admixture of five biomes and subdivisions within a relatively small geographic area. Here the Forest biome contains several elements: in the montane regions the easternmost patches of Southern Afrotemperate Forest and westernmost Southern Mistbelt Forest both occur as refugial patches embedded in a matrix of other biomes, and Southern Coastal Forest occurs at the coast. *C. alabastris* is found in these three forest types, mesic thicket, and dune strandveld. The lineage in the mistbelt forest patches on the mountain ridge south of Grahamstown is morphologically distinct (Fig. 4.4). *C. "amathole"* is found at Beggars Bush on the opposite ridge, separated by the drier intervening valley of the Blaaukrantz River in the catchment of the Kowie River. The Grahamstown form of *C. alabastris* and *C. "amathole"* occur sympatrically in Great Fish Thicket along the Kap River, a tributary of the Great Fish River on the west bank near the mouth. This is the easternmost record of *C. alabastris* and both species are very rare here while *C. bathrolophodes* of the largely coastal Eastern clade, is common.

Chondrocyclus "amathole" is found in Southern Mistbelt Forest throughout the Amathole Mountains and extends eastwards towards the Kei River in forest patches. The Amathole Range is an outlier of the southern end of the Drakensberg, isolated by the valleys of the Great Fish and Great Kei Rivers (Stuckenberg, 1962) and is known for endemicity of many low-vagility forest-dependent taxa, including molluscs (Connolly, 1939; Herbert & Moussalli, 2010; unpublished data), forest-floor spiders (Griswold, 1985), velvet worms (Daniels & Ruhberg,

2010), harvestmen (de Bivort & Giribet, 2010) and two amphibians, the Hogsback frog, *Anhydrophryne rattrayi* and the Amatola toad, *Vandijkophrynus amatolicus* (the latter also occurs in the Winterberg). The presence of *C. "amathole"* near the mouth of the Great Fish River provides evidence for a link between the coast and the Amathole Mountains and the Great Fish River basin has been identified as an area of persistence of thicket during the contractions of the LGM (Potts *et al.*, 2012). Migration between coastal areas and the Amatholes has also been suggested in other taxa. *Streptocarpus rexii* appears to be a very recent product of migration with speciation from the coast to the Amathole mountains and from there southwards into the southern Cape Afrotemperate forests, probably reaching its current range during the Holocene (< 8000 yr BP) (Hughes *et al.*, 2005). It is suggested that the lineage of rhytidid snails endemic to the Amatholes arose in Pondoland and migrated southwards and diverged into three lineages, one occurring in the Amatholes and one in more mesic southern parts of Albany Thicket (Herbert & Moussalli, 2010). This pattern is mirrored by *C. "amathole"* and *C. alabastris*. The mountains around Grahamstown, together with the Zuurberg, Boschberg and high ground in between, are defined as part of the south-eastern connection between the main Cape Floral Region and the Great Winterberg-Amatholes, based on evidence from several plant taxa (Weimarck, 1941; Clark *et al.*, 2010) and ancient montane lineages of invertebrates (Stuckenberg, 1962). This connection is also likely to have been instrumental in the biogeographical pattern of distribution in the S+E Cape clade throughout this region. The Great Winterberg-Amatholes share several endemic plants with the Boschberg at Somerset East (Clark *et al.*, 2010) but it is not known whether *C. "amathole"* occurs in the Southern Mistbelt forest patches on the Boschberg.

5.7 Western Cape

The "Cape" clades of *Chondrocyclus* occur in the western section of the Cape Floral Region. The Southwestern Cape clade (*C. convexiusculus*) occupies a relatively narrow known range in rugged mountainous areas of the Cape Fold belt to the east of the Cape Flats and on the Cape Peninsula (Fig. 3.4). The Overberg clade occupies a discontinuous area to the east of *C. convexiusculus* in the region known as the Overberg, with two apparently allopatric lineages, one in the southern Agulhas Plain (*C. "kevincolei"*) and the other in the foothills of the Langeberge (*C. "langebergensis"*) (Fig. 3.4). Montane populations of these Cape clades (*C. convexiusculus* and *C. "langebergensis"*) occupy relictual forest patches, usually confined to

sheltered gorges on steep slopes. These Western Cape Afrotemperate Forest and Western Cape Talus Forest types (Von Maltitz *et al.*, 2003) are the westernmost outliers of the Southern Afrotemperate Forest group, extending westwards from the large forest blocks in the southern Cape, in a series of isolated patches along the Cape Fold Mountains to the Cape Peninsula. On the relatively low-lying coastal region of the Agulhas Plain, populations of *C. "kevincolei"* occur in isolated patches of Western Cape Milkwood Forest of the Southern Coastal Forest group, on aeolianite and limestone outcrops; here the dominant floral element is subtropical although some Afrotemperate elements occur (Cowling *et al.*, 1988; Von Maltitz *et al.*, 2003). The two "Cape" clades have not been recorded sympatrically although they occur in close proximity inland in the upper Breede River valley and near the coast (Fig. 3.4). The Breede River valley separates the Langeberge from the mountains to the southwest and is considered an important barrier to gene flow (Weimarck, 1941; Linder 2003; Herbert & Moussalli, 2010; McDonald & Daniels, 2012). Other taxa also contain distinct clades in either the Hottentots-Holland Mountains or the Overberg which do not occur in the other region (e.g. Gouws *et al.*, 2010; Herbert & Moussalli, 2010; McDonald *et al.*, 2012; Daniels *et al.*, 2013). Molecular analyses show relatedness between the Western Cape clades and the S+E Cape clade, but the relationship of the clades to one another is not resolved here and requires further sampling on a finer geographic scale, as well as molecular studies using markers suitable for investigating deeper phylogenetic relationships.

There is a considerable body of information on cladogenesis and radiation in the Cape Floral Kingdom (e.g. Linder 2003, 2005, 2008; Cowling *et al.*, 2009; Verboom *et al.*, 2009). In the past two decades there have also been studies on diverse faunal taxa and common patterns of phylogeography are emerging for disparate faunal groups. Comparison of data on other taxa, particularly low-vagility forest specialists, showing similar distribution patterns to *Chondrocyclus*, provides insight into historical processes which may have influenced observed patterns. Drivers of diversification have been suggested to include mechanisms that fragment distribution ranges, such as climatic shifts leading to vegetation and sea-level changes, uplift, and isolation on either side of a barrier such as in disjunct watersheds. Ancestral floral clades and mature radiations are montane due to geomorphic and climatic stability (although low lying ancestral clades may have gone extinct) (Cowling *et al.*, 1996; Linder 2008; Verboom *et al.*, 2009; Cowling *et al.*, 2009). Low-lying populations of certain faunal taxa were derived from populations which had persisted and speciated in refugial montane habitats (Tolley *et al.*, 2006; Price *et al.*, 2007; Daniels *et al.*, 2013). In floral taxa there was no single trigger for

cladogenesis in the region and dates of divergence of various lineages are spread through time (e.g. Linder, 2005; Verboom, *et al.*, 2009). Lineage divergence in several faunal taxa dates to the Miocene, with further cladogenesis in the Pliocene and into the Quaternary (Tolley *et al.*, 2006; Tolley *et al.*, 2008; Moussalli *et al.*, 2009; Daniels *et al.*, 2009).

The high degree of similarity within either Afrotemperate or Coastal Forest groups suggests that they were already established before major fragmentation of forests began in the late Miocene (Geldenhuys, 1992b). During cooler, drier conditions commencing in the mid-Miocene, accentuated by uplift of the eastern escarpment which blocked the west from summer rainfall, a regime of winter rainfall and dry summers was initiated about 5 Mya and a transition from closed to open habitats progressed (Linder 2008; Cowling *et al.*, 2009). Fynbos taxa radiated and became the dominant vegetation type during the Pliocene (Scott *et al.*, 1997). These changes would have reduced suitable habitat for forest-dependent organisms like *Chondrocyclus* and limited dispersal between fragmented populations, although forest and its associated biota survived in dispersal corridors, including mountain chains and coastal dune systems (Geldenhuys, 1992b). The Pleistocene was characterized by prolonged glacial periods interrupted by short interglacials. Globally glacials were colder and drier periods resulting in marine regression, but in the southwestern Cape winter rainfall zone are associated with wetter conditions and expansion of forests (Linder, 2003; Chase & Meadows, 2007). Lower sea levels during glacial periods (Siesser & Dingle, 1981) may have enabled this vegetation to extend onto the exposed Agulhas bank allowing migration of terrestrial organisms.

Species comprising the Overberg clade appear to be morphologically similar, but careful examination including scanning electron microscopy, reveals differences, and together with molecular evidence, are considered sufficient to warrant recognition of at least two distinct species, *Chondrocyclus* "*langebergensis*" in the Langeberge and *C.* "*kevincolei*" consisting of geographically isolated populations in the Agulhas region (Figs. 4.13, 4.14). The Langeberge and Agulhas Plain are separated by the Breede River valley and by a belt of relatively arid vegetation, consisting mainly of Ruens Shale Renosterveld and Agulhas Limestone Fynbos (Rebelo *et al.*, 2006), which developed in the Pliocene (Cowling *et al.*, 2009). Molecular studies in unrelated faunal taxa also provide evidence for separate lineages in the Langeberge and the Agulhas Plain (e.g. Price *et al.*, 2007; Moussalli *et al.*, 2009; Gouws *et al.*, 2010; McDonald & Daniels, 2012) and for an absence of gene flow between these areas and within forests in the Langeberge (Myburgh & Daniels, 2015). This is a region of persistence of ancient

lineages: initial divergence of *Natalina s.l.* of the Gondwanan mollusc family Rhytididae split the ancestral stock into western and eastern lineages and the basal lineage remained an isolated lineage restricted to the Agulhas Plain (Moussalli *et al.*, 2009). In freshwater isopods, taxa in the Cape Fold Mountains are derived from the Agulhas Plain (Gouws *et al.*, 2010). Relatedness between montane and coastal lineages of the Overberg clade, and within other taxa, point to gene flow in the past. This may have occurred within the Overberg region, or it is also possible that the common ancestor of this clade may have dispersed to the current area of distribution from the Southern Cape, both along the Cape Fold Mountains and/or along the coast. The S+E Cape clade forms a monophyletic group with the two southwestern Cape clades but the relationships between these three clades is not resolved here. There is evidence in several unrelated taxa of evolutionary relationships between species in the southern Cape forests and those in the relict forests in the Langeberge although the latter are genetically distinct (e.g. Tolley *et al.*, 2006; Moussalli *et al.*, 2009). In freshwater isopods the species in the southern Cape is basal to the clade in the Overberg (Gouws *et al.*, 2010). Strong links between vegetation in the coastal lowland areas of the Eastern Cape and similar areas in the southern Cape, including the Agulhas Plain, may be explained in terms of floristic connections provided by past changes in sea level and the resultant exposure of the broad continental shelf (Agulhas Bank) between the two regions (Geldenhuys, 1992a; van Wyk & Smith, 2001; Linder, 2003). Hypotheses based on findings in other taxa could be formulated to investigate relationships between and within clades of *Chondrocyclus* in the southern and western Cape.

The long branch lengths of the isolated populations of *Chondrocyclus "kevincolei"* and a lack of sister species suggest lineage extinctions and isolation of species in shrinking refuges as arid-adapted vegetation replaced forest (see Tolley *et al.*, 2006; 2008). Recent radiations in faunal taxa are associated with adaptation to open habitats (Tolley *et al.*, 2006; Herbert & Moussalli, 2010). *Chondrocyclus* populations at Bredasdorp occur in relatively dry thicket. *C. "langebergensis"* at Pat Busch occurs in tall riverine fynbos at lower elevations than montane populations of the species and it appears that the former population is becoming adapted to drier conditions. Sea level changes have also had dramatic effects on vegetation of the Agulhas Plain (Linder, 2003) and its biota (e.g. Tolley *et al.*, 2006; Herbert & Moussalli, 2010). The Agulhas Plain experienced repeated marine transgressions, potentially restricting ancestral *Chondrocyclus* populations to refuges at higher elevations in Cape Fold outliers and thus driving allopatric divergence or eliminating closely related taxa at lower elevations (see Gouws *et al.*, 2010). Further sampling in the few unsampled forest/thicket patches on the Agulhas Plain

as well as in the Riviersonderendberge (where *Chondrocyclus* have not been found) would provide further information on relationships and cladogenesis between lineages in this clade. In rhytidid molluscs, separate species occur on the Agulhas Plain and in the Riviersonderendberge.

The Southwestern Cape clade, consisting of populations of *C. convexiusculus*, occurs on the Cape Peninsula and in the north-south running Hottentots-Holland and Limietberg Mountains at the western end of the Cape Fold Mountains (Fig. 3.4). On the Cape Peninsula *C. convexiusculus* occurs in refugial patches of Western Afrotemperate forest in ravines and gorges, which also support the persistence of fauna endemic to the Peninsula (Picker & Samways, 1996; Huber, 2003). The phylogeographic break between the Cape Peninsula and the adjacent interior is well documented (e.g. Daniels *et al.*, 2001; Wishart & Hughes, 2003; Gouws *et al.*, 2010; McDonald & Daniels, 2012; Cressey *et al.*, 2014) and cladogenesis of Peninsula clades has been dated to the mid-Pliocene – early Pleistocene (Wishart & Hughes, 2003; Daniels *et al.*, 2013). The forests of the Cape Peninsula have been isolated from the rest of the Cape Fold Mountains by successive marine transgressions (Siesser & Dingle, 1981) while the present arid conditions have prevailed at intervals since the late Miocene and Pliocene (Schalke 1973; Mucina & Geldenhuys, 2006; Neumann & Bamford, 2015). The distribution of the *C. convexiusculus* lineage also provides evidence for historic links between the forest patches on the Peninsula and those in the mountains to the east. The pattern in *Chondrocyclus* mirrors that in several other taxa with members of a lineage occur on both sides of the Cape Flats e.g. the *Peripatopsis capensis* and *P. balfouri* complexes of velvet worms (Daniels *et al.*, 2009; McDonald & Daniels, 2012; Daniels *et al.*, 2013) and *Bradypodion pumilum* chameleons (Tolley *et al.*, 2008). Forest has existed on the Cape Flats at various times since major cooling and drying caused fragmentation in the late Miocene and Pliocene. Palynological data suggest that during the past 50 000 years an extension of the mixed *Podocarpus* (Afrotemperate) forest to the central Cape Flats took place twice, the most recent interval being between 35500 and 33000 years B.P. (Schalke, 1973). Shared plant taxa between Cape Peninsula forests and those to the east along the coast, point to the possibility of a coastal corridor (Geldenhuys, 1992b).
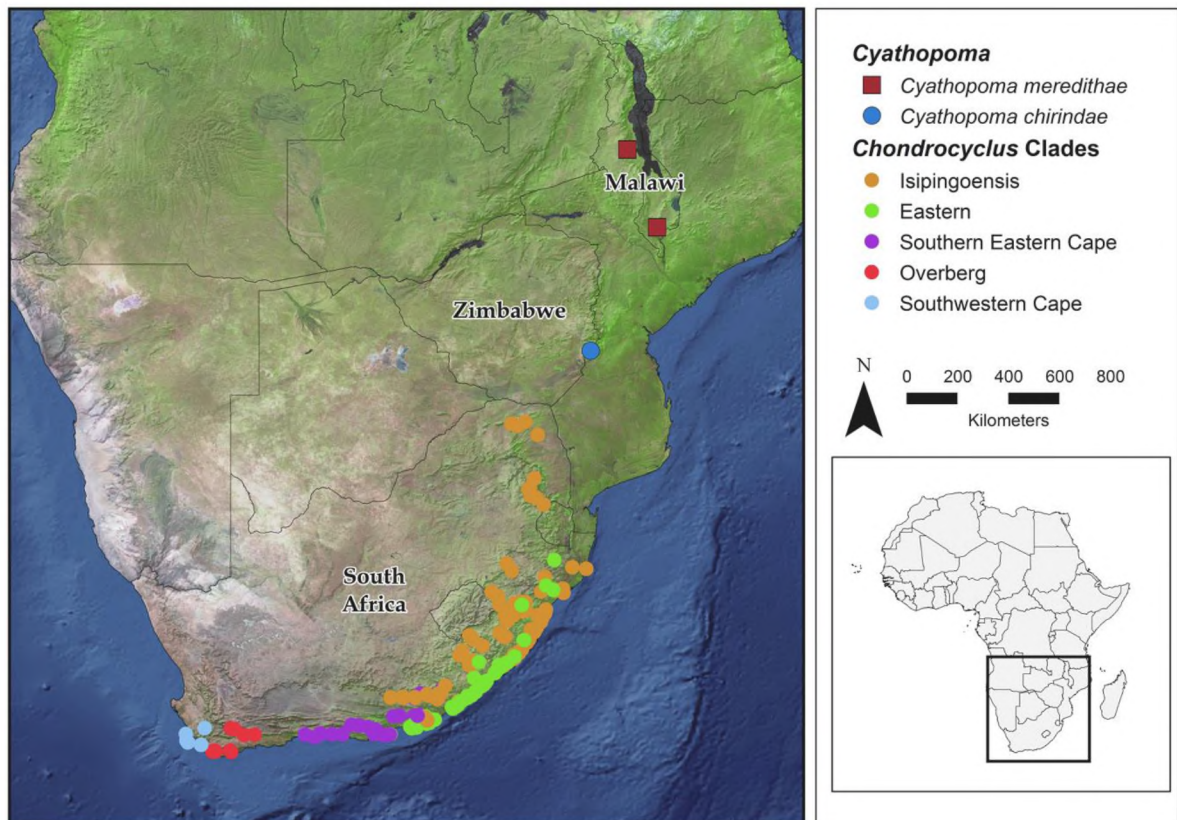
Figure 5.1 Map showing location of records of *"Cyathopoma" meredithae* and *"Cyathopoma" chirindae* (previously *"Chondrocyclus" meredithae* and *"C." chirindae*) in relation to distribution of major clades of *Chondrocyclus* in South Africa.

6 Conservation

6.1 Security of habitat

Chondrocyclus species occur in a variety of forest types and thickly vegetated habitats. The majority of *Chondrocyclus* diversity is concentrated in two of Africa's biodiversity hotspots: the Cape Floral Region and the Maputaland-Pondoland-Albany hotspot. The Forest Biome covers just over 3000 km^2, or 0.1% of the land surface of South Africa although at least 7% of the country is potential forest habitat owing to the favourable combination of climate and substrate for forest growth (Mucina & Geldenhuys, 2006; Eeley *et al.*, 1999). Much of the forest in SA is an archipelago of scattered islands among other biomes and most forests are surrounded by areas of high human population density (Mucina & Geldenhuys, 2006). The largest single forest is in the southern Cape (Knysna) area (approx. 260 km^2, part of a larger complex of 605 km^2 (Mucina & Geldenhuys, 2006)) and is owned by South African National Parks (SANParks), affording it the highest degree of protection. The second largest forest block is the Amathole forest complex (just over 400 km^2 (Mucina & Geldenhuys, 2006)), managed by various government departments, mainly Department of Agriculture, Fisheries and Forestry (DAFF), but management has deteriorated in recent years. Sections are managed by private forestry companies where better security improves compliance.

The habitat of most *Chondrocyclus* species falls within formally protected areas or private nature reserves (Table 6.1). Many indigenous forests are under statutory conservation and thus are afforded a degree of protection, although compliance is often lacking. Many forests outside proclaimed areas are well conserved, but their conservation status is insecure, although some are included in formal conservancies. Other privately owned forests are protected in theory since they fall under the National Forests Act of 1998 (Act No. 84 of 1998) and may not be cleared.

Conservation concerns pertaining to *Chondrocyclus* are those typical of terrestrial molluscs in general and of other low-vagility forest taxa: narrow-range endemism, patchy distribution within a forest, poor active dispersal ability and hence vulnerability to habitat loss (Solem, 1984; Fontaine *et al.*, 2007a; Stanisic *et al.*, 2007). The distributions of several *Chondrocyclus* species are highly fragmented and these forest patches may be extremely small. This in itself does not

necessarily imply these species are threatened. Studies of the effects of fragmentation on forest invertebrates are scarce and the few published studies on molluscs indicate that molluscs can be surprisingly resilient to forest fragmentation and degradation (Kappes *et al.*, 2009b; Raheem *et al.*, 2009), although the response is species-specific and seems to depend on habitat specialization (Kappes *et al.*, 2009a). Empirical evidence suggests that while loss of habitat has strong negative effects on biodiversity, fragmentation *per se* generally has weak effects that are as likely to be positive as negative (Fahrig, 2003). In both temperate and tropical forests, diversity of molluscs was shown to be independent of fragment size, but may be correlated with age of patch, pre-existing spatial gradients of species heterogeneity, soil moisture or limestone (Solem 1984; Fontaine *et al.*, 2007b; Kappes *et al.*, 2009b; Raheem *et al.*, 2009; Uys *et al.*, 2010). Small and/or degraded forest patches in Transkei contained surprisingly high levels of diversity and endemism and the value of conserving these habitats has been emphasised (Bursey & Herbert, 2004; Cole & Herbert, 2009). Such microrefugia provide areas for future expansion with attributes different from the matrix and as such should be prioritized for conservation (Solem *et al.*, 1981; Turner & Corlett, 1996; Fontaine *et al.*, 2007b; Raheem *et al.*, 2008; Mosblech *et al.*, 2011).

Gene flow is usually restricted concomitant with low active colonization ability (Myburgh & Daniels, 2015). However, passive dispersal does allow colonization of new habitats and wind-borne transport is regarded as an important mechanism (Gittenberger *et al.*, 2006; Kirchner *et al.*, 1997; Holland & Cowie 2007). In velvet worms, populations in small forest patches showed greater genetic diversity than in a larger forest and rare dispersal events were suggested to have enabled limited gene flow (Myburgh & Daniels, 2015).

6.2 Cryptic species

Ten new species are described by application of molecular systematics in conjunction with scanning electron microscopy (SEM) and gross morphology augmenting evidence from other studies that diversity of South African forest-dwelling invertebrates is underestimated (Huber, 2003; de Bivort & Giribet, 2010; McDonald *et al.*, 2012; Daniels *et al.*, 2013; Ruhberg & Daniels, 2013). Several cryptic species were revealed (defined as two or more distinct species that are erroneously classified under one species name (Bickford *et al.*, 2006)) (Table 6.2). These species were distinguishable on morphological criteria but had been overlooked previously due to lack of

fresh specimens displaying diagnostic morphological features. The importance of detecting cryptic species and their subsequent description for conservation purposes cannot be overestimated (Bickford *et al.*, 2006; Beheregaray & Caccone, 2007; Kahindo *et al.*, 2007). The majority of *Chondrocyclus* species occupy relatively narrow ranges and species or lineages within a cryptic species complex each have more limited distributions than previously realized (Fig. 3.2, Table 6.3). These taxa add to the cryptic species and/or lineages being discovered in South Africa across a variety of taxa (e.g. Griswold, 1990; Huber, 2003; Price *et al.*, 2007; Daniels *et al.*, 2009; Daniels & Ruhberg, 2010; de Bivort & Giribet, 2010; Gouws *et al.*, 2010; Herbert & Moussalli, 2010).

Conservation management and legislation are based on preservation of species units and therefore consideration of the delimitation of these units is relevant to conservation of *Chondrocyclus* species where an increase in the number of species is suggested. Application of different methods ("species concepts") for inferring boundaries of species can lead to different species identities, ranges and abundances (examples in Agapow *et al.*, 2004). Incompatibilities arise between species concepts because criteria adopted as necessary properties of the species category under different concepts (e.g. reproductive isolation, monophyly) arise at different times during the continuous process of lineage divergence (Ferguson, 2002; de Queiroz, 2007). With advances in molecular phylogenetics, the Phylogenetic Species Concept (PSC) is increasing in popularity (see Agapow *et al.*, 2004 and de Queiroz, 2007 for a summary of definitions under the concept), and it is widely recognized that the PSC will often split species determined under nonphylogenetic criteria, producing new groups with more restricted ranges and decreased abundance, and hence an increase in number of threatened species. However, incorrect splitting of species can be detrimental to conservation efforts by resulting in misdirected efforts (Harris & Rato, 2013; Zachos, 2013).

Under the Unified Species Concept, existence as a separately evolving metapopulation lineage, or more specifically, segment of such a lineage, is the only property of a species, and criteria used to define species under other concepts are considered lines of evidence relevant to assessment of a segment of a lineage as a species (de Queiroz, 2007). While any single property, if appropriately interpreted, is evidence of lineage divergence, hypotheses of the existence of separate species should be based on multiple lines of evidence (de Queiroz, 2007; Wiens, 2007; Zachos, 2013). In this study, species delimitation is based on morphology, monophyly and, in sympatric species,

intrinsic reproductive isolation. Systematic studies of molluscs tend to adopt an integrative approach (e.g. Pfenniger *et al.*, 2003, 2006; Depraz *et al.*, 2009; Moussalli *et al.*, 2009; Golding, 2014a,b; Golding *et al.*, 2014; Radea *et al.*, 2013; Wang *et al.*, 2014; Evangelisti *et al.*, 2016).

6.3 IUCN Threatened Species and assessment of risk

Assessments of the International Union for Conservation of Nature (IUCN) Threatened Species status are based mainly on decline in population or habitat quantified according to five criteria (IUCN, 2012). Criteria using geographic range (B and D) were used to evaluate if *Chondrocyclus* species belong to a threatened category (IUCN, 2016). The Extent of Occurrence (EOO) (Criterion B1) of species qualifying for Critically Endangered is < 100 km^2, for Endangered $<$ 5000 km^2 and for Vulnerable < 20000 km^2 (IUCN, 2012). The Area of Occupancy (AOO) (Criterion B2) for the respective categories is < 10 km^2, < 500 km^2 and < 2000 km^2. In addition to qualifying for a certain category based on EOO or AOO, observed or projected decline or extreme fluctuations in EOO, AOO, habitat quality or population size of a species are required to be demonstrated (IUCN, 2016). Nine species of *Chondrocyclus* species meet the criteria for Red Listing (Table 6.3). These data are essential for conservation in South Africa and without them threatened species and their habitats will not be given consideration in land use planning (M. Hamer, SANBI, pers. comm.). In addition, populations of *C. isipingoensis*, which may be a complex of several cryptic species, each with restricted ranges, may also be worthy of conservation efforts. These distinct genetic lineages were not described as new species due to insufficient samples for a comprehensive geographical, morphological and molecular study to provide multiple lines of evidence on which to base the descriptions. One lineage is described herein (*C. "oxygala"*) and it qualifies as Vulnerable (Table 6.3).

Measures of diversity in addition to, or instead of, species lists are proposed, but these require larger sample sizes than those used in this study. It has been suggested that evolutionary distinctiveness be incorporated into practical conservation measures including IUCN assessments of risk (Harris & Rato, 2013; Rosauer & Mooers, 2013). Evolutionary Significant Units are potentially useful for conservation management, but should be based on genetic and ecological information, with an emphasis placed on exchangeability rather than distinctiveness (Crandall *et al.*, 2000; Kappes *et al.*, 2009b). More extensive sampling of *Chondrocyclus* populations and further research to better understand their phylogenetic diversity and evolutionary processes

would help to guide efforts to ensure that their evolutionary potential (i.e. the network of genetic exchange) is protected (Crandall *et al.*, 2000; Wishart & Hughes, 2003; Tolley *et al.*, 2008).

Chondrocyclus exsertus is of high conservation concern and qualifies for listing as Critically Endangered based on AOO which is calculated to be only 6.43 km^2 and supporting conditions (IUCN, 2016). *C. exsertus* currently appears to be restricted to tiny patches of scarp forest inland of the coast and surrounded by sugarcane. Its habitat is severely fragmented and its population appears to be in decline since it has not been found during recent searches at sites where it was recorded prior to the 1930s, possibly due to habitat loss or degradation. The latter sites are on the South Coast of KwaZulu-Natal where human population densities are very high due to formal and informal developments. Most coastal forest in the region has been converted to sugar cane and although large areas remain climatically suitable for lowland forest insufficient area is currently protected (Eeley *et al.*, 1999). None of the forests where *C. exsertus* has been collected recently are within protected areas.

Chondrocyclus putealis meets the criteria for Endangered based on EOO and AOO and it also appears to be in decline. The species seems to have disappeared from its type locality on the KwaZulu-Natal South Coast, but has recently been found at one inland locality in this area and in a localized coastal area of Pondoland. Although part of this habitat falls within a provincial nature reserve (Mkhambati), it occurs in forest on a steep bank of the Mtentu River gorge, where raised sea level as a result of global warming could pose a future threat. Pondoland and southern KwaZulu-Natal are densely populated with multiple pressures on the forests including subsistence use, agriculture, tourism and mining (for limestone for cement). From a botanical stance alone, it has been expressed that every patch of the Pondoland Scarp Forests is of extremely high value and should be unconditionally protected (Mucina *et al.*, 2007).

Chondrocyclus trifimbriatus is Endangered based on EOO and AOO, and it has not been found in the Karkloof vicinity since its description and may have disappeared from its type locality. If specimens recorded in the small isolated scarp forests of Entumeni and Nkandla in Zululand are indeed *C. trifimbriatus* (as has been assumed here), its range may be more extensive than previously thought, but it still meets the criteria for listing as Endangered. It is recommended that increased attention should be devoted to the threats to the small patches of these Eastern Scarp Forests (Mucina *et al.*, 2007). Their relict character is of great scientific value since they carry

important messages about the evolutionary history of southern African forest biota (Mucina *et al.*, 2007).

There are several other examples of narrow-range endemic molluscs and other taxa which occur in only one or two of the Zululand scarp forests and not in others (Huber, 2003; Herbert & Kilburn, 2004; Tilbury & Tolley, 2009; Herbert & Moussalli, 2010). Predictions of climate change in South Africa present a growing concern for the conservation of forest-dependent species in northern KwaZulu-Natal because the predictions suggest decreased climatically-suitable habitat (Houiniet *et al.*, 2009). Eeley *et al.* (1999) showed with climate modeling that distribution of forests in Kwazulu-Natal are sensitive to climate change and have shown large-scale migrations under palaeoclimate change. Therefore, long-term forest preservation should require allowance for forest migration but isolation of forests by anthropogenic landscape change has limited their radiation potential and ability to track environmental change (Eeley *et al.*, 1999). Scarp forests, which were palaeo-refugia, are suggested to be important for the future conservation of forest biodiversity (Eeley *et al.*, 1999; Mucina *et al.*, 2007). Locations of refugia since the LGM and estimates of the magnitude of change in extent of suitable habitat were evaluated by comparing phylogeography of rainforest snails with predictions from palaeoclimate modelling, and snails were found to be good candidates for recovering details of historical biogeography (Hugall *et al.*, 2002). Similar studies in South African forests could be useful for application to conservation of forest biodiversity into the future.

The following six species occupy extremely small and severely fragmented forest patches, but since several have been newly discovered, a decline in population or habitat parameters cannot be estimated and hence they qualify for Vulnerable status. The majority have an AOO < 20km^2 and/or are known from only one location (Table 6.3). *C. "devilliersi"* is known from only one locality, Nqadu (Fig. 3.7), although more thorough sampling is required to establish if it is a point-endemic. The forests of the Transkei region are considered to be of major conservation importance due to their rich biodiversity and high levels of endemism, based on plants and vertebrates (Cooper & Swart, 1992; van Wyk & Smith, 2001). Analyses of invertebrate distributions indicate similar foci of diversity and endemism (Hamer & Slotow, 2002; Bursey & Herbert, 2004; Herbert & Kilburn, 2004; Cole & Herbert, 2009). Transkei forests have traditionally been utilized by local people as sources of natural products and for stock grazing. However, the sustainability of such practices has been compromised due to reduction in forest extent by direct clearing and increased

population density surrounding forests, leading to greater levels of utilization, and they represent a serious threat to the remaining forest (Cooper & Swart, 1992; Von Maltitz & Fleming, 2000; de Villiers & White, 2002; White, 2002; Cocks *et al.*, 2004). Activies that may have little impact on larger organisms, e.g. collection of fallen wood for fuel, may have profound effects on molluscs and other invertebrates (Simelane *et al.*, 2000; Kappes *et al.*, 2009a). These concerns also apply to *C.* *"cooperae"* and *C.* *"pondoensis"* occurring in several very small provincial protected areas where management is poor and uncontrolled use of forest resources is a conservation problem, albeit to a lesser degree than in forests outside protected areas where illegal hunting, trampling by cattle, fuelwood and muthi gathering, and direct clearing take place continually (personal observation).

C. *"pulcherrimus"* is a newly discovered species with its entire known range restricted to the Ngome forest, consisting of one large and several smaller patches of Southern Mistbelt forest totaling only 36.6 km^2 (Mucina & Geldenhuys, 2006). A proportion is protected in the Ntendeka Wilderness area.

Chondrocyclus *"kevincolei"* occurs in a few "islands" of forest on the Agulhas Plain. None of these localities falls within a protected area, but they include private nature reserves and a conservancy. Population level studies are required to better understand these genetically distinct lineages and assess their conservation status. While there are few other potentially suitable habitats on the Agulhas Plain, more extensive searching throughout the region, including in the Riviersonderendberge, is needed to document distribution more accurately and confirm that the observed structuring is not due to the limited coverage of sampling.

Chondrocyclus convexiusculus occupies an extremely small AOO, but a large proportion of its range falls within national and provincial parks. *C.* *"herberti"* also has an extremely small AOO within a relatively well-managed provincial protected area. It may be in the process of adapting to drier conditions since it is locally abundant, and may thus be of less conservation concern than other species with larger ranges.

Table 6.1 Ownership of land for recorded *Chondrocyclus* localities.

Species	Ownership of land
C. convexiusculus	National Park, Provincial Nature Reserves
C. alabastris	Small area of National Park, Provincial Nature Reserves, Municipal Nature Reserve, private land
C. "herberti"	Provincial Nature Reserve
C. "silvicolus"	National Park, Provincial Nature Reserve
C. "kevincolei"	Private land, conserved as Private Nature Reserves or conservancies
C. "langebergensis"	Provincial Nature Reserve, Private Nature Reserve
C. bathrolophodes	National Park, Municipal Nature Reserve, private land, tribal land
C. "amathole"	Department of Agriculture, Fisheries & Forestry, Provincial Nature Reserve, Municipal Nature Reserve, private land
C. "cooperae"	Provincial Nature Reserves, tribal land, private land
C. putealis	Provincial Nature Reserve, tribal land, private land
C. exsertus	Private land
C. trifimbriatus	Provincial Nature Reserves, tribal land, private land
C. "pulcherrimus"	Department of Agriculture, Forestry and Fisheries
C. "pondoensis"	Provincial Nature Reserve, tribal land, private land
C. "devilliersi"	Forestry concession
C. isipingoensis	Provincial Nature Reserves, tribal land, private land, forestry concessions
C. "oxygala"	Private land

Table 6.2 Cryptic *Chondrocyclus* species revealed in this study.

Cryptic species	Previous classification (Connolly, 1939; Herbert & Kilburn, 2004)
C. "kevincolei", C. "langebergensis", C. "silvicolus"	*C. convexiusculus*
C. "cooperae", C. "devilliersi"	*C. putealis*
C. "silvicolus", C. "amathole"	*C. alabastris*
C. "oxygala"	*C. isipingoensis*

Table 6.3 IUCN Red List (2016) categories and criteria used in assessment of risk of *Chondrocyclus* species. EOO = Extent of Occurrence, AOO = Area of Occupancy.

Species	EOO (km^2)	AOO (km^2)	Category	Criteria
C. exsertus		6.43	Critically endangered	B2 and a,b
C. putealis	1586	51.39	Endangered	B1 and B2; a,b
C. trifimbriatus	4593	114.49	Endangered	B1 and B2; a,b
C. "herberti"	487	0.303	Vulnerable	D2 AOO < 20 km^2
C. "kevincolei"	1083	4.31	Vulnerable	D2 AOO < 20 km^2
C. convexiusculus	5351	6.25	Vulnerable	D2 AOO < 20 km^2
C. "devilliersi"		8.69	Vulnerable	D2 AOO < 20 km^2; no. locations = 1
C. "pulcherrimus"	260	43.35	Vulnerable	D2 No. locations = 1
C. "oxygala"	961	51.02	Vulnerable	D2 No. locations = 2

7 Conclusions

The aim of this study was to revise the genus *Chondrocyclus*, the major South African group of the large family of operculate terrestrial molluscs, the Cyclophoridae, based on a molecular phylogeny and evidence from morphological examination. This is the first detailed systematic treatment of a group of Cyclophoridae in mainland Africa and the first to provide molecular data. This study will complement regional studies on the systematics of the family in Asia and will provide data for studies of higher level relationships within the Cyclophoridae.

Molecular and morphological data was congruent and provided independent sources of evidence for species delimitation. Informative features were morphology of the shell, protoconch, periostracum, operculum, radula and penis, and molecular data was based on regions of 16S and CO1 genes. Redescriptions of species regarded as members of the genus and descriptions of potentially new species are provided, together with detailed illustrations of characteristic morphological features. Museum collections have been boosted with the addition of fresh specimens and material from unsampled localities. Based on existing records, the genus is endemic to South Africa and does not include species in Afromontane regions of Zimbabwe and Malawi.

A molecular phylogeny is presented which showed *Chondrocyclus* to be monophyletic, and recovered five major clades. The Isipingoensis clade consisted of several well-supported groups of populations of "*Chondrocyclus isipingoensis*", considered here to be a species complex, with. *C. exsertus*, a species having unique morphological features, nested within it. The group at the western extremity of the clade was sister to all other populations and described as a new species, but the complex is not unravelled further here. The Isipingoensis clade is widely distributed along the length of the Great Escarpment and on the south-east coast. The other four clades encompass the area from Zululand to the Cape Peninsula with a pattern of east-west lineage turnover. Biogeography of the *Chondrocyclus* lineages is discussed and attention is drawn to concordant patterns in unrelated taxa.

The range of the Eastern clade on the southeast coast overlaps with populations of *C. "isipingoensis"* and contains seven species with complex patterns of sympatry and

disjunctions. At the western end of its range, the Eastern clade is sympatric with the clade occurring in the Albany Thicket biome (the Southerneastern Cape clade). Some populations of the latter appear to be adapted to drier habitats than is typical for the majority of *Chondrocyclus* species which are characteristic snails of mesic vegetation. This Southern-Eastern Cape clade extends westwards into the relatively large expanses of Afrotemperate forest in the southern Cape. Two clades occur in relictual forest patches in the western Cape Floristic Region. The Southwestern Cape clade occurs on the Cape Peninsula and to the east of the Cape Flats. The Overberg clade contains two apparently allopatric lineages, one in the southern Agulhas Plain and the other in the foothills of the Langeberge.

Diversity within the genus has more than doubled, from a previous seven South African species (and two species from north of South Africa) to seventeen. Several cryptic species were detected within previously widespread "species" and unrecorded narrowly endemic species were documented. Understanding of the terrestrial molluscan fauna of South Africa is improved with this revision of the major proportion of a family which hitherto was poorly documented. This study will complement other research on composition, spatial distribution and phylogenetic diversity of low-vagility invertebrates and expand the scientific evidence available for biodiversity conservation in South Africa.

Further research

This study has laid the foundation for further research on the systematics of *Chondrocyclus* and other Cyclophoridae on a local, African or global scale, and the historical biogeography of southern Africa. A proposed study which is underway, is to investigate relationships between the genera of Cyclophoridae (D. Raheem, pers. comm). Suggested topics for future studies include:

- Obtain a nuclear DNA dataset using a suitable marker for species-level taxonomy for comparison with the mitochondrial sequences
- Unravel the systematics of the *C. isipingoensis* species complex with the inclusion of more sampling localities from across its range

- Population genetic studies using microsatellites to investigate gene flow. There is wide scope for such studies in each of the five clades as well as between selected species within each clade.

- Investigate relationships between clades within *Chondrocyclus* using appropriate marker(s)

- Investigate relationship of *"Cyathopoma" chirindae* and *"Cyathopoma" meredithae* (recorded in Zimbabwe and Malawi respectively) to *Chondrocyclus* and the affinities of *Elgonocyclus* sp.

- Explore whether dating of the phylogeny is feasible.

Appendix 1 Identity, locality, date collected and museum registration number for specimens with same data as those used for sequencing. Specimens used for DNA extraction are destroyed in the process.

Genus and Species	Locality	Date	Latitude	Longitude	Accession Number
Acroptychia aequivoca	Madagascar, Nose Mangabe	2006-10-19	-15.493535	49.767888	NMSAL7326
Chondrocyclus alabastris	Grahamstown, Mountain Drive, south-facing slope	2011-02-06	-33.328129	26.500643	ELMD16889
Chondrocyclus alabastris	Van Stadens Pass, bottom of pass, west bank of river	2012-11-16	-33.909541	25.190462	ELMD17016
Chondrocyclus alabastris	Stinkhoutkloof, 11km N.E of Loerie	2012-11-17	-33.799255	25.096678	ELMD17034
Chondrocyclus alabastris	Van Stadens River gorge, east side of river	2011-09-27	-33.911650	25.204650	ELMW03638
Chondrocyclus alabastris	Ferndale, Patensie, Ratelkloof	2011-09-28	-33.716420	24.850300	ELMW03639
Chondrocyclus alabastris	Port Elizabeth, The Island Nature Reserve	2011-05-27	-33.986680	25.371510	ELMW03640
Chondrocyclus alabastris	Gamtoos River mouth, dune forest east of mouth	2011-05-28	-33.957441	25.047668	ELMW03641
Chondrocyclus alabastris	Grahamstown, Mountain Drive, south-facing slope	2011-02-06	-33.329150	26.499110	Extracted
Chondrocyclus alabastris	Olifantskop, Addo National Park	2011-09-29	-33.317315	26.499110	ELMW03643
Chondrocyclus alabastris	Berg River crossing, east bank, 9km E of Loerie	2012-11-17	-33.874608	25.119551	ELMW03668
Chondrocyclus alabastris	Addo National Park, Zuurberg section	2012-11-19	-33.340335	25.736193	ELMW03676
Chondrocyclus alabastris	Port Elizabeth, Lovemore Heights, south facing slope	2012-11-18	-33.992786	25.512132	ELMW03733
Chondrocyclus alabastris	Addo National Park, Zuurberg section	2012-11-19	-33.340335	25.736193	ELMW03738
Chondrocyclus alabastris	Paradise kloof, 8km SW of Grahamstown	2013-02-28	-33.344366	26.446569	ELMW03740
Chondrocyclus alabastris	Coleridge, near Stones Hill, 8km SE of Grahamstown	2013-03-02	-33.333394	26.615589	ELMW03741
Chondrocyclus amathole	Beggars Bush, 15km E of Grahamstown, south-facing	2013-02-25	-33.287080	26.688521	ELMD17289
Chondrocyclus amathole	Hogsback, forest above Hobbiton	2013-06-10	-32.595837	26.961697	ELMD17338
Chondrocyclus amathole	Fort Fordyce, south facing slope behind lookout	2015-01-17	-32.695607	26.485680	ELMD17860
Chondrocyclus amathole	Stutterheim, Contour path	2015-01-16	-32.536632	27.366781	ELMD17874
Chondrocyclus amathole	Hogsback, downstream of Madonna and Child Waterfall	2012-09-13	-32.606802	26.962248	ELMW03665
Chondrocyclus amathole	Patchwood Farm, forest at source of Quanti River	2012-12-18	-32.392392	27.446963	ELMW03695
Chondrocyclus amathole	Hogsback, downstream of Madonna and Child Waterfall	2014-04-06	-32.606802	26.962248	Extracted
Chondrocyclus bathrolophodes	Kap River, ravine on north bank	2011-05-13	-33.481175	27.087327	ELMD16927
Chondrocyclus bathrolophodes	The Glen on Pig Island Farm, Kleinemonde River	2013-02-26	-33.494645	26.934227	ELMD17355
Chondrocyclus bathrolophodes	Alexandria, top of ridge, near beacon tower	2009-11-23	-33.695096	26.354241	ELMW03658
Chondrocyclus bathrolophodes	Kap River, ravine on north bank	2012-11-22	-33.481175	27.087327	ELMW03756

Genus and Species	Locality	Date	Latitude	Longitude	Accession Number
Chondrocyclus bathrolophodes	Bathurst State Forest, near top of Kap River Pass	2013-02-25	-33.344051	26.865606	ELMW03759
Chondrocyclus bathrolophodes	Kobonqaba, coastal forest on east side of mouth	2015-04-23	-32.605755	28.493315	ELMW03868
Chondrocyclus bathrolophodes	Port Alfred, east side of Kowie River, dune forest	2011-04-06	-33.591692	26.904330	Extracted
Chondrocyclus convexiusculus	Cape Town, Simonstown	2011-06-25	-34.256750	18.472460	ELMD16879
Chondrocyclus convexiusculus	DuToits Kloof, Donkerkloof	2014-08-07	-33.753608	19.069556	ELMD17970
Chondrocyclus convexiusculus	Cape Town, Millers Point	2012-02-01	-34.256750	18.472946	ELMW03637
Chondrocyclus convexiusculus	Kogelberg N.R., near Leopards Gorge waterfall	2014-08-12	-34.340888	18.940717	ELMW03876
Chondrocyclus convexiusculus	Kogelberg N.R., Oudebosch	2014-08-12	-34.333662	18.948733	ELMW03877
Chondrocyclus cooperae	Mazeppa Bay, east bank of Sihlontlweni estuary	2015-04-23	-32.478317	28.646002	ELMW03867
Chondrocyclus cooperae	Xora, Bulungulu	2012-11-09	-32.152586	28.998814	Extracted
Chondrocyclus cooperae	Dwesa Nature Reserve, near camp	2011-02-20	-32.152817	28.841667	ELMD16935
Chondrocyclus cooperae	Dwesa Nature Reserve, forest east of camp	2011-02-21	-32.298624	28.829040	Extracted
Chondrocyclus cooperae	Umtiza Nature Reserve, east side of Buffalo pass road	2011-03-18	-33.014444	27.808056	ELMW03623
Chondrocyclus cooperae	Morgan Bay, Yellowwood Park	2011-03-06	-32.696670	28.334722	ELMD16968
Chondrocyclus cooperae	Xora, Nxeni Forest, east bank of Ntlonyane River	2012-11-08	-32.193325	28.957403	ELMW03813
Chondrocyclus devilliersi	Nqadu Forest, 16 km north of Mthatha as crow flies	2013-01-26	-31.424120	28.754750	ELMW03716
Chondrocyclus devilliersi	Nqadu Forest, 19 km north of Mthatha as crow flies	2015-04-16	-31.424120	28.754750	ELMW03861
Chondrocyclus exsertus	Frome Farm, Sunwich Port	2015-02-04	-30.649750	30.478640	ELMD17935
Chondrocyclus exsertus	Umzumbe, Clouds Hill	2015-02-04	-30.627491	30.530842	ELMD17936
Chondrocyclus exsertus	Frome Farm, Sunwich Port	2012-01-08	-30.649750	30.478640	ELMW03654
Chondrocyclus herberti	Baviaanskloof, Geelhoutbos, near hikers hut, in kloof	2015-03-09	-33.635662	24.245741	ELMD17986
Chondrocyclus herberti	Baviaanskloof, Geelhoutbos, near pool & weir	2015-03-09	-33.643001	24.242637	ELMD17990
Chondrocyclus herberti	Baviaanskloof, Poortjies	2011-01-26	-33.653700	24.527000	ELMW03691
Chondrocyclus herberti	Baviaanskloof, Poortjies	2015-03-09	-33.653700	24.527000	ExtracKny
Chondrocyclus isipingoensis	Umtiza Nature Reserve, east side of Buffalo pass road	2011-01-13	-33.014444	27.808056	ELMW03652
Chondrocyclus isipingoensis	Mount Frere, Buffalo Nek	2015-04-07	-30.854799	28.892971	ELMW03856
Chondrocyclus isipingoensis	Ingele Forest, Red Trail	2015-04-15	-30.533079	29.682669	ELMW03855
Chondrocyclus isipingoensis	Ongoye	2015-04-11	-28.842881	31.794020	Extracted
Chondrocyclus isipingoensis	Bedford, Maasstrom forest	2011-01-24	-32.648611	26.068333	ELMW03646

Genus and Species	Locality	Date	Latitude	Longitude	Accession Number
Chondrocyclus isipingoensis	Somerset East, Glen Avon	2011-01-25	-32.677000	25.636667	ELMW03647
Chondrocyclus isipingoensis	Kenneth Stainbank N.R, Durban	2011-04-12	-29.912175	30.938969	ELMW03648
Chondrocyclus isipingoensis	Phumalanga Farm, Bulura, riverine forest	2010-12-31	-32.806667	28.030556	ELMW03649
Chondrocyclus isipingoensis	Karkloof Falls, near top of gorge	2010-01-22	-29.408820	30.284040	ELMW03650
Chondrocyclus isipingoensis	Xora, Kumqolo Forest	2012-11-08	-32.158882	28.984821	Extracted
Chondrocyclus isipingoensis	Karkloof Falls, near top of gorge	2010-01-22	-29.408820	30.284040	ELMW03650
Chondrocyclus isipingoensis	Kei River Valley, Moonstone Farm, top of mountain	2012-12-19	-32.256500	27.568770	ELMD17097
Chondrocyclus isipingoensis	Langeni, Kambi Forest	2013-01-25	-31.468010	28.589330	ELMD17151
Chondrocyclus isipingoensis	Langeni, Phungela Valley, near forestry offices	2013-01-24	-31.473470	28.487180	Extracted
Chondrocyclus isipingoensis	Limpopo, Soutpansberg, Hanglip forest	2014-12-01	-22.999165	29.884389	ELMD18006
Chondrocyclus isipingoensis	Stutterheim, Kologha Forest, waterfall walk	2015-01-16	-32.533869	27.430833	Extracted
Chondrocyclus kevincolei	Platbos Forest near Gansbaai	2014-08-13	-34.567111	19.449516	ELMD18004
Chondrocyclus kevincolei	Gansbaai area, Grootbos Nat. Reserve	2005-02-13	-34.542050	19.415290	NMSAW5423
Chondrocyclus kevincolei	Gansbaai area, Grootbos Nat. Reserve	2007-10-07	-34.542050	19.415290	NMSAW5659
Chondrocyclus kevincolei	Bredasdorp, 7km south west on R43 to Elim	2014-08-11	-34.591246	19.999224	ELMD17983
Chondrocyclus kevincolei	Platbos Forest near Gansbaai	2012-04-18	-34.567111	19.449516	ELMW03659
Chondrocyclus agulhas	Grootbos Private N. R. betw Stanford & Gansbaai	2014-08-13	-34.541949	19.412233	ELMD18005
Chondrocyclus langebergensis	Marloth Nature Reserve, Swellendam, Duivelsbos	2005-02-23	-33.993430	20.458662	NMSAW5016
Chondrocyclus langebergensis	Pat Busch Nature Reserve	2012-03-03	-33.755348	19.994650	ELMD16920
Chondrocyclus langebergensis	Pat Busch N. R, Langeberge foothills	2014-08-07	-33.755130	19.994710	ELMD17981
Chondrocyclus langebergensis	Grootvadersbosch N. R, Melkhoutpad	2012-04-19	-33.981912	20.832153	ELMW03660
Chondrocyclus langebergensis	Grootvadersbosch Nature Reserve	2012-03-03	-33.981912	20.832153	ELMD16918
Chondrocyclus pondoensis	Umtamvuna Nature Reserve, Old Pont Road	2011-04-13	-31.060320	30.172487	ELMD16940
Chondrocyclus pondoensis	Simuma area, Hlokohloko Valley	2011-03-05	-30.663100	30.336850	NMSAW7844
Chondrocyclus pondoensis	Xora, Kumqolo Forest	2012-11-08	-32.158882	28.984821	Extracted
Chondrocyclus pulcherrimus	Ngome Forest, west of Nongoma	2010-01-19	-27.824405	31.419130	ELMD16939
Chondrocyclus silvicola	Knysna forest, Diepwalle section, Garden Route N.P.	2011-01-28	-33.967000	23.150000	ELMW03644
Chondrocyclus silvicola	Knysna forest, Diepwalle section, Garden Route N.P.	2015-03-11	-33.967000	23.150000	Extracted
Chondrocyclus silvicola	Tzitzikama, Storms River Bridge	2014-08-16	-33.967372	23.929261	ELMD17972

Genus and Species	Locality	Date	Latitude	Longitude	Accession Number
Chondrocyclus silvicola	Goukamma N.R., River Lodge	2015-03-12	-34.059119	22.938885	ELMW03869
Chondrocyclus silvicola	W. Cape, Wilderness N.P., west bank of Touw River	2015-03-12	-33.984350	22.607273	ELMW03871
Cyclotis sp.	Madagascar, Tsingy Beanlla	2011-09-01	-18.449861	44.720374	
Chondrocyclus sp. "nxaxo"	Nxaxo Forest, secondary dune forest	2014-07-03	-32.568333	28.541639	ELMD17756

Appendix 2 Glossary of terms used to describe morphology.

axial: longitudinal or parallel to main axis of shell

costa: a rib, referring to axial sculpture of the periostracum; these are flattened and hence described as lamellate costae

duplex (operculum): composed of two distinct parts

exserted (spire): conical or broadly tapering as opposed to flattened; "stretched or thrust out"

lamella: a flat plate or ridge

lenticular: lens-shaped; a disc, more or less convex on both sides

mammillate: nipple-shaped

malleate: pock-marked or dented as if beaten with a hammer (malleus = hammer, mallet)

operculum: hard disc on top of the hind part of the foot that closes the aperture when snail retracts inside its shell

periostracum: horny, outermost layer of the shell (organic)

peristome: rim around the aperture of shell

protoconch: shell formed by the developing larva or embryo and retained as the tip of the apex

rachidian (of radula): central tooth in each row

teleoconch: the remaining whorls of the shell after the protoconch

whorl: a single, complete 360° revolution in the spiral growth of a shell

Appendix 3 Material examined for redescriptions of *Chondrocyclus* species.

Chondrocyclus convexiusculus **(Pfeiffer, 1855)**

Type material: Syntypes of *Cyclostoma (Cyclophorus) convexiusculum* Pfeiffer, 1855 in NHMUK (20120231) (Fig. 4.1A).

Additional material examined (all ELM unless otherwise indicated): *W. Cape*: <u>Cape Peninsula</u>: Simonstown (-34.19119°S: 18.42109°E), M. Connolly (NMSA 2777); ditto, ex. M. Connolly coll. (NMSA A8004); Cape Town, 2.8 km south of Miller's Point (-34.25675°S: 18.472946°E), forest in a depression with a few invasive trees (*Eucalyptus* and Port Jackson), steep slope with rocks and root buttresses, thick and moist leaf litter, about a week of rain before collection, R. Daniels, 25/vi/2011 (D16879, W3636, NHMUK 20120276); ditto, R. Daniels, 01/ii/2012 (D16880, W3637, NHMUK 20120277, NMW.Z.2012.065.00007); DuToits Kloof, Donkerkloof (-33.753608°S: 19.069556°E), 462 m, patch of Southern Afrotemperate forest in steep ravine, M. Cole, 7/viii/2014 (D17970, W3891); Kogelberg Nature Reserve (-34.340888°S: 18.940717°E), 312 m, small patch of Southern Afrotemperate forest near Leopards Gorge waterfall, M. Cole, 12/viii/2014 (D17955, W03876); Kogelberg Nature Reserve, Oudebosch (-34.333662°S: 18.948733°E), 260 m, patch of Southern Afrotemperate forest in kloof with Oudebos River, M. Cole, 12/viii/2014 (D17975, W03877).

Chondrocyclus alabastris **(Craven, 1880)**

Type material: Syntypes of *Cyclotus alabastris* Craven, 1880 in NHMUK (1891.3.7.42-47) (Fig. 4.2A).

Additional material examined (all ELM unless otherwise indicated): *E. Cape*: Port Elizabeth, The Island Nature Reserve (-33. 98668°S: 25.37151°E), indigenous Southern Coastal forest in south facing valley, M. Cole, 18/ix/2008 (D15931); ditto, M. Cole, 27/v/2011 (D16885, W03640, NHMUK 20120270, NMW.Z.2012.065.00003); Port Elizabeth, Settlers Park (-33.9703°S: 25.6123°E), indigenous riverine forest, in leaf-litter, A. Moussalli & D. Stuart-Fox, 16/iii/2005 (NMSA W4602); Van Stadens River gorge (-33.91200°S: 25.20507°E) west of Port Elizabeth, tall forest on steep slope with stream running down to river, M. Cole, 22/ix/2008 (D15969); ditto, M. Cole, 27/ix/2011 (D16882, W03638); Loerie Restcamp, near PPC quarry (-33.79708°S: 24.96538°S), M. Cole, 22/ix/2008 (D15924); Maitland Nature Reserve, 2km from mouth on east side of river (-33.97740°S: 25.31207°E), forest on steep slope, M. Cole, D. Herbert, L. Davis, 26/ix/2011(D16881); Ningi, (formerly Yellowwoods Farm), on west side of Maitland River (-33.93036°S; 25.20825°E), riverine forest with large Yellowwoods 4.5 km upstream of mouth, M. Cole, D. Herbert, L. Davis 27/ix/2011 (D16883); Ferndale, Patensie, Ratelkloof (-33.71642°S: 24.85030°E), valley of Noaga River, M. Cole, D. Herbert, L. Davis 28/ix/2011 (D 16884, W03639); Gamtoos River mouth, dune forest east of mouth (-33.957441°S: 25.047668°E), 40 m, M. Cole, D. Herbert,

L. Davis 28/ix/2011 (D16886, W03641); Kap River, north bank(-33.483046°S: 27.080696°E), 30 m, indigenous riverine forest on shady, south-facing slope, M. Cole, 13/v/2011 (D16887); ditto, M. Cole, 30/xii/2002 (W03026); Olifantskop (-33.317315°S: 26.49911°E), Southern Mistbelt forest, M. Cole, D. Herbert, L. Davis , 9/ix/2011 (D16890, W03643); Van Stadens Pass, bottom of pass, west side of river (-33.909541°S: 25.190462°E), steep south facing slope, M & K. Cole, D. Herbert & L. Davis, 16/xi/2012 (D17016); Van Stadens Pass, near top of pass, steep north-facing slope (-33.913137°S: 25.204670°E), 163 m, M. Cole, 16/xi/2012 (D17222); Berg River crossing, east bank (-33.874608°S: 25.119551°E), 9 km E. of Loerie, 7.5 km N.W. of Van Stadens bridge, M & K. Cole, D. Herbert & L. Davis, 17/xi/2012 (D17026, W03668); Stinkhoutkloof, 11 km N.E of Loerie, 15 km N.W. of Van Stadens (-33.799255°S: 25.096678°E), M & K. Cole, D. Herbert , L. Davis & Edwards family, 17/xi/2012 (D17034); Addo National Park, Zuurberg section (-33.340335°S: 25.736193°E), 477 m, forest in valley of river, on 4 hour trail, M & K. Cole, 19/xi/2012 (D17045, W03676); Port Elizabeth, Lovemore Heights, south facing slope (-33.992786°S: 25.512132°E), 278 m, Southern Coastal forest, M & K. Cole, 18/xi/2012 (D17120, W03733); Grahamstown, Mountain drive, (-33.32813°S: 26.50064°E), south facing slope, in leaf-litter, M. Bursey & V. Ndibo, 10/iii/2007 (D15286); ditto, M. Cole, 20/xi/2009 (D16888, W03642, NHMUK 20120269); ditto (-33.32915°S: 26.49911°E), R. Daniels, 06/ii/2011 (D16889, W3690, NMW.Z.2012.065.00002); Grahamstown, Belmont Valley (-33.3152835°S: 26.586117°E), D. Herbert, 1978 (W581); Paradise Kloof, 8 km S.W. of Grahamstown (-33.344366°S: 26.446569°E), 710 m, runs down southwards into upper Howison's Poort (Palmiet River) from the Coldspring Ridge, collected at top of kloof, M. Cole, 28/ii/2013 (D17220, W03740); Coleridge, near Stones Hill, 8 km S.E. of Grahamstown (-33.333394°S: 26.615589°E), south facing slope, Southern Mistbelt Forest, M. & S. Cole, 2/iii/2013 (D17221, W03741).

Chondrocyclus isipingoensis **(Sturany, 1898)**

Type material: Holotype of *Cyclotus isipingoensis* Sturany, 1898 in Vienna Museum. Syntype of *Cyclophorus minimus* Melvill & Pfeiffer, 1898 in NHMUK (1902.10.1.7).

Additional material examined (all ELM unless otherwise indicated): SOUTH AFRICA: *N. Province*: Soutpansberg, Dundee Forest (-23.017°S: 29.515°E), sorted from leaf litter, C. Symons, 24/vii/1999 (NMSA V7513); Soutpansberg, Entabeni, Goede Hoep (-23.08330°S: 30.11170°E), +/-950 m, indigenous forest, in leaf-litter, D. Herbert, 20/xi/1997 (NMSA V5658); *Mpumalanga*: Buffelskloof Nat. Res. (-25.31690°S: 30.49900°E), 1300 m, indigenous forest, in leaf-litter, J. Horn, 15/iii/2006 (NMSA W4486); *KZN*: Ngoye Forest, lower section (-28.83300°S: 31.71700°E), +/-250 m, coastal scarp forest, in leaf litter, D. Herbert, 06/ix/1997 (NMSA V5861); Nkandla Forest Reserve, Mdonini area (-28.74531°S: 31.13567°E), +/-1050 m, mist-belt forest, under logs and in leaf-litter, Herbert, Bursey & Nangammbi, 21/x/2003 (NMSA W1103); Vernon Crookes Nat. Res. (-30.27500°S: 30.58300°E), small patch of scarp forest, in thin layer of leaf-litter on flat-topped boulder, D. Herbert, 01/i/2004 (NMSA W1441); Loteni,

Yellow-Wood Cave area (-29.41500°S: 29.48000°E), 1800 m, montane *Podocarpus* forest, in leaf-litter, D. Herbert, 25/x/1997 (V5752); Karkloof Falls, near top of gorge (-29.40882°S: 30.28404°E), Southern Mistbelt Forest, M. Cole, 22/i/2010 (D16902, W03650); Karkloof Nature Reserve (-29.31500°S:30.25000°E), 1350 m, M. Cole, 23/i/2010 (D16903); Kenneth Stainbank N.R, Yellowwood Park (-29.912175°S: 30.938969°E), M. Cole & K. Cole, 12/i/2010 (D16897); ditto, M. Cole, R. Daniels, L. Davis & D. Herbert, 12/iv/2011 (D16898, W03648, NHMUK 20120268, NMW.Z.2012.065.00001); Kranskop area, Ntumjambili (-28.93800°S: 30.95500°E), +/- 900 m, indigenous forest, in leaf-litter, D. Herbert, 09/viii/1997 (NMSA V5105); Kelso (-30.362215°S: 30.713157°E), 24 m, dune forest behind railway station, M. Cole, 31/x/2010 (D17635); Ingele Forest, 26 km east of Kokstad (-30.533079°S: 29.682669°E), 1234 m, large forest patch divided by N2, Red Trail on the west side of N2 approximately 0.5 km N.N.W. of hotel, M & K. Cole, 15/iv/2015 (D1791, W03855); Ingele Forest, Green Trail (-30.540611°S: 29.680174°E), 1208 m, small patch of forest approximately 0.5 km S.W. of hotel, M & K. Cole, 7/iv/2015 (D17900); *E. Cape*: Mtentu, north bank, inlet 1.5 km upstream to first waterfall from mouth (-31.238879°S: 30.034039°E) 30 m, east side of inlet, M. Cole, 13/i/2012 (D17086, W03604); Mtentu, north bank, inlet 3 km upstream of mouth (-31.229476°S: 30.018190°E), 43 m, west side of inlet, M. Cole, 12/i/2012 (D17006, W03605); Mkambati Nature Reserve, between Mkambati and Strandloper Falls (-31.27381°S: 30.02361°E), forest on east bank of Mkambati River, M. Cole, 15/ii/2011 (D16913, W03653); Mkambati, east bank Msikaba mouth (-31.31833°S: 29.96833°E), M. Cole, 16/ii/2011 (D16914); Mkambati, Gwe Gwe forest (-31.29040°S: 29.98970°E) forest above Gwe Gwe cottages, M. Cole, 05/iii/2001 (D17004); Mkambati Nature Reserve, Daza forest (-31.302504°S: 29.976667°E), M. Cole, 16/ii/2011 (W03688); Mbotyi, Ntsubane Forest, inland (-31.46154°S: 29.71286°E), accessed along KwaNyambalala River, M. Bursey, 03/iii/2003 (D17363); Mount Frere, just south of Buffalo Nek village (-30.854799°S: 28.892971°E), 1466 m, 10 km N.W. of Mount Frere, M. Cole, 7/iv/2015 (D17893, W03856); Langeni, Nocu forest (-31.42222°S: 28.49836°E), 840 m, large block of indigenous forest, in leaf-litter, M. Bursey, 18/ii/2006 (D14704); Langeni, Kambi Forest (-31.46801°S: 28.58933°E), M. Cole & V. Ndibo, 25/i/2013 (D17151); Xora, Kumqolo Forest (-32.158882°S: 28.984821°E), west bank of Xora river opposite Mangrove swamp, M. Cole, 13/viii/2011 (D17584); Qora, East Bank of Qora River (-32.43333°S: 28.66667°E), riverine forest, M. Cole, 07/xi/2009 (D16904, W03651); ditto, M Cole, 09/x/2011 (D17000); Phumalanga Farm, 7 km inland of Cintsa (-32.80667°S: 28.03056°E), riverine forest on Bulura River, Bursey, Wigley & Ndibo, 25/iv/2006 (D15030); ditto, M.Wigley, 12/xii/2008 (D15870); ditto, M. Cole & M. Wigley, 16/xi/2009 (D16899); ditto, M. Wigley, 01/xii/2009 (D16900, W03686); ditto, M. Cole, 31/xii/2010 (D16901, W03649); Moonstone Farm, Kei River valley, N.N.E. of Stutterheim (-32.25650°S: 27.56877°E), 1175 m, top of mountain, forest under sheer krantz, in leaf litter, M. Bursey, 7/iv/2005 (D14656*)*; ditto, M & K. Cole, 19/xii/2012(D17097); Umtiza Nature Reserve, Tree Dassie trail on east side of Buffalo Pass (-33.01688°S: 27.80923°E), M. Bursey, 21/iv/2006 (W03008); ditto, M. Cole, 08/vi/2010 (D16905); ditto, V. Ndibo, J. Glatz & R. Daniels, 13/i/2011 (D16906, W03652); ditto, M. Cole, 20/v/2011(D16907); ditto, M. Cole, 18/iii/2011 (D16908); ditto, M. Cole, 01/xii/2011 (D16909); Hogsback, downstream of Madonna and Child Waterfall (-32.606802°S: 26.962248°E), 1060 m, M.

Bursey, 25/i/2002 (W02835); Hogsback, Kettlespout, (-32.566667°S: 26.916667°E), forest above Hobbiton, Amathole Mountains, M. Cole, 31/xii/2008 (D17007); Amathole Mountains, Stutterheim, Kologha Forest, near picnic site (-32.53389°S: 27.43083°E), Southern Mistbelt forest, M. Cole, 22/xii/2009 (D16910); Stutterheim, Kologha Forest, forest drive near Protea Hill (-32.53389°S: 27.43083°E), M. Cole, 26/i/2010 (D16911); Stutterheim, Contour path (-32.536632°S: 27.366781°E) M. Cole, 16/i/2015 (D17873); Maden Dam, 18 km N.W. of King Williams Town (-32.73333°S: 27.28333°E), D-J. Hodgkinson, 26/iii/2011 (D16912); Fort Fordyce, kloof with watercourse and sheer krantz (-32.68930°S: 26.51212°E), 915 m, M. Cole, 29/xii/2008 (D16916); ditto, M. Cole, 06/x/2009 (D16961).

Chondrocyclus trifimbriatus **Connolly, 1929**

Type material: Holotype of *Chondrocyclus trifimbriatus* in NHMUK (1928.3.16.5) (Fig. 4.15A).

Additional material examined: *KZN*: Karkloof River valley, southwest of 'The Start' (-29.31500°S:30.25000°E), 1350 m, W. Falcon collection (NMSA A8000); Nkandla Forest Reserve, Chibini area (-28.7227°S: 31.1282°E) +/- 1200 m, scarp forest, under logs and in leaf litter, D. Herbert, M. Bursey & T. Nangammbi, 20/x/2003 (NMSA W1115); Entumeni Forest, 7 km west of Eshowe (-28.885219°S: 31.379702°E), 680 m, M. Cole, 29/x/2010 (ELM D16966, ELM W3692); ditto, 13/i/2010 (ELM D17003, ELM W03661).

Chondrocyclus bathrolophodes **Connolly, 1929**

Type material: Holotype of *Chondrocyclus bathrolophodes* Connolly, 1929 in NHMUK (1928.3.16.4) (Fig. 4.19A).

Additional material examined (All ELM unless otherwise indicated): *E. Cape*: Alexandria Forest, Langebos (-33.65333°S: 26.40833°E), vicinity of forest station, M. Cole, 02/ii/2009 (D15950); ditto, (33.695096°S: 26.354241°E) top of ridge with beacon tower, M. Bursey, 24/xi/2006 (D14938); ditto, M. Cole, 23/xi/2009 (D16960,W03658); ditto, (-33.699140°S: 26.363591°E) vicinity of hikers huts, M. Cole, 21/xi/ 2009 (D16924, W03617, NHMUK 20120274); Cannon Rocks (-33.73333°S: 26.55000°E), dune thicket, in leaf litter, M. Cole, 02/ii/2009 (D16002); Port Alfred, coastal forest east of Kowie River mouth (-33.59194°S: 26.90472°E), dune forest behind tall dunes, in leaf litter, M. Bursey & T. Moffat, 26/xi/2006, (D14998); ditto, M. Cole, 12/x/2009 (D16922, W03616, NHMUK 20120273, NMW.Z.2012.065.00005); ditto, R. Daniels, 06/iv/2011 (D16923); Tharfield, east bank of Riet River (-33.55889°S: 27.01500°E), dune forest, M. Cole, 30/i/2008 (D15882); The Glen on Pig Island Farm, (-33.48333°S: 26.93333°E), on Kleinemonde River, M. Bursey, 12/i/2007 (W03192, D15394); ditto, M. Cole, 01/ii/2009 (D16150, W03635); Kap River Nature Reserve, south bank (-33.482095°S: 27.075753°E), 35 m, thin strip of forest at base of dry north-facing cliffs, M. Bursey, 21/xii/2002 (D16925); Kap River Nat. Res., north bank (-

33.481175°S: 27.087327°E), 42 m, leaf litter in ravine, M. Bursey, 30/xii/2002 (D16926); ditto, M. Cole, 13/v/2011 (D16927, W03618); Gess farm (-33.480291°S: 27.063368°S), 31 m, indigenous forest in north-facing ravine leading into Kap river, M. Cole, 28/v/2011 (D16928, W03619); Kap River, south bank (-33.482095°S: 27.075753°E), 35 m, thin strip of forest at base of dry north-facing cliffs, Kap River, north bank (-33.483046°S: 27.080696°E), indigenous riverine forest on shady, south-facing slope, M Cole, 09/vi/2012 (D17002); Kobonqaba, coastal forest on east side of mouth (-32.605755°S: 28.493315°E), 17m, M. Cole, 23/iv/2015 (D17932; W03868); Port Elizabeth, Baakens River (-33.967°S: 25.333°E), ex Durban Museum, ix/1998 (V6683).

Chondrocyclus putealis Connolly, 1939

Type material: Syntypes of *Chondrocyclus putealis* Connolly, 1939 in NHMUK (1937.12.30.5087-5090). (Fig. 4.21A).

Additional material examined (all ELM unless otherwise indicated): *KZN*: Port Shepstone area, Marble Delta (-30.650933°S: 30.356017°E), Connolly, 10/v/ 2001 (NMSA V9390); *E. Cape*: Mkambati Nature Reserve, Mtentu River gorge, south bank, 4.25 km usptream of mouth (-31.231555°S: 30.010024°E), 31 m, M. Cole, 12/i/2012 (D16954, W03656, NHMUK 20120272, NMW.Z.2012.065.00004, RMNH.MOL 330498); Mtentu, north bank (-31.230998°S: 30.017351°E), 3.25 km upstream of mouth, scarp forest on steep slope with large rocks, M. Cole, 12/i/2012 (D16955, W03657).

Chondrocyclus exsertus Melville & Ponsonbyi, 1903

Type material: Holotype of *Chondrocyclus exsertus* Melville & Ponsonbyi, 1903 in NHMUK (1904.4.29.28). (Fig. 4.24A).

Additional material examined (all ELM unless otherwise indicated): *KZN*: Kelso junction (NMSA A8011); ditto, Ex Transvaal Museum (NMSA W465); Umzumbe, Trust Farm (-30.61000°S: 30.50694°E), 4.3 km inland of Umzumbe as crow flies, small patch of indigenous forest among sugar cane, M. Cole, D. Herbert, L. Davis, D. Kinsler 09/i/2012 (D16953, W03655, NHMUK 20120275); Farm Frome, Sunwich Port (-30.649750°S: 30.478640°E), 100 m, 3.8 km inland from coast, M. Cole, D. Herbert, L. Davis, R. Daniels, 14/iv/2011 (D16951); ditto, M. Cole, K. Cole, D. Kinsler, 08/i/2012 (D16952, W3654); ditto, D. Kinsler, 21/i/2012 (D17010, NMW.Z.2012.065.00006); ditto, D. Kinsler, 4/ii/2015 (D17935); Umzumbe, Clouds Hill (30.627491°S: 30.530842°E), 21 m, D. Kinsler, 13/ii/2012 (D17011); ditto, D. Kinsler, 4/ii/2015 (D17936).

References

Agapow, P. M., Bininda-Emonds, O. R. P., Crandall, K. A., Gittleman, J. L., Mace, G. M., Marshall, J. C., & Purvis, A. (2004). The impact of species concept on biodiversity studies. *The Quarterly Review of Biology, 79*(2), 161–179.

Ancey, C. F. (1898). Observsations sur les Mollusques terrestres et fluviatiles recueillies dans l'Indo-Chine et particulièrement au Laos, par M. Henri Counillon, accompagnées de remarques sur d'autres mollusques de cette region, par C.-F. Ancey. *Annales du Musée d'histoire naturelle de Marseille, 1*, 134–136.

Bauer, A., & Bauer, B. (1988). Individual movement patterns of the minute land snail *Punctum pygmaeum* (Draparnaud) (Pulmonata: Endodontidae). *The Veliger, 30*, 372–376.

Beheregaray, L. B., & Caccone, A. (2007). Cryptic biodiversity in a changing world. *Journal of Biology, 6*(4), 9.

Benson, W. H. (1856). New land shells collected by E. L. Layard Esq. and described by W. H. Benson, Esq. *Annals and Magazine of Natural History, XVIII*(CVIII), 233–439.

Bickford, D., Lohman, D. J., Sodhi, N. S., Ng, P. K. L., Meier, R., Winker, K., Ingram, K. K., & Das, I. (2006). Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution, 22*(3), 148–155.

Blanford, W. T. 1868. Monographie du genre *Cyathopoma. Journal de Conchyliogie, Paris., 16*, 256-263.

Bruggen, A. C. Van. (1965). Descriptions of three new species of Gulella (Mollusca, Gastropoda Pulmonata: Streptaxidae) from South Africa. *Annals of the Natal Museum, 18*(1), 21–26.

Bruggen, A. C. Van. (1966). The terrestrial Mollusca of the Kruger National Park: a contribution to the malacology of the Eastern Transvaal. *Annals of the Natal Museum, 18*(2), 315–399.

Bruggen, A. C. Van. (1978). Land molluscs. In M. J. A. Werger (Ed.), *Biogeography and ecology of southern Africa* (Biogeography, pp. 877–923). The Hague: Dr. W Junk.

Bruggen, A. C. Van. (1983). On some terrestrial operculates (Mollusca, Gastropoda Prosobranchia) from Malawi with the description of two new species. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, 86*(1), 1–14.

Bruggen, A. C. Van. (1985). *Neomazania coryli*, a new genus and species of Maizaniidae (Mollusca, Gastropoda Prosobranchia) from Malawi, south central Africa. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, 88*(4), 395–403.

Bruggen, A. C. Van. (1986). Further notes on Afrotropical prosobranch land molluscs (Gastropoda Prosobranchia: Maizaniidae, Cyclophoridae). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, 89*(4), 357–378.

Bruggen, A. C. Van. (2006). *Gulella johannae* spec. nov. (Gastropoda, Pulmonata, Streptaxidae), a new land snail from the Drakensberg range in Limpopo Province, South Africa, with notes on *G. johannesburgensis* (M. & P.). *Zoologische Mededelingen, 80*, 63–72.

Bruggen, A. C. Van. (2008). New studies on the land molluscs of Malawi, a second interim progress report. Prolegomena for a new checklist. *BASTERIA, 72*(4-6), 353–368.

Bursey, M. L., & Herbert, D. G. (2004). Four new narrow-range endemic species of Gulella from Eastern Cape, South Africa (Mollusca: Pulmonata: Streptaxidae). *African Invertebrates, 45*, 249–262.

This paper resulted from fieldwork in Transkei by the author (nee Bursey) and Herbert, assisted by members of the Border Shell Club. Many undescribed species and new records were added to the collections of the East London Museum and KwaZulu-Natal Museum. These four species were confirmed to be new by Herbert. I wrote the paper with input from Herbert. Herbert took the photographs and produced the maps.

Chase, B. M., & Meadows, M. E. (2007). Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews, 84*, 103–138.

Clark, V. R., Barker, N. P., McMaster, C., & Mucina, L. (2010). The Boschberg (Somerset East, Eastern Cape) - A floristic cross-roads of the southern Great Escarpment. *South African Journal of Botany, 77*(1), 94–104.

Clark, V. R., Barker, N. P., & Mucina, L. (2011). The Great Escarpment of southern Africa: A new frontier for biodiversity exploration. *Biodiversity and Conservation, 20*(12), 2543–2561.

Cocks, M. L., Dold, A. P., & Grundy, I. M. (2004). The trade in medicinal plants from forests in the Eastern Cape Province. In M. J. Lawes, H. A. C. Eeley, C. M. Shackleton, & B. G. S. Geach (Eds.), *Indigenous forests and woodlands in South Africa. Policy, people and practice.* (pp. 473–492). Pietermaritzburg: University of KwaZulu-Natal Press.

Cole, M. L., & Herbert, D. G. (2009). Description of four new species of *Gulella* Pfeiffer, 1856 from Eastern Cape, South Africa, with additional notes on two poorly known species (Mollusca: Eupulmonata: Streptaxidae). *Zoologische Mededelingen, 83*, 547–564.

This paper resulted from fieldwork in Transkei undertaken by the author and Herbert. These four species were confirmed to be new by Herbert. I wrote the paper, with input from Herbert. We both took the photographs and Herbert produced the maps.

Colgan, D. J., Ponder, W. F., Beacham, E., & Macaranas, J. (2007). Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). *Molecular Phylogenetics and Evolution, 42*(3), 717–737.

Connolly, M. (1929). New non-marine mollusca from South Africa. *Annals of the Natal Museum*, 6, 238.

Connolly, M. (1939). A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum, 33*, 1–660.

Cooper, K. H., & Swart, W. (1992). *Transkei forest survey*. Durban: Wildlife Society of southern Africa.

Cowling, R. M., Campbell, B. M., Mustart, P., McDonald, D. J., Jarman, M. L., Moll, & J, E. (1988). Vegetation classification in a floristically complex area: the Agulhas Plain. *South African Journal of Botany, 54*, 290–300.

Cowling, R. M., MacDonald, I. A. W., & Simmons, M. T. (1996). The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation, 5*(5), 527–550.

Cowling, R. M., Proches, S., & Vlok, J. H. J. (2005). On the origin of southern African subtropical thicket vegetation. *South African Journal of Botany, 71*(1), 1–23.

Cowling, R., & Pierce, S. (2009). *East of the Cape: Conserving Eden*. (L. Martin, Ed.). Fernwood Press.

Cowling, R. M., Proches, Ş., & Partridge, T. C. (2009). Explaining the uniqueness of the Cape flora: Incorporating geomorphic evolution as a factor for explaining its diversification. *Molecular Phylogenetics and Evolution, 51*(1), 64–74.

Cowling, R. M., & Potts, A. J. (2015). Climatic, edaphic and fire regime determinants of biome boundaries in the eastern Cape Floristic Region. *South African Journal of Botany, 101*, 73–81.

Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary process in Conservation Biology. *Trends in Ecology & Evolution, 15*(7), 290–295.

Craven, A. E. (1880). *Cyclotus alabastris. Proceedings of the Zoological Society*, p. 619.

Cressey, E. R., Measey, G. J., & Tolley, K. A. (2014). Fading out of view: the enigmatic decline of Rose's mountain toad *Capensibufo rosei. Oryx*, 1–8.

Daniels, S. R., Stewart, B. A., & Burmeister, I. (2001). Geographic patterns of genetic and morphological divergence amongst populations of a river crab (Decapoda, Potamonautidae) with the description of a new species from mountain streams in the Western Cape. *Zoologica Scripta, 30*, 181–197.

Daniels, S. R., Picker, M. D., Cowlin, R. M., & Hamer, M. L. (2009). Unravelling evolutionary lineages among South African velvet worms (Onychophora: *Peripatopsis*) provides evidence for widespread cryptic speciation. *Biological Journal of the Linnean Society, 97* (1), 200–216.

Daniels, S. R., & Ruhberg, H. (2010). Molecular and morphological variation in a South African velvet worm (*Peripatopsis moseleyi*) (Onychophora, Peripatopsidae): evidence of cryptic speciation. *Journal of Zoology, 282,* 171–179.

Daniels, S. R., McDonald, D. E., & Picker, M. D. (2013). Evolutionary insight into the *Peripatopsis balfouri sensu lato* species complex (Onychophora: Peripatopsidae) reveals novel lineages and zoogeographic patterning. *Zoologica Scripta, 42*(6), 656–674.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest2: more models, new heuristics and parallel computing. *Nature Methods, 9*(8), 772.

de Bivort, B. L., & Giribet, G. (2010). A systematic revision of the South African Pettalidae (Arachnida: Opiliones: Cyphophthalmi) based on a combined analysis of discrete and continuous morphological characters with the description of seven new species. *Invertebrate Systematics, 24,* 371–406.

Dépraz, A., Hausser, J., & Pfenninger, M. (2009). A species delimitation approach in the Trochulus sericeus/hispidus complex reveals two cryptic species within a sharp contact zone. *BMC Evolutionary Biology, 9,* 171-180.

de Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology, 56*(6), 879–886.

de Villiers, D. J., & White, R. M. (2002). Are current conservaton practices conserving indigenous forest fauna? In A. H. W. Seydack, T. Vorster, W. J. Vermeulen, & I. J. Van der Merwe (Eds.), *Natural forests and savannah woodlands symposium III. Multiple use management of natural forests and woodlands: policy refinements and scientific progress.* (pp. 110–121). Pretoria: Department of Water Affairs and Forestry.

de Winter, A. J. (2002). Notes on land operculates from Cameroon (Gastropoda: Cyclophoridae and Maizaniidae), including the description of two new species. In M. Falkner, K. Groh, & M. C. D. Speight (Eds.), *Collecteana Malacologia Festschrift für Gerhard Faulkner* (pp. 237–251). Hackenheim: ConchBooks.

Deacon, H. J. (1983). Another look at the Pleistocene climates of South Africa. *South African Journal of Science, 79*(8), 325–328.

Dépraz, A., Hausser, J., & Pfenninger, M. (2009). A species delimitation approach in the *Trochulus sericeus/hispidus* complex reveals two cryptic species within a sharp contact zone. *BMC Evolutionary Biology, 9,* 171.

Eeley, H. A. C., Lawes, M. J., & Piper, S. E. (1999). The influence of climate change on the distribution of indigenous forest in Kwazulu-Natal, South Africa. *Journal of Biogeography*, *26*, 595–617.

Emberton, K. C. (2002a). *Ankoravaratra*, a new genus of land snails endemic to northern Madagascar (Cyclophoroidea: Maizaniidae?). *The Veliger*, *45*(4), 278–289.

Emberton, K. C. (2002b). The genus *Boucardicus*, a Madagascan endemic. *Archiv Für Molluskenkunde*, *130*(1/2), 1–199.

Emberton, K. C. (2003). Madagascan *Cyathopoma sensu lato*. *Archiv Für Molluskenkunde*, *132*, 9–91.

Emberton, K. C. (2004). Madagascan *Georissa*, *Cyclotus*, *Omphalotropis* and so-called *Chondrocyclus* (Gastropoda: Caenogastropoda: Hydrocenidae, Cyclophoridae, Assimineidae). *Archiv Für Molluskenkunde*, *133*(1-2), 69–107.

Emberton, K. C. (2009). Operculate land snails from three rainforest transects in northeastern Madagascar, with description of nine new species and one new subspecies. *Archiv Für Molluskenkunde*, *138*, 1–41.

Emberton, K. C., & Pearce, T. A. (1999). Land caenogastropods of Mounts Mahermana, Ilapiry, and Vasiha, southeastern Madagascar, with conservation statuses of 17 species of *Boucardicus*. *The Veliger*, *42*(4), 338–372.

Emberton, K. C., Slapcinsky, J., Campbell, C. A., Rakotondrazafy, J. A., Andriamiarison, T. N., & Emberton, J. D. (2010). Terrestrial mollusks of Andriantantely Massif, Eastern Madagascar, with descriptions of 36 new species (Gastropoda: Caenogastropoda; Pulmonata). *Archiv Für Molluskenkunde*, *139*(1), 71–141.

Evangelisti, F., Bonfitto, A., Morassi, M., & Sabelli, B. (2016). How many native *Cerithium* species in the Mediterranean Sea? An integrative taxonomic approach. *Journal of Molluscan Studies*, *82*(2), 292–304.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics*, *34*(2003), 487–515.

Ferguson, J. W. H. (2002). On the use of genetic divergence for identifying species. *Biological Journal of the Linnean Society*, *75*, 509–516.

Fischer-Piette, E., Blanc, C. P., Blanc, F., & Salvat, F. (1993). Gasteropodes terrestres prosobranches. *Faune de Madagascar*, *80*, 1–281.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*, 294–297.

Fontaine, B., Gargominy, O., & Neubert, E. (2007a). Land snail diversity of the savanna/forest mosaic in Lope National Park, Gabon. *Malacologia, 49*(2), 313–338.

Fontaine, B., Gargominy, O., & Neubert, E. (2007b). Priority sites for conservation of land snails in Gabon: Testing the umbrella species concept. *Diversity and Distributions, 13*(6), 725–734.

Galley, C., Bytebier, B., Bellstedt, D. U., & Linder, H. P. (2007). The Cape element in the Afrotemperate flora: from Cape to Cairo? *Proceedings of the Royal Society B: Biological Sciences, 274*(1609), 535–543.

Geldenhuys, C. J. (1992a). Disjunctions and Distribution limits of forest species in the southern Cape. *South African Forestry Journal, 161*, 1–13.

Geldenhuys, C. (1992b). Richness, composition and relationships of the floras of selected forests in southern Africa. *Bothalia, 22*(2), 205–233.

Geldenhuys, C. J. (1997). Composition and biogeography of forest patches on the inland mountains of the southern Cape. *Bothalia, 27*(1), 57–74.

Gittenberger, E., Groenenberg, D. S. J., Kokshoorn, B., & Preece, R. C. (2006). Biogeography: molecular trails from hitch-hiking snails. *Nature, 439*(7075), 409.

Golding, R. E. (2014a). Molecular phylogeny and systematics of Australian and East Timorese Stenothyridae (Caenogastropoda: Truncatelloidea). *Molluscan Research, 34*(2), 102–126.

Golding, R. E. (2014b). Molecular phylogeny and systematics of Australian "Iravadiidae" (Caenogastropoda: Truncatelloidea). *Molluscan Research, 34*(4), 222–257.

Golding, R. E., Bieler, R., Rawlings, T. A., & Collins, T. M. (2014). Deconstructing *Dendropoma*: A Systematic Revision of a World-Wide Worm-Snail Group, with Descriptions of New Genera (Caenogastropoda: Vermetidae). *Malacologia, 57*(1), 1–97.

Gouws, G., Matthee, C. A., & Stewart, B. A. (2010). A multiple data set phylogeny for the endemic South African freshwater phreatoicidean isopod genus *Mesamphisopus*: Taxonomic and biogeographic implications. *Molecular Phylogenetics and Evolution, 55*(2), 541–551.

Griswold, C. E. (1985). A revision of the African spiders of the family Microstigmatidae (Araneae: Mygalomorphae). *Annals of the Natal Museum, 27*, 1–37.

Griswold, C. E. (1990). A revision and phylogenetic analysis of the spider subfamily Phyxelidinae (Araneae, Amaurobiidae). *Bulletin of the American Museum of Natural History, 196*, 1–206.

Guindon, S., & Gascuel, O. (2003). A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology, 52*, 696–704.

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series, 41*, 95–98.

Hamer, M. L., & Slotow, R. (2000). Patterns of distribution and speciation in the genus *Doratogonus* (Diplopoda: Spirostreptidae). *Fragmenta Faunistica, 43*, 295–311.

Hamer, M. L., & Slotow, R. H. (2002). Conservation application of existing data for South African millipedes (Diplopoda). *African Entomology, 10*(1), 29–42.

Harris, D. J., & Rato, C. (2013). Why are Red List species not on the EDGE? A response to Winter et al. *Trends in Ecology and Evolution, 28*(6), 321–322.

Hayes, K. A., Cowie, R. H., & Thiengo, S. C. (2009). A global phylogeny of apple snails: Gondwanan origin, generic relationships, and the influence of outgroup choice (Caenogastropoda: Ampullariidae). *Biological Journal of the Linnean Society, 98*(1), 61–76.

Hebert, P. D. N., Ratnasingham, S., & DeWaard, J. R. (2003). Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B: Biological Sciences, 270*, S96–S99.

Herbert, D. G. (1997). The terrestrial slugs of Kwazulu-Natal: diversity, biogeography and conservation (Mollusca: Pulmonata). *Annals of the Natal Museum, 38*, 197–239.

Herbert, D. G. (2006). Rediscovery of the type species of *Euonyma* (Subulinidae) and observations on South African species of *Gulella* (Streptaxidae), with description of two new species (Gastropoda: Eupulmonata). *Journal of Natural History, 40*(17-18), 1063–1081.

Herbert, D. G. (2007). Revision of the genus *Prestonella* (Mollusca: Gastropoda: Orthalicoidea: Bulimulidae s. l.), a distinctive component of the African land snail fauna. *African Invertebrates, 48*, 1–19.

Herbert, D., & Kilburn, D. (2004). *Field guide to the land snails and slugs of eastern South Africa.* Pietermaritzburg: Natal Museum.

Herbert, D. G., & Mitchell, A. (2009). Phylogenetic relationships of the enigmatic land snail genus *Prestonella*: The missing African element in the Gondwanan superfamily Orthalicoidea (Mollusca: Stylommatophora). *Biological Journal of the Linnean Society, 96*(1), 203–221.

Herbert, D. G., & Moussalli, A. (2010). Revision of the larger cannibal snails *Natalina* s. l. of southern Africa - *Natalina* s.s., *Afrorhytida* and *Capitina* (Mollusca: Gastropoda: Rhytididae). *African Invertebrates, 51*(1), 1–132.

Holland, B. S., & Cowie, R. H. (2007). A geographic mosaic of passive dispersal: population structure in the endemic Hawaiian amber snail *Succinea caduca* (Mighels, 1845). *Molecular Ecology, 16*(12), 2422–2435.

Houniet, D. T., Thuiller, W., & Tolley, K. A. (2009). Potential effects of predicted climate change on the endemic South African dwarf chameleons, *Bradypodion*. *African Journal of Herpetology, 58*(1), 28–35.

Huber, B. A. (2003). Southern African pholcid spiders: revision and cladistic analysis of Quamtana gen. and Spermophora Hentz (Araneae : Pholcidae), male-female covariation. *Zoological Journal Of The Linnean Society, 139*(4), 477–527.

Hugall, A., Moritz, C., Moussalli, A., & Stanisic, J. (2002). Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). *Proceedings of the National Academy of Sciences of the United States of America, 99*(9), 6112–6117.

Hughes, M., Moller, D., Bellstedt, D. U., Edwards, T. J., & Velliers, M. De. (2005). Refugia, dispersal and divergence in a forest archipelago: a study of *Streptocarpus* in eastern South Africa. *Molecular Ecology, 14*, 4415–4426.

International Commission on Zoological Nomenclature (2000). *International Code of Zoological Nomenclature. 4th edition.* Online.

IUCN. (2012). *IUCN Red List Categories and Criteria: Version 3.1. Second edition.* Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.

IUCN Standards and Petitions Subcommittee (2016). *Guidelines for Using the IUCN Red List Categories and Criteria. Version 12.* Prepared by the Standards and Petitions Subcommittee. Downloadable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Johnson, M. S., Hamilton, Z. R., Teale, R., & Kendrick, P. G. (2012). Endemic evolutionary radiation of *Rhagada* land snails (Pulmonata: Camaenidae) in a continental archipelago in northern Western Australia. *Biological Journal of the Linnean Society, 106*(2), 316–327.

Jonges, K. (1980). Genital ducts in several species of the cyclophorid genus *Leptopoma* (Mollusca, Mesogastropoda). *Bijdragen Tot de Dierkunde, 50 (2)*, 292–302.

Jørgensen, A., Kristensen, T. K., & Madsen, H. (2008). A molecular phylogeny of apple snails (Gastropoda, Caenogastropoda, Ampullariidae) with an emphasis on African species. *Zoologica Scripta, 37*(3), 245–252.

Kahindo, C., Bowie, R. C. K., & Bates, J. M. (2007). The relevance of data on genetic diversity for the conservation of Afro-montane regions. *Biological Conservation, 134*(2), 262–270.

Kappes, H. Jordaens, K., Hendrickx, F., Maelfait, J.-P., Lens, L. & Backeljau, T. (2009a). Response of snails and slugs to fragmentation of lowland forests in NW Germany. *Landscape Ecology, 24*, 685-697.

Kappes, H., Jordaens, K., Van Houtte, N., Hendrickx, F., Maelfait, J. P., Lens, L., & Backeljau, T. (2009b). A land snail's view of a fragmented landscape. *Biological Journal of the Linnean Society, 98*(4), 839–850.

Kasinathan, R. (1975). Some studies of five species of Cyclophorid snails from peninsular India. *Proceedings of the Malacological Society of London, 41*(5), 379–394.

Katoh, K., Misawa, K., Kuma, K., & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research, 30*, 3059–3066.

Katoh, K., & Toh, H. (2008). Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. *BMC Bioinformatics, 9*, 212.

Kirchner, C., Kratzner, R., & Welter-Schultes, F. W. (1997). Flying snail - how far can *Truncatellina* (Pulmonata: Vertiginidae) be blown over sea. *Journal of Molluscan Studies, 63*, 479–487.

Kobelt, W. (1902). Cyclophoridae. *Das Tierreich, 16*(I-XXXIX), 1–662.

Kohler, F. (2016). Rampant taxonomic incongruence in a mitochondrial phylogeny of *Semisulcospira* freshwater snails from Japan (Cerithioidea: Semisulcospiridae). *Journal of Molluscan Studies, 82*, 268–281.

Kohler, F., Panha, S., & Glaubrecht, M. (2010). Speciation and Radiation in a River: Assessing the Morphological and Genetic Differentiation in a Species Flock of Viviparous Gastropods (Cerithioidea: Pachychilidae). In M. Glaubrecht (Ed.), *Evolution in Action* (pp. 513–550). Berlin: Springer-Verlag.

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution, 29*(6), 1695–1701.

Lawes, M. J. (1990). The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Ceropithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. *Journal of Biogeography, 17*, 669–680.

Lawes, M. J., Eeley, H. A. C., Findlay, N. J., & Forbes, D. (2007). Resilient forest faunal communities in South Africa: a legacy of palaeoclimatic change and extinction filtering? *Journal of Biogeography, 34*(7), 1246–1264.

Lee, Y.-C., Lue, K.-Y., & Wu, W.-L. (2008a). A molecular phylogenetic investigation of *Cyathopoma* (Prosobranchia: Cyclophoridae) in East Asia. *Zoological Studies, 47*(5), 591–604.

Lee, Y.-C., Lue, K.-Y., & Wu, W.-L. (2008b). Molecular evidence for a polyphyletic genus *Japonia* (Architaenioglossa: Cyclophoridae) and with the description of a new genus and two new species. *Zootaxa, 1792*, 22–38.

Liew, T.-S., Vermeulen, J. J., Marzuki, M. E., & Schilthuizen, M. (2014). A cybertaxonomic revision of the micro-landsnail genus *Plectostoma* Adam (Mollusca, Caenogastropoda, Diplommatinidae), from Peninsular Malaysia, Sumatra and Indochina. *ZooKeys, 393*, 1–107.

Linder, H. P. (2003). The radiation of the Cape flora, southern Africa. *Biological Reviews, 78*(4), 597–638.

Linder, H. P. (2005). Evolution of diversity: The Cape flora. *Trends in Plant Science, 10*(11), 536–541.

Linder, H. P. (2008). Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 363*(1506), 3097–3105.

Marshall, B. A., & Barker, G. M. (2007). A revision of New Zealand landsnails of the genus *Cytora* Kobelt & Mollendorff, 1897 (Mollusca: Gastropoda: Pupinidae). *Tuhinga, 18*, 49–113.

Martin, A. R. H. (1968). Pollen analysis of Groenvlei Lake sediments, Knysna (South Africa). *Review of Palaeobotany and Palynology, 7*(1968), 107–144.

McDonald, D. E., & Daniels, S. R. (2012). Phylogeography of the Cape velvet worm (Onychophora: *Peripatopsis capensis*) reveals the impact of Pliocene Pleistocene climatic oscillations on Afromontane forest in the Western Cape, South Africa. *Journal of Evolutionary Biology, 25*, 824–835.

McDonald, D. E., Ruhberg, H., & Daniels, S. (2012). Two new *Peripatopsis* species (Onychophora: Peripatopsidae) from Western Cape province, South Africa. *Zootaxa, 3380*, 55–68.

Melvill, J. C., & Ponsonby, J. H. (1898). Descriptions of nine new species of terrestrial and fluviatile Mollusca from South Africa. *Annals and Magazine of Natural History, II*(XVIII), 125–130.

Melvill, J. C., & Ponsonby, J. H. (1899). Further contribution towards a check-list of the non-marine molluscan fauna of South Africa, with descriptions of fourteen new species. *Annals and Magazine of Natural History, IV*(XXI), 192–200.

Melvill, J. C., & Ponsonby, J. H. (1903). Descriptions of Thirty-one Terrestrial and Fluvatile Mollusca from South Africa. *Annals and Magazine of Natural History,* XII , 608.

Morgenthal, T. L., & Cilliers, S. S. (2000). Species composition and phytogeographical significance of an afromontane forest fragment in the Mpumalanga province, South Africa. *Southern African Forestry Journal, 189*, 81–102.

Morton, J. E. (1952). A Preliminary Study of the Land Operculate *Murdochia pallidum* (Cyclophoridae, Mesogastropoda). *Transactions of the Royal Society of New Zealand, 80*, 69–79.

Mosblech, N. A. S., Bush, M. B., & Van Woesik, R. (2011). On metapopulations and microrefugia: Palaeoecological insights. *Journal of Biogeography, 38*(3), 419–429.

Moussalli, A., Herbert, D. G., & Stuart-Fox, D. (2009). A phylogeny of the cannibal snails of the southern African genus *Natalina* sensu lato (Pulmonata: Rhytididae): Assessing concordance between morphology and molecular data. *Molecular Phylogenetics and Evolution, 52,* 167–182.

Mucina, L., & Geldenhuys, C. J. (2006). Afrotemperate, subtropical and azonal forests. In L. Mucina & M. C. Rutherford (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland.* (Strelitzia 19, pp. 585–614). Pretoria: SANBI.

Mucina, L., & Rutherford, M. C. (Eds.). (2006). *The vegetation of South Africa, Lesotho and Swaziland.* (Strelitzia 19). Pretoria: South African National Biodiversity Institute.

Mucina, L., Scott-Shaw, C. R., Rutherford, M. C., Camp, K. G. T., Matthews, W., Powrie, L. W., & Hoare, D. B. (2006). Indian Ocean Coastal Belt. In L. Mucina & M. C. Rutherford (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland.* (Strelitzia, pp. 569–583). Pretoria: SANBI.

Mucina, L., Pienaar, E., Van Niekerk, A., & Lötter, M. C. (2007). *Habitat-level classification of the Albany Coastal, Pondoland Scarp and Eastern Scarp forests.* Matieland: University of Stellenbosch.

Myburgh, A. M., & Daniels, S. R. (2015). Exploring the impact of habitat size on phylogeographic patterning in the Overberg velvet worm *Peripatopsis overbergiensis* (Onychophora: Peripatopsidae). *Journal of Heredity, 106,* 296–305.

Nantarat, N., Sutcharit, C., Tongkerd, P., Ablett, J., Naggs, F., & Panha, S. (2014a). An annotated catalogue of type specimens of the land snail genus *Cyclophorus* Monfort, 1810 (Caenogastropoda, Cyclophoridae) in the Natural History Museum, London. *ZooKeys, 411,* 1–56.

Nantarat, N., Wade, C. M., Jeratthitikul, E., Sutcharit, C., & Panha, S. (2014b). Molecular Evidence for cryptic speciation in the *Cyclophorus fulguratus* (Pfeiffer, 1854) species complex (Caenogastropoda: Cyclophoridae) with description of new species. *PLoS ONE, 9*(10), 1–15.

Nekola, J. C., Coles, B. F., & Horsak, M. (2015). Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. *Journal of Molluscan Studies, 81,* 196–216.

Neumann, F. H., & Bamford, M. K. (2015). Shaping of modern southern African biomes: Neogene vegetation and climate changes. *Transactions of the Royal Society of South Africa, 2015,* 1–18.

Ozgo, M., Orstan, A., Kirchenstein, M., & Cameron, R. A. D. (2015). Disperal of land snails by sea storms. *Journal of Molluscan Studies, 82*(2), 341–343.

Páll-Gergely, B., Fehér, Z., Hunyadi, A., & Asami, T. (2015). Revision of the genus *Pseudopomatias* and its relatives (Gastropoda: Cyclophoroidea: Pupinidae). *Zootaxa, 3937*(1), 1–49.

Palumbi, S. A., Martin, A., Ramano, S., McMillan, W., Stice, I., & Grabowski, G. (1991). *The simple fools guide to PCR*. Honolulu: Department of Zoology, University of Hawaii.

Partridge, T. C., Scott, L., & Hamilton, J. E. (1999). Synthetic reconstructions of southern African environments during the Last Glacial Maximum (21-18 kyr) and the Holocene Altithermal (8-6 kyr). *Quaternary International, 57-58*, 207–214.

Pfeiffer, C. (1855). *Cyclostoma (Cyclophorus) Convexiusculum. Proceedings of the Zoological Society*, p. 104.

Pfenninger, M., Eppenstein, A., & Magnin, F. (2003). Evidence for ecological speciation in the sister species *Candidula unifasciata* (Poiret, 1801) and *C. rugosiuscula* (Michaud, 1831) (Helicellinae, Gastropoda). *Biological Journal of the Linnean Society, 79*(4), 611–628.

Pfenninger, M., Hrabáková, M., Steinke, D., & Dèpraz, A. (2005). Why do snails have hairs? A Bayesian inference of character evolution. *BMC Evolutionary Biology, 5*(59), 1–11.

Pfenninger, M., Cordellier, M., & Streit, B. (2006). Comparing the efficacy of morphologic and DNA-based taxonomy in the freshwater gastropod genus *Radix* (Basommatophora, Pulmonata). *BMC Evolutionary Biology, 6*(100), 1–14.

Picker, M. D., & Samways, M. J. (1996). Faunal diversity and endemicity of the Cape Peninsula, South Africa - a first assessment. *Biodiversity and Conservation, 5*, 591–606.

Potts, A. J., Hedderson, T. A., Franklin, J., & Cowling, R. M. (2012). The Last Glacial Maximum distribution of South African subtropical thicket inferred from community distribution modelling. *Journal of Biogeography, 40*(2), 310–322.

Price, B. W., Barker, N. P., & Villet, M. H. (2007). Patterns and processes underlying evolutionary significant units in the *Platypleura stridula* L. species complex (Hemiptera: Cicadidae) in the Cape Floristic Region, South Africa. *Molecular Ecology, 16*(12), 2574–2588.

Price, B. W., Barker, N. P., & Villet, M. H. (2010). A watershed study on genetic diversity: Phylogenetic analysis of the *Platypleura plumosa* (Hemiptera: Cicadidae) complex reveals catchment-specific lineages. *Molecular Phylogenetics and Evolution, 54*(2), 617–626.

Radea, C., Parmakelis, A., Papadogiannis, V., Charou, D., & Triantis, K. (2013). The hydrobioid freshwater gastropods (Caenogastropoda, Truncatelloidea) of Greece: new records, taxonomic re-assessments using DNA sequence data and an update of the IUCN Red List Categories. *ZooKeys, 350*, 1–20.

Raheem, D. C., Naggs, F., Preece, R. C., Mapatuna, Y., Kariyawasam, L., & Eggleton, P. (2008). Structure and conservation of Sri Lankan land-snail assemblages in fragmented lowland rainforest and village home gardens. *Journal of Applied Ecology*, *45*, 1019–1028.

Raheem, D. C., Naggs, F., James Chimonides, P. D., Preece, R. C., & Eggleton, P. (2009). Fragmentation and pre-existing species turnover determine land-snail assemblages of tropical rain forest. *Journal of Biogeography*, *36*(10), 1923–1938.

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2014). Tracer v1.6. *Available from http://beast.bio.ed.ac.uk/Tracer*.

Rebelo, A. G., Boucher, C., Helme, N., Mucina, L., & Rutherford, M. C. (2006). Fynbos biome. In L. Mucina & M. C. Rutherford (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland*. (Strelitzia, pp. 52–219). Pretoria: SANBI.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*, *61*(3), 539–542.

Rosauer, D. F., & Mooers, A. O. (2013). Nurturing the use of evolutionary diversity in nature conservation. *Trends in Ecology & Evolution*, *28*(6), 322–3.

Rowson, B., Warren, B. H., & Ngereza, C. F. (2010). Terrestrial molluscs of Pemba Island, Zanzibar, Tanzania, and its status as an "oceanic" island. *Zookeys*, *70*, 1–39.

Ruhberg, H., & Daniels, S. R. (2013). Morphological assessment supports the recognition of four novel species in the widely distributed velvet worm *Peripatopsis moseleyi sensu lato* (Onychophora:Peripatopsidae). *Invertebrate Systematics*, *27*(2), 131–145.

Rundell, R. J. (2008). Cryptic diversity, molecular phylogeny and biogeography of the rock- and leaf litter-dwelling land snails of Belau (Republic of Palau, Oceania). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1508), 3401–3412.

Schalke, H. J. W. G. (1973). The Upper Quaternary of the Cape Flats Area (Cape Province, South Africa). *Scripta Geologica*, *15*, 1–67.

Scott, L., Anderson, H. M., & Anderson, J. M. (1997). Vegetation history. In R. M. Cowling, D. M. Richardson, & S. M. Pierce (Eds.), *Vegetation of southern Africa*. (pp. 62–84). Cambridge: Cambridge University Press.

Sengupta, M. E., Kristensen, T. K., Madsen, H., & Jørgensen, A. (2009). Molecular phylogenetic investigations of the Viviparidae (Gastropoda: Caenogastropoda) in the lakes of the Rift Valley area of Africa. *Molecular Phylogenetics and Evolution*, *52*(3), 797–805.

Siesser, W. G., & Dingle, R. V. (1981). Tertiary Sea-level movements around southern Africa. *Journal of Geology*, *89*(4), 523–536.

Simelane, T. S., Knight, M. H., & Kerley, G. I. H. (2000). Impact of fuelwood harvesting on conservation of invertebrate diversity. In A. H. W. Seydack, W. J. Vermeulen, & C. Vermeulen (Eds.), *Natural forests and savannah woodlands symposium II. Towards sustainable management based on scientific understanding of natural forests and woodlands.* (pp. 348–354). Pretoria.

Sirgel, W. F. (1985). A new subfamily of Arionidae (Mollusca, Pulmonata). *Annals of the Natal Museum, 26*(2), 471–487.

Solem, A. (1984). A world model of land snail diversity and abundance. In A. Solem & A. C. van Bruggen (Eds.), *World-wide snails. Biogeographical studies on non-marine Mollusca.* (pp. 6–22). Leiden: Brill/Backhuys.

Solem, A., Climo, F., & Roscoe, D. J. (1981). Sympatric species diversity of New Zealand land snails. *New Zealand Journal of Zoology, 8*, 453–485.

Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics, 2014, open access link: http://bioinformatics.oxfordjournals.org/content/early/2014/01/21/bioinformatics.btu033. abstract?keytype=ref&ijkey=VTEqgUJYCDcf0kP*.

Stanisic, J. (1998). Superfamily Cyclophoroidea. In P. L. Beesley, G. J. B. Ross, & A. Wells (Eds.), *Mollusca: The southern synthesis. Fauna of Australia. Vol. 5. Part B* (pp. 703–704). Melbourne.

Stanisic, J., Cameron, R. A. D., Pokryszko, B. M., & Nekola, J. C. (2007). Forest snail faunas from S. E. Queensland and N. E. New South Wales (Australia): patterns of local and regional richness and differentiation. *Malacologia, 49*(2), 445–462.

Stuckenberg, B. R. (1962). The distribution of the montane palaeogenic element in the South African invertebrate fauna. *Annals of the Cape Provincial Museums, 2*, 190–205.

Sturany, R. (1898). *Cyclotus isipingoensis* n. sp. *Anzeiger Der Akademie Der Wissenshaften in Wien, 35*, 161.

Sutcharit, C., Tongkerd, P., & Panha, S. (2014). The land snail genus *Pterocyclos* Benson, 1832 (Caenogastropoda: Cyclophoridae) from Thailand and Peninsular Malaysia, with descriptions of two new species. *The Raffles Bulletin of Zoology, 62*, 330–338.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution, 30*(12), 2725–2729.

Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research, 22*(22), 4673–4680.

Tielecke, H. (1940). Anatomie, phylogenie und tiergeographie der Cyclophoriden. *Archiv Für Naturgeschichte, 9*, 317–371.

Tilbury, C. R., & Tolley, K. A. (2009). A new species of dwarf chameleon (Sauria: Chamaeleonidae, *Bradypodion* Fitzinger) from Kwazulu-Natal South Africa with notes on recent climatic shifts and their influence on speciation in the genus. *Zootaxa, 2226*, 43–57.

Tolley, K. A., Burger, M., Turner, A. A., & Matthee, C. A. (2006). Biogeographic patterns and phylogeography of dwarf chameleons *Bradypodion* in an African biodiversity hotspot. *Molecular Ecology, 15*, 781–793.

Tolley, K. A., Chase, B. M., & Forest, F. F. (2008). Speciation and radiations track climate transitions since the Miocene Climatic Optimum: a case study of southern African chameleons. *Journal of Biogeography, 35*(8), 1402–1414.

Turner, I. M., & Corlett, R. T. (1996). The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology & Evolution, 11*(8), 330–3.

Uys, C., Hamer, M., & Slotow, R. (2010). Step process for selecting and testing surrogates and indicators of afrotemperate forest invertebrate diversity. *PLoS ONE, 5*(2), 1–10.

van Wyk, A. E., & Smith, G. F. (2001). *Regions of Floristic Endemism in Southern Africa.* (E. du Plessis & F. Steffens, Eds.). Umdaus Press .

Varón, A., Vinh, L. S., & Wheeler, W. C. (2010). POY version 4: Phylogenetic analysis using dynamic homologies. *Cladistics, 26*(1), 72–85.

Verboom, G. A., Archibald, J. K., & Bakker, F. T. (2009). Origin and diversification of the Greater Cape flora: ancient species repository, hot-bed of radiation, or both? *Molecular Phylogenetics and Evolution, 51*, 44–53.

Von Maltitz, G., & Fleming, G. (2000). The status of conservation of indigenous forests in South Africa. In A. H. W. Seydack, W. J. Vermeulen, & C. Vermeulen (Eds.), *Natural forests and savannah woodlands symposium II. Towards sustainable management based on scientific understanding of natural forests and woodlands.* (pp. 93–99). Pretoria: Department of Water Affairs and Forestry.

Von Maltitz, G., Mucina, L., Geldenhuys, C., Lawes, M., Eeley, H., Adie, H., Vink, D., Flemming, G., & Bailey, C. (2003). Classification system for South African indigenous forests: an objective classification for the Department of Water Affairs and Forestry. *Environmentek Report ENV-P-C 2003-017*, Environmentek, CSIR, Pretoria.

Wang, P., Xiao, Q., Zhou, W. C., & Hwang, C. C. (2014). Revision of three camaenid and one bradybaenid species (Gastropoda, Stylommatophora) from China based on morphological and molecular data, with description of a new bradybaenid subspecies from Inner Mongolia, China. *ZooKeys, 372*(1), 1–16.

Webster, N. B., Van Dooren, T. J. M., & Schilthuizen, M. (2012). Phylogenetic reconstruction and shell evolution of the Diplommatinidae (Gastropoda: Caenogastropoda). *Molecular Phylogenetics and Evolution, 63*(3), 625–638.

Weimarck, H. (1941). *Phytogeographical groups, centres and intervals within the Cape flora.* Leipzig: Lund.

White, R. M. (2002). Patterns of utilization of indigenous forest fauna and other natural resources in the Transkei Region, Eastern Cape. In A. H. W. Seydack, T. Vorster, W. J. Vermeulen, & I. J. van der Merwe (Eds.), *Natural forests and savannah woodlands symposium III. Multiple use management of natural forests and woodlands: policy refinements and scientific progress.* (pp. 340–349). Pretoria: Department of Water Affairs and Forestry.

Wiens, J. J. (2007). Species delimitation: new approaches for discovering diversity. *Systematic Biology, 56*(6), 875–878.

Wishart, M. J., & Hughes, J. M. (2003). Genetic population structure of the net-winged midge, *Elporia barnardi* (Diptera: Blephariceridae) in streams of the south-western Cape, South Africa: Implications for dispersal. *Freshwater Biology, 48*(1), 28–38.

Zachos, F. E. (2013). Species splitting puts conservation at risk. *Nature, 494*(7435), 35.