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*Molecular phylogeny, phylogeography and
evolutionary adaptation of foraging behaviour
amongst sympatric patellid limpets along the
southern African shoreline*

A thesis submitted in fulfillment of the requirements of the degree of

**Doctor of Philosophy
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by

Kolobe Lucas Mmonwa

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Supervisor: Prof. C.D. McQuaid (Distinguished Professor, Chair of Zoology and SARCI
Research Chair in Marine Ecosystem Research, Rhodes University)

Co-Supervisor: Prof. N.P. Barker (Head of Botany Department & Molecular Ecology and
Systematics Group, Rhodes University)



“In whom are hidden all the treasures of wisdom and knowledge”

(Colossians 2:3, ZCC Family Bible)

“I am fully in the know that the earth moves at about 100, 000 km/h around the sun, 1000 times faster than the speeds we go at on a highway, but I am not confused who God is”

The Honourable His Grace The Right Reverend Bishop Dr. BE Lekganyane

(Taung: Northwest Province, 11th March 2012)

“All religions, arts and sciences are branches of the same tree”

Albert Einstein (1879 – 1955)

“Gravity explains the motions of the planets, but it cannot explain who set the planets in motion”

Sir Isaac Newton (1642 – 1727)

ABSTRACT

The southern African shoreline is inhabited by a great diversity of patellid limpets of which most are endemic to South Africa. These limpets have evolved foraging mechanisms that partition ecological resources and reduce interspecific competition, resulting in ecological specialists and generalists. The evolution of ecological specialization or generalization remains poorly understood and there is no agreement on how such evolutionary transitions are correlated with levels of genetic diversity. This study investigated evolutionary correlations between territoriality in foraging and genetic structure of southern African patellid limpets (*Cymbula* and *Scutellastra* spp.) using stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, mitochondrial and nuclear DNA markers.

The outcomes of the study were best rationalized and understood in the context of the scale of analysis in terms of both space and taxonomy. At biogeographic scales and the interspecific level, the stable isotope signatures and genetic structure of these limpets are determined by extrinsic factors such as biogeography and oceanography. However, at the smallest site scales and the intraspecific level, the isotope signatures and genetic diversity of these limpets are significantly correlated to their foraging traits. At large scales, there are no correlations between foraging behaviour and either genetic structure or isotope signature. At smaller scales, territorial *Scutellastra* foragers display both isotopic enrichment and greater haplotype diversity than congeneric non-territorial foragers. Thus, the isotope signatures and genetic structure of these limpets are determined by intrinsic species-specific response linked to their foraging behaviour. However, this pattern was intriguing as differences between territorial and non-territorial limpets in both isotopic signature and genetic diversity were observed only along the south coast when the same species were compared in other biogeographic regions. The significant interaction effect between foraging behaviour and stable isotope signatures was only observed from the sites within the Agulhas Bank or which are strongly influenced by the Agulhas current. This south enrichment in isotopic ratios is due to the mixing differences between onshore and offshore waters as the Agulhas current moves from east to south.

At the generic level, the correlation between foraging behaviour and isotope signatures and genetic structure were particularly profound for *Scutellastra* species. The molecular phylogeny revealed deep evolutionary divergence between territorial and non-territorial *Scutellastra* spp. This divergence was concordant with morphological differences in shell shape and radula anatomy between territorial and non-territorial species. A taxonomic review of the scutellastrid spp. is proposed, suggesting possible re-consideration of the genus as two genera characterized by either territoriality or non-territoriality.

The divergence between territorial and non-territorial species in both *Scutellastra* and *Cymbula* took place approximately in the early Oligocene. Major climatic cooling and decreases in sea level occurred during the Oligocene and this probably exposed much of the lower intertidal zone, increasing new potential habitats and algal availability. The Oligocene exposure of rocky shores and algal abundance in the lower intertidal zone probably elicited resource partitioning amongst these patellid limpets and subsequently, the evolution of territorial and non-territorial species. Analyses of the demographic history of these patellid limpets revealed evidence of post-glacial spatial expansion around the Pleistocene, implying these limpets were at population equilibrium during the dramatic LGM sea temperatures. Thus, these limpets managed to expand their range during dynamic oceanographic oscillations and dramatic sea-level changes in the Pleistocene.

This study highlighted the importance of applying ecological traits as a subject to investigate and comprehend the evolutionary ecology of marine herbivores. The foraging traits of these true limpets are reflected in both their stable isotope ratios and genealogy, presumably as an evolutionary consequence of competition.

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GENESIS 1: 27-28

“So God created man in his own image, in the image of God he created him, male and female he created them. Rule over the fish of the sea and the birds of the air and over every living creature that moves on the ground”

(ZCC Family Bible)

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Dedications

This thesis is sincerely and solely dedicated to my dearest mother of greatness, Choene Agnes Mmonwa, for showing everlasting patience and support throughout my studies from undergraduates to the end of this thesis.

ISAIAH 66:13

“As a mother comforts her child, so I will comfort you, and you will be comforted over Jerusalem”

Declaration

I declare that this thesis constitutes my own original work except where acknowledgements are stated in the text. It has not been submitted for examination to any other university or academic institution for the recognition of doctorate degree. The views and opinions expressed herein are solely those of the author and do not necessarily reflect the views of the university.

Signature:A handwritten signature in black ink, consisting of several loops and a long horizontal stroke.**Date:** 04th September 2013

GENERAL INTRODUCTION



“It is as if a human would eat corn pone only, or cabbage, or onions, or cottage cheese, and never venture a baked potato, hot dog, or ice cream cone to vary the monotony. It was perhaps inevitable that, for many decades, discussions of the evolution of specialization were heavily colored by preconceptions based on human prejudices”

Berenbaum MR (1996, p78)

Territoriality and non-territoriality in patellid limpets

Intertidal shores are high-biodiversity marine ecosystems that are mostly inhabited by sessile or sedentary species which are likely to compete for ecological resources (i.e. habitat and food). In extreme cases the intensity of such inter-specific competition result in “ecological specialization” which eventually drives speciation (Hutchinson 1959, Branch 1985a, 1985b). Ecological specialization is an important aspect of biodiversity and understanding its underlying evolutionary effects is crucial to comprehending the whole process of speciation (Via & Hawthorne 2002). One of the basic problems in understanding how ecological specialization evolves is simply defining the term itself (Berenbaum 1996). The phrase “ecological specialization” is subjective and frequently refers either to diet- or habitat-specialists. However, species could also be classified as ecological specialists based on their thermal tolerance (Futuyma & Moreno 1988) or mate choice (Ferry-Graham et al. 2002).

The southern African coastline is home to approximately twenty species of patellogastropods (true limpets) and ecological specialization is very important in sustaining such great diversity. These patellid limpets have evolved interesting foraging mechanism to partition resources and reduce inter-specific competition (Branch 1971, 1974, 1975c). The pioneering interspecific studies by Branch (1971, 1974, 1975c, 1980, 1985a) subsequently categorized these limpets into two groups based on the differences in their foraging behaviour (territorial or non-territorial).

- 1) Territorial grazers occupy a narrow zone on the shore and forage on specific alga/e (Branch 1971, 1975b). Branch (1975c) described these limpets as the “non-migratory” group. These limpets are characterized by marked adult-juvenile differentiation with regard to habitat and diet (Branch 1971, 1975b, 1975c and Branch et al. 1992).

2) Non-territorial grazers occupy a wide range of the shore and forage on multiple algae (Branch 1971, 1975b). Branch (1975c) described these limpets as the “migratory” group. Unlike territorial grazers, these limpets do not exhibit marked adult-juvenile differentiation with regard to habitat and food (Branch 1971, 1975b, 1975c).

Nonetheless, segregation on the basis of foraging does not apply to all patellogastropods; some species display features of both groups and Branch (1975c) termed such species intermediate grazers. Such intermediate grazers often occur in low densities along their distributional range and this either hinders or reflects the intense inter-specific competition which drives ecological specialization (Branch 1975c). Such intermediate foragers possess morphological and ecological characters of territoriality and non-territoriality and include the bearded limpet *Scutellastra barbara* (Linnaeus, 1758) and Argenville’s limpet *Scutellastra argenvillei* (Krauss, 1848). The bearded limpet *Scutellastra barbara* defends territories of the filamentous algae only along the south coast but not along the west coast (Ridgway et al. 1999).

The term “territoriality” here refers to an adaptive behaviour of permanent habitation of an area and defense against intruders and evolves due to intense intra- or inter-specific competition for algal food (Stimson 1970, 1973, Branch 1971, 1975c, 1976, 1981, 1984 and Branch et al. 1992).

The territorial grazers occur low on the shore and defend territories of encrusting non coralline or coralline algae on which they primarily forage. Adjacent territories can touch but do not overlap and are defended by pushing other limpets away, leaving only a garden of fine red, turfy algae in some species (i.e. *S. longicosta* Lamarck, 1819) and *S. tabularis* Krauss 1848). The limpets form scars on the rock in the center of their territory and forage by rotating on the scar, grazing their algal garden or the encrusting algae in the vicinity of the scar (Branch 1975c). The non-territorial grazers settle as larvae low on the shore and migrate progressively upwards to the high shore as they grow, thus occupying a wider range. These limpets are generalized grazers, non-aggressive to their own species and have a random to aggregated distribution (Branch 1975c).

The study species

Territorial foragers

The territorial pear limpet *Scutellastra cochlear* (Born, 1778) and the encrusting coralline alga *Spongites yendoi* (Foslie) occur in mutual symbiosis along the coastline. The limpet excludes other algae from its territory leaving a garden of the red algae, *Gelidium micropterum* (Kuetzing) or *Herposiphonia heringii* (Harvey) (Branch 1975c, 1976). Juvenile *Scutellastra cochlear* avoid predation by inhabiting the shells of the adult limpets covered with *Spongites yendoi* and after two years they move to the surrounding rock to establish their own scars (Branch 1975c). Gut content analysis of *S. cochlear* has confirmed that the limpet forages primarily on *Spongites yendoi*, which comprised 85% of the contents analysed (Maneveldt & Keats 2008). The remaining percentage comprised a mixture of fleshy algae, diatoms, invertebrates, microscopic algae and unidentifiable organic matter.

The territorial long-spined limpet *Scutellastra longicosta* (Lamarck, 1819) and giant limpet *S. tabularis* (Krauss 1848) are found in symbiosis with the encrusting algae *Ralfsia verrucosa* or *R. expansa* and *Zeacarpa leiomorpha* respectively (Branch 1975c, 1981). *S. longicosta* changes its habitat at different life stages and this reduces competition between these age groups (Branch 1971, 1974, 1975c). The juveniles inhabit the shell of limpets and other species and in the second year they move on to the rock and feed on *Spongites yendoi* until they establish their own territory or occupy a vacant home scar and territory (Branch 1975c).

The territorial kelp limpet *Cymbula compressa* (Linnaeus, 1758) is found in symbiosis with the sea bamboo *Ecklonia maxima* only along the west coast. The limpets form obvious scars on the kelp and intruders are sensed through tentacles and forcefully pushed away from the scar (Branch 1971). The adult limpets occupy the stipes whereas the juveniles inhabit the fronds where they are protected from wave force and predators (Branch 1971, 1974, 1975c). The territorial pink-rayed limpet *C. miniata* (Born, 1778) is found in symbiosis with the encrusting coralline alga *Spongites yendoi*.

Non-territorial foragers

The granular limpet, *Scutellastra granularis* (Linnaeus, 1758) is one of the most widely distributed of these limpets, occurring from the Namibian coast to the north-eastern coast of South Africa (Branch et al. 2010). This limpet displays marked variation in shell size and morphology in relation to different oceanographic conditions throughout its range (Bustamante et al. 1995). Two sister species have been recognised at the western and eastern edges of the *S. granularis* distributional range. *Scutellastra miliaris* (Phillip, 1848) is restricted to the north-western Angolan shoreline (Branch GM, personal communication) and *S. natalensis* (Krauss, 1848) is restricted to the north-eastern South African shoreline (Ridgway et al. 1998b). These three parapatric granular sister species are non-territorial foragers, high shore inhabitants, mobile and have generalized algal diets.

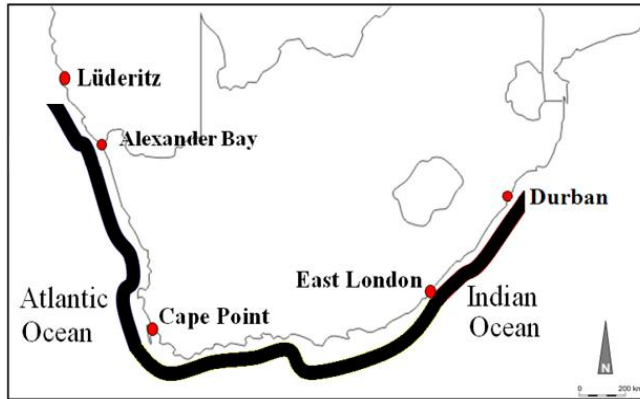
Gut content analysis of the non-territorial granular limpet *S. granularis* comprised 47% of *Spongites yendoi* and 53% of turf or foliose algae (Maneveldt & Keats 2008). This further corroborates the fact that *Scutellastra granularis* is indeed a feeding-generalist, foraging on a range of algae. Interestingly, the coralline algae *Spongites yendoi* and *Ralfsia verrucosa* have been proven to be as nutritious as or even more nutritious than turf or foliose algae (Maneveldt et al. 2006).

The goat's eye limpet *Cymbula oculus* (Born, 1778) and the granite limpet *C. granatina* (Linnaeus, 1758) are amongst the ubiquitous non-territorial foragers along the high intertidal zone. These limpets show no algal preferences and forage on any available algae (Branch 1971, 1975b, Maneveldt et al. 2009). Like all other non-territorial foragers, they are characterized by relatively high growth rates and high gonad output (Branch 1975b and Branch & Newell 1978).

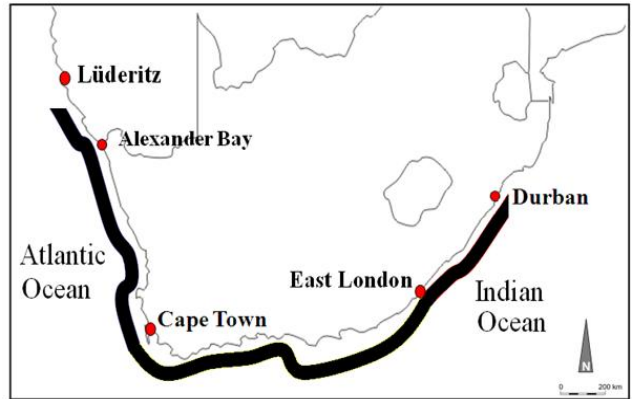
The habitats of southern African patellid limpets discussed in this study and the type of their larval development are given below in Table 1. The distributional ranges of these species are illustrated on the maps in Figures 1a – l.

Table 1: The habitats (along the tidal zone), mode of larval dispersal and distributional ranges of sympatric southern African patellid limpets. Foraging Behaviour: ^T = Territorial, ^{NT} = Non-territorial, ^{IM} = Intermediate. Three main Biogeographic regions: CB = cool-temperate Benguela region, WA = warm-temperate Agulhas region, SE = subtropical East coast region.

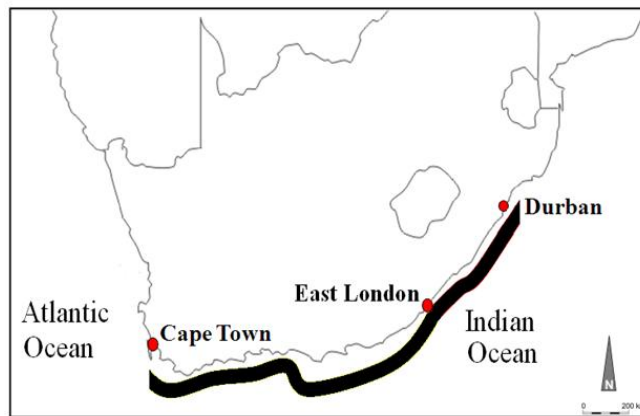
Species	Habitat	Larval development	Distributional Range
<i>Scutellastra</i>			
<i>S. barbara</i> ^{IM}	Low shore	Planktonic	across three regions (CB, WA and SE)
<i>S. cochlear</i> ^T	Low shore	Planktonic	across three regions (CB, WA and SE)
<i>S. longicosta</i> ^T	Low shore	Planktonic	across the warm-temperate Agulhas region
<i>S. tabularis</i> ^T	Subtidal zone	Planktonic	across the warm-temperate Agulhas region
<i>S. argenvillei</i> ^{IM}	Low shore	Planktonic	across three regions (CB, WA and SE)
<i>S. granularis</i> ^{NT}	High shore	Planktonic	across two regions (CB and WA)
<i>S. natalensis</i> ^{NT}	High shore	Planktonic	across the subtropical East coast region
<i>S. miliaris</i> ^{NT}	High shore	Planktonic	Along the Angolan coastline
<i>Cymbula</i>			
<i>C. compressa</i> ^T	Low shore	Planktonic	across the cool-temperate Benguela region
<i>C. miniata</i> ^T	Low shore	Planktonic	across three regions (CB, WA and SE)
<i>C. granatina</i> ^{NT}	High shore	Planktonic	across the cool-temperate Benguela region
<i>C. oculus</i> ^{NT}	Mid shore	Planktonic	across two regions (WA and SE)
<i>Helcion</i>			
<i>H. concolor</i> ^{NT}	High shore	Planktonic	across two regions (WA and SE)



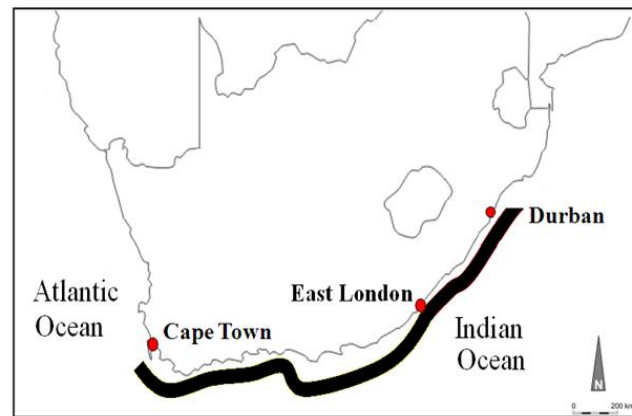
a) *Scutellastra barbara*^T



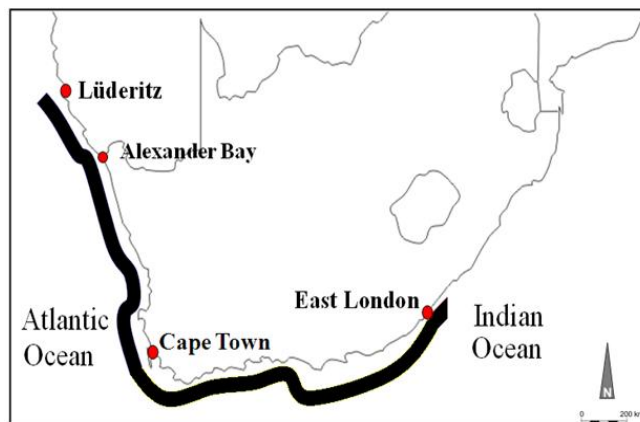
b) *Scutellastra cochlear*^T



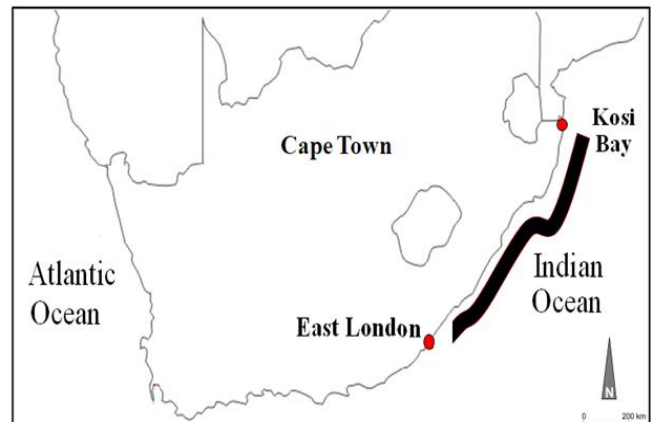
c) *Scutellastra longicosta*^T



d) *Scutellastra tabularis*^T

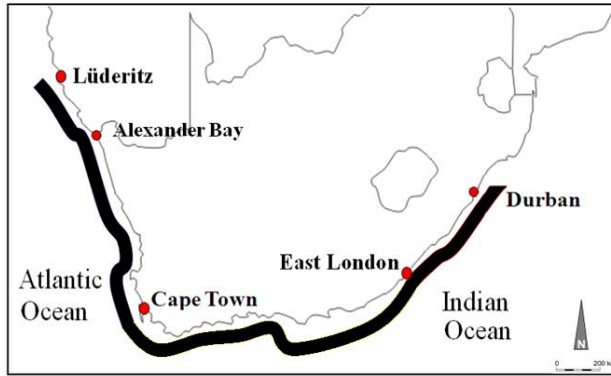


e) *Scutellastra granularis*^{NT}

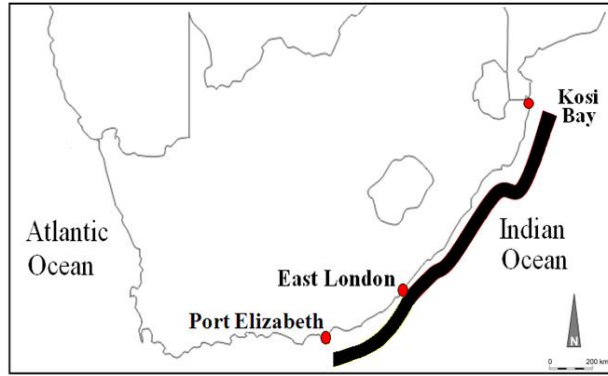


f) *Scutellastra natalensis*^{NT}

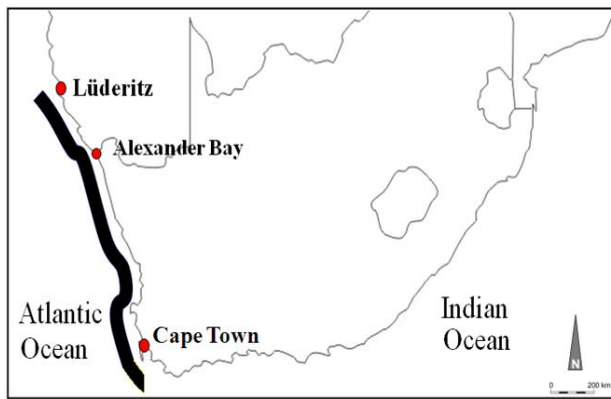
Figures 1a - f: The South African maps showing distributional ranges of the patellid limpets analysed in this study (Branch et al. 2010). ^T = Territorial foragers, ^{NT} = Non-territorial foragers.



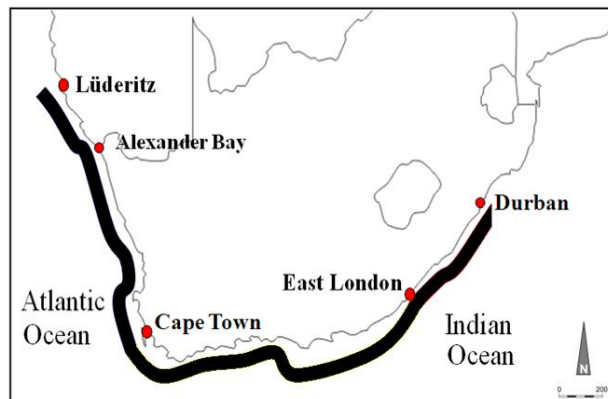
g) *Scutellastra argenvillei*^{NT}



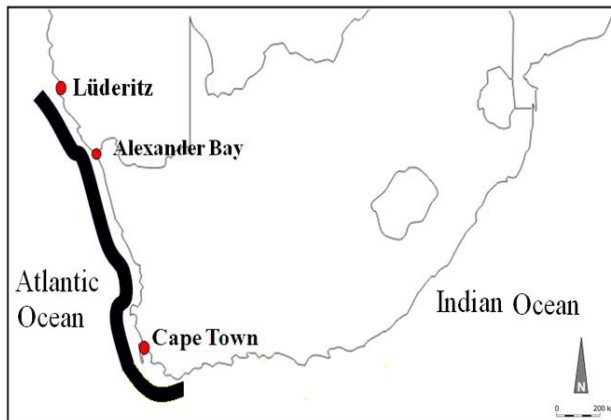
h) *Helcion concolor*^{NT}



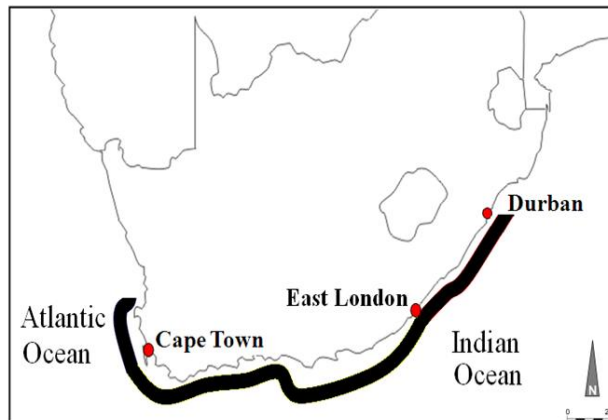
i) *Cymbula compressa*^T



j) *Cymbula miniata*^T



k) *Cymbula granatina*^{NT}



l) *Cymbula oculus*^{NT}

Figures 1g - l: The South African maps showing distributional ranges of the patellid limpets analysed in this study (Branch et al. 2010). ^T = Territorial foragers, ^{NT} = Non-territorial foragers.

The feeding apparatus of territorial and non-territorial foragers

The patellogastropods display marked differences in anatomical adaptations of their feeding apparatus between territorial and non-territorial grazers (Steneck & Watling 1982, Simison & Lindberg 1999). The radula teeth of the territorial *Scutellastra cochlear* have three anatomical features that are well adapted to excavate encrusting coralline algae (Figure 2). Firstly, the teeth of this species are blunt and shovel-like (Figures 2A and 2B), unlike the sharp and rake-like teeth of the non-territorials *S. argenvillei* and *S. granularis* (Figures 2C and 2D). Secondly, the radula of territorial *Scutellastra cochlear* is long and narrow (Figures 2A and 2B) in contrast to a short and broad radula in the non-territorial grazers (Figures 2C and 2D). Thirdly, the teeth of the territorial *Scutellastra cochlear* are hard and stone-like due to a high content of iron and silica, which occurs in low amounts in the teeth of non-territorial *S. argenvillei* and *S. granularis* (Maneveldt 1995, Maneveldt et al. 2006). Moreover, the first lamellar layer is arranged circularly and radially in non-territorial and territorial foragers respectively (Koufopanou et al. 1999).

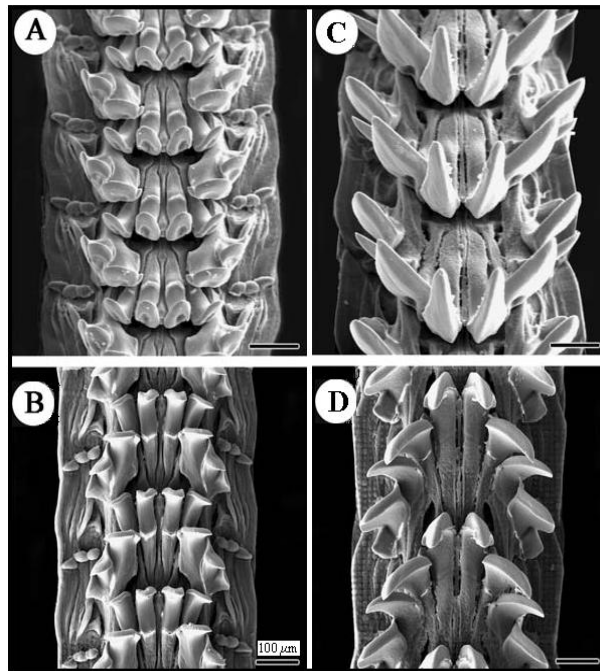


Figure 2: The SEM illustration of the differences in the radula anatomy between territorial *Scutellastra cochlear* (A and B) and non-territorial *S. argenvillei* and *S. granularis* (C and D) patellid limpets, modified from Maneveldt et al. (2006).

Possible effects of genetic structure in patellid limpets

Genetic breaks or phylogeographic structure in populations of these limpets could correspond with the prevailing biogeographic limits (Figure 3) as has generally been found in other organisms (Ridgway et al. 1998b, Teske et al. 2006, 2007a, 2008, 2009, Zardi et al. 2007). These biogeographic limits are not necessarily the cause of genetic breaks but act to maintain genetic breaks evoked by ancient climate changes (Teske et al. 2011a, 2011b). The patellogastropods are broadcast spawners with pelagic lecithotrophic larvae (Thorson 1961, Kay & Emlet 2002) which could disperse widely over open water via currents, circumventing nearshore dispersal barriers. These larvae on their own have relatively limited dispersal potential (Bird et al. 2007) and gene flow is driven mainly by oceanic currents (Hadfield et al. 1997, Bird et al. 2011). Nonetheless, using the life history of the organism to predict its genetic structure has proven problematic in most cases, especially in a dynamic marine realm like the southern African shoreline. Several potential long-distance dispersing invertebrates were unexpectedly found to display immense genetic variability (Teske et al. 2007c, Zardi et al. 2007). In spite of the larval potential for long-distance dispersal, abiotic factors such as ancient oceanographic oscillations and habitat availability have also been shown to shape the genetic structure of various marine taxa (Barber et al. 2002, Kirkendale & Meyer 2004, Teske et al. 2006, Maggs et al. 2008, Marko et al. 2010).

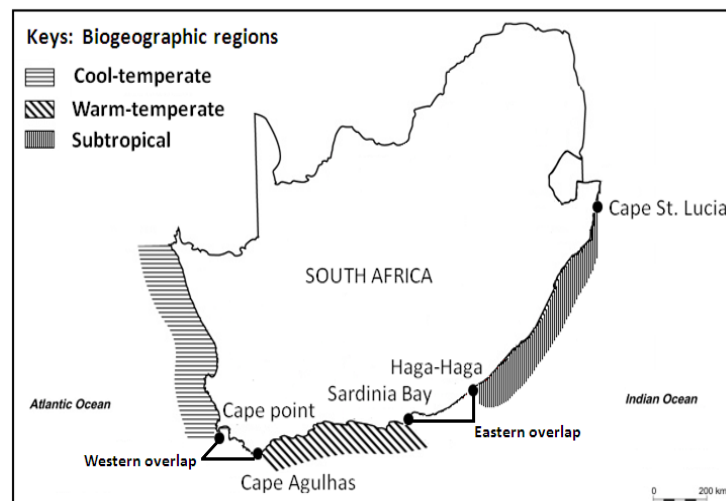


Figure 3: The map of South Africa showing the three main prevailing biogeographic regions (Bustamante et al. 1995, Griffiths et al. 2010).

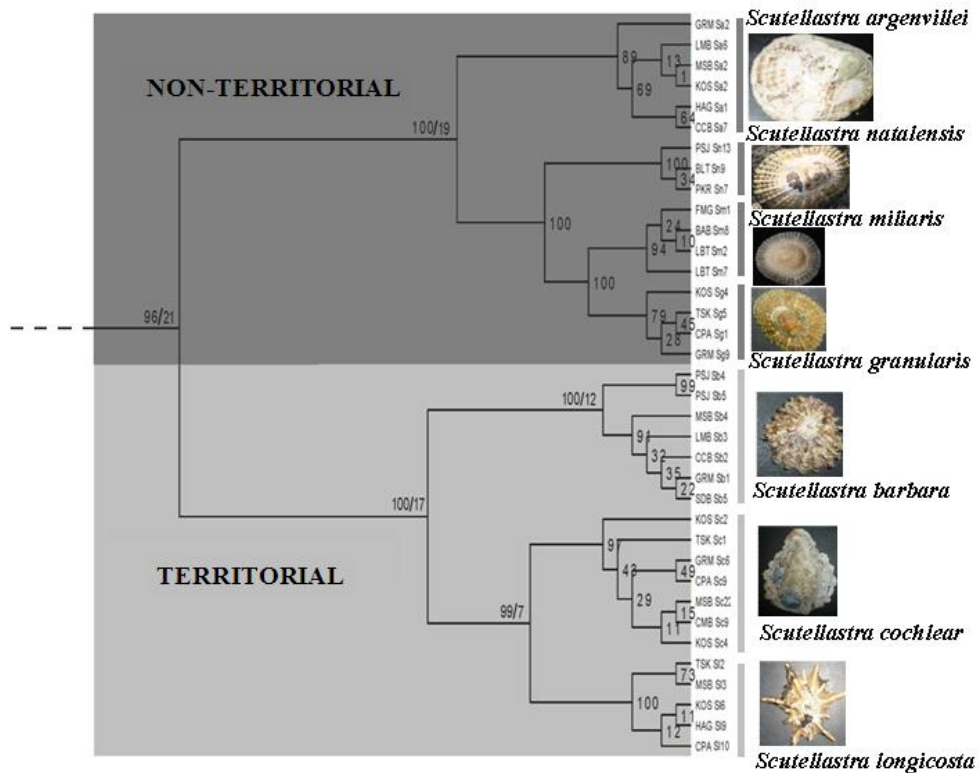
The main research questions and objectives

In contrast to terrestrial ecosystems, there is limited documented evidence of co-evolutionary adaptations in marine invertebrates. This is not because there are no such evolutionary adaptations amongst marine herbivores, but because such questions are rarely addressed (Hay 1992, 1996, Targett & Arnold 2001). In marine realms, traits of seaweeds could shape the evolution of small herbivorous invertebrates (Hay et al. 1987). The only studies to date articulating such genetic adaptation amongst populations of marine invertebrates have concerned herbivorous amphipods (Sotka & Hay 2002, Sotka et al. 2003). Different seaweed traits such as palatability (Bolser & Hay 1996, Taylor et al. 2003) and chemical defense (Sotka & Hay 2002, Sotka 2003, Sotka et al. 2003) have been proven to cue genetic adaptation amongst marine herbivores. Our knowledge and understanding on the role that seaweeds play in the evolution of marine invertebrates is minimal and restricted to amphipods (Sotka et al. 2003, Sotka 2005). To my knowledge, this will be the first study to investigate the evolutionary effects of ecological specialization on foraging ecology and genetic structure of patellid limpets along the southern African coastline.

Foremost, this study will address molecular phylogeny (chapter one) of the southern African patellid limpets to identify any taxonomic problems and reveal the evolutionary relationships between territorial and non-territorial grazers. Subsequent chapters will examine and compare interspecific phylogeographic distribution (chapter two) and intraspecific phylogeography or genetic diversity (chapter three) between territorial and non-territorial grazers in both *Scutellastra* and *Cymbula* species. The final chapter (chapter four) will address foraging behaviour of these limpets using stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures at local and biogeographic scales. Stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures are advantageous over gut contents analysis in that they provide information on the diet of the animal over relatively long periods of time. This would be essential in unraveling long term diet variation between territorial and non-territorial foragers. Ultimately, the results of stable isotope analysis and genetic analysis of these limpets will be integrated (Synthesis) to determine if territorial and non-territorial foraging traits are expressed isotopically or genetically or both.

CHAPTER ONE

Molecular phylogeny of the southern African sympatric patellid limpets (Gastropoda: Patellogastropoda) based on mitochondrial and nuclear markers



1.1 Introduction

1.1.1 *Molecular phylogeny of the patellogastropods*

The patellogastropods (commonly known as patellid limpets) are abundant and ubiquitous inhabitants of intertidal rocky shores throughout the world from tropical to polar regions (Branch 1985a, 1985b, Lindberg 1988). This monophyletic group of limpets has been used to address many research questions in evolutionary biology due to its phenotypic plasticity and supposition to be the sister-taxon to all other extant gastropod orders (Haszprunar 1988, Ponder & Lindberg 1997, Koufopanou et al. 1999, Yoon & Kim 2007). However, the most recent molecular phylogeny, derived using seven different markers has disputed the basal position of the patellogastropods, indicating that the order is only sister-taxon to the Vetigastropoda (Aktipis & Giribet 2010).

Historical taxonomic studies based on the shell and radular structure classified this order into three families: Acmaeidae, Lepetidae and Patellidae (Powell 1973). Subsequent phylogenetic studies based on morphological characters (Jamieson et al. 1991, Ridgway et al. 1998a) and molecular characters (Harasewych & McArthur 2000, Yoon & Kim 2007, Nakano & Ozawa 2007) reclassified the order into six families: Acmaeidae, Lepetidae, Lottidae, Nacellidae, Neolepetopsidae and Patellidae. The most recent review of the molecular phylogenetics of the patellogastropods further re-reclassified the order into seven families. The families Acmaeidae and Lottidae were placed into one family (Lottidae) and two more new families emerged, the Eoacmaeidae and Pectinidontidae (Nakano & Sasaki 2011). This phylogenetic uncertainty in reclassification of the patellogastropods clearly signals systematic problems within the order.

Previous comprehensive molecular phylogenetic studies of the patellogastropods were biased towards three families: Lottidae (Simison & Lindberg 1999), Nacellidae (Goldstein et al. 2006, Aranzamendi et al. 2009, González-Wevar et al. 2010) and Patellidae (Koufopanou et al. 1999, Sà-Pinto et al. 2005). This can be attributed to the fact that the other families comprise deep subtidal and hydrothermal vent species which are not readily accessible (Nakano & Sasaki 2011).

The family Patellidae (Rafinesque 1815) is the most studied group and so far 39 patellid species (Table 1.1) have been described and identified worldwide (Ridgway et al. 1998a and Nakano & Sasaki 2011). Amongst these, 20 species are endemic to the southern African shoreline from Angola on the west coast to northern Kwazulu-Natal on the east coast (Koufopanou et al. 1999). The family Patellidae has been recognised as the sister-taxon to all other patellogastropod families based on morphological characters (Lindberg 1988, 1998 and Lindberg & Hedegaard 1996). Recent molecular studies were also congruent with this placement and consequently, the entire family is recognised as monophyletic (Koufopanou et al. 1999, Nakano & Ozawa 2004 and 2007).

Table 1.1: The total estimated number of Patellidae species globally (Nakano & Sasaki 2011).

Genus	Estimated number of species
<i>Scutellastra</i> Quoy & Gaimard, 1834	17
<i>Cymbula</i> H & A Adams, 1854	9
<i>Helcion</i> Monfort, 1810	4
<i>Patella</i> Linnaeus, 1815	9
Total patellid species globally	39

Morphological and molecular phylogenetic analyses of the family Patellidae recognised four main monophyletic clades which comprised the following genera (Table 1.1): *Patella*, *Helcion*, *Cymbula* and *Scutellastra* (Ridgway et al. 1998a, Koufopanou et al. 1999, Harasewych & McArthur 2000, Nakano & Ozawa 2004 and Yoon & Kim 2007). The evolutionary relationships amongst these genera have been comprehensively documented (Koufopanou et al. 1999, Nakano & Ozawa 2004, 2007 and Yoon & Kim 2007).

1.1.2 *Origin, divergence and dispersal routes of the patellid limpets*

Analyses of the fossil records and Cretaceous paleogeographic patterns further indicated that the patellid limpets originated in the northern parts of Gondwanaland, along the southern coast of the Tethys Sea in the mid to late Cretaceous (Figure 1.1). The Tethys Sea was broadly open and connected to the Pacific Ocean in the mid to late Cretaceous, providing a possible trans-oceanic dispersal route (Figure 1.1). Consequently, they diverged and dispersed following different trans-oceanic currents of the Cretaceous, which resulted in an antitropical distribution (Koufopanou et al. 1999, Nakano & Ozawa 2004, 2007).

The approximate divergence time of the family Patellidae and its genera has been well estimated and explained by Nakano & Ozawa (2004, 2007) based on both fossil records and molecular markers (Table 1.2). The most recent taxonomic split within this family was during the early Eocene.

Table 1.2: The approximate divergence times (and 95% credibility intervals) of the family Patellidae (Nakano & Ozawa 2004, 2007).

Taxa	Divergence Time (Mya)	Geological Time
Patellidae vs. other patellogastropods	191 (128 – 272)	Early Jurassic
<i>Patella</i>	163 (121 – 231)	Mid Jurassic
<i>Scutellastra</i> (South African + (Australian vs. Indo-Pacific subclades)	67 (90 – 50)	Late Cretaceous
<i>Cymbula</i> vs. <i>Helcion</i>	53 (24 – 91)	Early Eocene

The genus *Patella* Linnaeus, 1815 was the first group to diverge from the ancestral taxon, and followed a westward dispersal route to inhabit the northeastern Atlantic and the Mediterranean Sea. To date, approximately nine *Patella* species have been identified and described. The molecular phylogeny and phylogeography of this genus was addressed by Sà-Pinto et al. (2005 and 2008) and found genetic divergence between continental and islands populations.

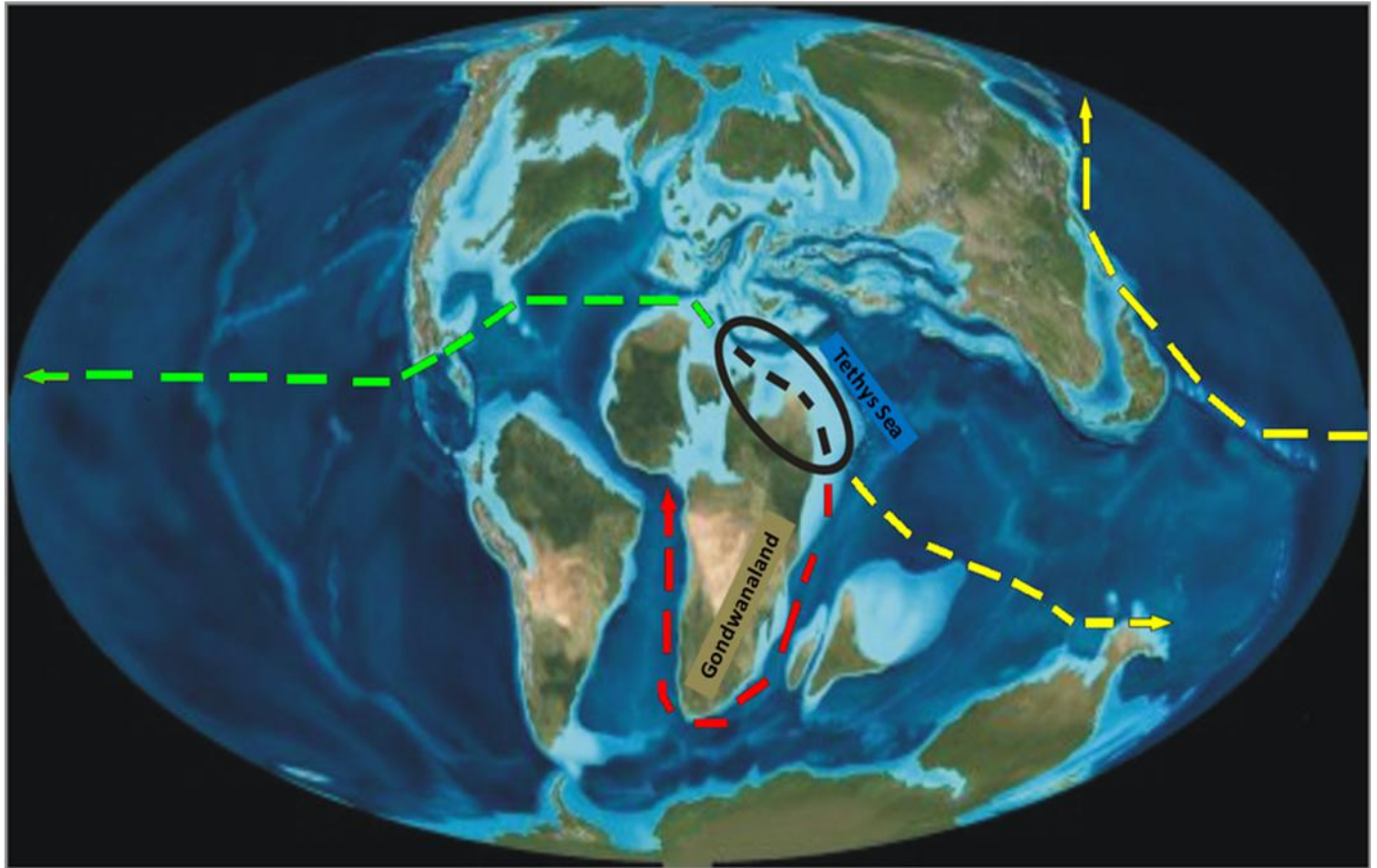


Figure 1.1: The global paleogeographic map indicating the origin (circled dotted black lines) and proposed migratory routes (coloured dotted lines) of the patellid limpets during the mid to late Cretaceous period, modified from Nakano & Ozawa (2004). Migratory routes: dotted green lines (*Patella* spp.), dotted yellow lines (Australian and Indo-Pacific *Scutellastra* spp.) and dotted red lines (southern African patellid spp. including *Helcion*, *Cymbula* and *Scutellastra*).

The genera *Cymbula* Adams, 1854 and *Helcion* Monfort, 1810 dispersed southwestwards to inhabit the southern and western African shorelines. Nine *Cymbula* spp. and four *Helcion* spp. are endemic to southern Africa (Nakano & Ozawa 2004, 2007, Nakano & Sasaki 2011 and Espinosa et al. 2011).

Scutellastra Quoy & Gaimard, 1834 is the most broadly distributed genus and it followed different dispersal routes to colonize the Indo-Pacific, southern Australian and southern African shorelines (Figure 1.1). The genus diverged and dispersed southwards to the South African shoreline (Figure 1.1). On a different migratory route, the genus dispersed eastwards to inhabit both the Indo-Pacific and southern Australia (Figure 1.1). To date, 17 *Scutellastra* spp. are recognised and distributed across the tropical Indo-Pacific from southern African to the Mexican coasts (Nakano & Ozawa 2007 and Nakano & Sasaki 2011). Molecular phylogenetic analysis (Nakano & Ozawa 2004, 2007 and Lindberg 2007) subdivided the genus into three monophyletic subclades corresponding to their spatial range in South Africa, southern Australia and the Indo-Pacific (Figure 1.2). These subclades are distinguishable at the genus level and further deliberation is required to fully understand their evolutionary patterns and taxonomic status (Nakano & Sasaki 2011).

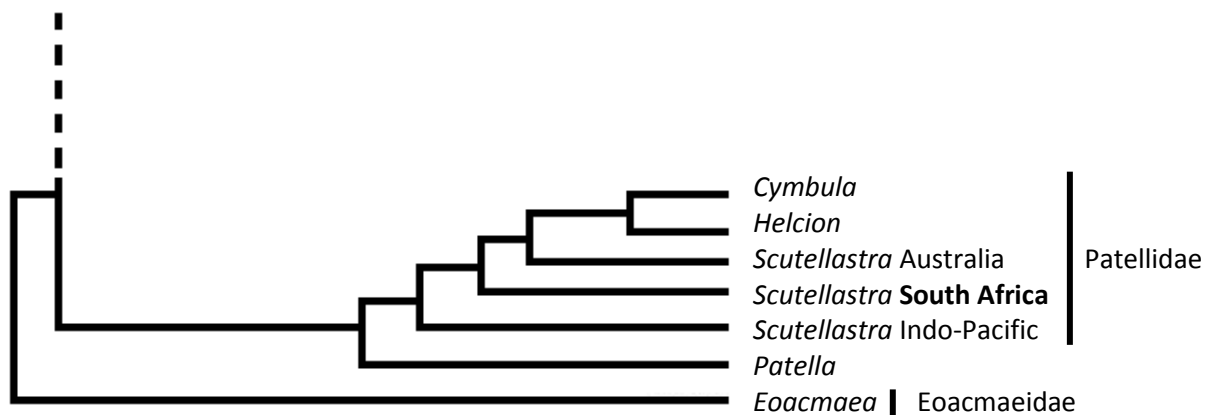


Figure 1.2: The part of the phylogenetic tree illustrating the resolution of the genus *Scutellastra* into three spatial subclades based on combined 12S rRNA, 16S rRNA and CO1 genes (Nakano & Ozawa 2007).

1.1.3 *Evolution of ecological specialization and generalization*

The patellid limpets have evolved interesting foraging mechanisms which resulted in ecological specialization (territorial foraging) and ecological generalization (non-territorial foraging). Understanding the evolution of ecological specialization and generalization remains one of the most enigmatic phenomena in evolutionary biology (Simpson 1953, Levins & MacArthur 1969, Futuyma 1976, Futuyma & Moreno 1988, Futuyma & McCafferty 1990 and Berenbaum 1996). Historical and recent studies on the evolution of ecological specialization have discovered evolutionary transitions both from generalization to specialization (Courtney 1986, Losos et al. 1994, Funk et al. 1995, Kelley & Farrell 1998, Crespi & Sandoval 2000) and from specialization to generalization (Lanyon 1992, Muller 1996, Armbruster & Baldwin 1998 and Crespi & Abbot 1999). Therefore, not all studies are congruent with the traditional model of generalists evolving into specialists and this has been attributed to different abiotic or biotic factors driving each ecological or evolutionary transition (Crespi & Sandoval 2000).

Lindberg (2007) superimposed foraging traits of patellid limpets on their phylogenic tree based on published 16S rRNA sequences obtained mainly from Koufopanou et al. (1999). He discovered that territorial species are resolved as the basal clades and suggested that territoriality is an ancestral trait in patellogastropods. This study will investigate this speculation further using two relatively conserved mitochondrial DNA (12S rRNA, 16S rRNA), nuclear (ATPS β) and rapidly evolving mitochondrial (CO1) markers. The application of multiple markers is advantageous in providing robust phylogenetic resolution when the markers are congruent. However, the difficulties in aligning ribosomal genes and differences in evolutionary rates between mitochondrial and nuclear markers could contribute to incorrect phylogenetic resolution in various taxa (Harasewych 2002, Nakano & Ozawa 2007, Aktipis & Giribet 2010 and Nakano & Sasaki 2011). The relatively fast evolving mitochondrial markers have been suggested to be more informative in reconstructing relationships in patellogastropods (Harasewych & McArthur 2000, Nakano & Ozawa 2007).

1.1.4 *The main aims and objectives of the study*

The southern African shoreline is inhabited by 11 described *Scutellastra* spp. of which seven are endemic to South Africa (Branch et al. 1994). The genus *Cymbula* and *Helcion* were consistently resolved as monophyletic (Koufopanou et al. 1999, Nakano & Ozawa 2004, 2007, Lindberg 2007). Most studies have consistently resolved *Scutellastra* as a paraphyletic group (Koufopanou et al. 1999, Nakano & Ozawa 2004, 2007, Lindberg 2007) whereas a few of these studies (see Nakano & Ozawa 2004, 2007) resolved some of the *Scutellastra* spp. (*S. argenvillei*, *S. granularis* and *S. miliaris*) as monophyletic (Table 1.3). The general consensus amongst most studies is that *Scutellastra* as a whole is paraphyletic (Lindberg 2007, Nakano & Ozawa 2011). However, there is no coherent opinion on whether the southern African *Scutellastra* subclade is paraphyletic or monophyletic (Table 1.3).

It is clear *Scutellastra* is the most taxonomically problematic group within the patellogastropods and the evolutionary relationship within *Scutellastra* is poorly understood (Nakano & Sasaki 2011). There is thus a need to thoroughly examine evolutionary relationships within the South African *Scutellastra* subclade (Figure 1.2). As noted before, more than half of the patellid limpets described worldwide are endemic to the southern African shoreline; hence understanding the evolutionary relationships amongst these taxonomically problematic limpets would be a major contribution in ascertaining phylogenetic resolution amongst *Scutellastra* species.

The evolutionary relationships amongst several *Scutellastra* species remain a mystery due to their lack of common ancestry or synapomorphic characters. Thus, the phylogeny of these patellid limpets remains controversial due to their lack of morphologically synapomorphic characters (Yoon & Kim 2007). There are also studies that have documented evidence of cryptic species in these morphologically variable limpets (Simison & Lindberg 2003, Nakano & Spencer 2007 and Nakano et al. 2009). While the integration of morphological and genetic characters is generally considered to improve the resolution of phylogenetic trees; in this case, the phylogenetic incongruence between these two approaches further complicates the systematics of this group.

Table 1.3: The phylogenetic resolution of various southern African patellid limpets included in previous studies. Foraging Behaviour: ^T = Territorial, ^{NT} = Non-territorial, ^{IM} = Intermediate.

Species	Monophyletic/ Paraphyletic	Localities	Studies
<i>Scutellastra</i>			
<i>S. aphanes</i> ^T	Paraphyletic	Munster (South Africa)	Koupofanou et al. (1999) Nakano & Ozawa (2004, 2007)
<i>S. barbara</i> ^{IM}	Paraphyletic	Kommetjie (Cape Town)	ii
<i>S. cochlear</i> ^T	Paraphyletic	Kommetjie (Cape Town)	ii
<i>S. longicosta</i> ^T	Paraphyletic	Kommetjie (Cape Town)	ii
<i>S. obtecta</i> ^T	Paraphyletic	Cape Vidal (Cape Town)	ii
<i>S. argenvillei</i> ^{IM}	Monophyletic	Kommetjie (Cape Town)	ii
<i>S. granularis</i> ^{NT}	Monophyletic	Kommetjie (Cape Town)	ii
<i>S. miliaris</i> ^{NT}	Monophyletic	Mocámedes (Angola)	ii
<i>Cymbula</i>			
<i>C. compressa</i> ^T	Monophyletic	Kommetjie (Cape Town)	ii
<i>C. miniata</i> ^T	Monophyletic	Kommetjie (Cape Town)	ii
<i>C. granatina</i> ^{NT}	Monophyletic	Kommetjie (Cape Town)	ii
<i>C. oculus</i> ^{NT}	Monophyletic	West Bank (Cape Town)	ii
<i>Helcion</i>			
<i>H. concolor</i>	Monophyletic	West Bank (East London)	ii
<i>H. dunkeri</i>	Monophyletic	Bloubergstrand (Cape Town)	ii
<i>H. pectunculus</i>	Monophyletic	Kommetjie (Cape Town)	ii
<i>H. pruinusus</i>	Monophyletic	Dalebrook (Cape Town)	ii

The southern African *Scutellastra* species which were included in previous phylogenetic studies included samples mostly from Kommetjie along the west coast (Table 1.3). This study will reconstruct phylogeny of southern African patellid limpets using multiple samples from multiple populations. This phylogeny will subsequently be used to assess the evolution of life history traits related to foraging behaviour with special attention to the *Cymbula* and *Scutellastra* species complexes. To my knowledge, this is the first study to investigate molecular phylogeny of the southern African patellid limpets and the evolution of foraging traits.

The objectives of this study are two-fold:

- 1) To reconstruct a comprehensive molecular phylogeny of southern African patellid limpets using multiple markers and further assess their generic relationships and monophyly.
- 2) To use this phylogeny to evaluate the evolution of foraging traits within the southern African patellid limpets.

1.2 Materials and Methods

1.2.1 Selection of the study species and sampling

A list of the identified and described southern African patellid limpets is presented in Table 1.4. The study species (Figures 1.3, 1.4, 1.5 and 1.6) were primarily selected based on their well documented foraging behaviour. As a result, sampling was biased towards species with foraging behaviour of interest, for example territorial and non-territorial foragers. The species were identified based on their shell morphology following Branch et al. (2010). The samples were collected across 18 localities along the South African shoreline (Figure 1.7). At least five specimens of each species were collected randomly from each locality and immediately fixed in 100% ethanol. The samples of *Scutellastra miliaris* were sourced from three Angolan shorelines, namely Baia do Bengo, Lobito and Flamingo (Figure 1.7) and kindly provided by Branch GM.

Table 1.4: A list of the described southern African patellid limpets. The species endemic to the South African shoreline are indicated by * (Branch et al. 2010, Ridgway et al. 1999a and 2000).

♦ = The species which were not sampled in this study but GenBank sequences included.

<i>Scutellastra</i> spp.	<i>Cymbula</i> spp.	<i>Helcion</i> spp.
1. <i>S. aphanes</i> *♦	1. <i>C. adansonii</i>	1. <i>H. concolor</i>
2. <i>S. argenvillei</i>	2. <i>C. canescens</i> ♦	2. <i>H. dunkeri</i> ♦
3. <i>S. barbara</i>	3. <i>C. compressa</i>	3. <i>H. pectunculus</i> ♦
4. <i>S. cochlear</i>	4. <i>C. decepta</i> ♦	4. <i>H. pruinus</i> *♦
5. <i>S. exusta</i> ♦	5. <i>C. granatina</i>	
6. <i>S. granularis</i>	6. <i>C. miniata</i>	
7. <i>S. longicosta</i> *	7. <i>C. oculus</i> *	
8. <i>S. miliaris</i>	8. <i>C. safiana</i> ♦	
9. <i>S. natalensis</i> *	9. <i>C. sanguinans</i> *	
10. <i>S. obtecta</i> *		
11. <i>S. tabularis</i> *		

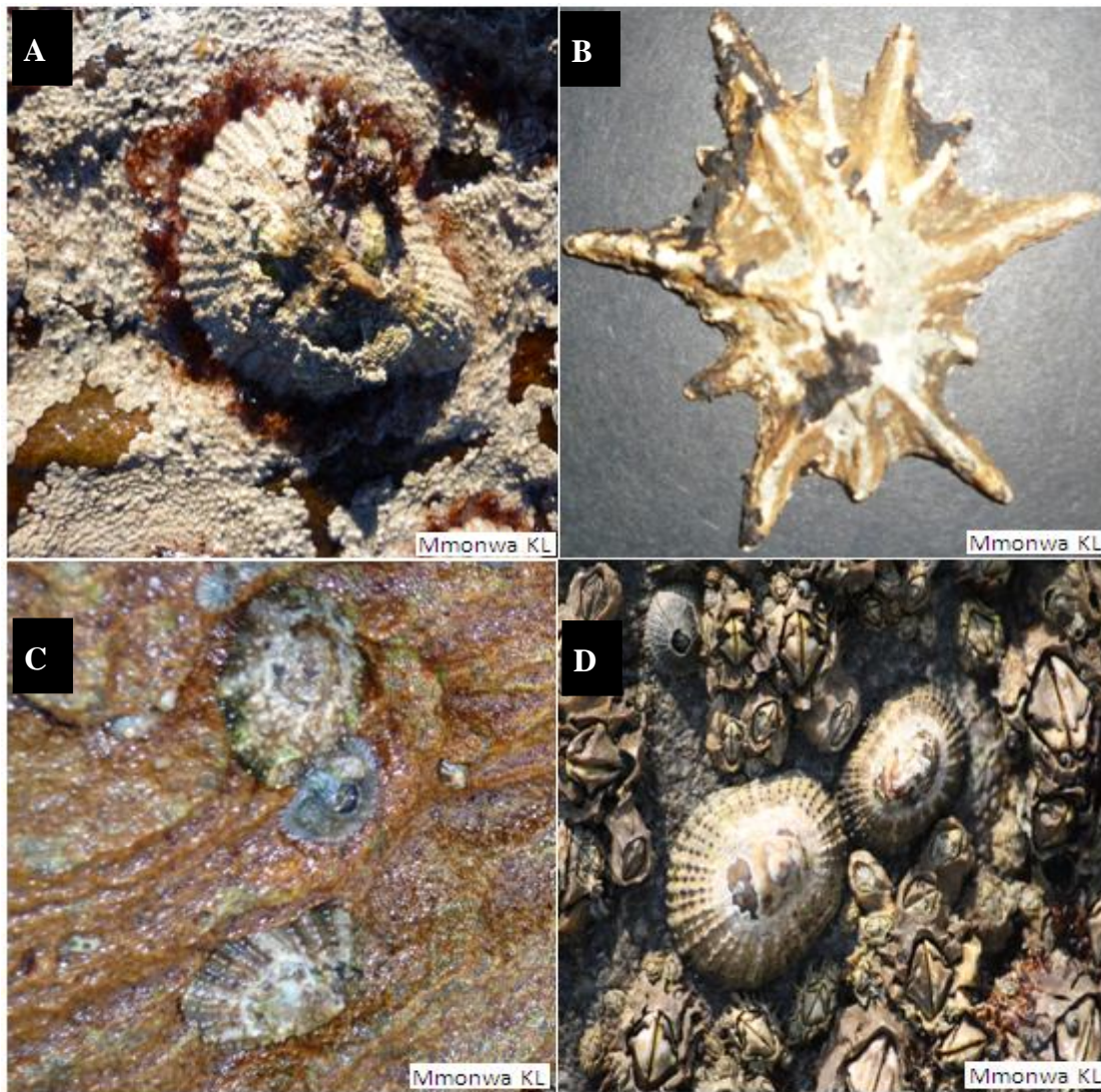
1.2.2 *The study species*

Figure 1.3: **A.** Territorials *Scutellastra cochlear* and **B.** *Scutellastra longicosta*
C. Non-territorials *Scutellastra granularis* and **D.** *Scutellastra natalensis*.

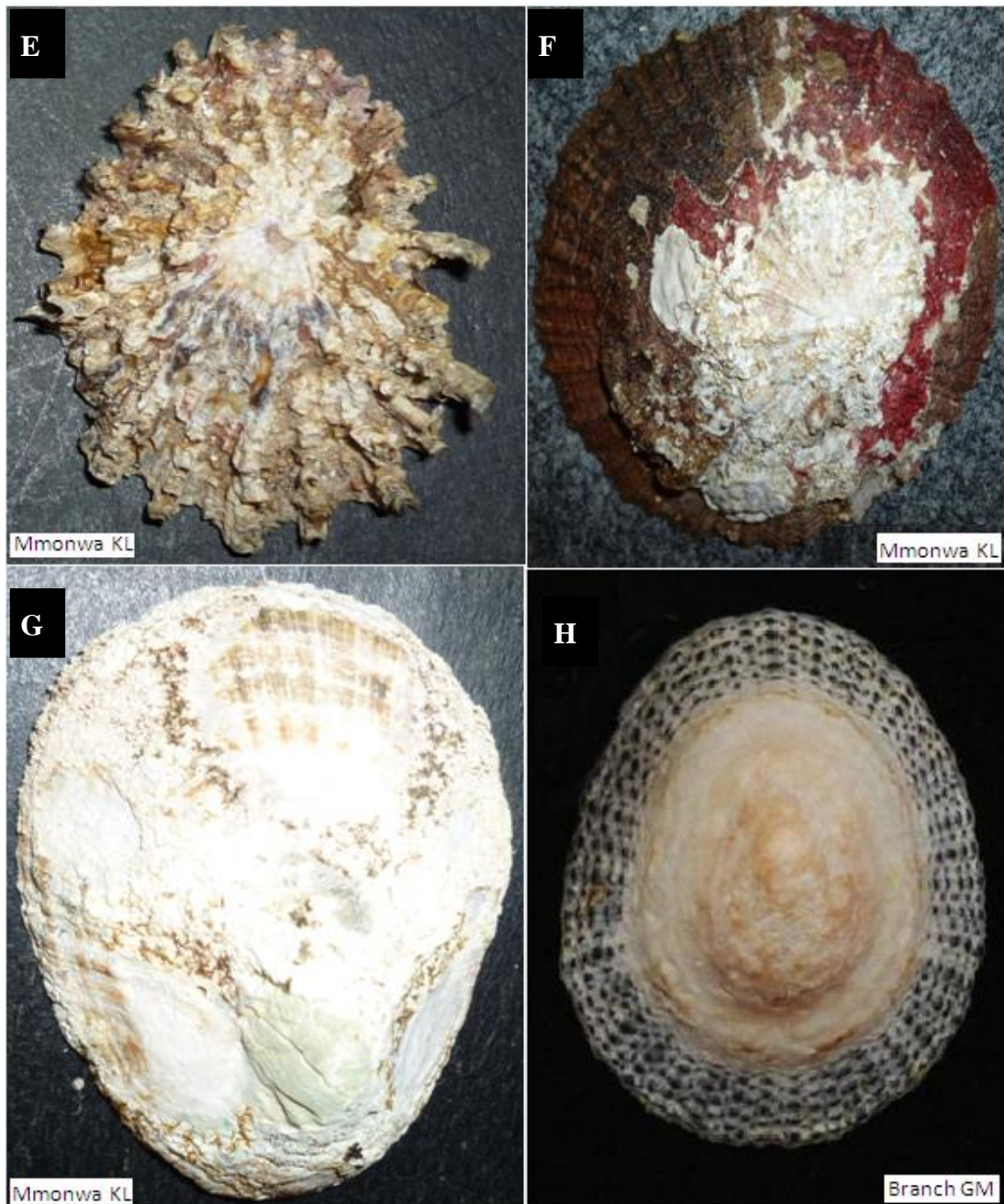


Figure 1.4: E. Intermediate *Scutellastra barbara* and F. Territorial *Scutellastra tabularis*
G. Intermediate *Scutellastra argenvillei* and H. Non-territorial *Scutellastra miliaris*.

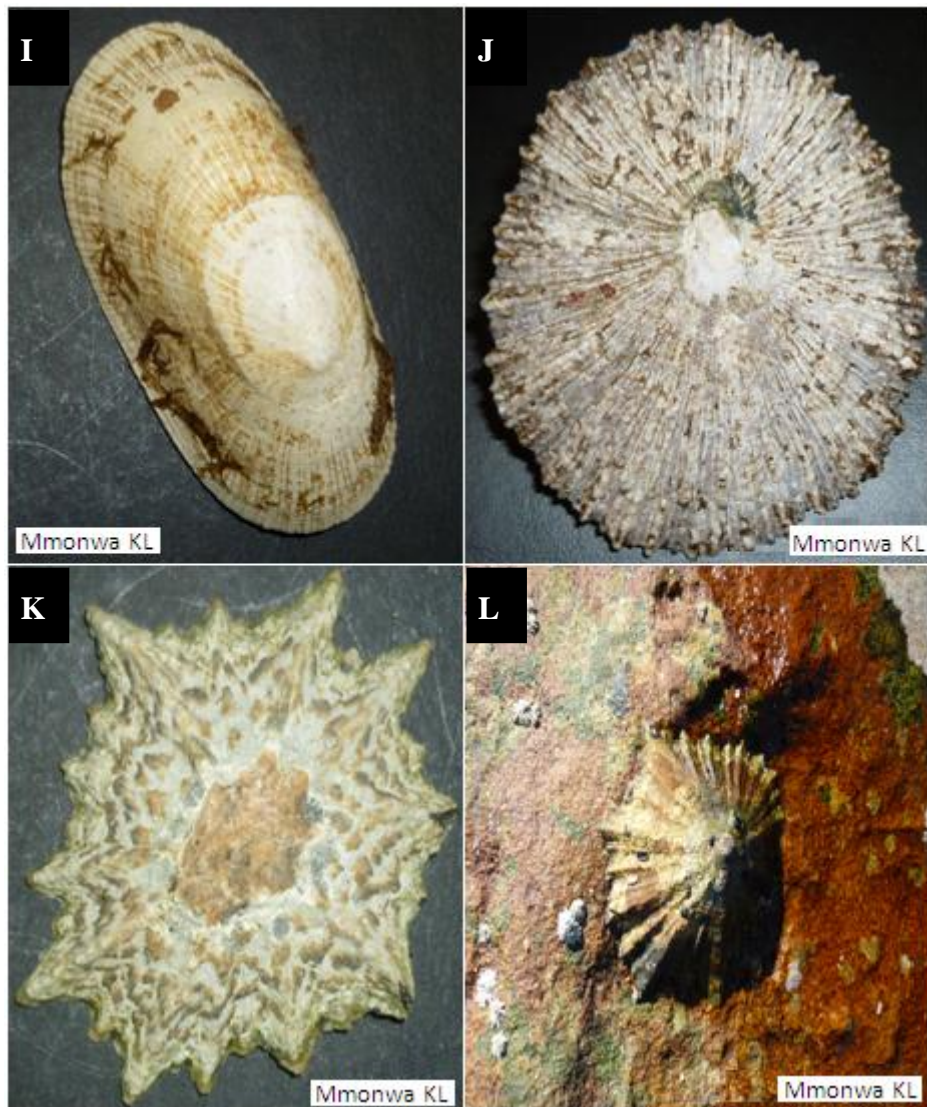


Figure 1.5: I. Territorials *Cymbula compressa* and J. *Cymbula miniata*.
K. Non-territorials *Cymbula granatina* and L. *Cymbula oculus*

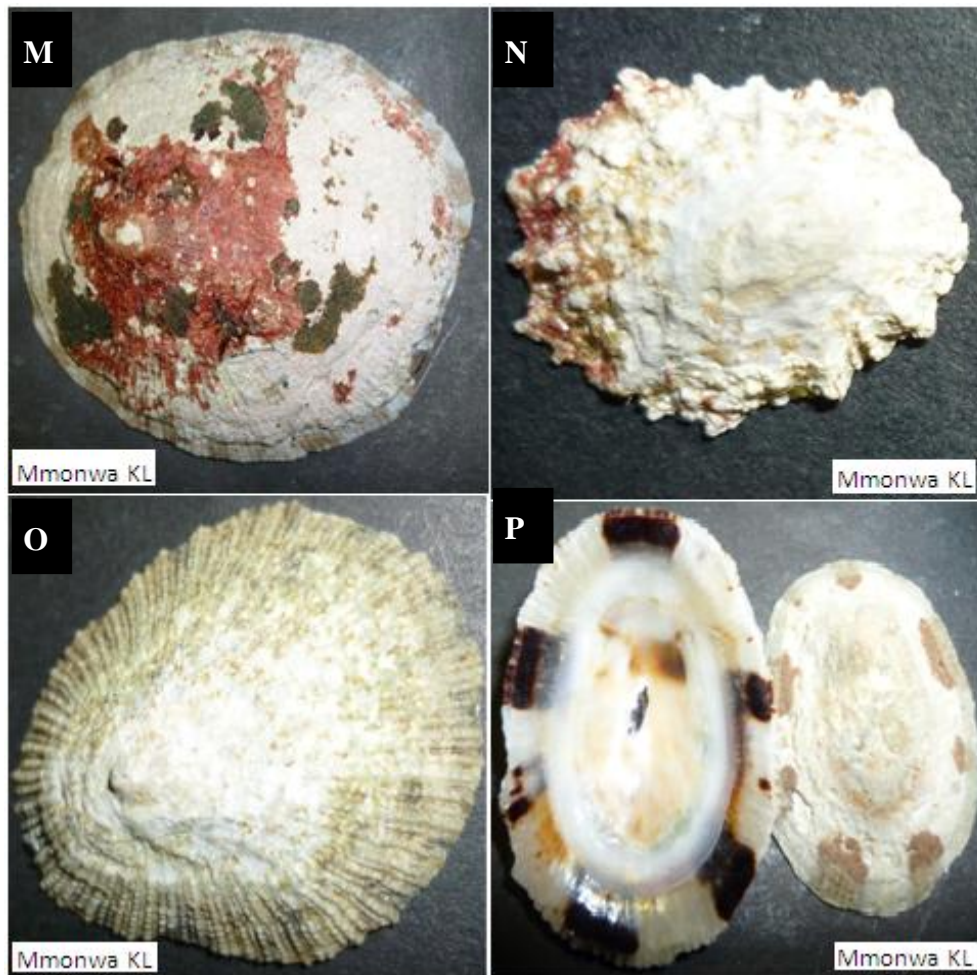


Figure 1.6: M. Territorials *Cymbula sanguinans* and N. *Scutellastra obtecta*
O. The non-territorial *Helcion concolor* and P. The outgroup *Cellana capensis*.

1.2.2 Sampling localities

The sampling localities along the Angolan and South African shorelines are presented below in Table 1.5 and illustrated in Figure 1.7.

Table 1.5: The sampling localities and the GPS co-ordinates along the Angolan and South African coastline.

Sampling localities	GPS points(Latitude, Longitude)	Collector
Angolan shoreline		
1. Baia do Bengo (BAB)	8°48'35.07"S, 13°13'58.97"E	Branch GM
2. Lobito (LBT)	12°21'38.98"S, 13°31'34.40"E	Branch GM
3. Flamingo (FMG)	12°36'57.80"S, 13°13'38.55"E	Branch GM
South African shoreline		
4. Groenriviermond (GRM)	30°51'53.68"S, 17°34'46.42"E	Mmonwa KL
5. Doring Bay (DRB)	31°49'0.00"S, 18°13'60.00"E	Mmonwa KL
6. Lamberts Bay (LMB)	32° 5'38.86"S, 18°18'18.85"E	Mmonwa KL
7. Paternoster (PTN)	32°48'25.26"S, 17°53'9.20"E	Mmonwa KL
8. Cape Columbine (CCB)	33° 6'22.65"S, 17°57'2.17"E	Mmonwa KL
9. Camps Bay (CMB)	33°56'51.68"S, 18°22'38.51"E	Mmonwa KL
10. Muizenberg (MZB)	34° 5'43.46"S, 18°30'36.13"E	Mmonwa KL
11. Strandfontein (STF)	34° 4'29.30"S, 18°41'8.68"E	Branch GM
12. Cape Agulhas (CPA)	34°50'7.71"S, 19°59'44.28"E	Mmonwa KL
13. Mossel Bay (MSB)	34°11'43.43"S, 22° 8'38.93"E	Mmonwa KL
14. Tsitsikamma (TSK)	33°59'42.77"S, 23°43'45.20"E	Mmonwa KL
15. Sardinia Bay (SDB)	34° 2'8.01"S, 25°30'24.71"E	Mmonwa KL
16. Kenton-on-Sea (KOS)	33°40'51.81"S, 26°41'45.52"E	Mmonwa KL
17. Haga Haga (HAG)	32°45'56.59"S, 28°14'56.69"E	Mmonwa KL
18. Port St. Johns (PSJ)	31°38'0.29"S, 29°33'7.41"E	Mmonwa KL
19. Port Edward (PED)	31° 2'44.13"S, 30°13'44.77"E	Mmonwa KL
20. Park Rynie (PKR)	30°19'47.80"S, 30°44'13.86"E	Mmonwa KL
21. Ballito (BLT)	29°31'40.68"S, 31°13'34.97"E	Mmonwa KL

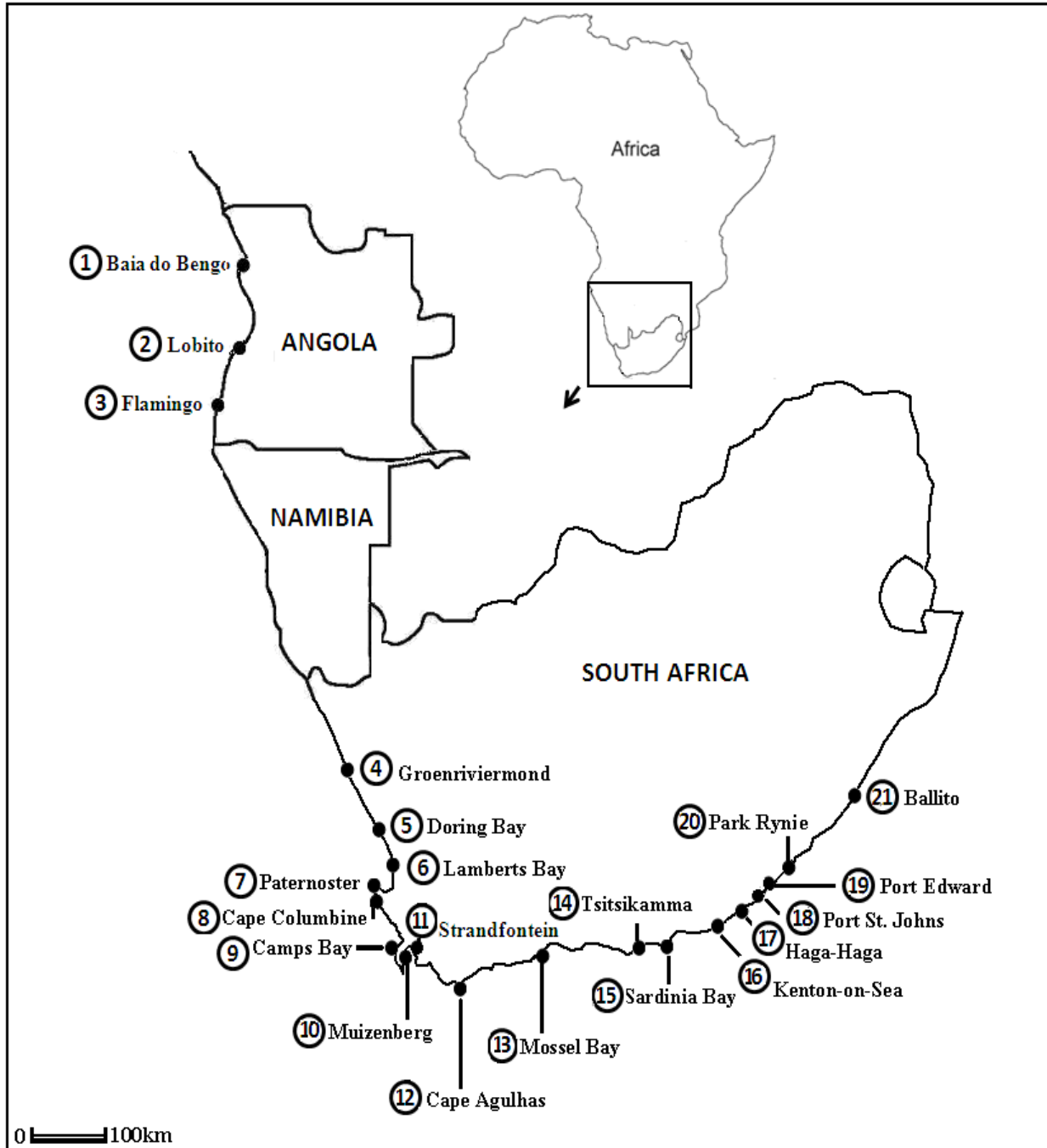


Figure 1.7: A map of southern Africa showing the sampling localities along the South African shoreline and the sampling localities of *Scutellastra miliaris* along the Angolan shoreline.

The species collected from each shore are indicated in Table 1.6 below, the sampling for each species was largely delimited by species` range and availability.

Table 1.6: The species and the number of individual samples collected from each site. *S* = *Scutellastra*, *C* = *Cymbula* and *H* = *Helcion*. Site numbers as per Figure 1.7 and abbreviations in Table 1.5.

Study species	Sites																					
	BAB	LBT	FMG	GRM	DRB	LMB	PTN	CCB	CMB	MZB	STF	CPA	MSB	TSK	SDB	KOS	HAG	PSJ	PED	PKR	BLT	
	①	②	③	④	⑤	⑥	⑦	⑧	⑨	⑩	⑪	⑫	⑬	⑭	⑮	⑯	⑰	⑱	⑲	⑳	㉑	
<i>S. argenvillei</i>				5		5		5					5								6	
<i>S. barbara</i>				5		6		7			5	6	5	5	7	5	6	5				
<i>S. cochlear</i>				6	5	5	5	5	5	5		6	6	5	6	5	7					
<i>S. granularis</i>				5	5	5	5	5	5	5		5	5	5	5	6	5					
<i>S. longicosta</i>										5		5	5	5	5	6	5					
<i>S. natalensis</i>																				6	6	6
<i>S. miliaris</i>	10	10	10																			
<i>S. obtecta</i>																					3	
<i>S. tabularis</i>																					4	
<i>C. compressa</i>				10	10		10	10	10		10											
<i>C. granatina</i>				10	10		10	10	10													
<i>C. miniata</i>				5		5							5	6	6							
<i>C. oculus</i>												5	6	6	6	5	6			3		
<i>C. sanguinans</i>														3								
<i>H. concolor</i>														4								
<i>Cellana capensis</i> (outgroup)														3								

1.2.3 DNA extraction, PCR and Sequencing

Muscle tissue from the foot was dissected using alcohol-sterilized razor blades. The tissue was rinsed with double distilled water (ddH₂O) and left in TE buffer overnight. Total genomic DNA was then extracted using the cetyltrimethyl ammonium bromide (CTAB) protocol by Doyle & Doyle (1987). The partial fragments of both mitochondrial and nuclear sequences were amplified by PCR for each sample. Three mitochondrial markers (12S rRNA, 16S rRNA and CO1) and one nuclear marker (ATPS β intron) were amplified.

The amplification reagents were prepared in a 50 μ l reaction volume consisting of 16 μ l 5X buffer (50 mM KCL, 10 mM Tris-HCL, pH 8.0), 5 μ l of 5 mM MgCl₂, 2 μ l dNTPs, 2 μ l of each primer (forward and reverse), 0.5 μ l Taq Polymerase, 5 μ l template DNA and 17.5 μ l ddH₂O to fill-up the reaction medium to 50 μ l. The PCR amplifications were conducted on a ThermoHybaid PCR Sprint Temperature Cycling System under the following parameters: initial denaturation at 95 °C for three minutes, followed by 30 cycles of denaturation at 95 °C for 45 seconds, annealing at 48 °C (CO1), 54 °C (12S rRNA and 16S rRNA) and 58 °C (ATPS β) for 45 seconds and extension at 72 °C for 3 minutes. A final extension of 10 minutes at 72 °C was included at the end of the PCR run. The universal CO1 primers by Folmer et al. (1994) failed to amplify in territorial *Scutellastra* species and internal primers were designed using the primer designer software *CLC Main Workbench 6.7* (CLC Bio). The details of all the primers used are presented in Table 1.7 for each of the four markers.

The PCR products were purified using the Promega Magic PCR Preps TM, QIAGEN® QIAquick™ following the manufacturer's instructions. The purified PCR products were used for cycle sequencing reactions prepared for both forward and reverse sequences. The sequencing reactions were conducted on ABI Prism BigDye Terminator v3.0 or v3.1 Ready Reaction Cycle Sequencing Kit (Applied Biosystematics) under the following cycling parameters: 95 °C for 45 seconds, 50 °C for 45 seconds and 60 °C for 3 minutes repeated for 30 cycles. Cycle sequencing products were precipitated using an EDTA/Sodium Acetate procedure according to manufacturer's instructions. Sequences were then generated for both directions on ABI 3100 genetic analyzer at Rhodes University's Sequencing Unit.

Table 1.7: The table showing the details of the primers used for all four regions amplified.

Marker	Primers	Primer sequences	Author
1. CO1	LCO1490 HCO2198	5'-TCAACAAATCAYAAAGAYATTGG -3' 5'- AATTAATAATRTAWACTTCTGG -3'	Folmer et al. 1994
2. CO1 (Territorial <i>Scutellastra</i>)	Scut F1 Scut R1	5`-TCWGGYYTAGTHGGRAC-3` 5`- CAYARWASCATAGTRATDGC-3`	This study
3. 12S rRNA	12Sar 12Sbr	5`- CTGGGATTAGATACCCCACTA-3` 5`-TGAGGAGGGTGACGGGCGGT-3`	Kocher et al. 1989
4. 16S rRNA	16Sar 16Sbr	5`- CGCCTGTTTATCAAAAACAT-3` 5`- GCCGGTCTGAACTCAGATCACGT-3`	Palumbi 1996
5. ATPS β	ATPS β f1 ATPS β f2	5'-TGRATTCCCTGATGTTTTTGTGAG-3' 5'- CGGGCACGGGCRCCDGGNGGTTCGT-3'	Jarman et al. 2002

1.2.4 Sequence editing and alignment

The forward and reverse sequences were assembled, checked and edited using SequencherTM version 3.1.1 and version 4.2.2. (Gene Codes Corporation) and aligned by eye using MacClade version 4.0.6. (Maddison & Maddison 2000). The alignments were edited and formatted into different files for different phylogenetic analyses using DAMBE version 5.3.8 (Xia & Xie 2001). The ATPS β sequences of some of the samples (for all the species) comprised different introns and exons of variable nucleotide lengths. In such cases, the exons were trimmed and the final alignment comprised only introns of equivalent lengths. The aligned intron regions were comparable amongst different taxa and probably have similar evolutionary origins.

1.2.5 Genbank samples

For the samples not sequenced in this study, their published sequences were downloaded from GenBank (Table 1.8) and included in the analyses. The nuclear ATPS β data comprised exclusively southern Africa samples sequenced in this study and is thus a smaller data set.

Table 1.8: The samples and their accession numbers downloaded from GenBank.

Taxon	Location	CO1	12S rRNA	16S rRNA
<i>Cymbula</i>				
<i>C. adansonii</i>	South Africa		AF058190	
<i>C. canescens</i>	South Africa		AF058191	
<i>C. safiana</i> 1&2	Spain	AB238573	AF058198 & AB238327	
<i>Helcion</i>				
<i>H. dunkeri</i> 1&2	South Africa		AF058175 & AB238329	
<i>H. pectunculus</i>	South Africa		AF058176	
<i>H. pruinosis</i> 1&2	South Africa		AF058177 & AB238330	
<i>Scutellastra</i>				
<i>S. aphanes</i>	South Africa		AF058178	
<i>S. exusta</i> 1&2	South Africa & Madagascar		AF058189 & AB238336	
<i>S. flexuosa</i> 1&2	Western Samoa		AF058183 & AB106433	
<i>S. optima</i>	Japan		AB106434	
<i>S. sp.</i> ESU1	Madagascar		AB238339	
<i>Patella</i>				
<i>P. aspera</i>	Portugal	AJ291545	AF058203	AF058249
<i>P. caerulea</i>	Spain	AB238577		
<i>P. candei</i>	Portugal	JF763830.1		AF058255
<i>P. depressa</i> 1&2	Portugal	EU073891 & EU073893		AF058257
<i>P. depressa</i> 4&5	Spain	EF462972 & EF462974	AF058208	
<i>P. lugubris</i>	Cape Verde	EU073889.1		AF058259
<i>P. pellucida</i> 1&2	Portugal & UK	DQ089620 & DQ089621		AF058223
<i>P. rustica</i>	Spain	AB238579		
<i>P. vulgata</i>	UK	AB238580	AF058213	

1.2.6 Phylogenetic analyses

The phylogenies were reconstructed separately for each marker using a maximum likelihood (ML) approach with RAxML HPC version 7.2.6 (Stamatakis 2006). Gaps were treated as missing data and uncertainties as ambiguity characters. The program assumes the GTR + I + G substitution model and 1000 bootstrap replications were run to generate likelihood support values for the branch nodes. These ML trees were all rooted using *Cellana capensis* (Gmelin, 1791), as the Nacellidae have been consistently identified as the evolutionarily closest taxon to the patellid limpets (Nakano & Ozawa 2004 and González-Wevar et al. 2011b). The mitochondrial markers (CO1, 12S rRNA and 16S rRNA) were congruent in their resolution of the major clades and the sequences were concatenated to make a single data set.

The concatenated data set comprised only southern African samples which had CO1, 12S rRNA and 16S rRNA in common. The *Patella* spp. were chosen as the outgroup taxa for the concatenated data set based on their basal resolution in the ML analysis of the three markers (CO1, 12S rRNA and 16S rRNA). The concatenated data set was subjected to Bayesian Inference (BI), maximum likelihood (ML) and maximum parsimony (MP) analyses.

The ATPS β sequences were not included in the concatenated data set due to several critical problems in the sequences which complicated alignment. The high number of indels and variable nucleotide length in ATPS β sequences resulted in alignment uncertainty. Additionally, the determined substitution model for the ATPS β (Table 1.9) was in conflict with the SYM + G substitution model determined for the three mitochondrial markers (CO1, 12S rRNA and 16S rRNA). Consequently, the ATPS β was analysed separately using BI, ML and MP analyses.

Bayesian phylogenetic inference (BI) was performed using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003). The GTR + I + G substitution model was applied as the approximate substitution model closest to the SYM + G model determined by jModelTest 0.1.1 (Posada 2008)

for the concatenated markers (Table 1.9). Two chains were run concurrently for 20,000,000 generations each and trees were sampled every 2000 generations. The final majority rule consensus phylogram was generated after removing the first 10% of the trees as burn-in. The posterior probability values which indicate the node support were determined using the Metropolis-coupled Markov chain Monte Carlo (MCMC) criterion.

Table 1.9: The results of the jModelTest for the four markers as determined using the corrected Akaike Information Criterion (AICc).

Marker	AICc negative log Likelihood	Model selected
CO1	7312.6	SYM + G
12S rRNA	2358.3	SYM + G
16S rRNA	2991.4	SYM + G
ATPS β	3763.1	TPM3 + G

The maximum parsimony (MP) analyses were conducted using PAUP* version 4.0b (Swofford 2002). The characters were equally-weighted. The Heuristic search and tree bisection reconnection (TBR) plus branch-swapping option were selected as the criteria to reconstruct the phylogenetic tree. The node support was assessed using bootstrap values which were determined using the non-parametric bootstrapping with 1000 pseudo-replicates (Felsenstein 1981).

1.2.7 Estimation of divergence times

The concatenated data set (CO1, 12S rRNA and 16S rRNA) was analysed in Beast v. 1.41 (Drummond & Rambaut 2007) to estimate the approximate divergence time amongst major clades. The height nodes and branch length were converted into divergence times calibrated using a minimum reference date of 163 millions year ago (Mya) for the ancestral *Patella* species (Nakano & Ozawa 2007).

1.3 Results

1.3.1 Phylogenetic analyses

The details of each of the five data sets used to reconstruct maximum likelihood phylogenetic trees are presented in Table 1.10 below.

Table 1.10: The details of each of the five data sets used to reconstruct phylogenetic trees

Data set	Ingroup taxa	Final alignment Length	No. of variable characters (%)	No. of parsimony informative characters(%)
CO1	80	658	325 (49%)	312 (96%)
12S rRNA	70	323	196 (61%)	163 (83%)
16S rRNA	70	523	226 (43%)	179 (79%)
ATPS β	70	232	161 (69%)	160 (99%)
Concatenated data (CO1, 12S rRNA and 16S rRNA)	62	1518	639 (42%)	599 (94%)

The ML tree reconstructed using the CO1 data set recovered seven major clades (Figure 1.8) which conformed to the following genera or taxa: *Patella*, *Scutellastra argenvillei*, *Cymbula*, *Helcion*, *Scutellastra B*, *Scutellastra A* and *Cymbula compressa*. The latter taxon was resolved as a sister taxon to the rest of the clades followed by *Patella* which was resolved as sister taxon to the remaining clades (100% maximum likelihood support). The resolution of *C. compressa* as a distinct lineage or taxon was very weak and not supported at all. The mitochondrial CO1 sequence of *C. compressa* was very distinct and distant from CO1 sequences of other *Cymbula* spp. The genus *Patella* was resolved as the basal clade with 100% maximum likelihood support. Strikingly, *S. argenvillei* was resolved separately from other *Scutellastra* species. The species was resolved as a sister taxon to the *Cymbula* - *Helcion* clade but with only weak support (70%). The analysis resolved the remaining *Scutellastra* spp. as paraphyletic, comprising two main clades, *Scutellastra A* (territorial species) and *Scutellastra B* (non-territorial species).

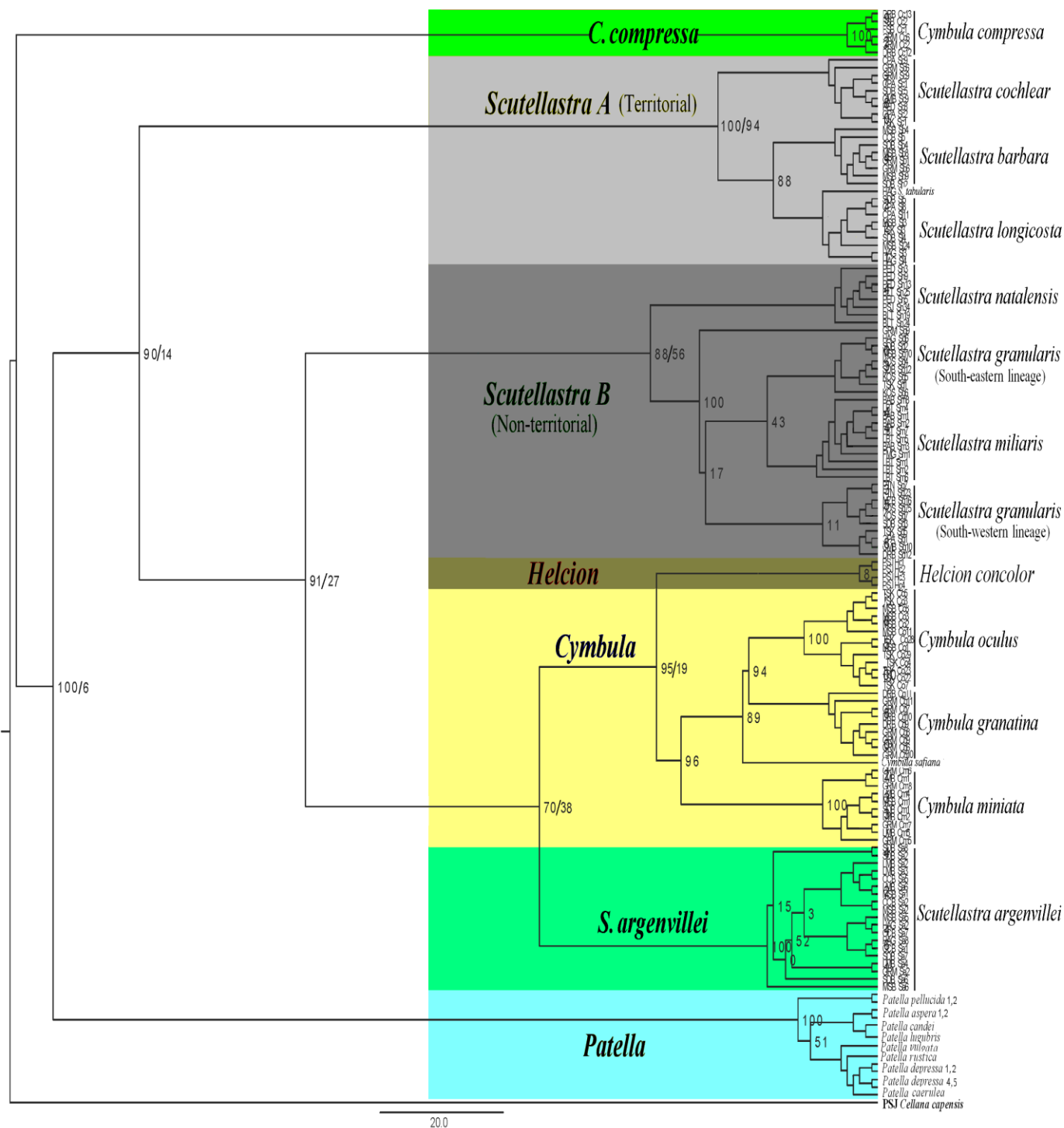


Figure 1.8: The Maximum likelihood (ML) phylogenetic tree reconstructed using CO1 data set recovered seven major clades indicated by different colours. The values at the branch nodes indicate the likelihood support of the diverging taxa based on 1000 bootstrap replicates/branch lengths for major clades.

The ML tree reconstructed using the 16S rRNA data set recovered five major clades (Figure 1.9) which conformed to the following genera: *Patella*, *Helcion*, *Scutellastra B*, *Scutellastra A* and *Cymbula*. The genus *Patella* was resolved as the sister clade to the rest, with 93% maximum likelihood support. The genus *Helcion* was resolved as a monophyletic sister clade to *Scutellastra A*, *Scutellastra B* and *Cymbula*. In contrast to CO1, 16S rRNA resolved *Scutellastra A* (territorial) and *Scutellastra B* (non-territorial) as monophyletic sister taxa with 96% maximum likelihood support (Figure 1.9). *Scutellastra* as a whole was resolved as sister taxa to *Cymbula* with 86% maximum likelihood support. In contrast to CO1, the 16S rRNA resolved *C. compressa* together with the rest of *Cymbula spp* (Figure 1.9).

The ML tree reconstructed using the 12S rRNA data set recovered six major clades (Figure 1.10) which conformed to the following genera: *Patella*, *Scutellastra A*, *Scutellastra B*, *Cymbula*, *Helcion* and *Scutellastra* (Indo-Pacific). Overall, the 12S rRNA analysis yielded the most poorly resolved ML tree with weak bootstrap support values for most of the clades. For example, the non-territorials *Cymbula oculus* and *C. granatina* were resolved as paraphyletic with weak bootstrap support of 61% and 72% respectively. *Cymbula canescens* and *C. safiana* (GenBank samples) were also resolved as paraphyletic with weak bootstrap support of 54%. Additionally, the territorial *Scutellastra A* and *Scutellastra B* were resolved as paraphyletic with weak bootstrap support of 75% and 73% respectively. The poor resolution of the 12S rRNA tree may be attributed to insertions and deletions (indels) which complicated sequence alignment (Doyle & Gaut 2000) and thus a poorly resolved phylogenetic tree.

The genus *Helcion* was weakly resolved as a monophyletic sister taxa to the territorial *Cymbula* species (47% likelihood support). The *Scutellastra* clade comprising samples from the Indo-Pacific (GenBank samples) were resolved as sister taxa to *Scutellastra A*, *Scutellastra B*, *Cymbula* and *Helcion* (98% maximum likelihood support). *Patella* was resolved as the sister clade to the rest with 100% maximum likelihood support (Figure 1.10).

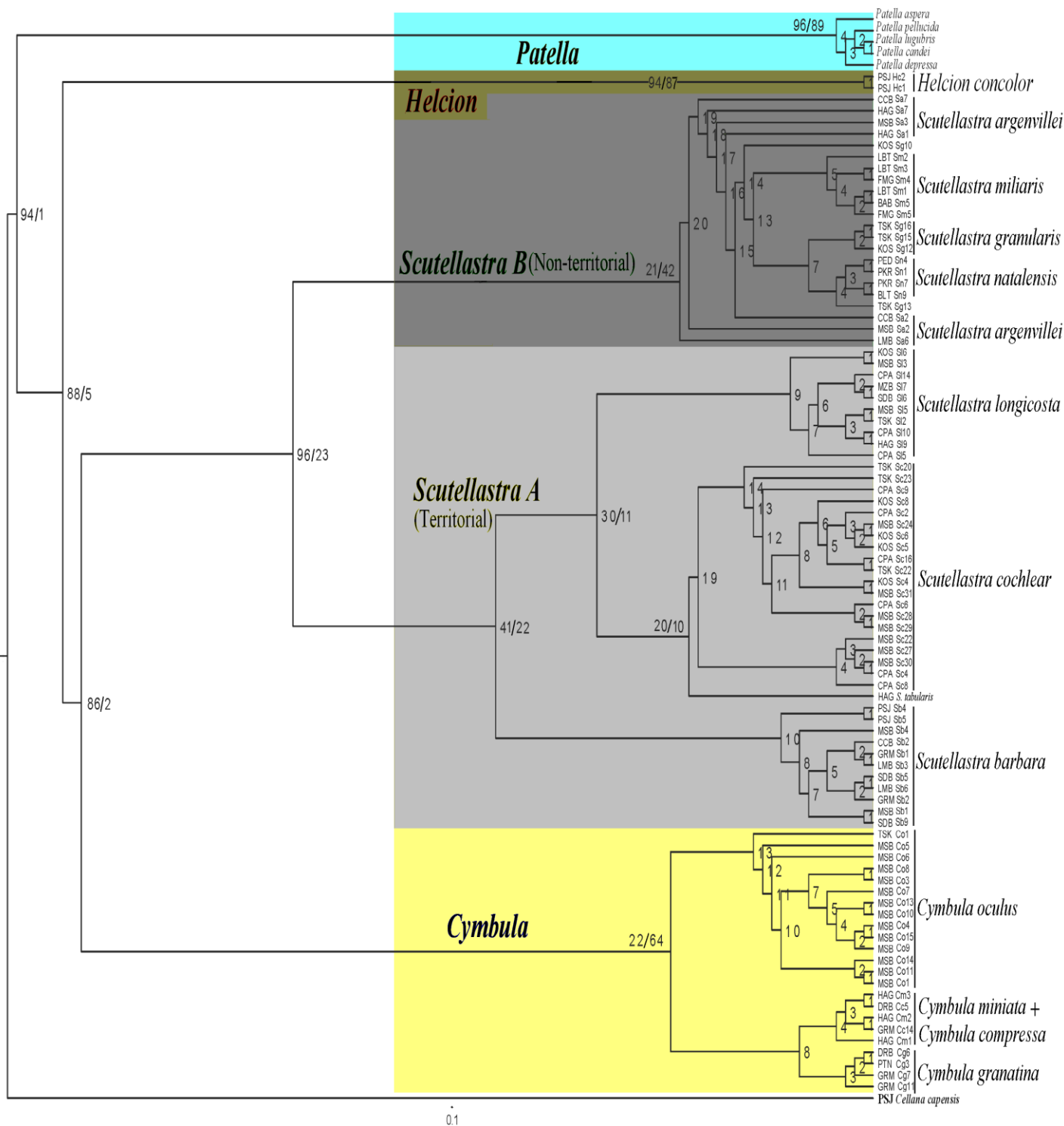


Figure 1.9: The Maximum likelihood (ML) phylogenetic tree reconstructed using 16S rRNA data set recovered five major clades indicated by different colours. The values at the branch nodes indicate the likelihood support of the diverging taxa based on 1000 bootstrap replicates/branch lengths for major clades.

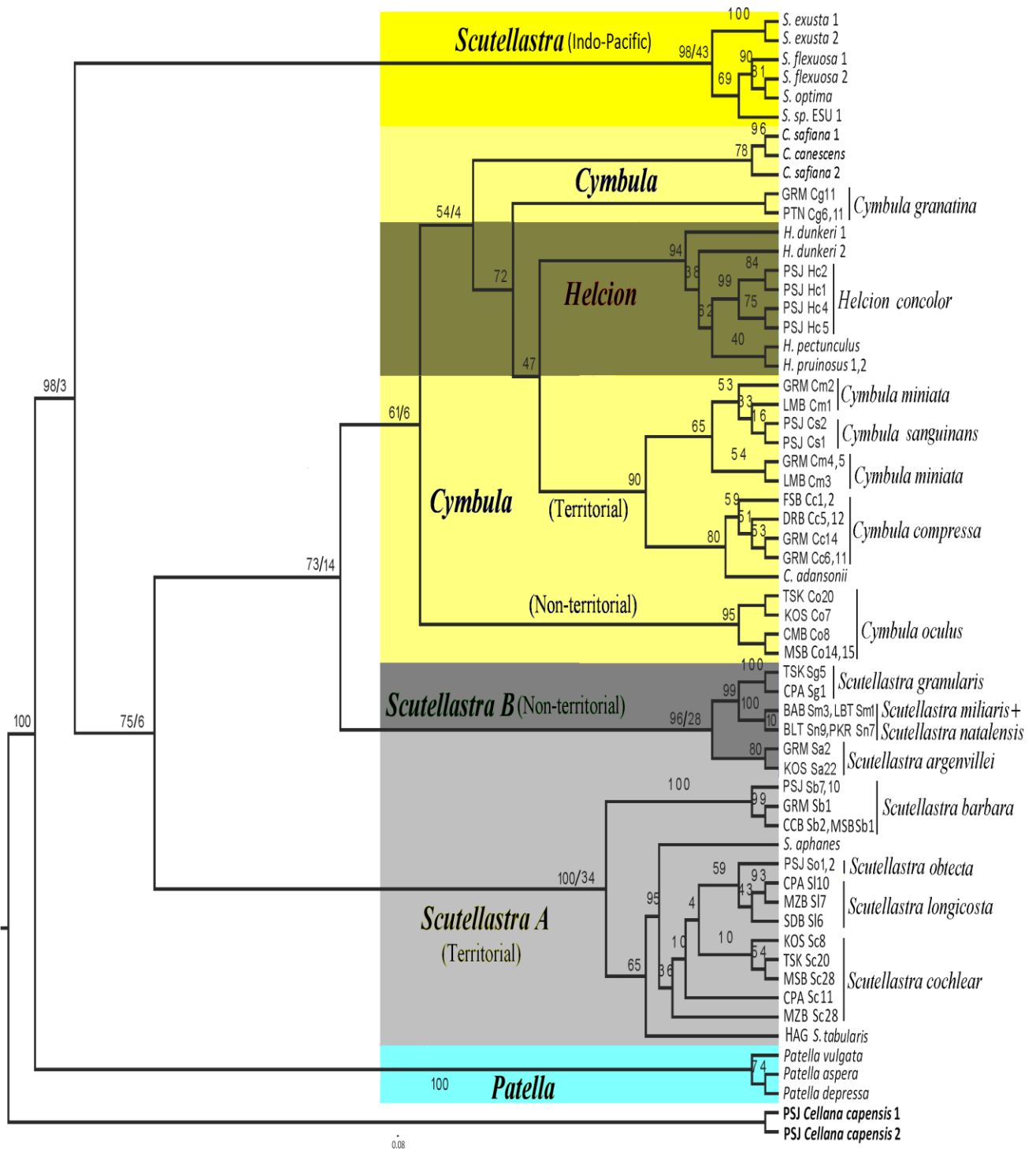


Figure 1.10: The Maximum likelihood (ML) phylogenetic tree reconstructed using 12S rRNA data set recovered six major clades indicated by different colours. The values at the branch nodes indicate the likelihood support of the diverging taxa based on 1000 bootstrap replicates/branch lengths for major clades.

The four main recovered clades (*Scutellastra A*, *Scutellastra B*, *Cymbula* and *Helcion*) were common in ML trees of CO1, 12S rRNA and 16S rRNA. The three markers were not congruent in resolution of most of the clades. For example, CO1 resolved *C. compressa* and *S. argenvillei* as distinct clades whereas they were resolved with their congeneric species in 12S rRNA and 16S rRNA analyses. The 16S rRNA resolved territorial *Scutellastra A* and non-territorial *Scutellastra B* as monophyletic sister taxa, whereas CO1 and 12S rRNA resolved *Scutellastra A* as paraphyletic.

The BI, ML and MP analyses of the concatenated data set recovered four main clades which conformed to the following genera: *Helcion*, *Cymbula*, *Scutellastra A* and *Scutellastra B*. The BI and ML phylogenetic reconstruction revealed similar phylogenetic trees with the same tree topology (Figures 1.11 and 1.12). The analyses resolved *Helcion* as sister taxon to the rest of the taxa, with a posterior probability of 1.0 (Figure 1.11) and 100% likelihood support (Figure 1.12). *Scutellastra A* (territorial) and *Scutellastra B* (non-territorial) were resolved as sister taxa with posterior probability of 1.0 (Figure 1.11) and 96% maximum likelihood support (Figure 1.12). *Cymbula* was resolved as a monophyletic sister taxa to both *Scutellastra A* and *B* with posterior probability of 0.93 (Figure 1.11) and 92% maximum likelihood support (Figure 1.12). *Cymbula* was further resolved into two sister subclades corresponding to territorial and non-territorial species with posterior probability of 1.0 (Figure 1.11) and 98% maximum likelihood support (Figure 1.12).

The MP phylogenetic reconstruction was slightly different to the BI and ML analyses in the resolution of evolutionary relationships amongst the four clades (Figure 1.13). The MP analysis resolved *Scutellastra A* as paraphyletic taxon (100% bootstrap support) to the rest of the clades. *Scutellastra B* was resolved as a monophyletic sister taxon to both *Cymbula* and *Helcion* which themselves were resolved as sister taxa with 82% bootstrap support. The *Cymbula* clade (87% bootstrap support) was further subdivided into two sister subclades corresponding to territorial (85% bootstrap support) and non-territorial (100% bootstrap support) species.

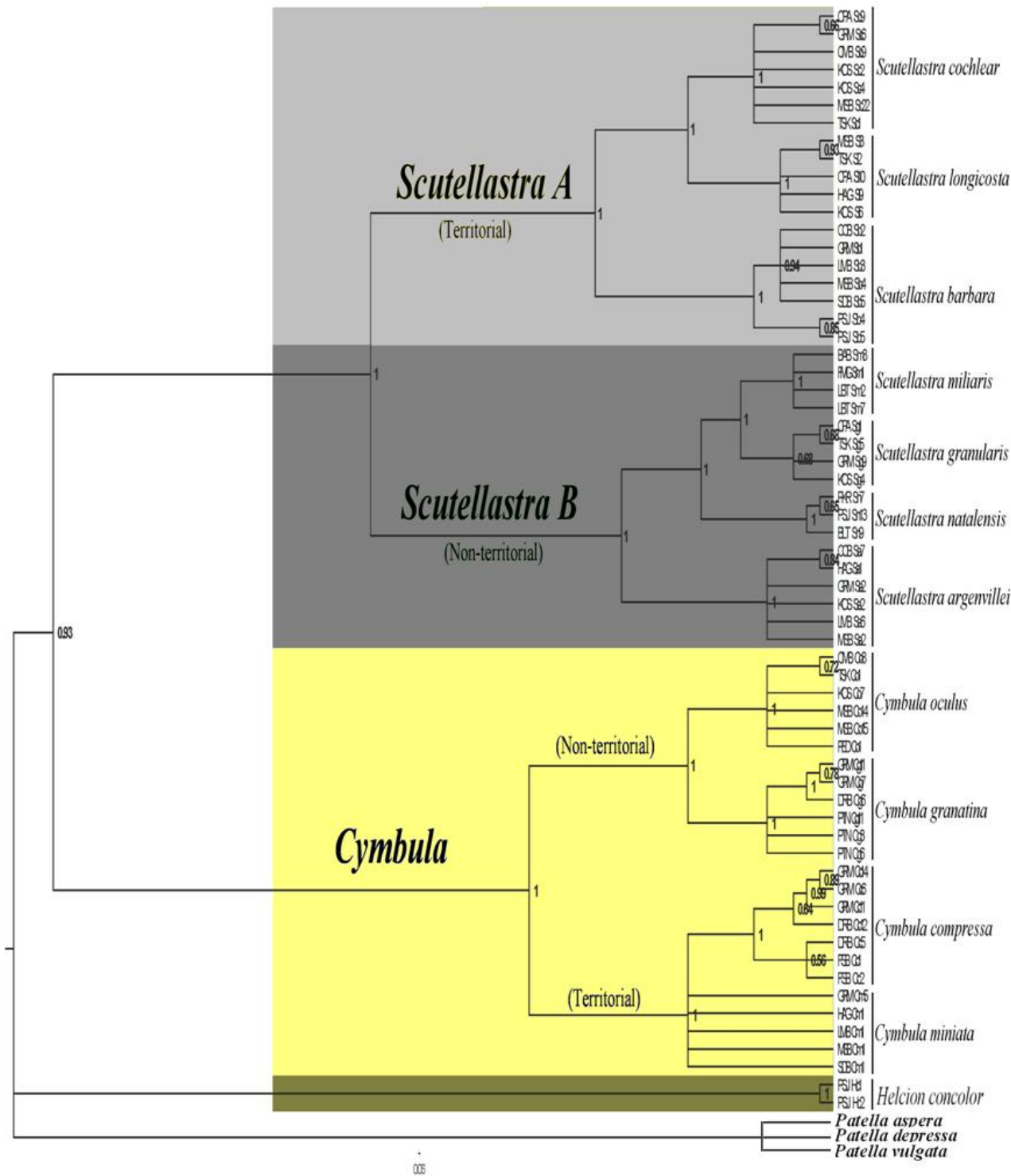


Figure 1.11: The Bayesian Inference (BI) phylogenetic tree reconstructed using the concatenated data set (12S rRNA, 16S rRNA and CO1) recovered four major clades indicated by different colours. The numbers above the branch nodes are the posterior probability values of the diverging clades based on 1000 replicates.

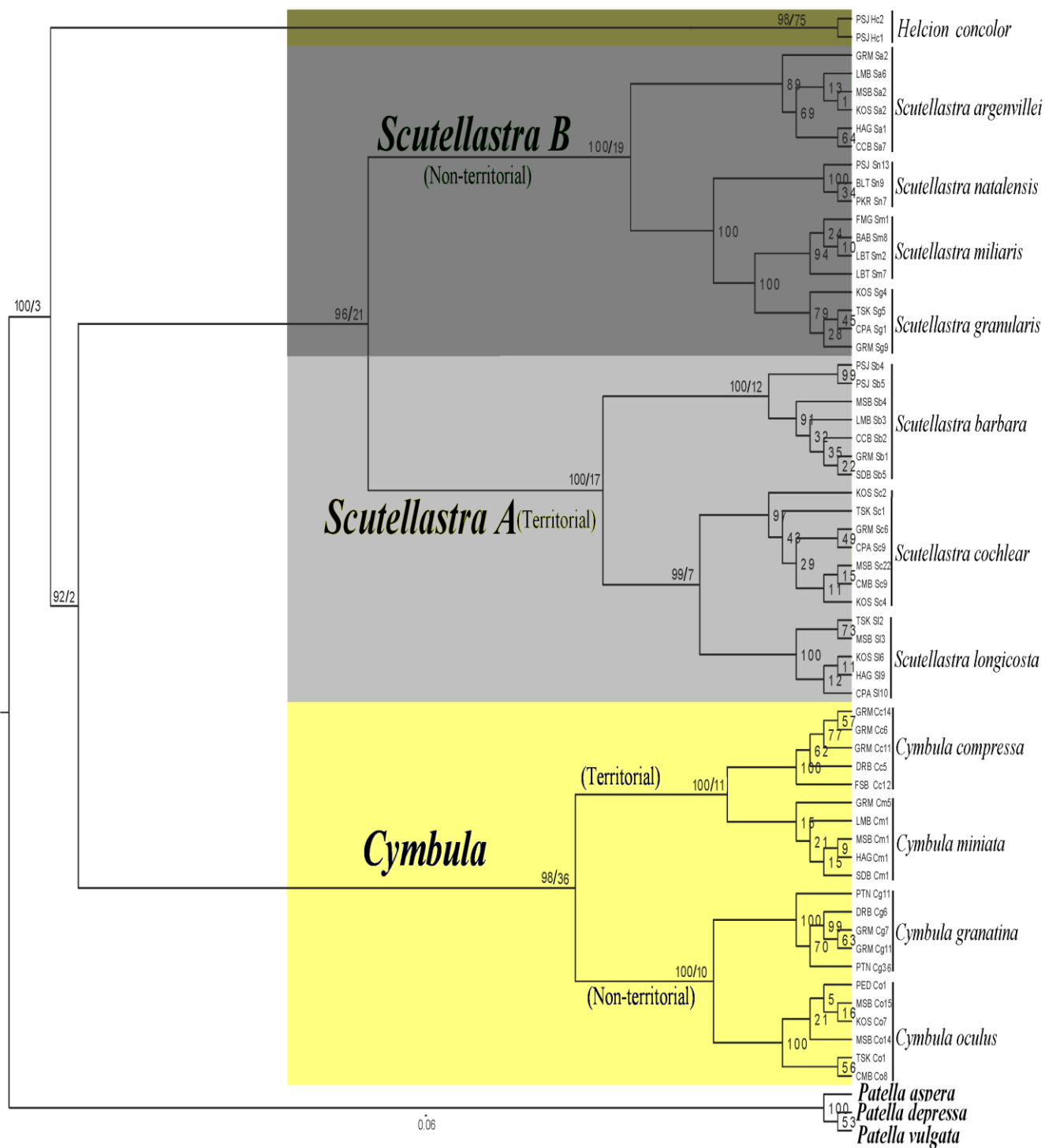


Figure 1.12: The Maximum likelihood (ML) phylogenetic tree reconstructed using the concatenated data set recovered four major clades indicated by different colours. The numbers above the branch nodes indicate the maximum likelihood support of the diverging taxa based on 1000 bootstrap replicates/branch lengths for major clades.

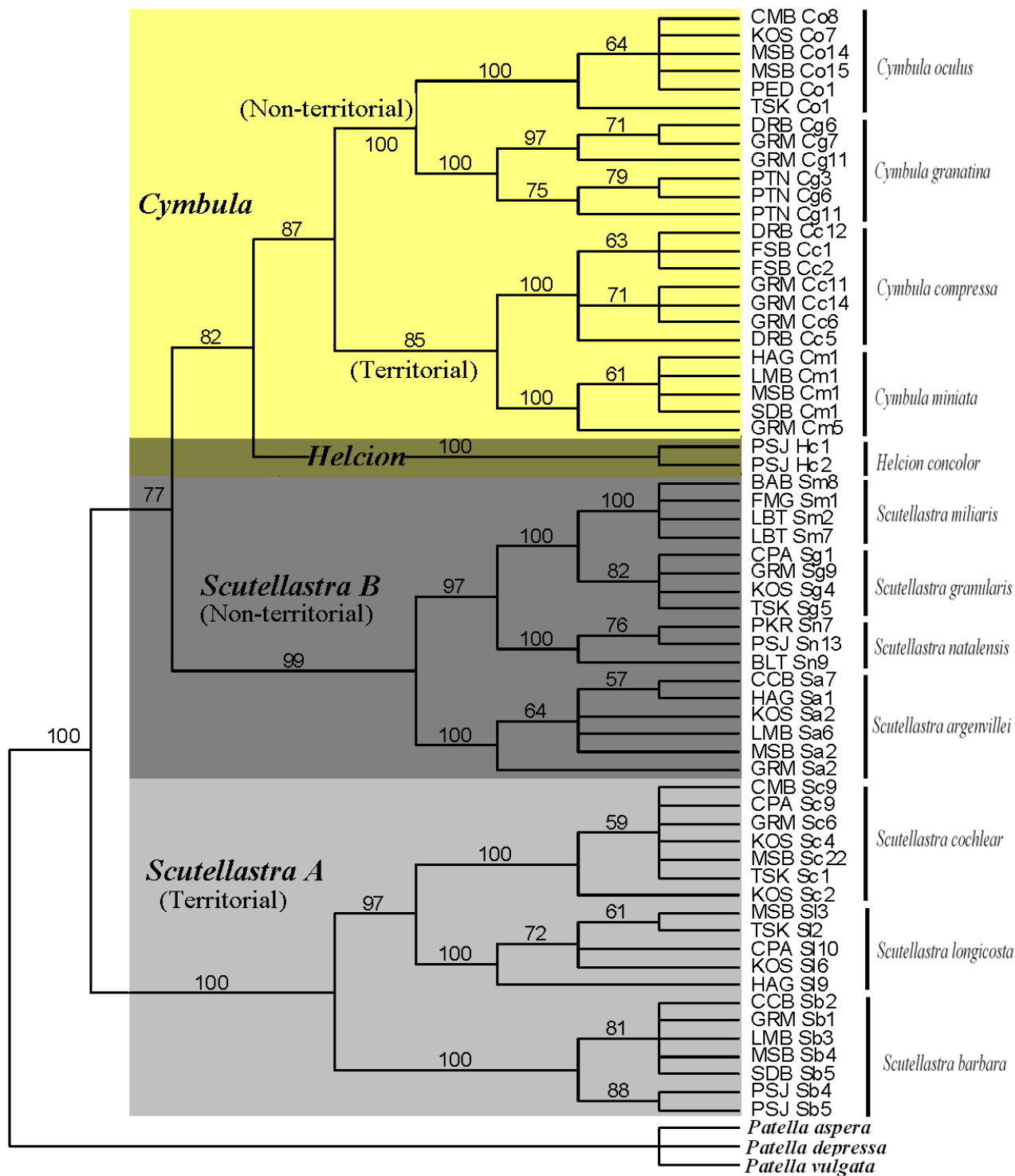


Figure 1.13: The Maximum parsimony (MP) phylogenetic tree reconstructed using the concatenated data set recovered four major clades indicated by different colours. The numbers above the branch nodes indicate the bootstrap support of the diverging taxa based on 1000 bootstrap replicates.

The BI, ML and MP phylogenetic reconstruction using the ATPS β data set recovered four main clades (Figures 1.14, 1.15 and 1.16) which conformed to the following genera: *Helcion*, *Cymbula*, *Scutellastra A* and *Scutellastra B*. The genus *Helcion* was resolved within the *Cymbula* clade (Figure 1.14), however the ML and MP analyses resolved the genus as a separate clade (Figures 1.15 and 1.16). The territorial and non-territorial *Cymbula* species were resolved as paraphyletic with weak bootstrap support of 23% and 10% respectively (Figures 1.15). The *Cymbula*, *Scutellastra A* and *Scutellastra B* clades were resolved as monophyletic with 100% support for sister relationship between *Scutellastra A* (territorial) and *Scutellastra B* (non-territorial) (Figures 1.14, 1.15 and 1.16). The whole of the *Scutellastra* clade was resolved as a sister taxa to the *Cymbula* clade (Figures 1.14, 1.15 and 1.16).

The ML analysis retrieved sister relation between territorial *Cymbula* and the whole of *Scutellastra* with a weak 23% likelihood bootstrap support (Figure 1.15). The non-territorial *Cymbula* species were weakly resolved as paraphyletic to *Scutellastra* with a weak 10% likelihood bootstrap support (Figure 1.15). Thus, the ML resolution of *Cymbula* into territorial and non-territorial subclades was very weak (Figure 1.15).

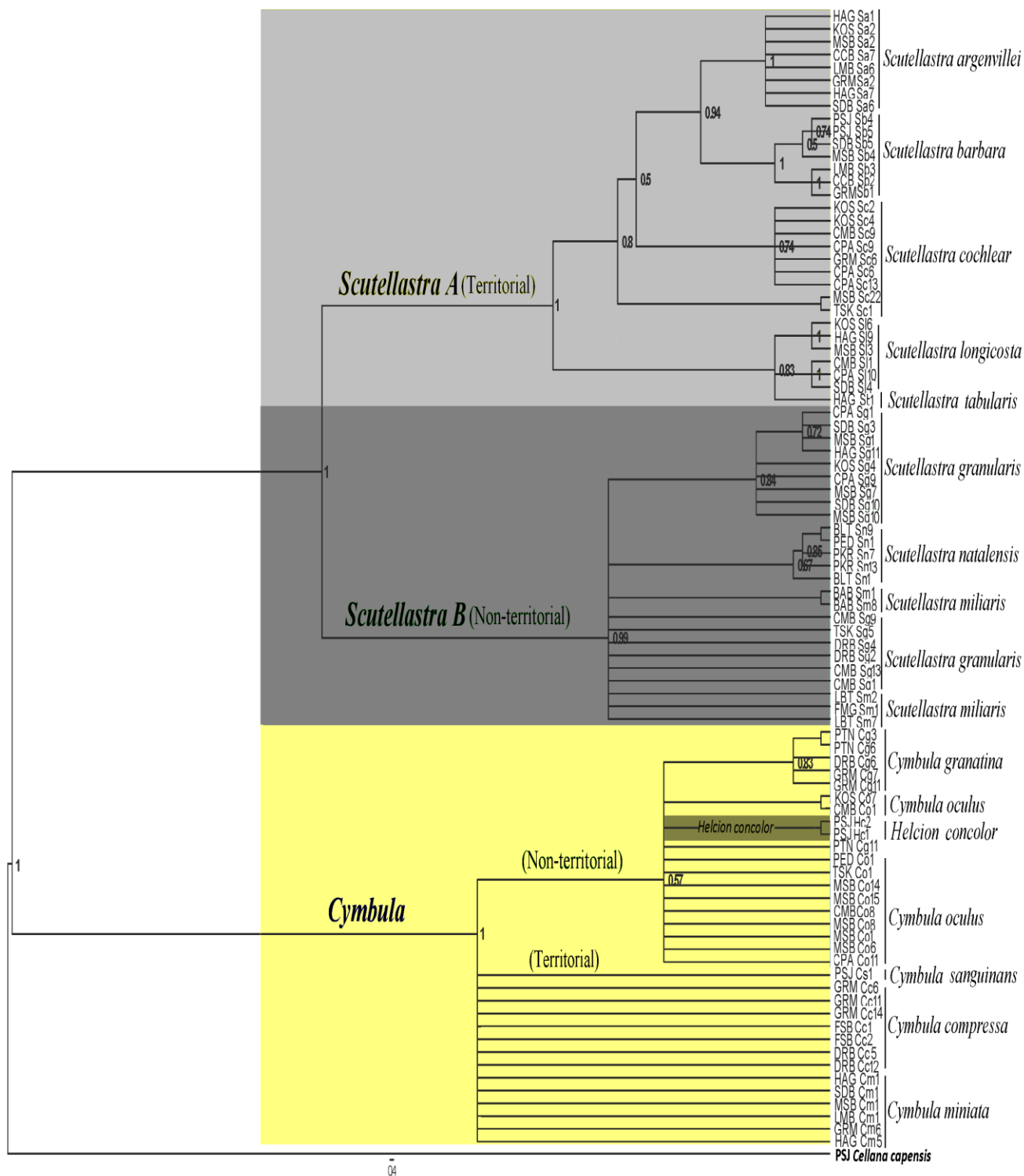


Figure 1.14: The Bayesian inference (BI) phylogenetic tree reconstructed using the ATPS β data set recovered four major clades indicated by different colours. The numbers at the branch nodes indicate the posterior probability support of the diverging taxa based on 1000 replicates.

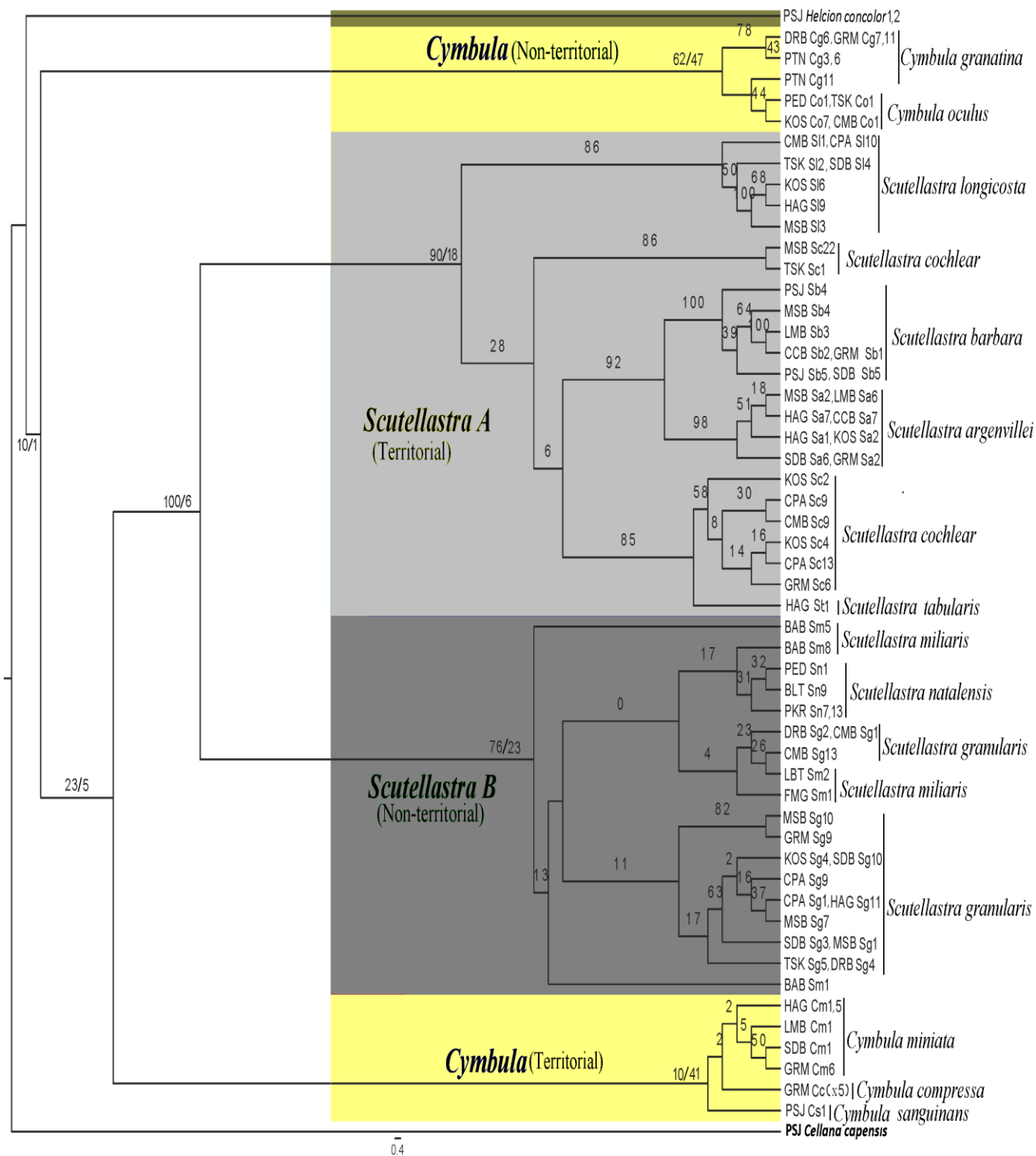


Figure 1.15: The Maximum likelihood (ML) phylogenetic tree reconstructed using the ATPS β data set recovered four major clades indicated by different colours. The values at the branch nodes indicate the likelihood support of the diverging taxa based on 1000 bootstrap replicates/branch lengths for major clades.

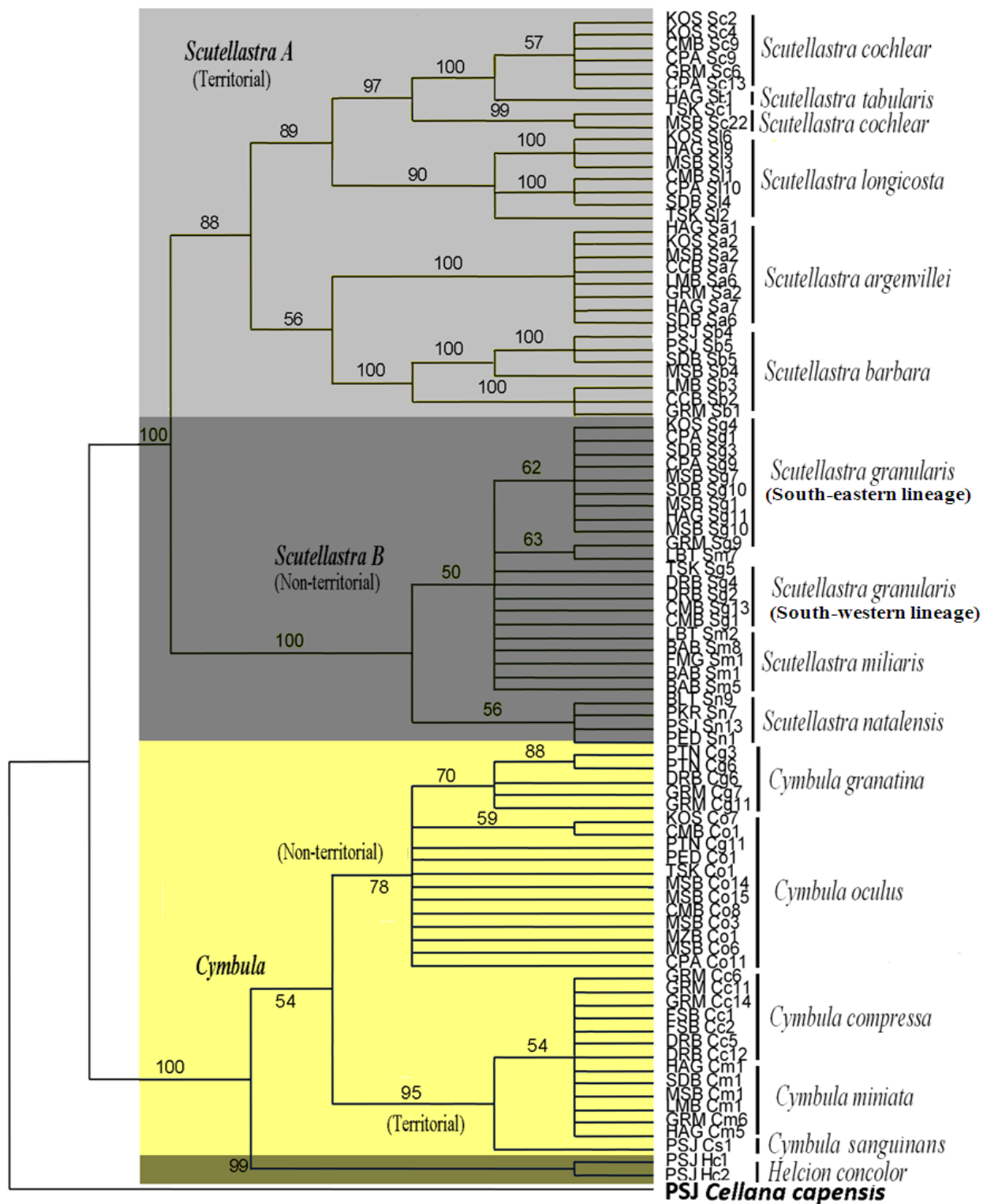


Figure 1.16: The Maximum parsimony (MP) phylogenetic tree reconstructed using ATPS β data set recovered four major clades indicated by different colours. The values at the branch nodes indicate the likelihood support of the diverging taxa based on 1000 bootstrap replicates.

1.3.2 Estimates of molecular divergence amongst the discovered clades

The Bayesian majority rule chronogram tree illustrating estimates of divergence times amongst discovered clades is presented in Figure 1.17. The major divergence times are summarised below in Table 1.11. The three South African patellid genera (*Helcion*, *Cymbula* and *Scutellastra*) started to diverge from the ancestral *Patella* species from the early Cretaceous (145 Mya) until the early Eocene (52 Mya). The *Helcion* was the first group to diverge (≈ 78 Mya), then followed by both *Cymbula* and *Scutellastra* simultaneously (≈ 47 Mya). The evolution or divergence of territorial and non-territorial species occurred almost within the same evolutionary time frame ($\approx 32 - 30$ Mya). The divergence times amongst territorial and non-territorial species dates approximately 32 and 30 Mya in *Scutellastra* and *Cymbula* species respectively. The divergence amongst the three parapatric granular limpets *Scutellastra granularis* and *S. miliaris* dates approximately 4 Mya whereas the sister species *S. natalensis* diverged from *S. granularis* approximately 2 Mya.

Table 1.11: The approximate divergence times (and 95% credibility intervals) in millions years ago (Mya) amongst major clades and genera of the southern African patellid limpets.

Taxa/Taxon	Divergence Time	Geological Time
<i>Scutellastra/Cymbula</i> vs. <i>Helcion</i>	78 (52 - 145) Mya	Late Cretaceous
<i>Scutellastra</i> vs. <i>Cymbula</i>	47 (28 - 69) Mya	Mid Eocene
<i>Scutellastra</i> A vs. <i>Scutellastra</i> B (Territorial) (Non-Territorial)	32 (18 - 50) Mya	Early Oligocene
<i>Cymbula</i> vs. <i>Cymbula</i> (Territorial) (Non-Territorial)	30 (14 - 44) Mya	Early Oligocene
<i>S. granularis</i> vs. <i>S. natalensis</i>	8 (4 - 15) Mya	Late Miocene
<i>S. granularis</i> vs. <i>S. miliaris</i>	4 (1 - 5) Mya	Mid Pliocene

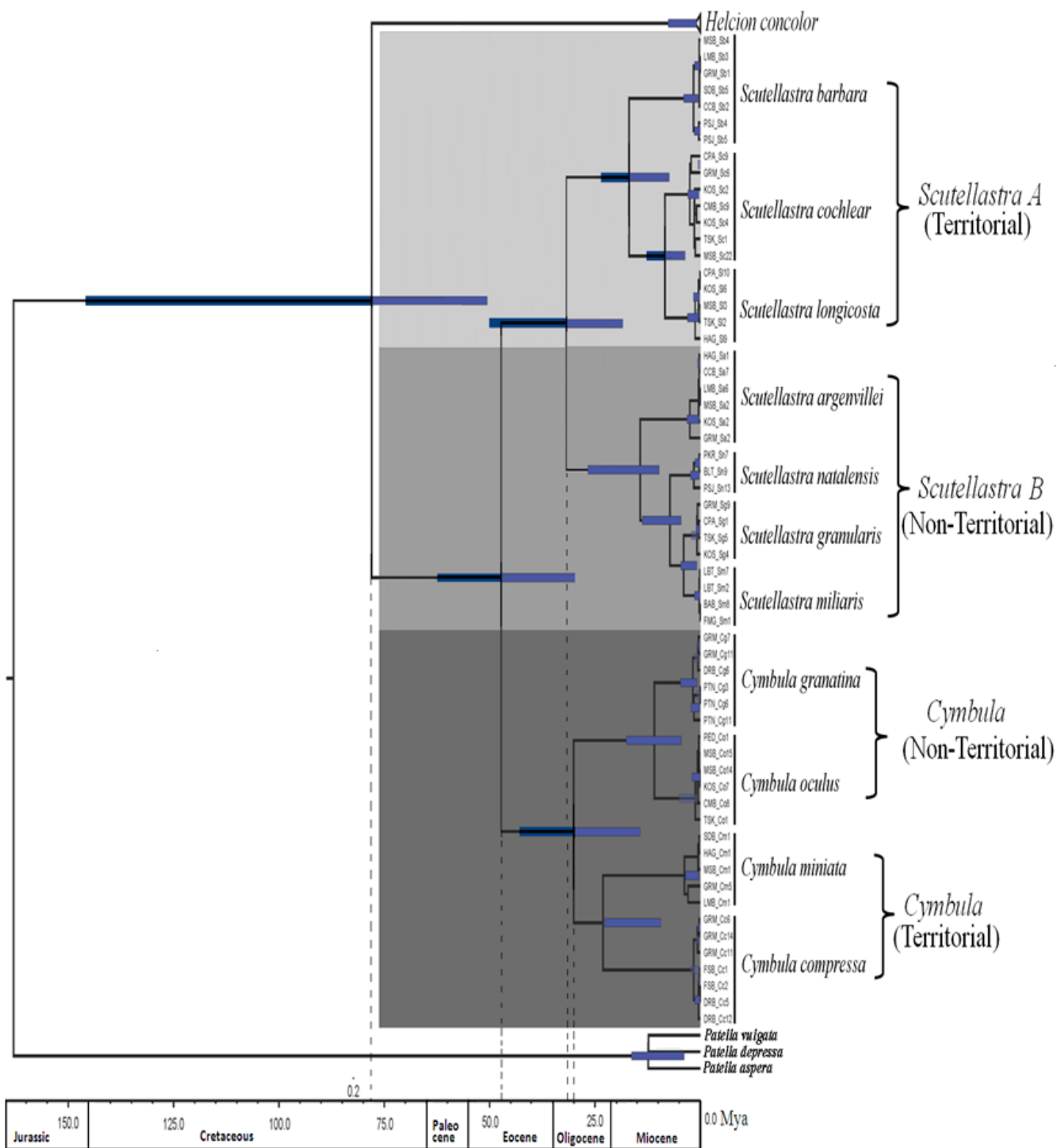


Figure 1.17: The Majority rule Bayesian chronogram tree generated in BEAST based on the concatenated data set (12S rRNA, 16S rRNA and CO1). The shaded bold line indicates 95% credibility intervals for each estimate of divergence time measured in millions years ago (Mya).

1.4 Discussion

1.4.1 Phylogenetic analyses

The phylogenetic reconstruction of each marker and the concatenated data retrieved five main patellid clades: *Patella*, *Helcion*, *Cymbula*, *Scutellastra A* and *Scutellastra B*. The congruent BI and ML trees from the concatenated data set are likely the best representation of the phylogeny of these limpets. *Patella* was consistently resolved as the sister taxa to the rest of the clades. The inclusion of the *Patella* spp. was essential for robust phylogenetic resolution but the genus will not be discussed any further. *Helcion* comprises only four southern African endemics with little information on their foraging ecology, though Branch (1975c) described *H. concolor* as non-territorial. and there is no evidence that any of the other South African *Helcion* spp. are territorial (C McQuaid personal communication).”The genus was resolved as a paraphyletic sister to *Scutellastra* and *Cymbula* (combined BI and ML). This discussion will exclusively focus on the two most species-rich genera, *Cymbula* and *Scutellastra*, the foraging ecology of which is very well understood (Branch 1975c and 1980).

The BI, ML and MP phylogenetic reconstructions of the concatenated data set consistently and strongly resolved *Cymbula* into two subclades, corresponding to territorial and non-territorial taxa. The territorial subclade comprises *C. compressa* and *C. miniata*, while the non-territorial subclade comprises *C. oculus* and *C. granatina*. The phylogenies further resolved *Cymbula* as a monophyletic sister taxon to the whole of *Scutellastra* (except in the concatenated MP analyses).

The most intriguing evolutionary resolution of *Cymbula* was observed in the phylogeny of the CO1 tree. This marker resolved the territorial *C. compressa* as the sister clade to all other clades. The sequences of these samples were re-checked, re-aligned and different samples re-sequenced and in all instances, the final sequences were similar. Additionally, the test for the stop codons ruled out the possibility that the sequenced CO1 fragment might be a pseudo-gene. It is highly unlikely that *C. compressa* is the sister clade to all other southern African patellid limpets for

two reasons. Firstly, the other three markers (12S rRNA, 16S rRNA and ATPS β) which are relatively conserved, and were derived from the same samples as the CO1 data, resolved *Cymbula compressa* with other *Cymbula* spp. Secondly, the paleogeographic evolutionary theories suggest all the patellid limpets originated from the Cretaceous Tethys coastline and migrated to the southern African shoreline, not *vice versa* (Koufopanou et al. 1999 and Nakano & Ozawa 2004). The distinct contemporary CO1 genealogy within *C. compressa* could possibly have arisen due to ancient hybridization between *C. compressa* and other sympatric patellid species.

The phylogenetic reconstructions based on the concatenated data set resolved *Scutellastra argenvillei* and *S. barbara* in the non-territorial and territorial clades respectively. These species were described as intermediate grazers based on the admixture of their ecological characters used to categorize them as either territorial or non-territorial grazers (Branch 1975c). As in other non-territorial grazers, the first lamellae layer of the radula is arranged circularly in *S. argenvillei* (Maneveldt 1995 and Koufopanou et al. 1999), further supporting phylogenetic resolution of this species in the non-territorial clade. This study highlights the potential application of phylogenetic tools in resolving or categorizing species as territorial or non-territorial grazers in cases where ecological characters are overlapping or not abruptly separated. Thus, *S. argenvillei* and *S. barbara* will be referred to as non-territorial and territorial foragers respectively in the subsequent chapters.

The strong monophyletic sister relationship between *Scutellastra A* and *Scutellastra B* suggests these two *Scutellastra* clades are more evolutionarily related to each other than to either *Cymbula* or *Helcion*. In both *Cymbula* and *Scutellastra*, the territorial species are more closely related to each other than to their congeneric non-territorial species. This implies a very deep and stable evolutionary divergence between territorial and non-territorial taxa in both genera. The common ancestral patellid taxa possibly possessed either territorial or non-territorial foraging mechanism and thus, either of these foraging traits could be an apomorphic character.

The BI, ML and MP analyses of the concatenated data revealed strongly supported territorial and non-territorial clades amongst species of both *Cymbula* and *Scutellastra* (Figures 1.14 - 1.16). Thus, territorial foraging independently evolved twice in these patellid limpets to give rise to both territorial *Cymbula* and *Scutellastra* species. The BI, MP and ML phylogenetic reconstructions based on the concatenated data set and ATPS β recovered a robust resolution of *Scutellastra* into two clades corresponding to their foraging traits. *Scutellastra A* comprised territorial foragers while *Scutellastra B* comprised non-territorial foragers (Table 1.12).

Table 1.12: The patellid species comprising *Scutellastra A* and *Scutellastra B* clades.

<i>Scutellastra A</i> (territorial foragers)	<i>Scutellastra B</i> (non-territorial foragers)
1. <i>S. barbara</i>	1. <i>S. argenvillei</i>
2. <i>S. cochlear</i>	2. <i>S. granularis</i>
3. <i>S. longicosta</i>	3. <i>S. miliaris</i>
4. <i>S. obtecta</i>	4. <i>S. natalensis</i>
5. <i>S. tabularis</i>	

The territorial *Scutellastra* species are generally characterized by a flat and specialized shell shape compared to the congeneric non-territorial grazers. For example, in the two scutellastrid clades, the shells of the territorial *Scutellastra A* are flat compared to the shells of the non-territorial *Scutellastra B* (Figure 1.18). Additionally, the other noticeable conchological difference between *Scutellastra A* and *Scutellastra B* is the general shell morphology (Figure 1.18). The shells of the territorial *Scutellastra A* are characterized by high morphological plasticity ranging from the flat and ring-like shell of *S. barbara* to a giant, elevated ray-like shell of *S. tabularis* (Figure 1.18a). The shells of the non-territorial *Scutellastra B* are simple and characterized by less morphological variability, generally taking a granular and cone-like form (Figure 1.18b). Thus, the granular cone-like shell appears to be a synapomorphic character in the *Scutellastra B* clade. The differences in shell shape between territorial and non-territorial species could be attributed to different adaptations to wave exposure between low shore (territorial) and

high shore (non-territorial) species (see Branch & Marsh 1978). Despite remarkable variation in conchological morphology, there is no significant variation in shell size between the two scutellastrid clades (Figure 1.18).

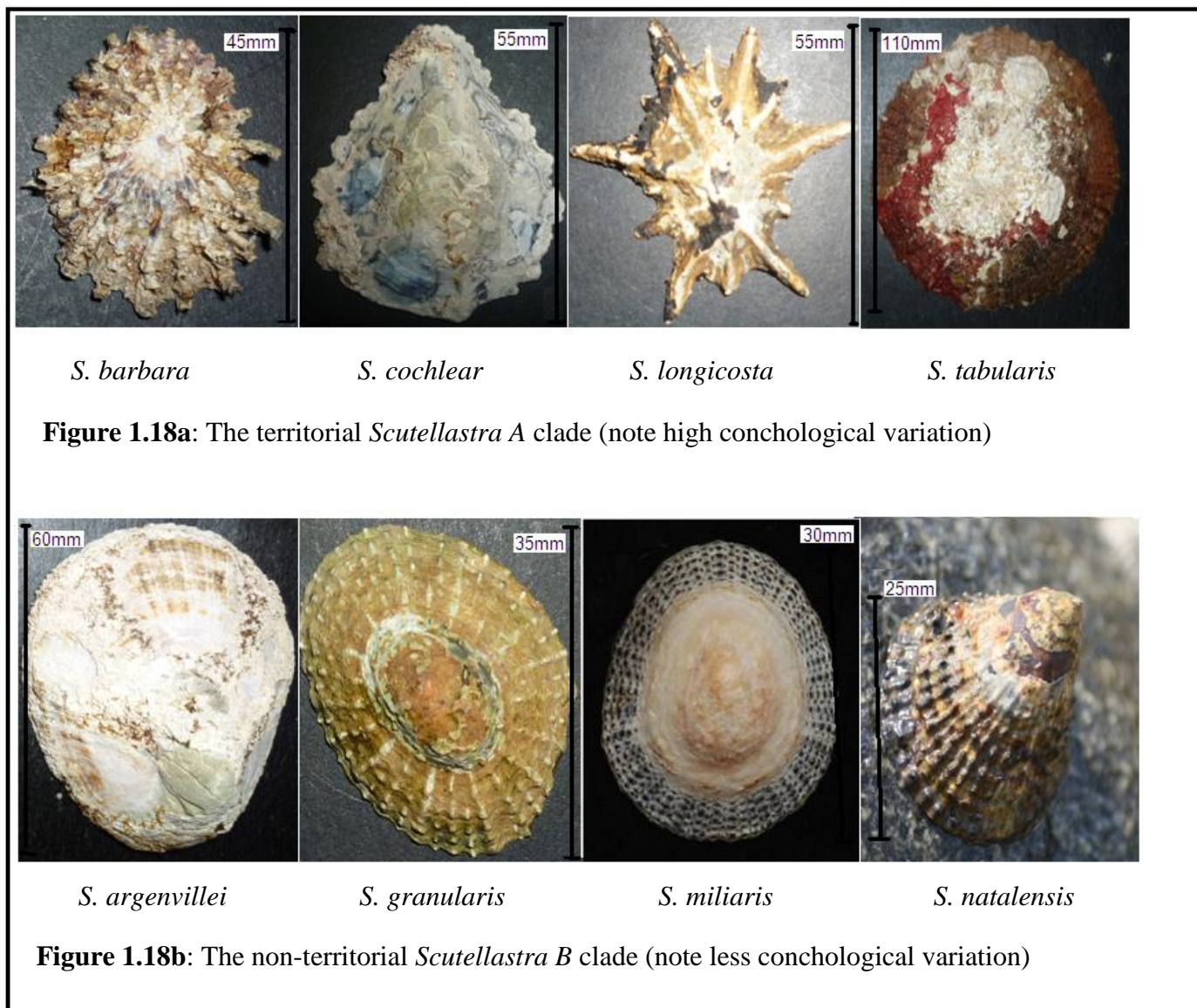


Figure 1.18: The shells of species comprising *Scutellastra* A and *Scutellastra* B clades.

The remarkable morphological differences between these evolutionarily closely related scutellastrid clades (Figure 1.18) suggest the evolutionary adaptation of their foraging behaviour. However, with the exception of *C. compressa*, which has a shell shape highly modified for attachment to the stipes of kelp, there are no remarkable differences in shell shape and morphology amongst *Cymbula* taxa (Figure 1.5). Thus, evolutionary and morphological divergence between the territorial and non-territorial *Cymbula* taxa is not as robustly established as in the scutellastrid taxa.

The deep evolutionary divergence between the territorial *Scutellastra A* and the non-territorial *Scutellastra B* clades suggests they both warrant recognition at the generic level. The high conchological variability between these two clades corresponds to their deep genetic divergence, strongly suggesting possible distinction at the generic level. However, a thorough examination of anatomical and morphological characters would be crucial to substantiate the need for such a subdivision into two genera. The radula anatomy has long been recognised as a useful taxonomic character in both species and generic classification (Powell 1973, Lindberg 1998, Ridgway et al. 1998b, 1999a and 2000). The remarkable differences in radula tooth between the territorial and non-territorial foragers (Maneveldt et al. 2006) should prompt further examination of other morphological characters which are taxonomically essential to distinguish taxa at the genus level.

Additionally, the CO1 sequence divergence between the territorial *Scutellastra A* and the non-territorial *Scutellastra B* was estimated to be 10% (Table 1.13). This estimate almost corresponds with other CO1 sequence divergence amongst recognised limpets genera estimated based on the substitution rate from the CO1 phylogenetic trees. The BI and the ML trees based on the concatenated data set resolved *Helcion* as paraphyletic whereas *Cymbula*, *Scutellastra A* and *Scutellastra B* were resolved as monophyletic (Table 1.14).

Table 1.13: The main generic clades amongst patellid genera and their approximate sequence divergence discovered using mitochondrial CO1.

Genus	Clades	Sequence divergence (CO1)	Study
<i>Scutellastra</i>	<i>Scutellastra</i> A (Territorial) vs. <i>Scutellastra</i> B (Non-territorial)	10%	This study
<i>Nacella</i>	<i>Nacella</i> (Antarctica) vs. <i>Nacella</i> (South America)	7.5%	González-Wevar et al. (2010) Aranzamendi et al. (2009)
<i>Patella</i>	Clade I vs. Clade II/III/IV	10%	Sá-Pinto et al. (2005)

Table 1.14: The main generic clades discovered in this study and their phylogenetic resolutions based on the concatenated Bayesian Inference (BI) and Maximum Likelihood trees (ML)

Genus/Clade	Phylogenetic tree	Monophyletic/Paraphyletic
<i>Helcion</i>	BI and ML	Paraphyletic
<i>Cymbula</i>	BI and ML	Monophyletic
<i>Scutellastra</i> A	BI and ML	Monophyletic
<i>Scutellastra</i> B	BI and ML	Monophyletic

The robust congruency in the recognition of the two *Scutellastra* clades amongst four different markers reflects the strong effects of ecological specialization (territorial foraging) in the evolution of patellogastropods. The evolutionary adaptations of territorial and non-territorial foraging are ecologically manifested within these true limpets and noticeable even at the generic level amongst closely related taxa. Although the evolutionary adaptations and divergence of foraging traits were apparent amongst *Cymbula* spp., they were not as robust or divergent as in *Scutellastra* species.

The Cretaceous antitropical distribution of these patellogastropods along the southern African shoreline was followed by synchronized evolution and diversification into territorial and non-territorial species. The phylogenetic reconstruction of these patellid limpets has not only provided insight into the evolutionary relationship amongst these true limpets but also shed lights on the evolutionary scenarios that led to such high species diversity.

1.4.2 Divergence times amongst the discovered clades

The divergence times estimated in this study amongst major genera (i.e. *Scutellastra*/*Cymbula* vs. *Helcion* and *Scutellastra* vs. *Cymbula*) correspond with times estimated in previous studies (Koufopanou et al. 1999, Nakano & Ozawa 2004, 2007). The genus *Helcion* diverged from the ancestral *Patella* in the late Cretaceous whereas the genera *Scutellastra* and *Cymbula* diverged in the mid Eocene (Nakano & Ozawa 2004, 2007 and this study).

The divergence between territorial and non-territorial species in both *Scutellastra* and *Cymbula* took place approximately in the early Oligocene. The major climatic cooling and decreases in sea level occurred during the Oligocene (Miller et al. 2008, Liu et al. 2009, Teske and Beheregaray 2009). This probably exposed much of the lower intertidal zone, increasing new potential habitats and algal availability. The encrusting algae (including *Spongites yendoi* and *Ralfsia verrucosa*) date back to the early Cretaceous (Moussavian et al. 1993, Arias et al. 1995) and these algae expanded rapidly in the early Oligocene as global sea levels drops (Aguirre et al. 2000, 2010). These crustose coralline algae have the broadest cosmopolitan distribution and abundance of any group of marine algae (Steneck 1986). The Oligocene exposure of rocky shores and algal abundance on the lower intertidal zone probably elicited resource partitioning amongst these patellid limpets and subsequently, the evolution of territorial and non-territorial species.

The evolution of territoriality or resource specialization first occurred within *Scutellastra* species (≈ 32 Mya) and then within *Cymbula* species (≈ 31 Mya). It is probable this synchronized convergent evolution (early Oligocene) of territorial foraging was elicited by different ecological needs or adaptations in both genera. For example, unlike the sedentary territorial *Scutellastra* species, the territorial *C. compressa* is mobile and inhabits exclusively the stipes of the kelp, not rocky substratum (Branch 1971, 1974, 1975c). Nevertheless, , different evolutionary strategies of

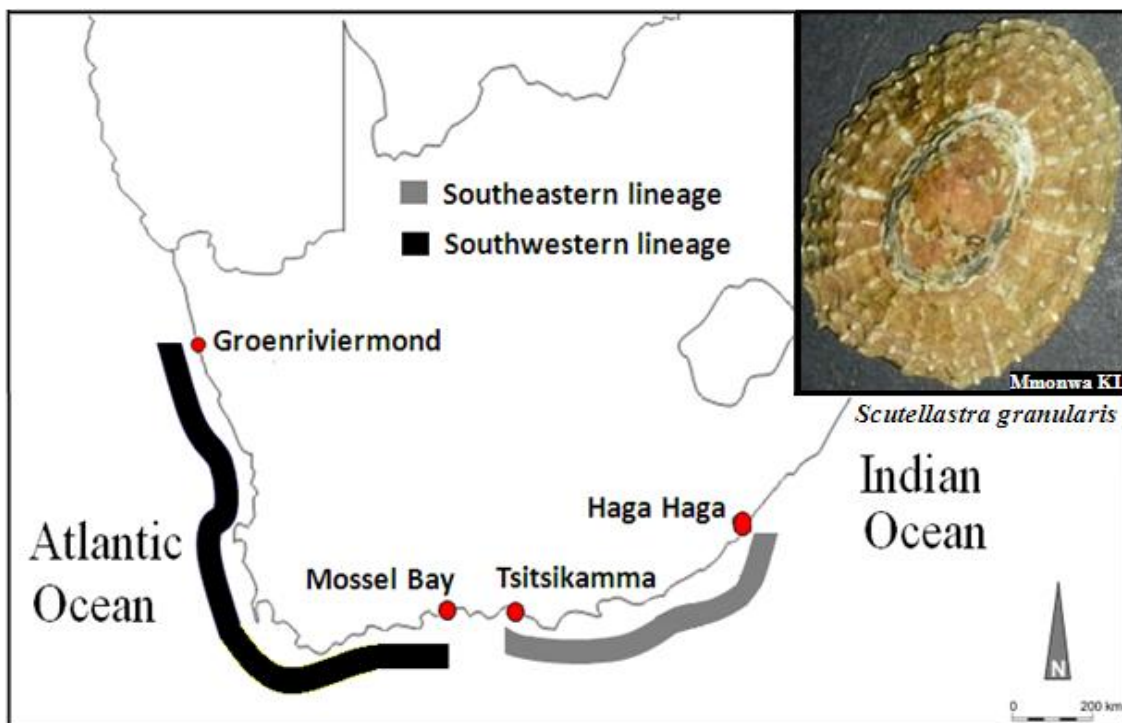
resources specialization in both territorial *Scutellastra* and *Cymbula* species resulted in a unique and prudent feeding behaviour, territorial foraging.

Territorial foraging is a well studied and understood ecological trait within the patellogastropods, however it is not yet clear which foraging trait is ancestral between territorial and non-territorial foraging (Lindberg 2007). This study discovered that territoriality or resource partitioning amongst southern African patellid limpets arose in two separate lines. This independent evolution of territoriality in both *Scutellastra* and *Cymbula* makes it difficult to ascertain which foraging trait is ancestral. In neither genus did the territorial species evolve from the non-territorial species or *vice versa*, instead both genera radiated independently within the same evolutionary time frame (early Oligocene). The sister relationship and synchronized evolution of territorial and non-territorial species suggest their concurrent evolution from ancestral taxa. The ancestral *Patella* species are presumed be non-territorial foragers based on their high shore migration, generalized algal diet and lack of foraging territories (Lewis & Bowman 1975).

It is possible that territorial/non-territorial *Scutellastra* species could have evolved from these non-territorial *Patella* taxa (see Lindberg 2007). However, on the second independent evolution of resource partitioning (*Cymbula* spp.), territorial/non-territorial species could have evolved from territorial taxa. This reflects an evolutionary scenario whereby non-territorial taxa evolved into both territorial and non-territorial taxa of which either evolved into more territorial and non-territorial taxa. This study is in agreement with suggestion that territoriality is an apomorphic trait in scutellastrid species (Lindberg 2007). The same applies in *Cymbula*, though through the independent evolution of a similar ecological trait of resource partitioning. The synchronized evolution of these species and their foraging traits suggest their foraging behaviour could also be reflected in their genotype (see chapter three).

CHAPTER TWO

Phylogeography of sympatric intertidal patellid limpets (Gastropoda: Patellogastropoda) with different foraging behaviours from the South African shoreline



2.1 Introduction

Phylogeography is the subfield of biogeography focused on how physical and biological factors have shaped the spatial distribution of genetic lineages (Avice et al. 1987, Avice 1992, 1998, 2004, Beheregaray 2008, Teske et al. 2009, 2011 and Hickerson et al. 2010). Historical (vicariance and dispersal) and contemporary (climate change and hydrological cycles) processes are the fundamental vagaries shaping spatial distribution of these genetic lineages (Bernardi et al. 2003, Templeton 2003, Rocha et al. 2007, Arbogast & Kenagy 2008, Waters 2008a and Pleines et al. 2009). Contemporary processes such as variation in oceanographic currents, upwelling cells, sea-surface temperature and coastal topographical features (e.g. bays and habitat availability) have been evoked to explain genetic breaks amongst marine taxa (Banks et al. 2007, Waters, 2008b, Pelc et al. 2009, Teske et al. 2009, 2010, 2011a and Zardi et al. 2007, 2011). The most important factor shaping spatial distribution of these genetic lineages is larval dispersal and duration (Bernardi et al. 2003, Waters & Roy 2004a, Waters 2008a and Teske et al. 2009).

The phylogeographic patterns observed amongst most marine taxa are the result of the interaction between historical/contemporary factors and an organism's larval dispersal (Palumbi 1994). The period the larvae spend in the planktonic stage is often correlated with the dispersal distance, which can influence or determine an organism's genetic structure. Thus, genetic structure can be hypothesized to be directly or indirectly related to the organism's larval biology (Avice 1992, Kyle & Boulding 2000, Bowen et al. 2006, Teske et al. 2007b, 2011a). The assumption would be that species with long planktonic larval stage will show no or little genetic structure whereas species with short or non-planktonic larval stages will tend to show high genetic structure (Palumbi 1994, Chambers et al. 1996, 1998, Bohonak 1999, Dawson 2001, Bernardi et al. 2003, Bowen et al. 2006, Rocha et al. 2007, Bell 2008 and Pelc et al. 2009). In such taxa, genetic units or lineages are often confined to recognised biogeographic regions (Avice 1994), but other studies have showed incongruence between phylogeographic and biogeographic boundaries (Burton 1998, Irwin 2002, Kou & Avice 2004, Bilodeau et al. 2005, Teske et al. 2006, York et al. 2008 and Pelc et al. 2009).

Phylogeographic analyses have also provided a powerful tool for identifying cryptic or sibling species that are often difficult or impossible to distinguish based on morphological features (Templeton 2003, Beheregaray & Caccone 2007, Teske & Beheregaray 2009, Teske et al. 2009, 2011c and Azuma et al. 2011). Phylogeography is also useful in management or conservation studies since it can be used to estimate population connectivity as well as levels and patterns of genetic diversity within and between populations (Féral 2002, Rawson et al. 2003, Palumbi 2004, Rocha et al. 2007, von der Heyden 2008, 2009, Ni et al. 2012, Provan & Maggs 2012). In addition to advancing understanding of evolutionary processes driving genealogical distribution, phylogeographic findings can also provide science-based advice for the management and conservation of marine protected areas (von der Heyden 2008, 2009 and Teske et al. 2010).

A recent review of southern African marine phylogeography emphasized that the recognized coastal biogeographic boundaries do not affect the phylogeography of all marine invertebrates in the same way (Teske et al. 2011a). In most scenarios, species show phylogeographic structure that coincides with biogeographic boundaries (Ridgway et al. 1998b, Evans et al. 2004, Norton 2005, Teske et al. 2006, 2007a, Zardi et al. 2007, van der Merwe 2009, von der Heyden 2009 and von der Heyden et al. 2008, 2011). However, there are other cases where biogeographic boundaries have no impact on the phylogeography of species (Klopper 2005, Tolley et al. 2005, Oosthuizen 2007, Teske et al. 2007b, von der Heyden et al. 2007a, Neethling et al. 2008, Mmonwa 2009 and Teske et al. 2010).

Oceanographic conditions, with their influence on historical habitat availability and larval dispersal play a major role in shaping the phylogeographic structure of various marine animal taxa along the South African shoreline (Teske et al. 2006, 2008, 2011a, von der Heyden et al. 2008, Ross et al. 2009, Sivasundar & Palumbi 2010 and Muller et al. 2012). The two main oceanic circulations driving larval dispersal are the cold northward flowing Benguela on the west coast and the warm southward flowing Agulhas currents on the east and south coasts (Figure 2.1). For example, larvae dispersing southward via the Agulhas current may be unable to reach

rocky shore habitats as they can be deflected offshore by the Agulhas Retroflexion (Teske et al. 2006).

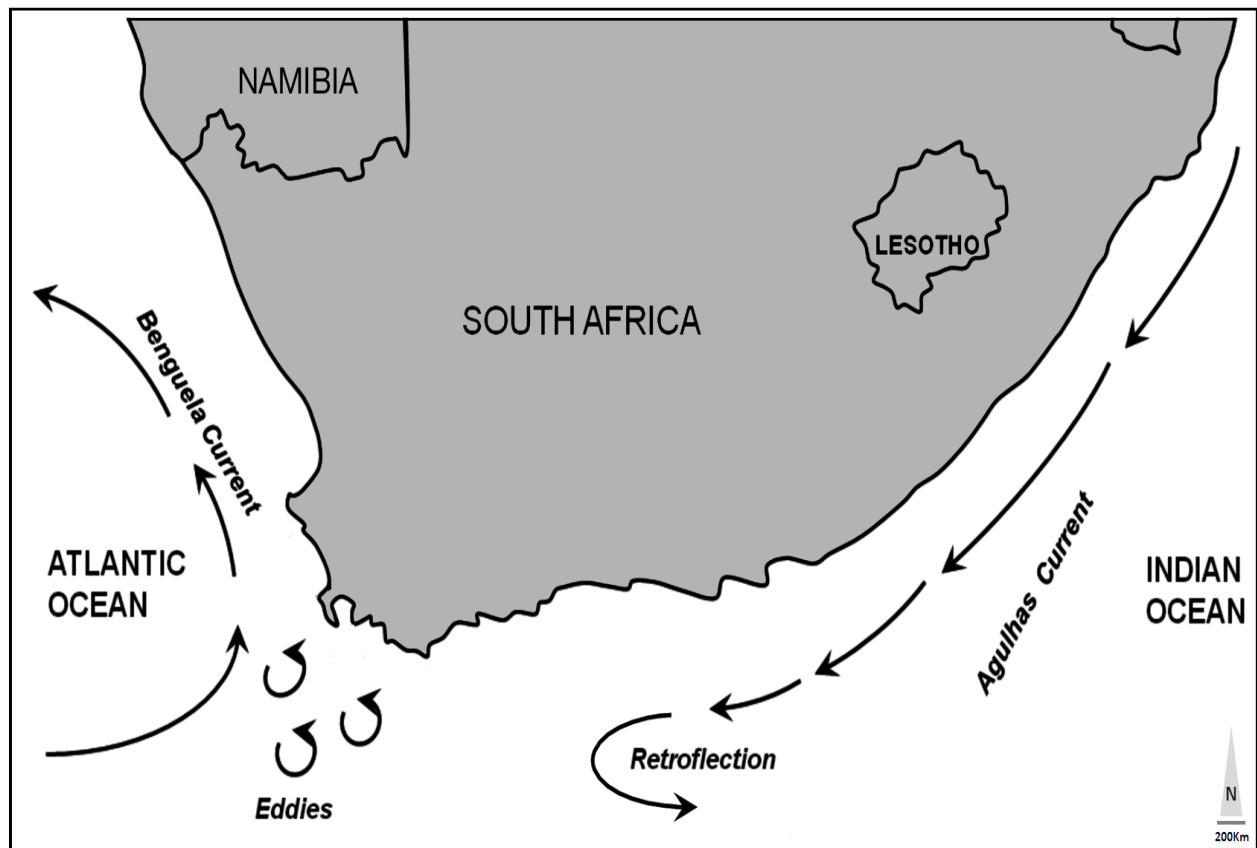


Figure 2.1: Map of South Africa showing the cold-temperate northward flowing Benguela current and the warm-temperate southward flowing Agulhas current (Griffiths et al. 2010)

The sympatric territorial and non-territorial patellid limpets presumably have similar larval histories (all have lecithotrophic larvae, Hadfield et al. 1997, Kay & Emlet 2002 and Paulay & Meyer 2006) and are exposed to similar oceanographic circulations. The larvae have a brief planktonic stage (\approx 3-11 days) after which they metamorphose into a juvenile phase (Goldstein et al. 2006, Bird et al. 2007, González-Wevar et al. 2010) that may migrate up the shore as they age (non-territorial foragers) or settle low on the shore (territorial foragers). Thus, these two types of

foragers are expected to be characterized by similar large-scale phylogeographic structure given their similar larval biology. The interaction between historical and contemporary processes and larval dispersal is likely to have yielded similar genetic structure in both territorial and non-territorial foragers. Furthermore, both types of foragers are expected to reveal almost correlated levels of genetic differentiation or similarity from site to site.

The comparison of spatial patterns of genealogical distribution or comparative phylogeography (see Bermingham & Moritz 1998 and Arbogast & Kenagy 2001) allows one to test if co-distributed taxa have congruent phylogeographic distribution. This study adopts a comparative approach to investigate large scale phylogeographic differences or similarities amongst territorial and non-territorial patellid limpets along the South African coastline. Comparative phylogeographic studies are more effective at disentangling evolutionary patterns and processes than single taxon studies, which can provide misleading conclusions (Marko 2004, Lourie et al. 2005, Goldstein et al. 2006, Teske et al. 2006, 2011a, von der Heyden 2009 and von der Heyden et al. 2013). This study analysed the mitochondrial CO1 marker to investigate phylogeographic patterns and Φ_{ST} genetic differentiation amongst territorial and non-territorial foragers in both *Cymbula* and *Scutellastra* species. The Φ_{ST} statistics have commonly been used to analyse and compare the degree of population genetic structure within species (Bird et al. 2007, González-Wevar et al. 2011a and von der Heyden et al. 2011, 2013).

This study adopts a comparative approach to investigate phylogeographic structure of patellid limpets with two different type of foraging behaviours. The objective was to test the following hypothesis: Large scale biogeographic factors such as historical climate changes and contemporary oceanographic circulations shaped the genealogical distribution of these limpets in similar patterns. Therefore, it is expected that sympatric territorial and non-territorial foragers will be characterized by similar phylogeographic distributions as measured by Φ_{ST} population genetic differentiation.

2.2 Materials and Methods

2.2.1 Study sites and sampling procedure

The study sites comprised 16 rocky shores across the entire South African shoreline (Figure 2.2). From each site, at least five individual samples of each species were collected randomly at approximately 5m apart and immediately fixed in 100% ethanol.

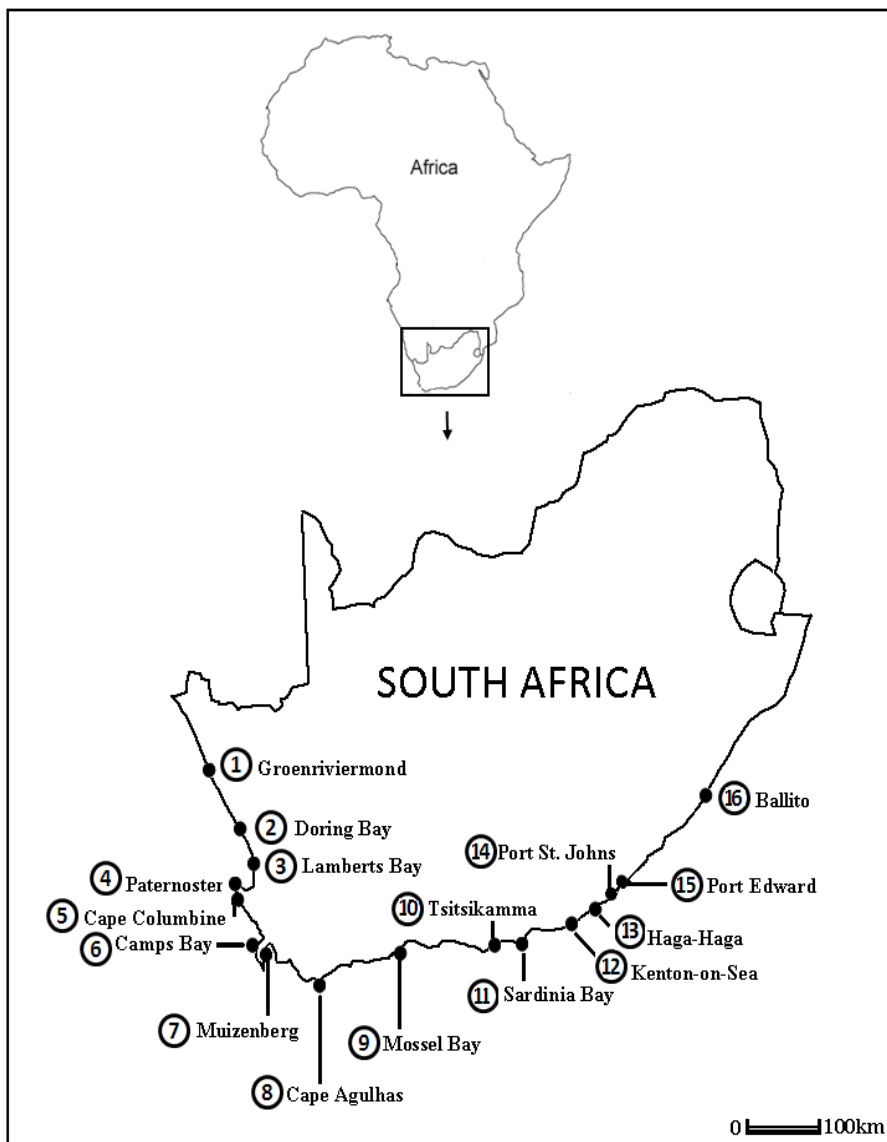
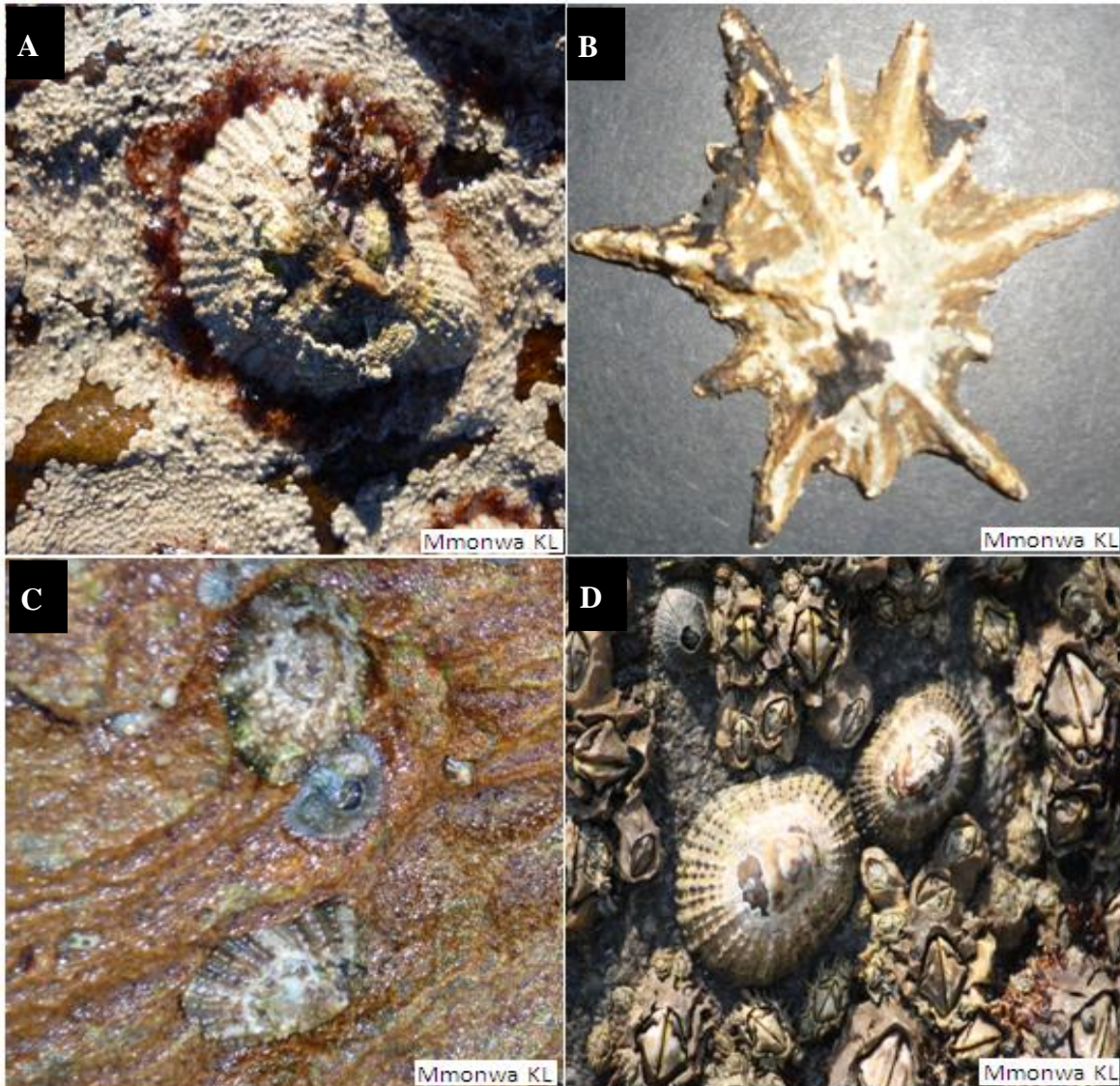
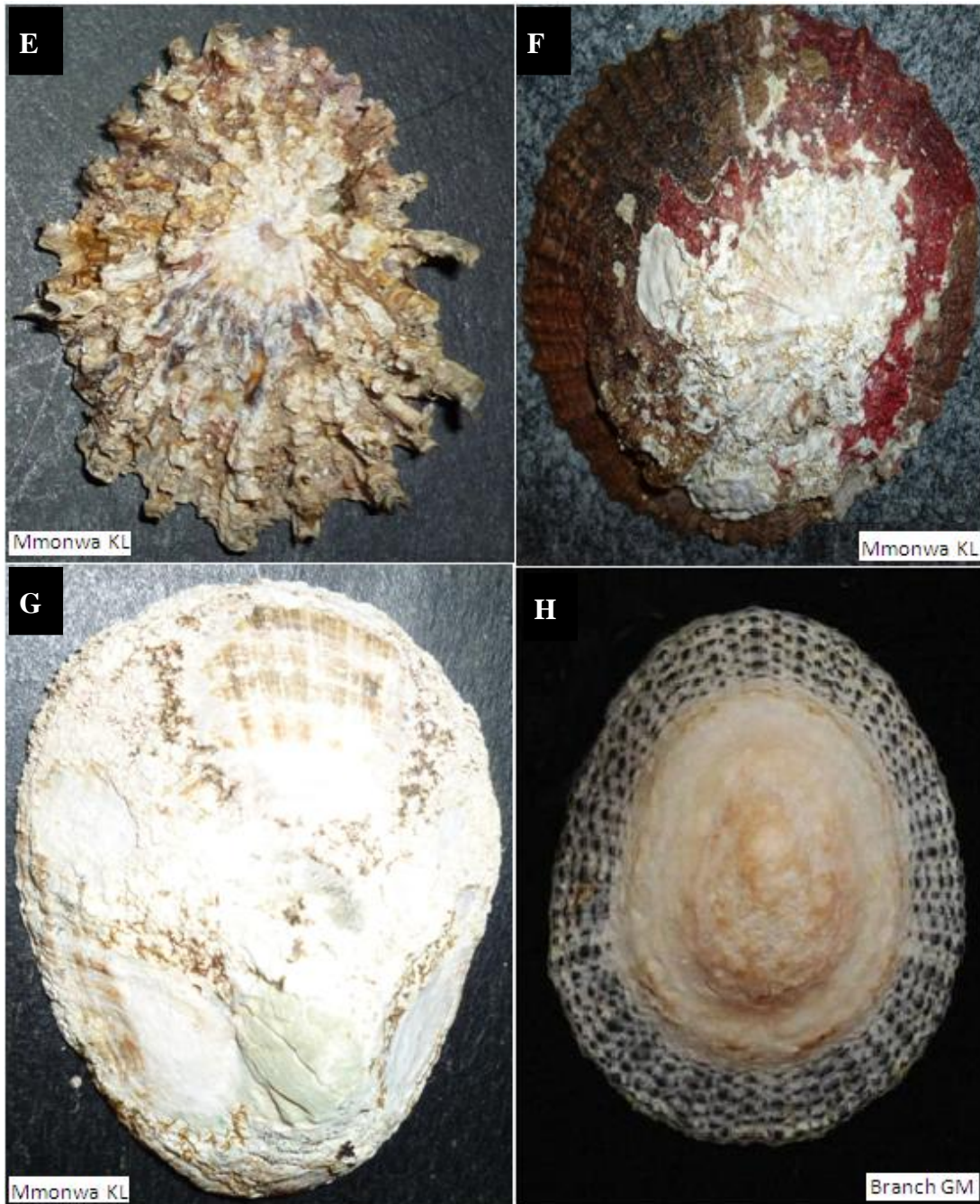


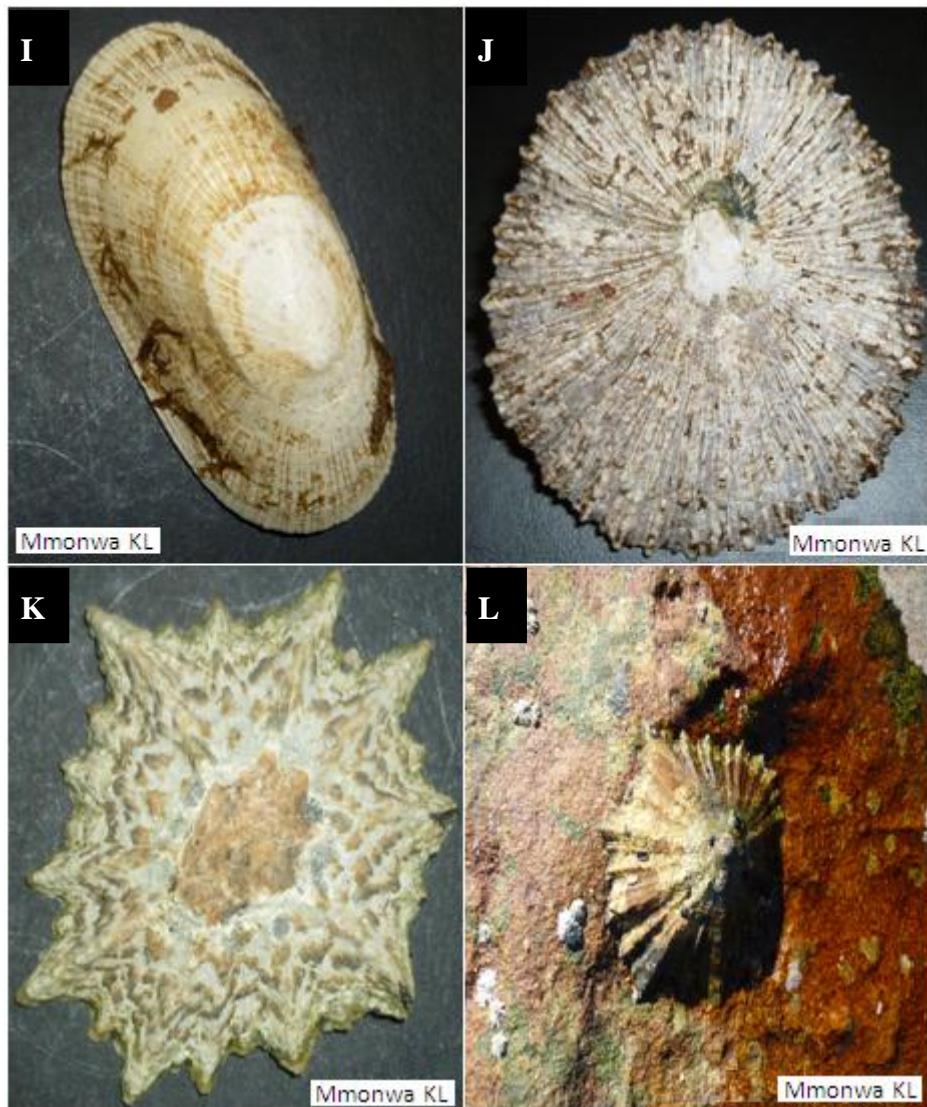
Figure 2.2: The map of the South African shoreline showing the sampling localities.

2.2.2 *The study species*

Figures 2.3A - D: **A.** Territorials *Scutellastra cochlear* and **B.** *Scutellastra longicosta*
C. Non-territorials *Scutellastra granularis* and **D.** *Scutellastra natalensis*.



Figures 2.3E - H: E. Territorials *Scutellastra barbara* and F. *Scutellastra tabularis*
 G. Non-territorials *Scutellastra argenvillei* and H. *Scutellastra miliaris*.



Figures 2.3I - L: **I.** Territorials *Cymbula compressa* and **J.** *Cymbula miniata*.
K. Non-territorials *Cymbula granatina* and **L.** *Cymbula oculus*.

2.2.3 *Materials and Methods* (described in chapter one)

2.2.4 *Analyses of genetic differentiation and structure*

The Φ_{ST} statistics (Nei 1982) was developed to investigate population substructure by measuring the average nucleotide distance between haplotypes using Arlequin version 3.1 (Excoffier et. al. 1992, 2006). The index compares average nucleotide diversity within and between populations by determining how different each haplotype is from the other (Rousset 1996, Excoffier et. al. 2006). The Φ_{ST} statistic is calculated using the following formula: $\Phi_{ST} = \pi_B/\pi_T$, where π_B is the average nucleotide diversity among subpopulations and π_T is the expected nucleotide diversity in a randomly mating total population (Nei 1982). The level of statistical significance of the pairwise Φ_{ST} values is based on the proportion of permutations leading to the Φ_{ST} value that is larger to or equal to the observed one (Excoffier et. al. 1992, 2005, 2006).

Haplotype networks were reconstructed using the software package TCS version 1.21 (Clement et al. 2000) for all the species. The Neighbor Joining trees were constructed using default settings in DAMBE version 5.3.8 (Xia & Xie 2001) and the program PAUP* version 4.0b10 (Swofford 2002). All the analyses produced congruent trees, this was critical in making robust comparison of phylogeographic structure between territorial and non-territorial grazers. The robustness of the tree topology was tested through bootstrap analyses with 1,000 replicates. The bootstrap values indicate the percentage of times that a particular divergence is supported when characters are randomly sampled to create a new data matrix (Graur & Li 2000).

2.3 Results

Genetic differentiation and Phylogeographic analyses

The analyses of genetic structure estimated using the Φ_{ST} indices revealed significant genetic differentiation among populations of the territorial *Scutellastra barbara* (Table 2.1), *S. cochlear* (Table 2.2), *S. longicosta* (Table 2.3) and the non-territorial *S. granularis* (Table 2.4). The analyses of Φ_{ST} did not reveal significant genetic differentiation among populations of the non-territorial *S. argenvillei*, *S. miliaris* or *S. natalensis* (see Appendices). In *Cymbula spp.*, non-significant Φ_{ST} indices were observed amongst populations of the territorial *C. miniata*, *C. compressa* and the non-territorial *C. granatina* (see Appendices). Significant genetic differentiation was observed between only two populations (Kenton-on-Sea and Mossel Bay) in the non-territorial *Cymbula oculus* (see Appendices).

2.3.1 *Scutellastra barbara*

Table 2.1: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) among populations of the territorial *Scutellastra barbara*. * = significant at $p < 0.0500$ and ns = not significant.

	PSJ	HAG	SDB	MSB	CCB	LMB	GRM
Port St. Johns (PSJ)		ns	*	*	*	*	*
Haga Haga (HAG)	0.127		*	*	*	*	*
Sardinia Bay (SDB)	0.050	0.000		ns	ns	ns	ns
Mossel Bay (MSB)	0.002	0.000	1.000		ns	ns	ns
Cape Columbine (CCB)	0.000	0.000	1.000	1.000		ns	ns
Lamberts Bay (LBT)	0.045	0.000	0.464	0.300	0.527		ns
Groenriviermond (GRM)	0.018	0.000	0.464	1.309	0.209	0.182	

The Neighbor Joining analysis of *Scutellastra barbara* revealed two main clusters, the eastern cluster (Port St. Johns population) and the southwestern lineage comprising all the samples from Groenriviermond (GRM) to Haga Haga (HAG). The divergence between these two clusters was strongly supported with a bootstrap support of 90% (Figure 2.4).

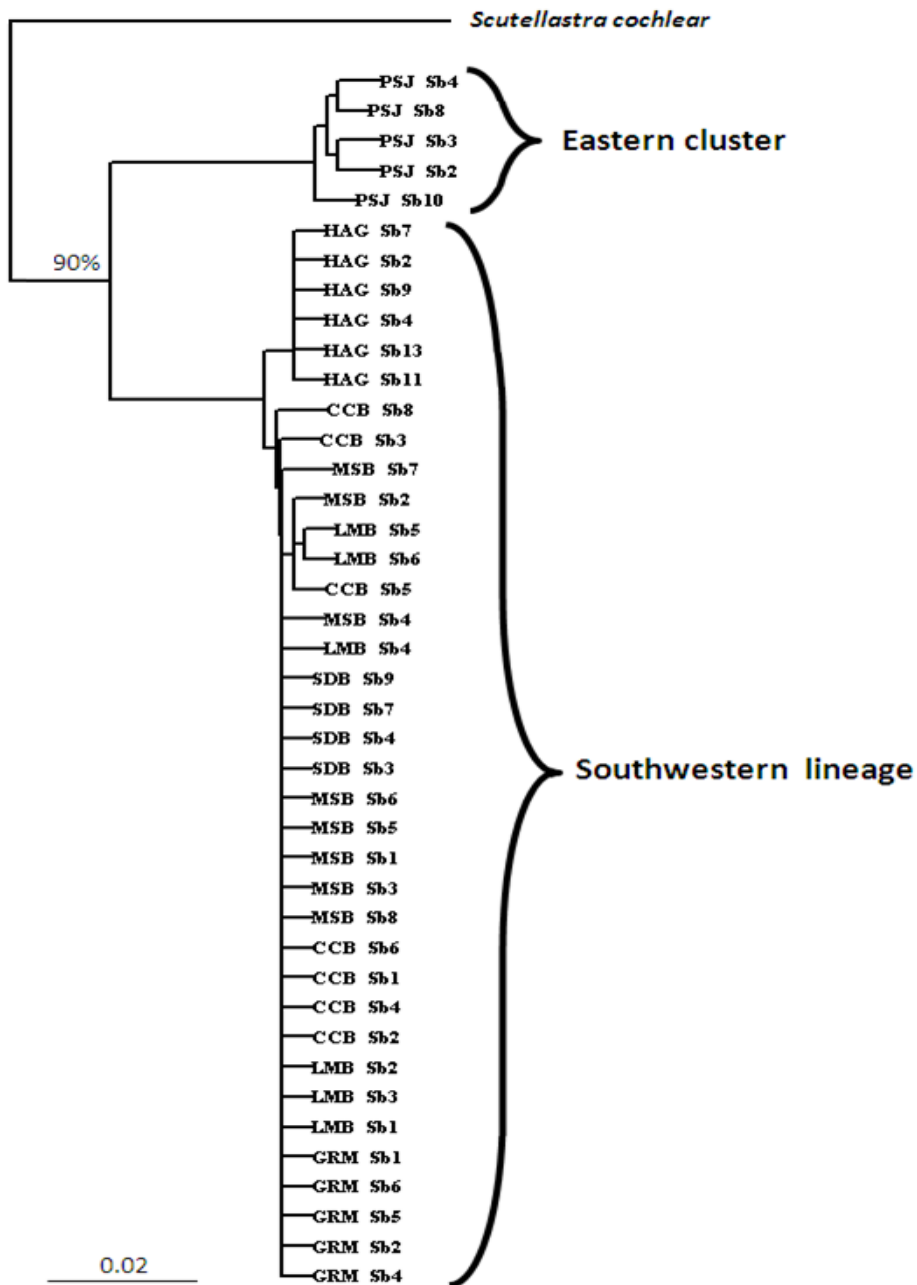


Figure 2.4: The CO1 Neighbor Joining tree of the territorial *Scutellastra barbara*.

The haplotype network reconstruction of *Scutellastra barbara* (Figure 2.5) also revealed two main clusters, the eastern cluster (Port St. Johns population) and the southwestern lineage comprising all the samples from Groenriviermond (GRM) to Haga Haga (HAG).

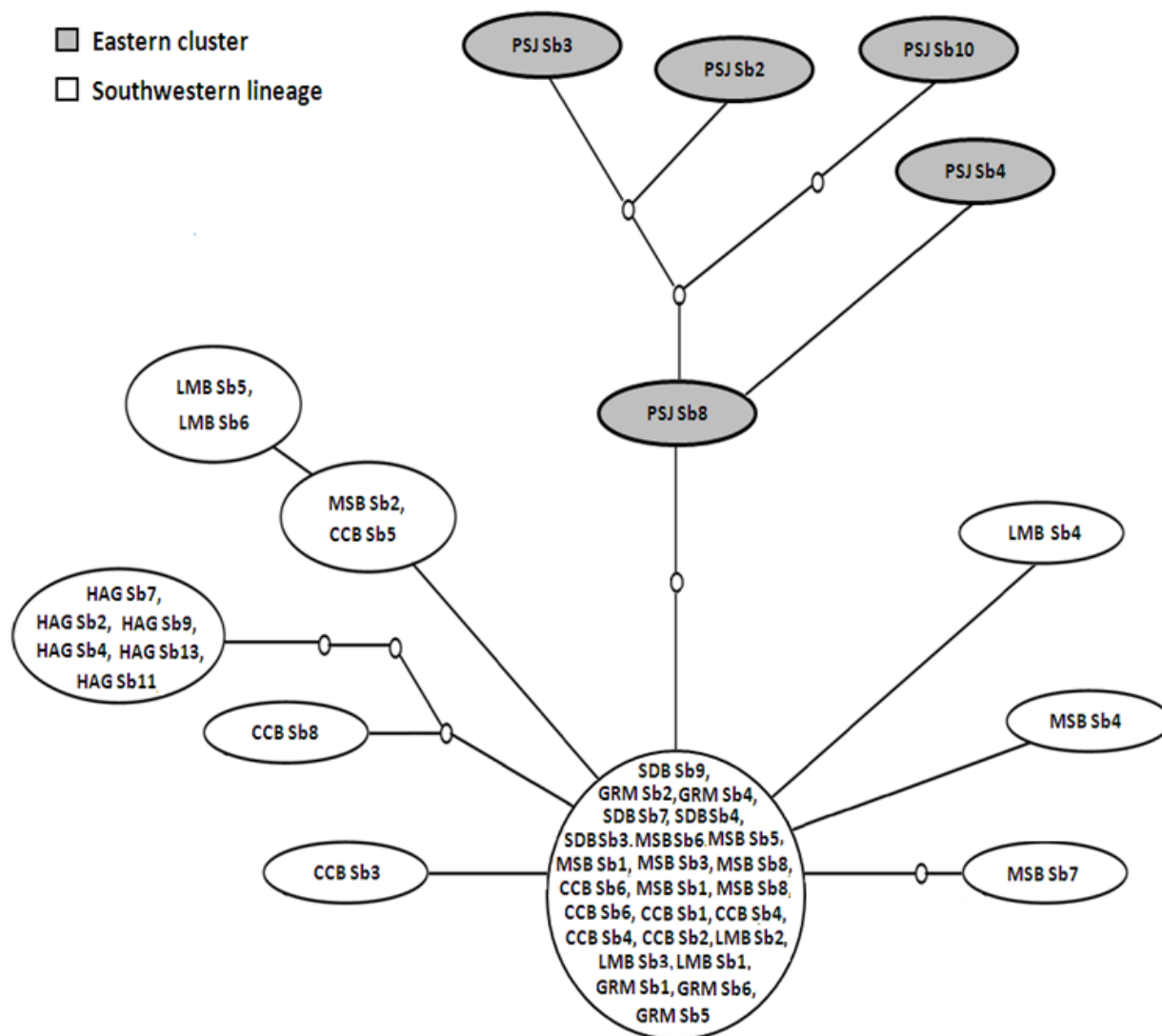


Figure 2.5: The COI haplotype network of *Scutellastra barbara*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotype names are site abbreviation followed by individual species` sample. Port St. Johns (PSJ), Haga-Haga (HAG), Sardinia Bay (SDB), Mossel Bay (MSB), Cape Columbine (CCB) and Lamberts Bay (LMB).

2.3.2 *Scutellastra cochlear*

The analyses of genetic structure estimated using the Φ_{ST} indices revealed significant genetic differentiation amongst populations of the territorial *Scutellastra cochlear* (Table 2.2).

Table 2.2: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) amongst populations of the territorial *Scutellastra cochlear*. * = significant at $p < 0.0500$ and ns = not significant. Port St. Johns (PSJ), Haga Haga (HAG), Sardinia Bay (SDB), Tsitsikamma (TSK), Mossel Bay (MSB), Cape Agulhas (CPA), Muizenberg (MZB), Camps Bay (CMB), Paternoster (PTN), Doring Bay (DRB), Groenriviermond (GRM).

	P SJ	HAG	KOS	SDB	TSK	MSB	CPA	MZB	CMB	PTN	DRB	GRM
PSJ		ns	*	ns	ns	ns	ns	*	ns	ns	ns	ns
HAG	0.500		*	ns	ns	ns	ns	*	ns	ns	*	ns
KOS	0.000	0.018		ns	ns	ns	ns	*	*	ns	*	ns
SDB	0.000	0.227	0.118		ns	ns	ns	*	*	ns	*	ns
TSK	0.218	0.209	0.127	0.082		ns	ns	ns	ns	ns	ns	ns
MSB	0.218	0.527	0.136	0.191	0.727		ns	ns	ns	ns	ns	ns
CPA	0.254	0.545	0.054	0.100	0.454	1.000		ns	ns	ns	ns	ns
MZB	0.000	0.000	0.000	0.000	0.027	0.036	0.164		*	*	*	*
CMB	0.073	0.064	0.045	0.009	0.236	0.282	0.264	0.027		ns	*	ns
PTN	0.364	0.709	0.600	1.000	0.636	1.000	1.000	0.000	0.736		ns	ns
DRB	0.072	0.036	0.036	0.018	0.136	0.282	0.164	0.072	0.045	0.136		*
GRM	0.273	0.300	0.300	0.273	0.218	0.436	0.673	0.000	0.345	1.000	0.027	

The haplotype network (Figure 2.6) and Neighbor Joining (Figure 2.7) analyses revealed no phylogeographic structure within *Scutellastra cochlear* across its entire range along the South African coastline. The haplotypes were randomly distributed across all the three biogeographic regions. However, the species has remarkable haplotype diversity

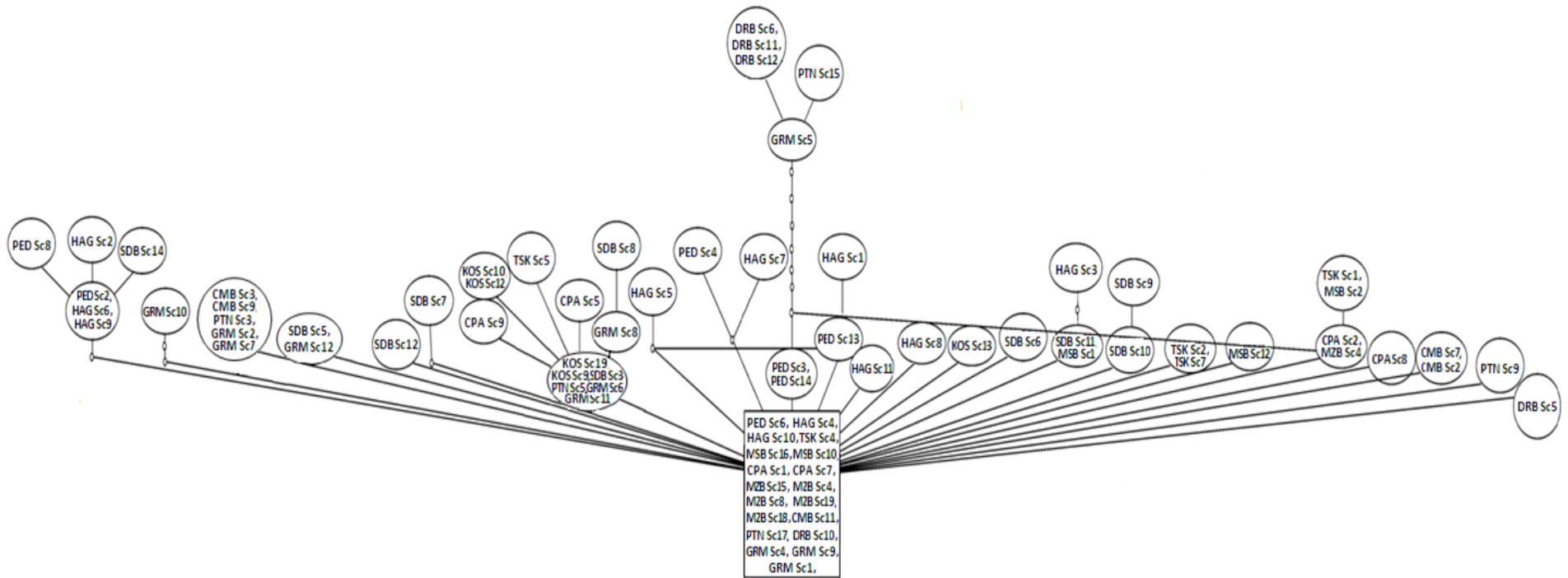


Figure 2.6: The CO1 haplotype network of *Scutellastra cochlear*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by individual species` sample. Sites abbreviations: Port Edward (PED), Haga-Haga (HAG), Kenton-on-Sea (KOS), Sardinia Bay (SDB), Tsitsikamma (TSK), Mosel Bay (MSB), Cape Agulhas (CPA), Camps Bay (CMB), Paternoster (PTN), Doring Bay (DRB) and Groenriviermond (GRM).

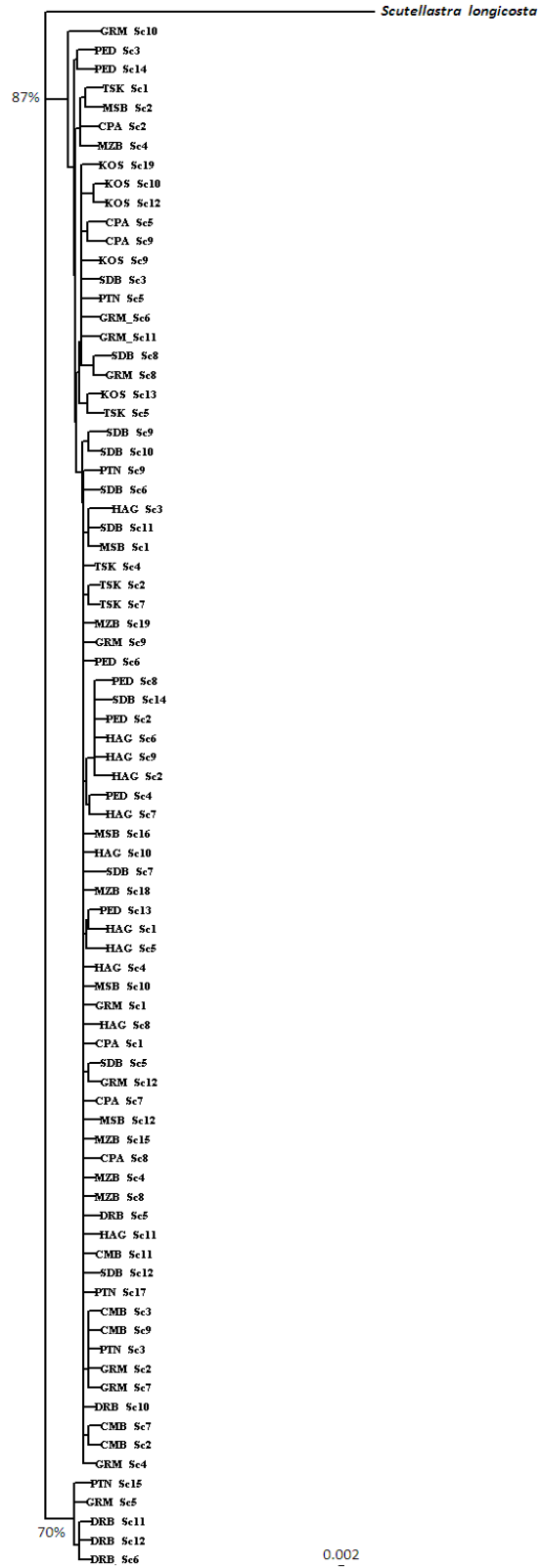


Figure 2.7: The CO1 Neighbor Joining tree of the territorial *Scutellastra cochlear*.

2.3.3 *Scutellastra longicosta*

The analyses of genetic structure estimated using the Φ_{ST} indices revealed significant genetic differentiation amongst populations of the territorial *Scutellastra longicosta* (Table 2.3).

Table 2.3: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) among populations of the territorial *S. longicosta*. * = significant at $p < 0.0500$ and ns = not significant.

	PSJ	HAG	KOS	SDB	TSK	MSB	CPA	MZB
Port St. Johns (PSJ)		ns	ns	*	*	*	*	*
Haga Haga (HAG)	0.091		ns	ns	*	*	ns	ns
Kenton-on-Sea (KOS)	1.000	0.100		*	*	*	*	*
Sardinia Bay (SDB)	0.073	0.091	0.036		*	*	*	ns
Tsitsikamma (TSK)	0.018	0.001	0.000	0.000		*	*	*
Mossel Bay (MSB)	0.018	0.182	0.009	0.036	0.000		ns	ns
Cape Agulhas (CPA)	0.045	0.391	0.182	0.045	0.036	0.318		ns
Muizenberg (MZB)	0.036	0.173	0.054	0.054	0.736	0.073	0.227	

The haplotype network (Figure 2.8) and Neighbor Joining (Figure 2.9) analyses of *Scutellastra longicosta* revealed two distinct lineages, a south-western and an eastern lineages. The southwestern lineage comprised samples from Muizenberg to Kenton-on-Sea whereas the eastern lineage comprised samples from Haga-Haga and Port St. Johns. The phylogeographic break between these two lineages is positioned between Haga-Haga and Kenton-on-Sea along the southeastern coast, coinciding with the biogeographic boundary between the warm-temperate Agulhas region and the Subtropical east coast region.

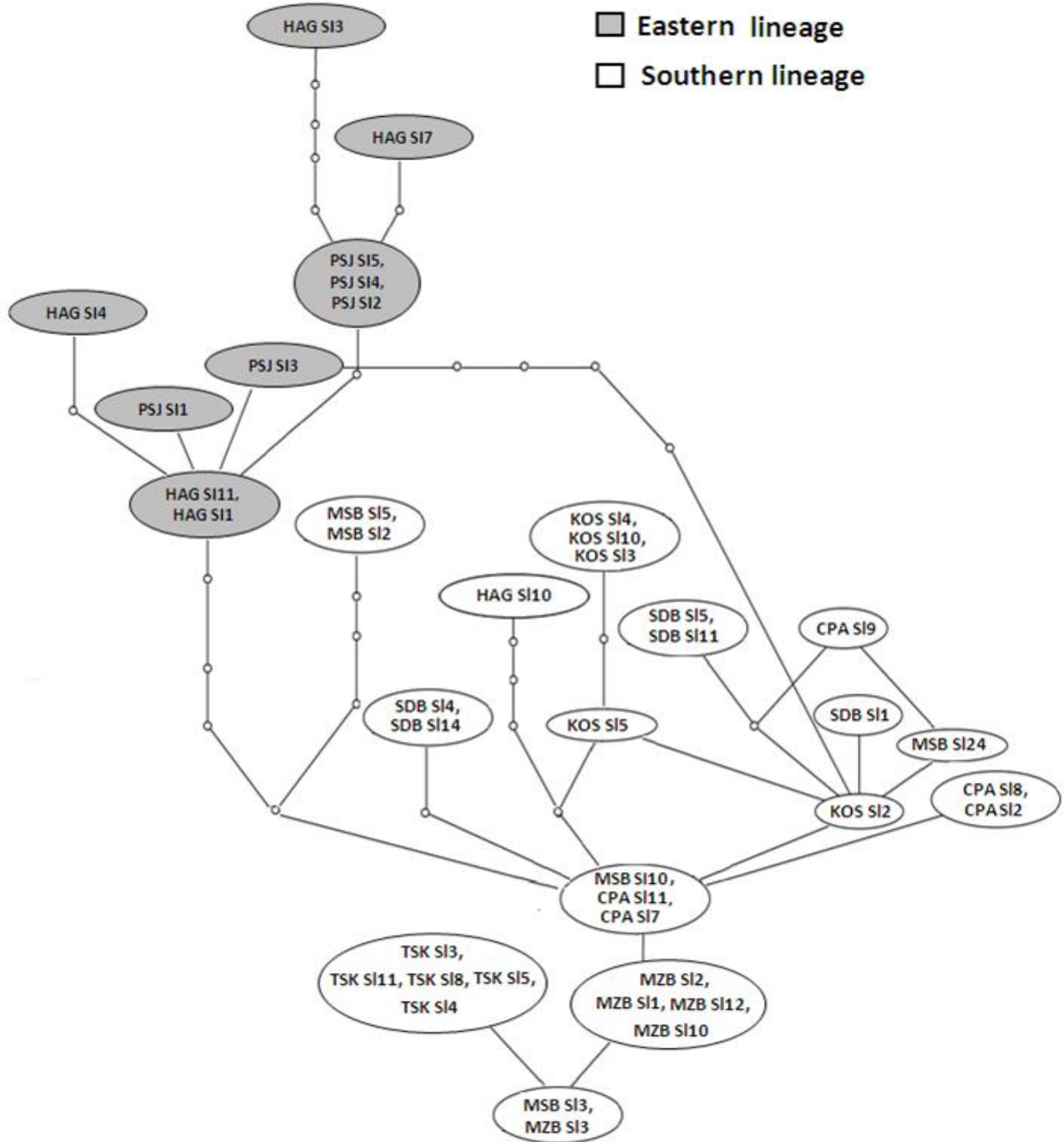


Figure 2.8: The CO1 haplotype network of *S. longicosta*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotype names are site abbreviation followed by individual species` sample. Sites abbreviations: Port St. Johns (PSJ), Haga-Haga (HAG), Kenton-on-Sea (KOS), Sardinia Bay (SDB), Mossel Bay (MSB) and Muizenberg (MZB).

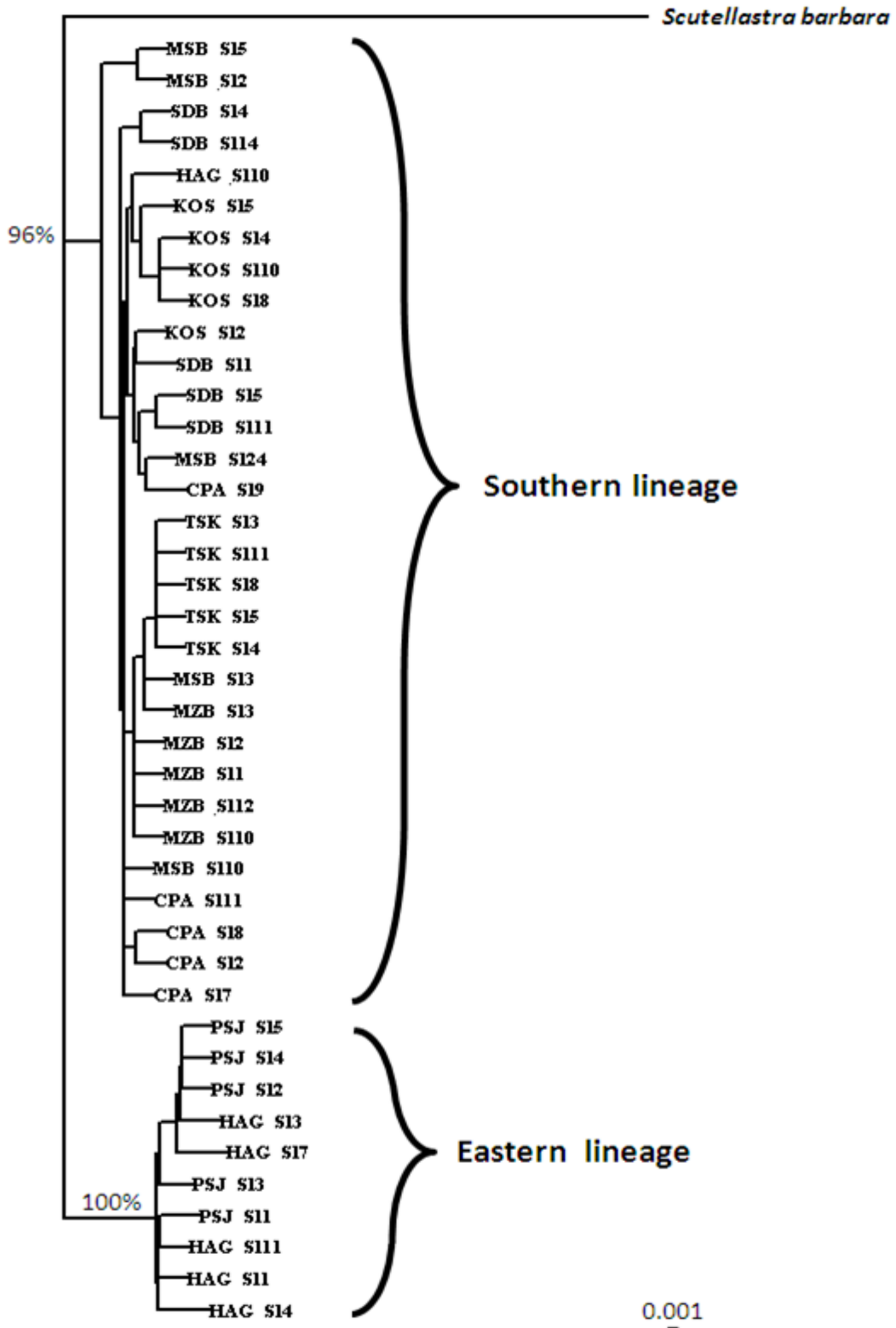


Figure 2.9: The CO1 Neighbor Joining tree of the territorial *Scutellastra longicosta*.

2.3.4 *Scutellastra granularis*

The analyses of genetic structure estimated using the Φ_{ST} indices revealed significant genetic differentiations amongst populations of the non-territorial *Scutellastra granularis* (Table 2.4).

Table 2.4: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) amongst populations of *Scutellastra granularis*. * = significant at $p < 0.0500$ and ns = not significant. Haga Haga (HAG), Kenton-on-Sea (KOS), Sardinia Bay (SDB), Tsitsikamma (TSK), Mossel Bay (MSB), Cape Agulhas (CPA), Muizenberg (MZB), Camps Bay (CMB), Paternoster (PTN), Doring Bay (DRB) and Groenriviermond (GRM).

	HAG	KOS	SDB	TSK	MSB	CPA	MZB	CMB	PTN	DRB	GRM
HAG		*	ns	*	ns	ns	*	*	*	ns	ns
KOS	0.045		ns	*	*	ns	*	*	*	*	*
SDB	0.036	0.036		*	ns	ns	*	*	*	*	*
TSK	0.000	0.009	0.000		*	*	*	*	*	*	*
MSB	0.045	0.000	0.000	0.000		ns	*	*	*	*	*
CPA	0.473	0.182	0.045	0.009	0.045		*	*	*	ns	ns
MZB	0.000	0.009	0.009	0.000	0.045	0.000		*	*	*	*
CMB	0.009	0.009	0.000	0.009	0.000	0.027	0.000		*	*	*
PTN	0.000	0.027	0.000	0.009	0.000	0.091	0.000	0.018		*	*
DRB	0.064	0.036	0.000	0.000	0.000	0.136	0.009	0.000	0.018		*
GRM	0.045	0.045	0.000	0.027	0.000	0.191	0.000	0.018	0.000	0.045	

The haplotype network (Figure 2.10) and Neighbor Joining (Figure 2.11) analyses of *Scutellastra granularis* revealed two distinct lineages, a southwestern lineage (GRM, DRB, PTN, CMB, MZB, CPA and MSB) and southeastern lineages (TSK, SDB, KOS and HAG). The genetic break between these two lineages is between Mossel Bay and Tsitsikamma along the mid south coast.

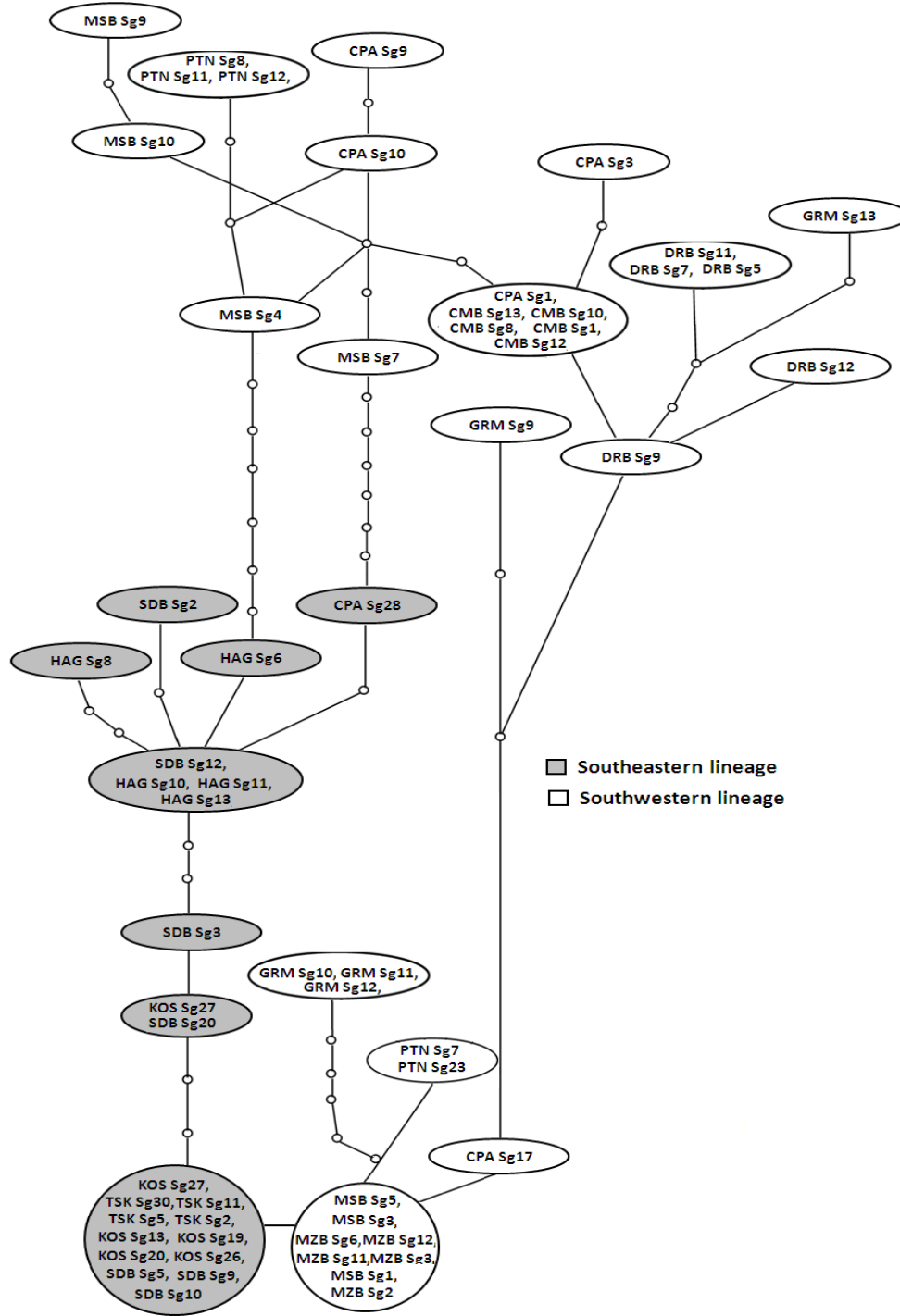


Figure 2.10: The CO1 haplotype network of *Scutellastra granularis*. Samples are represented as site abbreviation followed by specimen number. Open circles indicate mutations and samples are represented as site abbreviation followed by individual species` sample. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations given in Table 2.4.

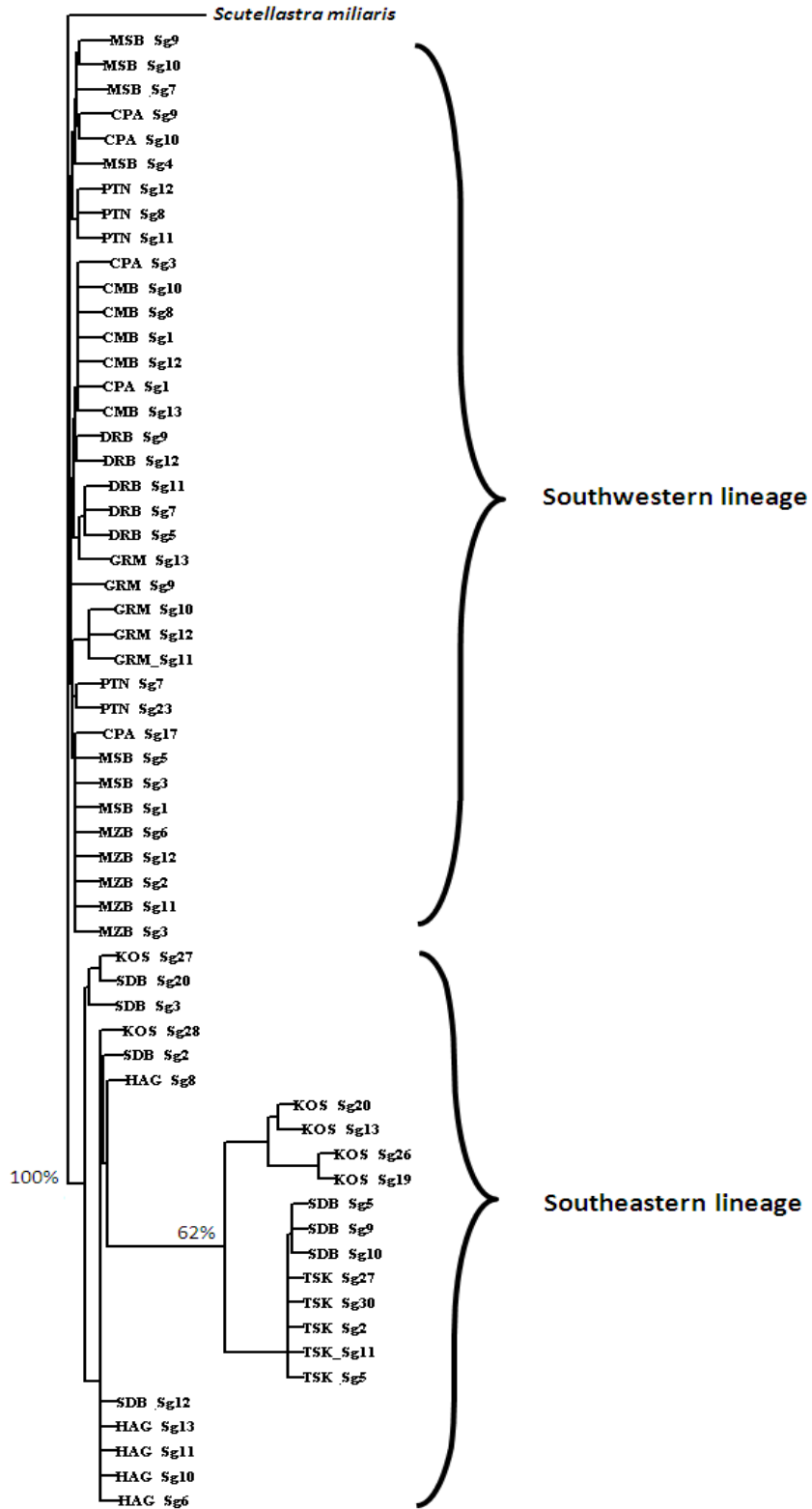


Figure 2.11: The COI Neighbor Joining tree of the non-territorial *Scutellastra granularis*.

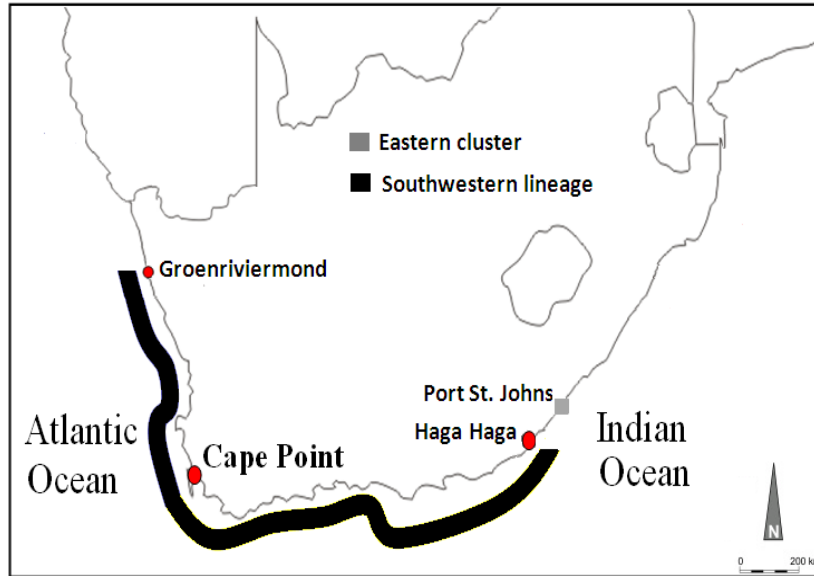
2.4 Discussion

Phylogeographic distribution of territorial and non-territorial foragers

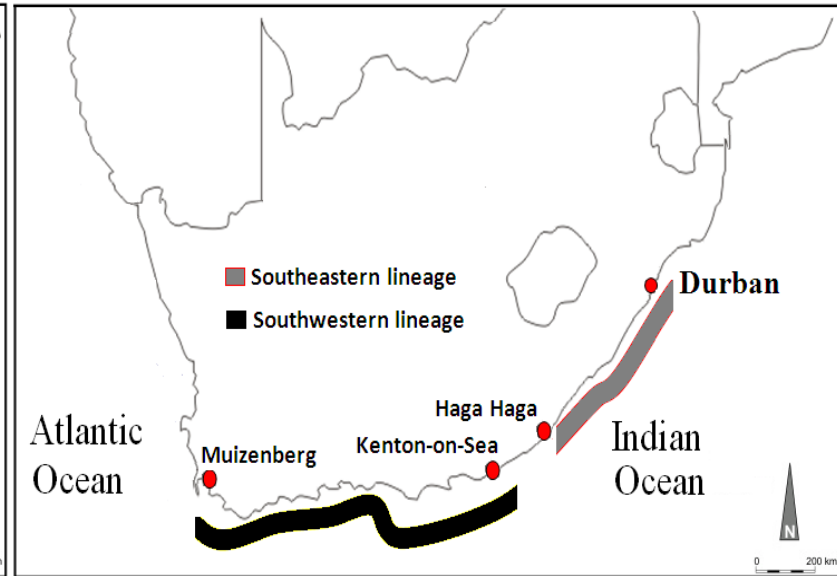
The territorial and non-territorial grazers did not show common Φ_{ST} population genetic differentiation and phylogeographic patterns as expected. The analyses revealed two lineages in the territorial *Scutellastra longicosta* (southern and eastern lineages) and in the non-territorial *Scutellastra granularis* (southwestern and southeastern lineages). The territorial *S. cochlear* displayed no phylogeographic structure, but significant Φ_{ST} genetic differentiation. The territorial *S. barbara* revealed a southwestern lineage which was distinct from the most northeastern population (Port St. Johns, Figure 2.12a). The observed genetic disjunction coincides with the biogeographic boundary between the warm-temperate Agulhas region and the Subtropical region. Interestingly, an electrophoresis analysis of 17 loci failed to recover this phylogeographic break amongst populations of *S. barbara* (Ridgway et al. 1999b).

The analysis of Φ_{ST} genetic differentiation, neighbor joining analysis and haplotype network reconstruction revealed two distinct genetic lineages within the territorial *Scutellastra longicosta* (Figure 2.12b). The phylogeographic boundary between the two lineages of *S. longicosta* was located between Kenton-on-Sea and Haga-Haga, coinciding with the biogeographic break between the warm-temperate Agulhas region and the Subtropical region. The phylogeographic break observed within the territorials *S. barbara* and *S. longicosta* coincides with the biogeographic boundary between the warm-temperate Agulhas region and the Subtropical east coast region (Figures 2.12a and 2.12b). This is concordant with previous studies which found phylogeographic breaks in this region for various estuarine and marine invertebrates including mudprawns, crabs, shrimps and intertidal mussels (Teske et al. 2006, 2007a, 2009 and Zardi et al. 2007). This has been attributed to the flow of Agulhas current which deflects offshore along this region, creating a semi-permeable barrier to gene flow (Teske et al. 2006, Zardi et al. 2011).

a)



b)



Figures 2.12a and b: The map of South Africa showing distribution of **a)** the break between the southwestern lineage and the most northeastern population (Port St. Johns) within the territorial *Scutellastra barbara* and **b)** the southwestern and southeastern lineages discovered within the territorial *Scutellastra longicosta*.

This phylogeographic boundary (Figure 2.12) is maintained by the offshore deflection of the Agulhas current which carries the entrained larvae away from the intertidal zone (Teske et al. 2006, 2008, 2011a, 2013b, Zardi et al. 2007, 2011a). The two lineages in *S. longicosta* overlap along this region, a pattern also discovered in the endemic South African brown mussel *Perna perna* (Zardi et al. 2007). Post-glacial sea level fluctuations have also been invoked to explain genetic disjunction within species of the pulmonate limpet *Siphonaria* along this region (Teske et al. 2011b, 2013b).

The analysis of Φ_{ST} genetic differentiation, neighbor joining analysis and haplotype network reconstruction revealed two distinct genetic lineages within the non-territorial *Scutellastra granularis*. This phylogeographic break between these lineages was located along the mid south coast between Mossel Bay and Tsitsikamma (Figure 2.13). However, allozyme analyses of this species (Ridgway et al. 1998b, Vat 2000) failed to recover this break. A phylogeographic break in this region has been recorded before for marine demersal fishes (von der Heyden 2009 and von der Heyden et al. 2008). This phylogeographic boundary (between Mossel Bay and Tsitsikamma) has been attributed to the flow of the Agulhas current in relation to the continental shelf, the current flows further from the shore along this region deflecting dispersing larvae offshore and thus creating a barrier to gene flow (von der Heyden et al. 2007b, 2008).

The distributional break between the parapatric granular sister taxa, *S. granularis* and *S. natalensis* is positioned between Haga-Haga and Port St. Johns, coinciding with the biogeographic boundary between the warm-temperate Agulhas region and the Subtropical east coast region. The genetic distinction of Haga-Haga samples could be attributed to hybridization between these parapatric sister taxa if not larval recruitment.

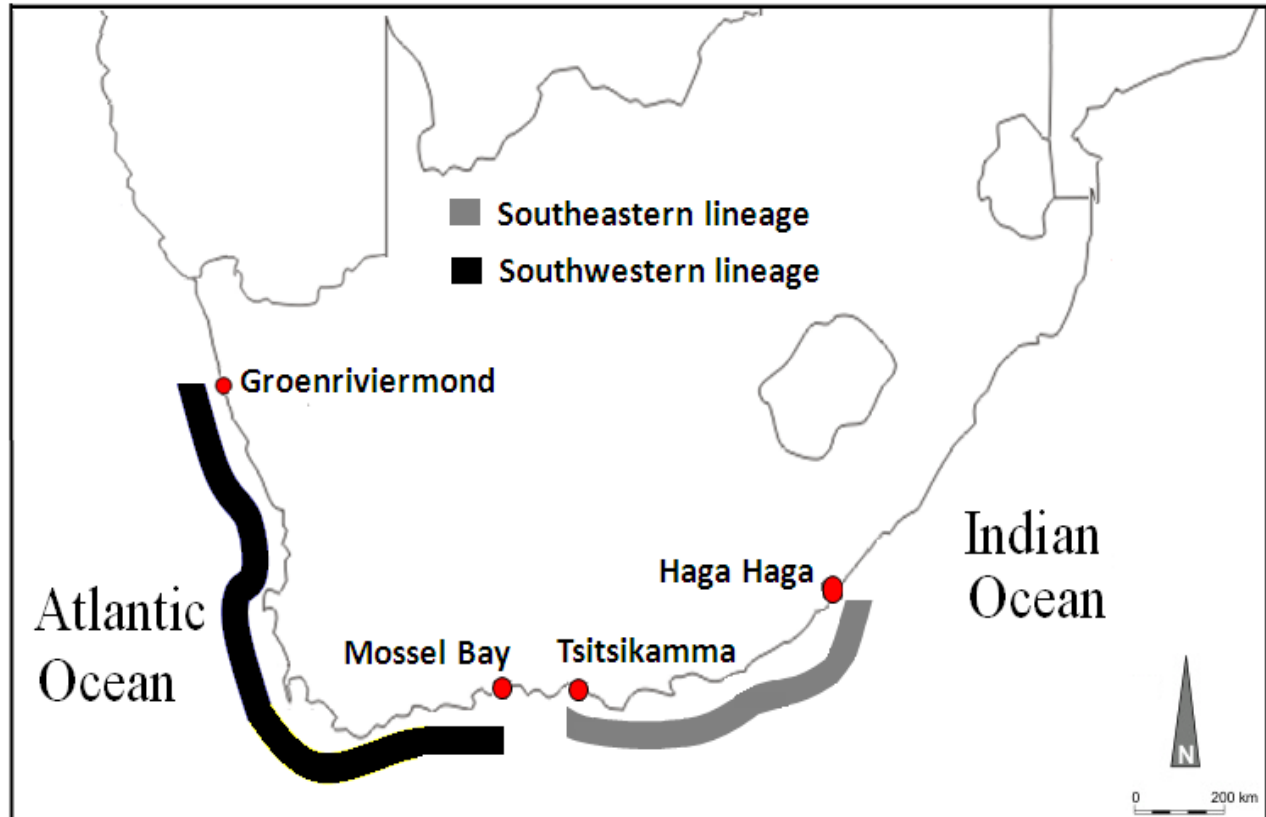


Figure 2.13: The map of South Africa showing distribution of the southwestern and southeastern lineages discovered within the non-territorial *Scutellastra granularis*.

The territorial and non-territorial species did not reveal similar patterns of variation in either phylogeographic structure or Φ_{ST} genetic differentiation. Three territorial species (*S. barbara*, *S. cochlear*, *S. longicosta*) and one non-territorial species (*S. granularis*) revealed significant Φ_{ST} population genetic differentiation (Table 2.5). Two territorial species (*Scutellastra barbara* and *S. longicosta*) revealed a common phylogeographic boundary, whereas the non-territorial *S. granularis* revealed a different phylogeographic break (Table 2.13). The most striking genetic pattern was observed within the territorial *Scutellastra cochlear*, this species revealed no phylogeographic structure but significant Φ_{ST} population genetic differentiation. This probably implies that external vagaries such as oceanographic circulations and biogeographic boundaries have no impact on the observed genetic structure within this species.

Table 2.5: The summary of large scale (biogeographic) genetic structure amongst sympatric southern African patellid limpets. ^T = Territorial foragers, ^{NT} = Non-territorial foragers.

Species	Phylogeographic Structure (Yes/No)	Significant Φ_{ST} Genetic Differentiation (Yes/No)
<i>Scutellastra barbara</i> ^T	Yes	Yes
<i>Scutellastra cochlear</i> ^T	No	Yes
<i>Scutellastra longicosta</i> ^T	Yes	Yes
<i>Scutellastra argenvillei</i> ^{NT}	No	No
<i>Scutellastra granularis</i> ^{NT}	Yes	Yes
<i>Scutellastra miliaris</i> ^{NT}	No	No
<i>Scutellastra natalensis</i> ^{NT}	No	No
<i>Cymbula compressa</i> ^T	No	No
<i>Cymbula miniata</i> ^T	No	No
<i>Cymbula granatina</i> ^{NT}	No	No
<i>Cymbula oculus</i> ^{NT}	No	No

This study highlighted the potential of the CO1 marker in recovering genetic structure in cases where allozyme analyses have limitations (i.e. *Scutellastra granularis*: Ridgway et al. 1998b, Vat 2000 and *S. barbara*: Ridgway et al. 1999b). The incongruent phylogeographic boundaries discovered amongst these species suggest different interaction effects between their larval history and oceanographic oscillations. The territorial and non-territorial foragers do not show similar trends in phylogeographic structure or Φ_{ST} indices, rejecting the original hypothesis. The two territorial species with congruent phylogeographic boundary may have different larval dispersal compared to the non-territorial *Scutellastra granularis* which revealed a phylogeographic boundary along the mid south coast. Thus, the evolutionary processes determining large scale (biogeographic) genetic structure of these sympatric patellid limpets seem to be species-specific.

CHAPTER THREE

Genetic diversity and demographic history of sympatric intertidal patellid limpets (Gastropoda: Patellogastropoda) with different foraging behaviours from the southern African shoreline



3.1 Introduction

South African intertidal rocky shores are conspicuously inhabited by limpets, with the true limpets or patellogastropods dominating in terms of both species richness and diversity (Branch 1976, 1981, 1984, 1985a). Intense interspecific competition for ecological resources such as habitat (i.e. high or low shore) and food (i.e. algae) played a core role in the evolution of territorial and non-territorial foraging in these true limpets (Branch 1985b). These limpets are unevenly distributed between the tidal heights, with a high diversity of territorial grazers inhabiting the low shore, where primary production is greater and a low diversity of non-territorial grazers inhabiting the high shore (Branch 1976, 1981, 1984, 1985a, Branch & Newell 1978).

This partitioning of ecological resources (habitat and algal food) can be explained in the context of the adaptive strategies of environmental grain and trophic resource stability (Levins & MacArthur 1966, Schoener 1974, Valentine 1976 and Vellend 2006). In accordance with this adaptive strategy, if food resources are inconsistent or unstable, the most adaptive strategy is to forage on almost everything and to live in a wide variety of habitats, increasing the chances of finding food. Contrarily, if food resources are consistent or stable, the best adaptive strategy is predicted to be to inhabit a restricted zone and eat only what is best, minimizing interspecific competition (Valentine 1976).

The availability of algal food is unpredictable in time and space for high shore species due to the receding and peaking tides, presumably the limpets there are able to search for algal food and forage when conditions are favourable. The best adaptive strategy there would be to be a highly mobile general forager, which would improve the chances of finding algal food. The ecological dynamics of the high shore promote ecological generalization for both food and habitat and thus limpets on the high shore tend to be non-territorial foragers (Branch 1985a).

However, algal availability is greater and more stable on the low shore, and limpets there have evolved a strategy of ecological specialization probably to reduce interspecific competition. This adaptive strategy entails foraging only on specific alga(e) and inhabiting a fixed place. In patellid limpets, the territorial grazers not only inhabit a fixed place but also actively defend it against intruding limpets. Stability and consistency in the availability of food resources permit the persistence of species with specialized habitats and diets (Branch 1981 and 1985b).

Over the mid to late 20th century there was an upsurge in population genetic studies across a wide range of phyla following the advent of electrophoretic techniques (Ayala et al. 1974). Consequently, there was a burning aspiration to comprehend the rationale behind genetic variation in natural populations. As a result, ecological geneticists reviewed most of these population genetic studies in an endeavour to develop theories and hypotheses that could best explain the genetic variation discovered within and amongst species. Amongst the theories postulated was the common ecological niche-width variation hypothesis (Levene 1953 and van Valen 1965).

This hypothesis presumes that levels of genetic polymorphism or heterogeneity are directly proportional to the breadth and heterogeneity of the niche occupied by a species (Powell 1971, MacDonald & Ayala 1974, Bryant 1976, Gillespie 1978, Nevo 1978 and Nevo et al. 1984). This is based on the rationale that species inhabiting a heterogeneous environment will accumulate and retain or express multimeric alleles to adapt to the dynamics of their environment, whereas species inhabiting homogenous environments will express the few alleles that are optimal for their that environment (Fincham 1972, Campbell et al. 1975 and Clarke 1979). A vast literature of ecological studies based on allozyme analyses of marine gastropods has long been in concordance with this hypothesis (Lavie & Nevo 1981, 1986, Noy et al. 1987 and Nevo 1978) although it was contradicted by some allozyme studies (Valentine 1976 and Valentine & Ayala 1977).

Notwithstanding the discordant results, evolutionary ecologists used the hypothesis to develop a habitat specialist-generalist model to explain the evolution of ecological specialization or generalization (Valentine 1976 and Smith & Fujio 1982). According to the model, a habitat-specialist perceives its habitat as heterogeneous and is affected by its patchiness; the species will express several narrow-ranging alleles resulting in higher genetic variability at the species level. In contrast, a habitat-generalist perceives its habitat as homogenous and is less affected by patchiness; the species will express a few wide-ranging alleles resulting in lower genetic variability (Smith & Fujio 1982). Subsequently, it has been a common doctrine in evolutionary ecology to equate “ecological specialization” with apomorphic rather than plesiomorphic characters (Futuyma & Moreno 1988).

Studies based on microsatellites and isozyme electrophoresis of various taxa including carabid insects (Brouat et al. 2004), marine teleosts (Smith & Fujio 1982) and crustaceans (Nelson & Hedgecock 1980) were congruent with this model. On the other hand, limited genetic studies using both isozyme electrophoresis and DNA analysis were in conflict with the model (Valentine 1976, Valentine & Ayala 1977, Haynie et al. 2009 and Fine et al. 2012). For example, the ecological woodrat specialists (diet and habitat), *Neotoma stephensi* and *N. magister* were characterized by lower heterozygote diversity than congeneric generalists (Haynie et al. 2009).

Considering the conflicting findings, there is no consensus on whether specialist species, presumed to be characterized by apomorphic characters, display higher genetic heterogeneity than sympatric generalists. Patellogastropods are good model organisms for the investigation of the correlation between “ecological specialization” and genetic diversity. Territorial grazers have restricted food and habitat (Branch 1975c), with a foraging trait that encapsulates both habitat and feeding specialization.

The evolution of resource partitioning is likely to have culminated in dissimilar genetic structure between territorial and non-territorial foragers amongst these limpets. The non-territorial grazers inhabit the low shore and migrate to the high shore as they mature and do not occupy a fixed home range or foraging area. These species occupy a broad, heterogeneous ecological niche and are predicted to be characterized by low genetic variability by the ecological specialist-generalist model. In contrast, the territorial grazers permanently inhabit an area on the low shore and can be perceived as occupying a narrow, homogeneous ecological niche (Noy et al. 1987). In compliance with the ecological specialist-generalist model, territorial grazers should be characterized by greater genetic variability than sympatric non-territorial grazers.

Genetic diversity of these limpets could well have been affected by past climatic oscillations. Most marine animal taxa underwent bottleneck or founder effect during dramatic Pleistocene sea-level fluctuations because of the intrusion of ice-sheets into suitable habitats (Hewitt 2004, Wilson 2006, Waltari et al. 2007, Larmuseau et al. 2009 and Marko et al. 2010). Sea-level fluctuated dramatically along the southern African coast during the mid and late Pleistocene, when most present day coastlines were formed (Ramsay & Cooper 2002 and Fisher et al. 2010). Pleistocene sea-levels in South Africa were similar to those of the Caribbean Sea (Ramsay & Cooper 2002) and numerous studies have documented how Pleistocene sea-levels and the Last Glacial Maximum (LGM) climatic fluctuations have shaped the demographic distribution of marine taxa along the Caribbean Sea and worldwide (Gysels et al. 2004, Olsen et al. 2004, Sa-Pinto et al. 2005, Domingues et al. 2005, 2007, Hoarau et al. 2007, Maggs et al. 2008, Larmuseau et al. 2009 and Neto et al. 2012). During periods of glaciation, ice-cover rendered many habitats unsuitable for most coastal species, which were presumably restricted to one or a few refugial habitats (Larmuseau et al. 2009). Post-glacial Pleistocene demographic expansions have been documented along the South African coastline for seahorses (Teske et al. 2003), demersal fishes (von der Heyden et al. 2010), sea urchins (Muller et al. 2012), barnacles (Reynolds 2011) and false limpets (Teske et al. 2007b, 2011b). Post-glacial sea-level fluctuations are likely to have affected demographic history of both territorial and non-territorial foragers in the same way.

In addition to investigating the specialist-generalist model, this study will also test for evidence of demographic population expansion in both territorial and non-territorial patellid limpets. The main hypothesis of this study was to test the specialist-generalist model on the genetic structure of these limpets at two scales of analyses: within species and within sites. The model predicts that at small, local or within-site scales, territorial grazers should be characterized by higher values of molecular indices than congeneric non-territorial foragers.

3.2 Materials and Methods

3.2.1 Study sites and sampling procedure

Limpets were sampled from 16 rocky shores across the entire South African shoreline (Figure 3.1). From each site, at least five individual specimens of each species were collected randomly at approximately 5m intervals and immediately preserved in 100% ethanol.

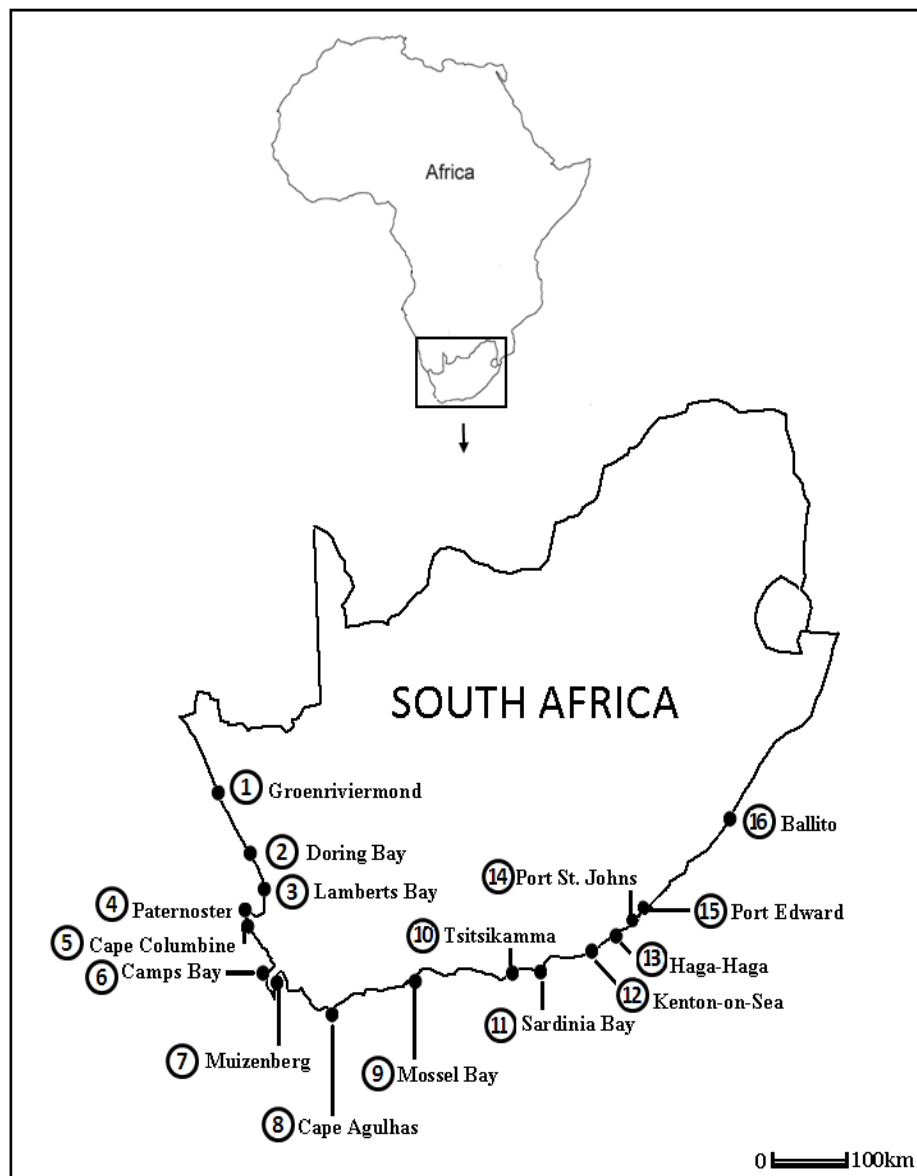


Figure 3.1: The map of the South Africa showing the sampling localities.

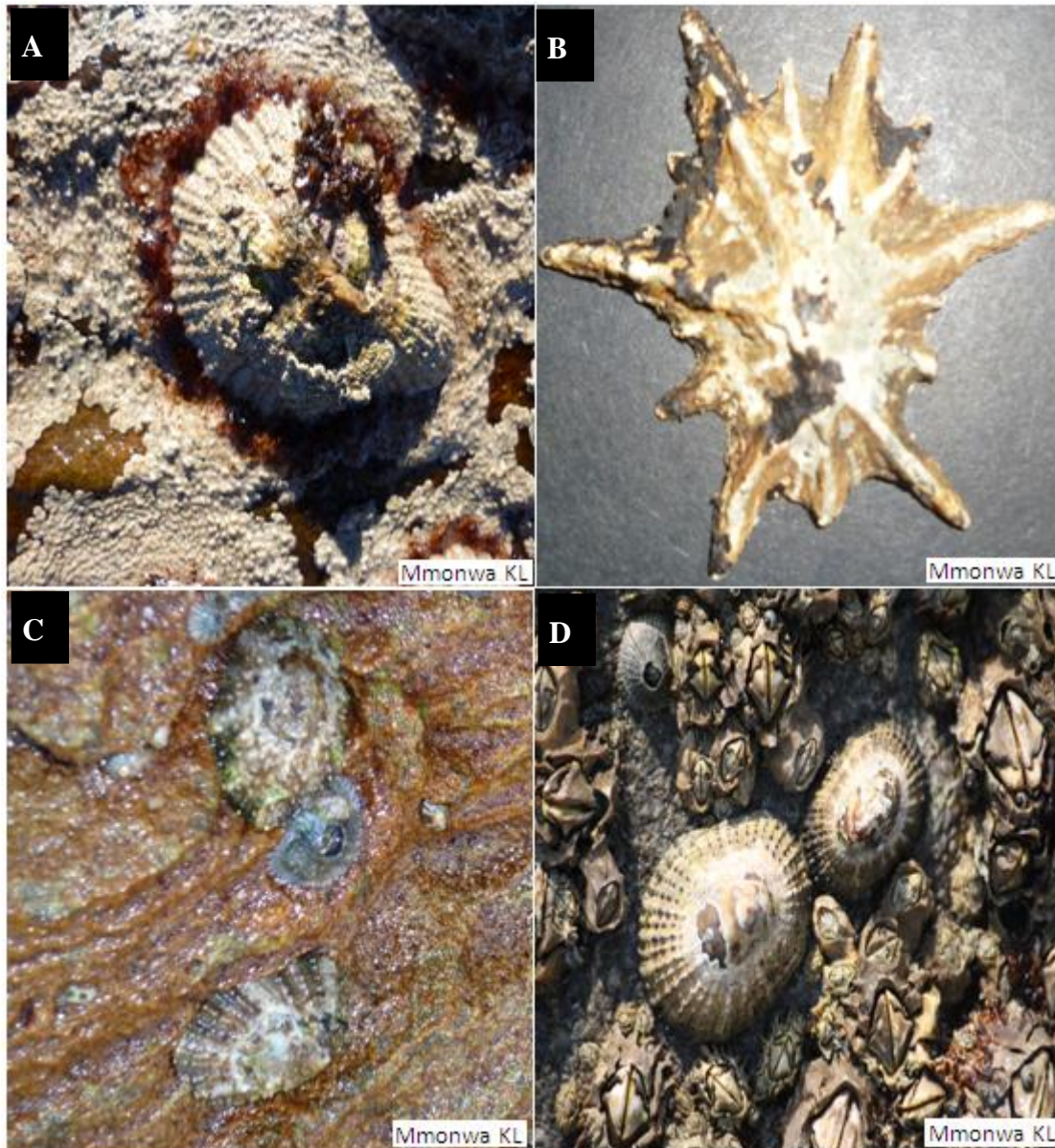
3.2.2 *The study species*

Figure 3.2: A. Territorials *Scutellastra cochlear* and B. *Scutellastra longicosta*
C. Non-territorials *Scutellastra granularis* and D. *Scutellastra natalensis*.

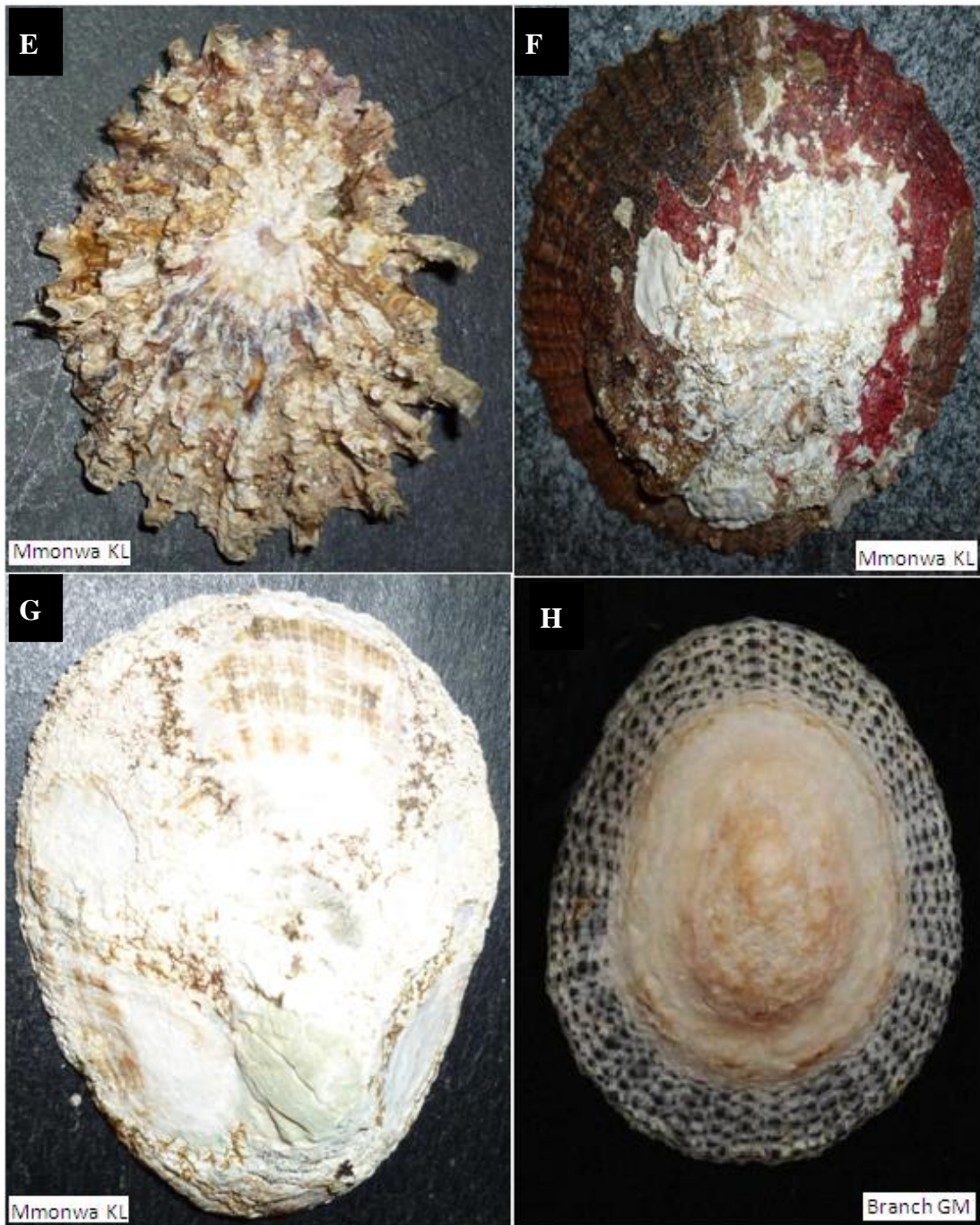


Figure 3.2: **E.** Territorials *Scutellastra barbara* and **F.** *Scutellastra tabularis*
G. Non-territorials *Scutellastra argenvillei* and **H.** *Scutellastra miliaris*.

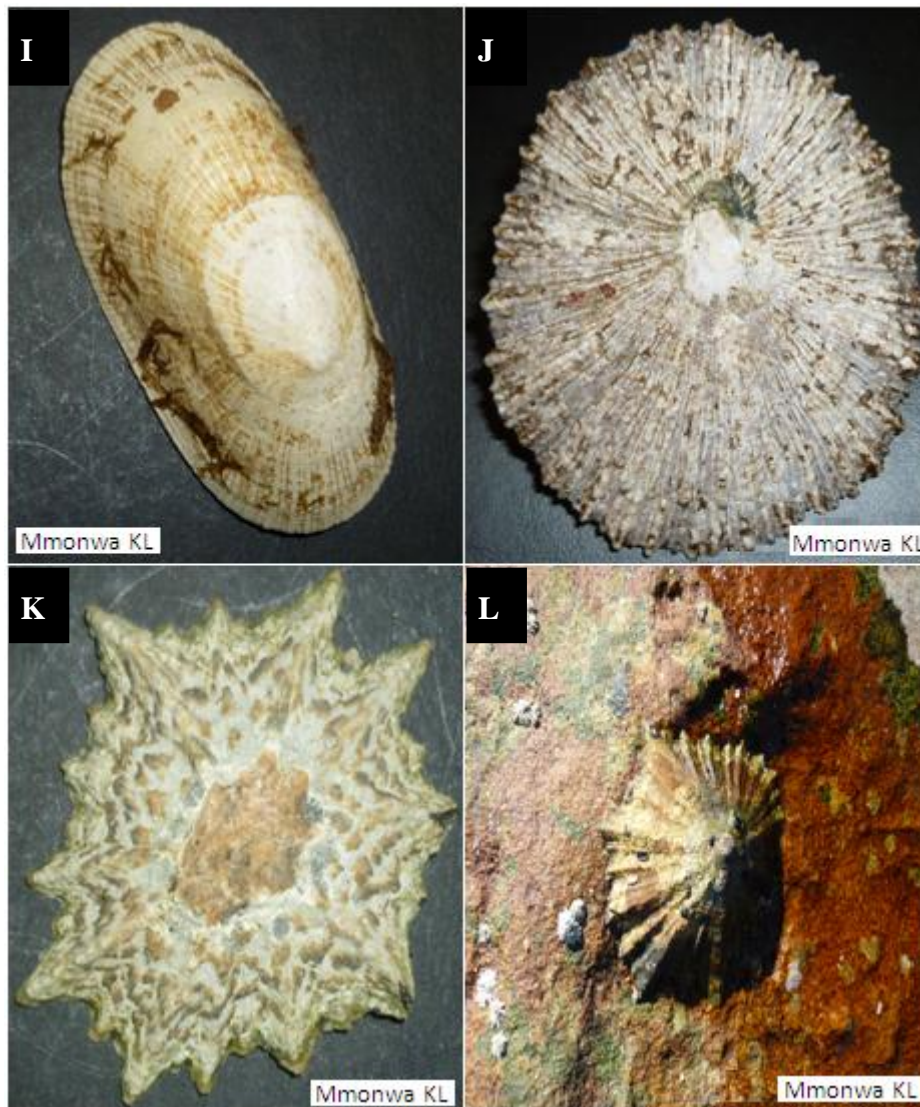


Figure 3.2: I. Territorials *Cymbula compressa* and J. *Cymbula miniata*.
K. Non-territorials *Cymbula granatina* and L. *Cymbula oculus*

3.2.3 *Materials and Methods* (described in chapter one)

3.2.4 *Genetic diversity indices for all the species*

Genetic diversity was calculated using the software package DnaSP version 5.00.07 (Librado & Rozas 2009) for all the selected study species. A partial fragment of the mtDNA Cytochrome Oxidase subunit 1 (CO1) was used to compare the levels of genetic diversity in territorial and non-territorial patellid limpets. For each species, the input data set comprised at least five samples of partial fragments of CO1 sequences from each population. The level of genetic differentiation amongst populations was estimated using F_{ST} index (Wright 1951 and 1965) using DnaSP5.00.07 (Librado & Rozas 2009). The levels of genetic diversity were estimated for the following standard molecular indices (Nei 1987): number of samples (n), number of haplotypes (k), average nucleotide differences (D) polymorphic sites (S), haplotype diversity (h) and nucleotide diversity (π). Selective neutrality tests were calculated using both Tajima's D (Tajima 1989) and Fu and Li's D (Fu & Li 1993) statistics.

3.2.5 *Genetic diversity indices within phylogeographic and biogeographic regions*

The numbers of localities and samples analysed were different for each species depending on the species' biogeographic limits and sampling efforts (Table 3.1). Additionally, phylogeographic reconstruction (chapter two) revealed genetic clusters or lineages which were confined to biogeographic regions for *Scutellastra barbara* and *S. longicosta* but not *S. granularis*. All of these may present skewed haplotype distribution and diversity from site to site due to sampling bias and different genetic clusters or lineages in question. Consequently, sites were grouped into biogeographic regions (Table 3.1) and phylogeographic clusters or lineages to counteract the effects of sample size and different lineages in question. Levels of genetic heterogeneity were estimated for the same genetic diversity indices amongst territorial and non-territorial grazers confined to each and biogeographic region and phylogeographic region (*S. granularis*).

Table 3.1: The species examined, number of individuals analysed from each site and the grouping of sites into regions. Foraging traits: ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Regions	West coast						South coast						East coast		Angolan coast		Total samples		
Sites	GRM	DRB	LMB	PTN	CCB	CMB	MZB	CPA	MSB	TSK	SDB	KOS	HAG	PSJ	PED	BLT		BAB	LBT
Sites Number	①	②	③	④	⑤	⑥	⑦	⑧	⑨	⑩	⑪	⑫	⑬	⑭	⑮	⑯	⑰	⑱	
Scutellastra																			
<i>S. barbara</i> ^T	5		6		7				8		6		6	5					43
<i>S. cochlear</i> ^T	10	5		5		5	5	6	5	5	7	5	11		6				81
<i>S. longicosta</i> ^T							5	5	5	5	5	6	5						41
<i>S. argenvillei</i> ^{NT}			5			5			5				5						20
<i>S. granularis</i> ^{NT}	5	5		5		5	5	5	6	5	7	6	5						60
<i>S. miliaris</i> ^{NT}																	7	7	14
<i>S. natalensis</i> ^{NT}															5	5			10
Cymbula																			
<i>C. compressa</i> ^T	10	10		10		10													40
<i>C. miniata</i> ^T			5						5				5	5					20
<i>C. oculus</i> ^{NT}					5	5	5	8	6	6	5								40
<i>C. granatina</i> ^{NT}	10	10		10		10													40

3.2.6 *Molecular diversity indexes within sites*

Theta parameters are useful in estimating levels of genetic differentiation within and between populations (Excoffier et al. 2005, 2006). Differences in molecular diversity were estimated using Arlequin version 3.1 (Excoffier et al. 2006) for various theta (θ) parameters. The various population parameters of genetic differentiation were computed in Arlequin version 3.1 (Excoffier et al. 2006) using the following formula: $\theta = 2M\mu$, where M is equal to N for haploid populations and μ is the overall mutation rate at the haplotype level (Excoffier et al. 2006). The following parameters of genetic differentiation were estimated: π (nucleotide diversity estimated using the mean number of pairwise nucleotide differences), $\theta\pi$ (estimated from the infinite-site equilibrium relationship between the mean number of pairwise differences (π) and θ (Tajima 1983), θ_S (estimated from the infinite-site equilibrium relationship between the number of segregating sites (S) and the sample size (n)), θ_k (estimated from the infinite-haplotype equilibrium relationship between the expected number of haplotypes (k), sample size (n) and θ (Ewens 1972)). The computed molecular diversity indices were compared between territorial and non-territorial foragers within each site.

3.2.7 Demographic and spatial expansion analyses

A signature of historical demographic expansion was estimated using both Tajima's D (Tajima 1989) and Fu's F_s (Fu 1996) statistics based on 1000 coalescent simulations in Arlequin version 3.1 (Excoffier et al. 2006). These test statistics are sensitive to departures from both selective neutrality and from population size equilibrium caused by expansions or bottlenecks (Tajima 1996, Fu 1997). Significantly negative Tajima's D (Tajima 1989) and Fu's F_s (Fu 1996) statistics indicate population expansion (Ray et al. 2003) or a selective sweep, whereas positive values are expected under balancing selection of recent bottlenecks (Teixeira et al. 2011). However, even populations displaying uniform genetic structure (non-significant F_{ST} values) may infer recent demographic expansion (Walker et al. 1998, Espinosa et al. 2010 and Teixeira et al. 2011). Thus, departures from both selective neutrality and population size equilibrium were estimated for all the species inclusive of those characterized by lack of genetic structure.

To determine whether these patellid limpets underwent a range expansion, the spatial expansion model was investigated in Arlequin version 3.1 (Excoffier et al. 2006). The goodness-of-fit of the observed mismatch distribution to that expected under the spatial expansion model was estimated using the sum of squared deviations (SSD) statistic for pooled samples. The model of spatial expansion assumes that subdivided populations expanded their distribution range and increased the total number of individuals (Excoffier et al. 2006). A significant SSD value is taken as evidence of departure from the estimated demographic model of spatial expansion and a non-significant SSD values indicates evidence of spatial expansion (Excoffier et al. 2005, 2006). Demographic changes amongst these patellid limpets were also examined by calculating the Raggedness index of the observed mismatch distribution for each of the populations according to the population expansion model (Excoffier et al. 2005, 2006). This statistic quantifies the smoothness of the observed mismatch distribution, smaller values indicates sudden population expansion, whereas higher values (greater raggedness) indicate a more stable population (Harpending 1994).

The plots of mismatch distribution were computed using the software package DnaSP version 5.00.07 (Librado & Rozas 2009). Mismatch distributions were plotted for each species with all populations pooled together in cases where there was no significant genetic differentiation amongst populations. For the species which revealed two distinct genetic lineages across their range (*Scutellastra barbara*, *Scutellastra longicosta* and *Scutellastra granularis*), each lineage was analysed separately. Molecular signatures of a unimodal mismatch distribution characterize sudden demographic expansion while a multimodal mismatch distribution indicates populations at demographic equilibrium (Slatkin & Hudson 1991, Rogers & Harpending 1992, Ray et al. 2003 and Excoffier et al. 2006). However, even spatial population expansion could be characterized by unimodal mismatch distribution if gene flow is high amongst neighbouring populations (Ray et al. 2003 and Excoffier 2004).

The spatial expansion model further estimated tau (τ) or the demographic expansion factor, with 95% confidence intervals and the initial and final mutational parameter, theta (θ). Initial theta is estimated as $\theta_i = 2N_i\mu$ (before the population growth) and final theta is $\theta_f = 2N_f\mu$ (after the population growth). The time since population expansion took place was estimated using the formula: $t = \tau/2\mu k$, where t is the time (in years) since population expansion took place, τ is the estimated number of generations since the expansion, μ is the mutation rate per site per generation and k is the sequence length. A mutation rate of 1.0% per million years per site was used for patellid limpets as estimated for *Cellana* species (González-Wevar et al. 2010, 2011a). The demographic expansion parameters were estimated using the nonlinear least-squared approach implemented in Arlequin version 3.1 (Schneider & Excoffier 1999). The time since population expansion take place was estimated online using the mismatch calculator (<http://www.uni-graz.at/zoowww/mismatchcalc/mmc3.php>). The mismatch calculator provides an advantage of avoiding rounding errors and allowing four different options of substitution rates to estimate time since population expansion (Schenekar & Weiss 2011).

3.3 Results

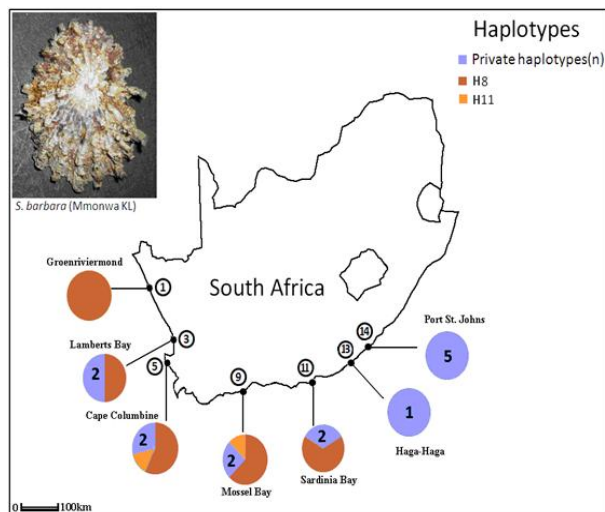
3.3.1 Species-specific genetic diversity indices

The results of the genetic diversity indices and genetic differentiation are presented in Table 3.2 and summarised in Figures 3.3a – j for all species along their core distributional range.

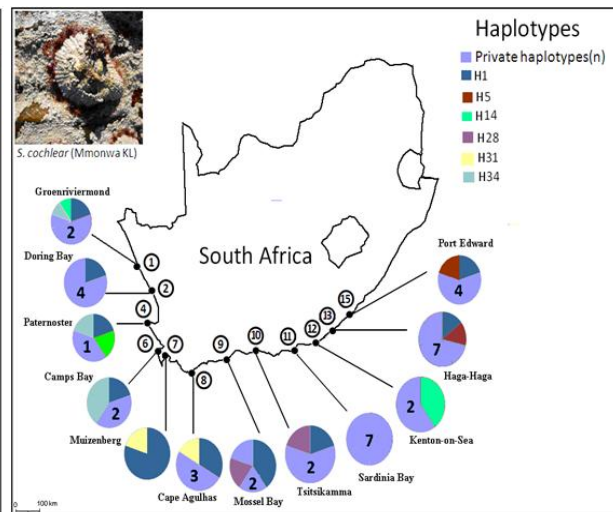
Table 3.2: The results of genetic diversity indices and F_{ST} genetic differentiation for all the species. Number of samples (n), Number of haplotypes (k), Average nucleotide differences (II), Polymorphic sites (S), Haplotype diversity (h), Nucleotide diversity (π), Significant * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and ns (not significant). ^T = Territorial, ^{NT} = Non-territorial grazers.

Species	n	CO1 Length	k	II	S	h	π	F_{ST}
<i>Scutellastra</i>								
<i>S. barbara</i> ^T	43	539bp	16	16.25	145	0.749	0.03114	0.001***
<i>S. cochlear</i> ^T	81	538bp	42	3.18	48	0.935	0.00592	0.006**
<i>S. longicosta</i> ^T	41	546bp	17	4.37	24	0.928	0.00877	0.000***
<i>S. argenvillei</i> ^{NT}	20	541bp	10	1.27	10	0.800	0.00234	0.556(ns)
<i>S. granularis</i> ^{NT}	60	680bp	30	61.64	221	0.958	0.09078	0.000***
<i>S. miliaris</i> ^{NT}	14	603bp	8	1.46	7	0.824	0.00242	0.539(ns)
<i>S. natalensis</i> ^{NT}	10	537bp	5	2.267	9	0.756	0.00422	0.991(ns)
<i>Cymbula</i>								
<i>C. compressa</i> ^T	20	689bp	2	0.087	1	0.087	0.00013	0.653(ns)
<i>C. miniata</i> ^T	20	711bp	7	3.14	8	0.874	0.39286	0.509(ns)
<i>C. granatina</i> ^{NT}	40	689bp	7	1.28	7	0.759	0.00186	0.289(ns)
<i>C. oculus</i> ^{NT}	40	689bp	7	0.97	7	0.612	0.00140	0.251(ns)

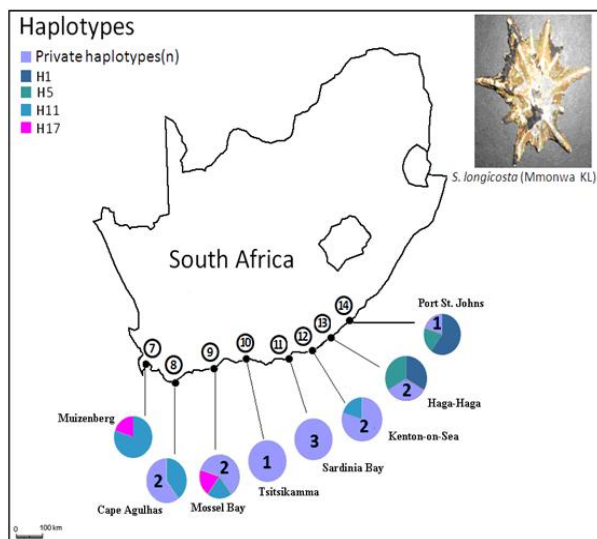
The F_{ST} tests revealed significant genetic differentiation amongst populations of the territorial species *Scutellastra barbara*, *S. cochlear*, *S. longicosta* and the non-territorial *S. granularis* (Table 3.2). The haplotype frequency and diversity within each species are summarized on the maps below.



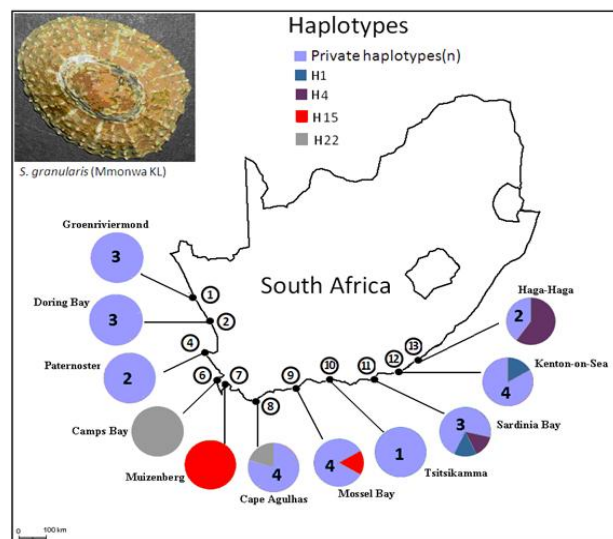
a) *Scutellastra barbara*^T



b) *Scutellastra cochlear*^T

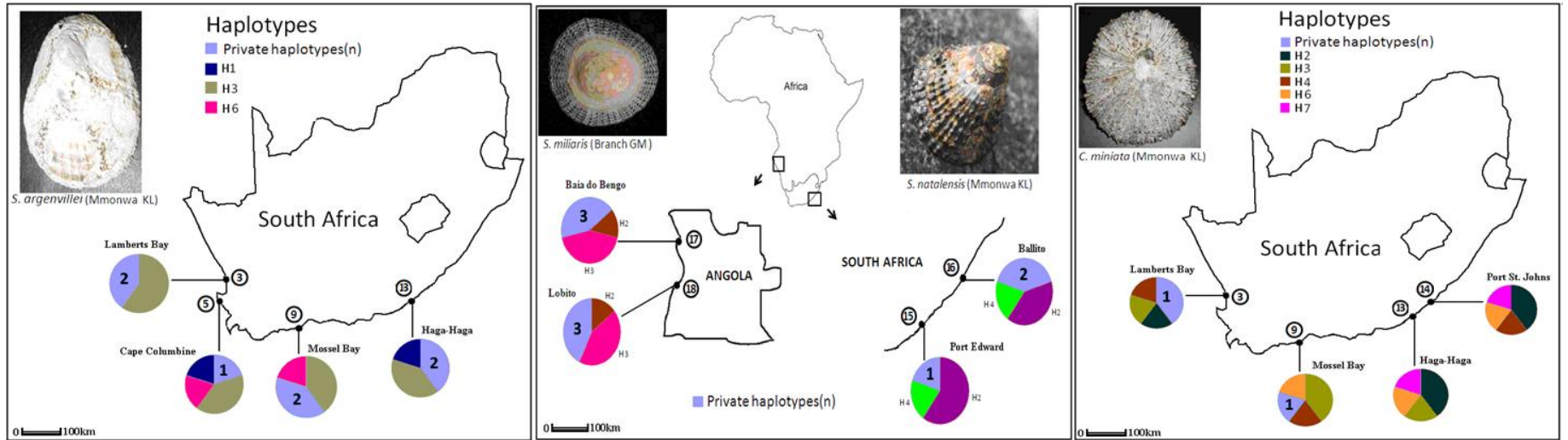


c) *Scutellastra longicosta*^T



d) *Scutellastra granularis*^{NT}

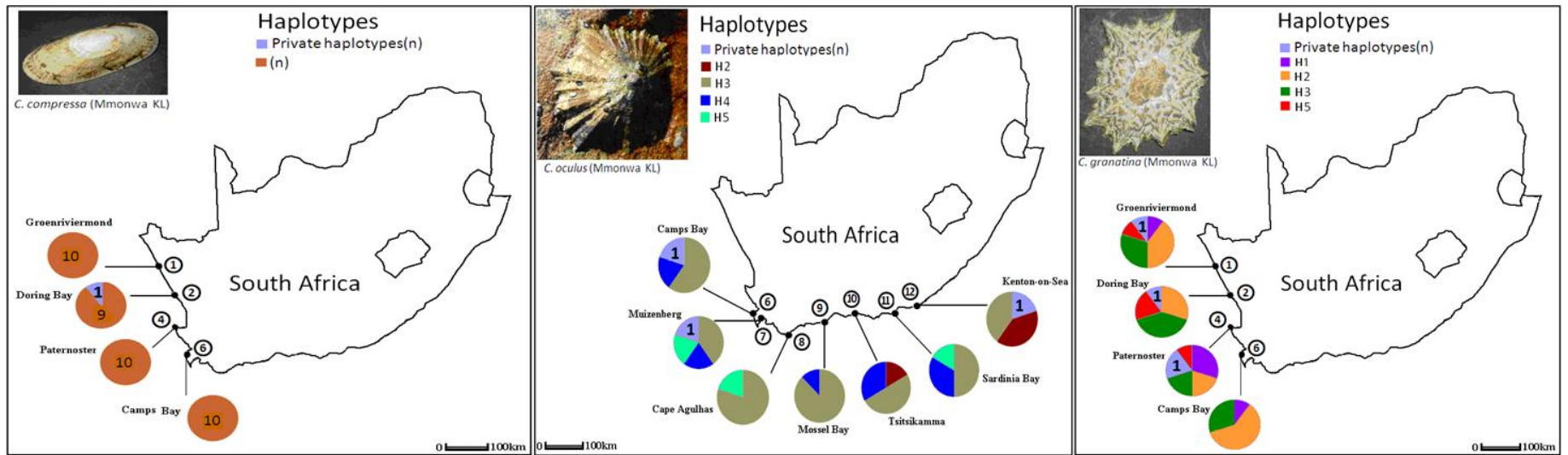
Figures 3.3a - d: The map summarizing haplotype frequency and diversity for all of the species at the core of their distribution range. ^T = Territorial grazers and ^{NT} = Non-territorial grazers.



e) *Scutellastra argenvillei*^{NT}

f) *S. miliaris*^{NT} and *S. natalensis*^{NT}

g) *Cymbula miniata*^T



h) *Cymbula compressa*^T

i) *Cymbula oculus*^{NT}

j) *Cymbula granatina*^{NT}

Figures 3.3e - j: The map summarizing haplotype frequency and diversity for all of the species at the core of their distribution range. ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

The territorial *Scutellastra* species were all characterized by high numbers of haplotypes and private haplotypes at sites across the species' ranges (Table 3.3). Non-territorial *Scutellastra* spp. had lower numbers of haplotypes and private haplotypes, with the important exception of *S. granularis*. Overall, *Cymbula* spp. were characterized by lower numbers of haplotypes and private haplotypes than *Scutellastra* spp. In contrast to *Scutellastra*, the non-territorial *Cymbula* species had higher numbers of haplotypes and private haplotypes than the congeneric territorial species (Table 3.3). Nevertheless, the number of sampled haplotypes is related to sampling effort and this could have influenced the observed results since sampling effort differed amongst species.

Table 3.3: The total number of haplotypes and private haplotypes sampled within each species at its core distributional range. ^T = Territorial, ^{NT} = Non-territorial foragers

Species	Number of sites analysed	Number of Haplotypes	Private Haplotypes
<i>Scutellastra</i>			
<i>S. barbara</i> ^T	7	16	14
<i>S. cochlear</i> ^T	12	42	36
<i>S. longicosta</i> ^T	8	17	13
<i>S. argenvillei</i> ^{NT}	4	10	17
<i>S. granularis</i> ^{NT}	11	30	26
<i>S. miliaris</i> ^{NT}	2	8	6
<i>S. natalensis</i> ^{NT}	2	5	3
<i>Cymbula</i>			
<i>C. compressa</i> ^T	4	2	1
<i>C. miniata</i> ^T	4	7	2
<i>C. granatina</i> ^{NT}	4	7	3
<i>C. oculus</i> ^{NT}	7	7	3

3.3. 2. Genetic diversity within phylogeographic regions

There was no consistent pattern of variation in h and π amongst territorial and non-territorial grazers within phylogeographic regions (Table 3.4). The non-territorial and territorial grazers had the highest numbers of h and π within the western, southern and eastern lineages without any obvious trends of one type of grazer consistently revealing higher/lower values.

Table 3.4: The results of genetic diversity indices and neutrality tests within three of the phylogeographic lineages discovered in this study. *S* = *Scutellastra* and *C* = *Cymbula*. Foraging traits: ^T = Territorial grazers and ^{NT} = Non-territorial grazers. * $p < 0.05$, ** $p < 0.02$.

▼ = Southwestern lineage, ● = Southern lineage and ■ = Southeastern/Eastern lineage.

Phylogeographic regions	Species	Haplotype diversity (h)	Nucleotide diversity (π)	Tajima's D	Fu and Li's D
Western lineage/group	<i>S. barbara</i> ^{T▼}	0.562	0.00176	-1.50374	-1.46752
	<i>S. cochlear</i> ^T	0.902	0.00841	-0.6416	-0.64593
	<i>S. granularis</i> ^{NT▼}	0.895	0.00712	0.03517	0.32029
	<i>C. granatina</i> ^{NT}	0.759	0.00186	-0.91186	-1.40761
Southern lineage/group	<i>S. cochlear</i> ^T	0.96	0.00438	-2.13911*	-2.72810*
	<i>S. longicosta</i> ^{T●}	0.911	0.00613	-0.37106	1.09797
	<i>S. granularis</i> ^{NT}	0.803	0.11787	2.06779*	1.65532**
	<i>C. oculus</i> ^{NT}	0.51	0.001	-0.33707	-0.20284
Eastern lineage/group	<i>S. barbara</i> ^{T■}	1	0.00594	-0.33192	-0.33192
	<i>S. cochlear</i> ^T	0.952	0.00478	-0.5177	-0.29833
	<i>S. longicosta</i> ^{T■}	0.927	0.08887	1.81719	0.49352
	<i>S. granularis</i> ^{NT■}	0.927	0.12856	-1.25898	1.50690**
	<i>S. natalensis</i> ^{NT}	0.756	0.00422	-1.25898	-1.0008

3.3.3. Genetic diversity within biogeographic regions

Similarly, there was no consistent pattern of variation in h and π amongst territorial and non-territorial grazers within biogeographic regions (Table 3.5). The territorial *Scutellastra cochlear* and the non-territorial *S. granularis* revealed higher h and π along both the western and southern coasts. Again, there were no obvious trends of one type of grazer consistently revealing higher/lower values in h and π along the eastern coast (Table 3.5).

Table 3.5: The results of genetic diversity indices and neutrality tests for each biogeographic region analysed. *S* = *Scutellastra* and *C* = *Cymbula*. Foraging traits: ^T = Territorial grazers and ^{NT} = Non-territorial grazers. * $p < 0.05$, ** $p < 0.02$.

Biogeographic regions	Species	Haplotype diversity (h)	Nucleotide diversity (π)	Tajima's D	Fu and Li's D
West coast	<i>S. barbara</i> ^T	0.562	0.00176	-1.50374	-1.46752
	<i>S. cochlear</i> ^T	0.902	0.00841	-0.6416	-0.64593
	<i>S. argenvillei</i> ^{NT}	0.778	0.00214	-1.38818	-1.34803
	<i>S. granularis</i> ^{NT}	0.895	0.00712	0.03517	0.32029
	<i>C. granatina</i> ^{NT}	0.759	0.00186	-0.91186	-1.40761
South coast	<i>S. barbara</i> ^T	0.604	0.00679	2.13560**	-2.37818*
	<i>S. cochlear</i> ^T	0.96	0.04638	-2.13911*	-2.72810*
	<i>S. longicosta</i> ^T	0.911	0.00613	-0.37106	1.09797
	<i>S. granularis</i> ^{NT}	0.942	0.12013	2.06770*	1.65532**
	<i>C. oculus</i> ^{NT}	0.51	0.001	-0.33707	-0.20284
East coast	<i>S. barbara</i> ^T	1	0.00594	-0.33192	-0.33192
	<i>S. cochlear</i> ^T	0.967	0.00536	-1.58515	-1.73282
	<i>S. longicosta</i> ^T	0.909	0.00926	0.86075	0.49352
	<i>S. granularis</i> ^{NT}	0.927	0.08887	1.81719	0.08690
	<i>S. natalensis</i> ^{NT}	0.756	0.00422	-1.25898	-1.00080

3.3.4 Molecular diversity indexes within sites

There was no uniform pattern of variation in molecular diversity indexes (π , $\theta\pi$, θ_S and θ_K) between territorial and non-territorial species sampled from each site (Tables 3.6a – l), although territorial grazers had higher values than non-territorial grazers at most of sites (≥ 7). Nucleotide diversity (π) was higher for territorial grazers than non-territorial grazers at seven sites (Tables 3.6a, 3.6b, 3.6e, 3.6h, 3.6i, 3.6j and 3.6k). The theta parameters based on the number of nucleotide differences ($\theta\pi$) and segregating sites (θ_S) were higher for territorial grazers than non-territorial grazers at eight sites (Tables 3.6a, 3.6b, 3.6e, 3.6f - $\theta\pi$, 3.6h, 3.6i, 3.6j, 3.6k and 3.6l - θ_S). There was no consistent or predominant pattern of variation in θ_K indexes between territorial and non-territorial grazers from site to site. The θ_K values were higher for territorial grazers than non-territorial grazers at six sites (Tables 3.6a, 3.6b, 3.6e, 3.6f, 3.6i and 3.6l). The non-territorial grazers had higher molecular diversity indices (π , $\theta\pi$, and θ_S) than territorial grazers at the following four sites: Kenton-on-Sea (Table 3.6c), Sardinia Bay (Table 3.6d), Mossel Bay (Table 3.6f) and Cape Agulhas (Table 3.6g).

Tables 3.6a - l: Site-specific comparisons of molecular diversity indexes between territorial and non-territorial grazers in both *Scutellastra* and *Cymbula* species. h = haplotype diversity, T = Territorial grazers and NT = Non-territorial grazers. All values are means.

a) Port St. Johns

Species	h (\pm SD)	π (\pm SD)	$\theta\pi$ (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. barbara</i> ^T	1.000(\pm 0.126)	0.006(\pm 0.004)	3.200(\pm 2.314)	3.360(\pm 2.000)	-
<i>S. cochlear</i> ^T	0.952(\pm 0.095)	0.005(\pm 0.003)	2.571(\pm 1.971)	2.857(\pm 1.599)	16.777(3.88, 75.10)
<i>S. longicosta</i> ^T	0.700(\pm 0.218)	0.011(\pm 0.007)	6.000(\pm 4.025)	1.440(\pm 1.016)	2.225(0.53, 9.41)
<i>S. natalensis</i> ^{NT}	0.700(\pm 0.218)	0.002(\pm 0.002)	1.400(\pm 1.191)	1.440(\pm 1.016)	2.225(0.53, 9.41)
<i>C. miniata</i> ^T	0.900(\pm 0.161)	0.004(\pm 0.003)	2.800(\pm 2.067)	3.360(\pm 2.000)	7.106(1.54, 33.08)

b) Haga- Haga

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. barbara</i> ^T	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>S. cochlear</i> ^T	0.964(\pm 0.051)	0.006(\pm 0.003)	3.000(\pm 1.192)	4.097(\pm 1.937)	20.730(6.30, 73.78)
<i>S. longicosta</i> ^T	0.867(\pm 0.129)	0.017(\pm 0.011)	9.333(\pm 5.779)	4.817(\pm 2.595)	4.063(1.05, 16.12)
<i>S. argenvillei</i> ^{NT}	0.800(\pm 0.161)	0.003(\pm 0.002)	1.600(\pm 1.319)	1.920(\pm 1.267)	7.106(1.54, 33.08)
<i>S. granularis</i> ^{NT}	0.700(\pm 0.218)	0.002(\pm 0.002)	1.600(\pm 1.318)	1.920(\pm 1.267)	2.225(0.53, 9.41)

c) Kenton-on-Sea

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	0.800(\pm 0.164)	0.003(\pm 0.002)	1.400(\pm 1.191)	1.440(\pm 1.061)	2.225(0.53, 9.41)
<i>S. longicosta</i> ^T	0.700(\pm 0.218)	0.003(\pm 0.002)	1.600(\pm 1.318)	1.440(\pm 1.016)	2.225(0.53, 9.41)
<i>S. granularis</i> ^{NT}	0.933(\pm 0.122)	0.139(\pm 0.081)	94.67(\pm 55.058)	76.64(\pm 36.246)	1.442(2.58, 52.03)
<i>C. oculus</i> ^{NT}	0.800(\pm 0.164)	0.003(\pm 0.002)	2.000(\pm 1.570)	1.920(\pm 1.267)	2.225(0.53, 9.41)

d) Sardinia Bay

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. barbara</i> ^T	0.600(\pm 0.215)	0.102(\pm 0.059)	54.80(\pm 32.040)	60.44(\pm 28.659)	1.696(0.43, 6.60)
<i>S. cochlear</i> ^T	1.000(\pm 0.045)	0.003(\pm 0.002)	1.600(\pm 1.319)	7.106(\pm 1.543)	-
<i>S. longicosta</i> ^T	0.857(\pm 0.164)	0.009(\pm 0.006)	4.600(\pm 3.172)	1.920(\pm 1.267)	2.225(0.53, 9.41)
<i>S. granularis</i> ^{NT}	0.800(\pm 0.137)	0.140(\pm 0.079)	95.00(\pm 53.475)	67.75(\pm 30.590)	6.40(1.74, 24.42)
<i>C. oculus</i> ^{NT}	0.733(\pm 0.155)	0.001(\pm 0.001)	0.933(\pm 0.852)	0.876(\pm 0.684)	1.70(0.427, 6.60)

e) Tsitsikamma

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	0.900(\pm 0.161)	0.004(\pm 0.003)	2.200(\pm 1.695)	2.400(\pm 1.513)	7.106(1.54, 33.08)
<i>S. longicosta</i> ^T	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>S. granularis</i> ^{NT}	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>C. oculus</i> ^{NT}	0.733(\pm 0.155)	0.001(\pm 0.001)	0.933(\pm 0.852)	0.876(\pm 0.684)	1.696(0.43, 6.60)

f) Mossel Bay

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. barbara</i> ^T	0.643(\pm 0.184)	0.002(\pm 0.001)	1.000(\pm 0.852)	1.543(\pm 0.960)	2.501(0.73, 8.44)
<i>S. cochlear</i> ^T	0.900(\pm 0.161)	0.003(\pm 0.002)	1.600(\pm 1.319)	1.920(\pm 1.267)	7.106(1.54, 33.08)
<i>S. longicosta</i> ^T	0.900(\pm 0.161)	0.010(\pm 0.007)	5.400(\pm 3.659)	3.840(\pm 2.243)	7.106(1.54, 33.08)
<i>S. argenvillei</i> ^{NT}	0.800(\pm 0.160)	0.002(\pm 0.002)	1.200(\pm 1.062)	1.440(\pm 1.016)	7.106(1.54, 33.08)
<i>S. granularis</i> ^{NT}	0.857(\pm 0.137)	0.006(\pm 0.004)	4.190(\pm 2.710)	4.082(\pm 2.156)	6.397(1.74, 24.42)

g) Cape Agulhas

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	0.933(\pm 0.122)	0.003(\pm 0.003)	1.867(\pm 1.426)	2.190(\pm 1.341)	11.44(2.58, 52.03)
<i>S. longicosta</i> ^T	0.800(\pm 0.164)	0.005(\pm 0.004)	2.600(\pm 1.944)	1.440(\pm 1.016)	2.22(0.527, 9.41)
<i>S. granularis</i> ^{NT}	0.700(\pm 0.126)	0.006(\pm 0.004)	4.000(\pm 2.805)	3.840(\pm 2.243)	-
<i>C. oculus</i> ^{NT}	0.400(\pm 0.237)	0.001(\pm 0.001)	0.800(\pm 0.797)	0.960(\pm 0.758)	0.691(0.15, 3.18)

h) Muizenberg

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_s (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	0.333(\pm 0.215)	0.001(\pm 0.001)	0.333(\pm 0.439)	0.438(\pm 0.438)	0.592(0.13, 2.63)
<i>S. longicosta</i> ^T	0.400(\pm 0.237)	0.003(\pm 0.002)	1.600(\pm 1.318)	0.960(\pm 0.758)	0.691(0.15, 33.18)
<i>S. granularis</i> ^{NT}	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>C. oculus</i> ^{NT}	0.900(\pm 0.161)	0.002(\pm 0.002)	1.400(\pm 1.191)	1.440(\pm 1.016)	7.106(1.54, 33.08)

i) Camps Bay

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_s (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	0.800(\pm 0.164)	0.002(\pm 0.002)	1.200(\pm 1.062)	0.960(\pm 0.758)	2.225(0.53, 9.41)
<i>S. granularis</i> ^{NT}	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>C. oculus</i> ^{NT}	0.700(\pm 0.218)	0.001(\pm 0.001)	1.000(\pm 0.931)	0.960(\pm 0.758)	2.225(0.53, 9.41)
<i>C. granatina</i> ^{NT}	0.600(\pm 0.130)	0.001(\pm 0.001)	0.733(\pm 0.670)	0.707(\pm 0.539)	1.052(0.29, 3.58)

j) Paternoster

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_s (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	1.000(\pm 0.126)	0.010(\pm 0.007)	5.200(\pm 3.538)	6.240(\pm 3.446)	-
<i>S. granularis</i> ^{NT}	0.600(\pm 0.175)	0.004(\pm 0.003)	2.400(\pm 1.820)	1.920(\pm 1.267)	0.691(0.15, 3.18)
<i>C. compressa</i> ^T	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>C. granatina</i> ^{NT}	0.867(\pm 0.071)	0.002(\pm 0.001)	1.467(\pm 1.094)	1.41(\pm 0.861)	3.30(\pm 1.07, 10.05)

k) Doring Bay

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. cochlear</i> ^T	0.700(\pm 0.218)	0.012(\pm 0.008)	6.400(\pm 4.268)	5.280(\pm 2.965)	2.225(0.53, 9.41)
<i>S. granularis</i> ^{NT}	0.500(\pm 0.418)	0.003(\pm 0.002)	2.200(\pm 1.695)	5.760(\pm 3.206)	2.225(0.53, 9.41)
<i>C. compressa</i> ^T	0.222(\pm 0.166)	0.000(\pm 0.000)	0.222(\pm 0.327)	0.368(\pm 0.368)	0.455(0.103, 1.92)
<i>C. granatina</i> ^{NT}	0.778(\pm 0.091)	0.002(\pm 0.002)	1.533(\pm 1.312)	1.767(\pm 1.014)	1.956(0.60, 6.12)

l) Groenriviermond

Species	h (\pm SD)	π (\pm SD)	θ_{π} (\pm SD)	θ_S (\pm SD)	θ_K (95% CI)
<i>S. barbara</i> ^T	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>S. cochlear</i> ^T	0.909(\pm 0.066)	0.006(\pm 0.004)	3.454(\pm 2.15)	5.463(\pm 2.479)	7.237(2.48, 21.37)
<i>S. granularis</i> ^{NT}	0.700(\pm 0.218)	0.008(\pm 0.005)	5.800(\pm 3.903)	5.760(\pm 3.206)	2.225(0.53, 9.41)
<i>C. compressa</i> ^T	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(\pm 0.000)	0.000(0.00, 0.00)
<i>C. granatina</i> ^{NT}	0.800(\pm 0.100)	0.002(\pm 0.001)	1.044(\pm 0.85)	1.060(\pm 0.704)	3.301(1.07, 10.05)

3.3.5 Summary of Molecular diversity indices within sites

The results for estimates of molecular diversity (h , π , θ_π , θ_S and θ_K) are summarised below in Table 3.6. The territorial grazers had greater haplotype diversity (h) than non-territorial grazers within all sites except Kenton-on-Sea (Table 3.7). Furthermore, the one-way ANOVA revealed significant differences in haplotype diversity ($p < 0.005$) between territorial and non-territorial foragers in *Scutellastra* spp. (Table 3.8). This was confirmed by one-way ANOVA comparing territorial and non-territorial species of *Scutellastra*. Because not all species occurred at all sites, territorial species were represented by either one or both of two species (*S. longicosta* or *S. cochlear*) and the non-territorial species by one or two out of three species (*S. granularis*, *S. argenvillei* or *S. natalensis*), depending on which were present at each site. This analysis revealed significant differences in haplotype diversity ($p < 0.005$) between territorial and non-territorial foragers (Table 3.8).

Table 3.7: The summary of the genetic and molecular diversity indexes amongst the territorial (T) and non-territorial (NT) species within *Scutellastra*. h = haplotype diversity and π = nucleotide diversity.

Sites	h	π	θ_π	θ_S	θ_K
Port St. Johns	T > NT	T > NT	T > NT	T \geq NT	T \geq NT
Haga-Haga	T > NT	T > NT	T > NT	T > NT	T > NT
Kenton-on-Sea	NT > T	T \geq NT	NT > T	NT > T	NT > T
Sardinia Bay	T > NT	NT > T	NT > T	NT > T	NT > T
Tsitsikamma	T > NT	T > NT	T > NT	T > NT	T > NT
Mossel Bay	T > NT	NT \geq T	T > NT	NT > T	T \geq NT
Cape Agulhas	T > NT	NT > T	NT > T	NT > T	-
Muizenberg	T > NT	T > NT	T > NT	T > NT	NT > T
Camps Bay	T > NT	T > NT	T > NT	T \geq NT	T \geq NT
Paternoster	T > NT	T > NT	T > NT	T > NT	NT > T
Doring Bay	T > NT	T > NT	T > NT	T > NT	T \approx NT
Groenriviermond	T > NT	NT > T	NT > T	T > NT	T > NT

Table 3.8: One-way ANOVA test of significance in haplotype diversity values between territorial and non-territorial *Scutellastra* species amongst sites. * = Significant at $P < 0.05$.

<i>Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	2.671955229	11	0.242905	3.551454	0.001917*	2.066608
Within Groups	2.46225375	36	0.068396			
Total	5.134208979	47				

There was no uniform intrasite pattern of variation between territorial and non-territorial grazers for the remaining molecular indexes (π , $\theta\pi$, θ_S and θ_K , Table 3.5). The following molecular indexes (π , $\theta\pi$, and θ_K) were higher for territorial grazers than non-territorial grazers at eight sites (Port St. Johns, Haga Haga, Tsitsikamma, Mossel Bay (only h and $\theta\pi$), Muizenberg, Camps Bay, Paternoster and Doring Bay). The same indexes (π , $\theta\pi$, and θ_S) were higher for non-territorial grazers than territorial grazers at four sites (Kenton-on-Sea, Sardinia Bay, Cape Agulhas and Groenriviermond).

3.3.6 Demographic and spatial population expansion

The analyses of demographic expansion revealed non-significant values of Tajima's D (Tajima 1989) and Fu's Fs (Fu 1996) statistics (Table 3.9) for all species ($p > 0.05$) except for the non-territorial *Scutellastra miliaris*. This species revealed significant departure from selective neutrality only in the Fu's Fs ($p < 0.05$). However, complimentary tests of selective neutrality (Tajima's D, Tajima 1989 and Fu and Li's D, Fu & Li 1993) computed in DnaSP revealed non-significant departure from demographic equilibrium ($p > 0.05$).

The analyses of demographic history under a spatial expansion model revealed non-significant SSD values and Raggedness indices ($p > 0.05$) for all species, suggesting spatial population expansion (Table 3.9). The non-significant SSD and Raggedness index values suggest the observed data do not significantly differ from the data expected under a spatial expansion model (Lorenzo-Carballa et al. 2012). The evidence of past spatial population expansion was further supported by the plots of mismatch distribution of pairwise haplotype difference against haplotype frequency (Figures 3.4a - k).

The mismatch distribution (Table 3.9) were analysed separately for each lineage for those species which revealed phylogeographic structure (*Scutellastra barbara*, *S. longicosta* and *S. granularis*). However, for the territorial *S. barbara*, only the southwestern lineage was analysed since it comprised all the populations except the most northeastern population (Port St. Johns).

Table 3.9: Results for tests of demographic expansion estimated using various tests statistics for all the species. ^T = Territorial, ^{NT} = Non-territorial foragers and * = Significant at $p < 0.050$.

▪ = Southwestern lineage • = Southern lineage and ▼ = Southeastern lineage.

Species	SSD (p)	Raggedness (p)	Tajima's D (p)	Fu's FS (p)
<i>Scutellastra</i>				
<i>S. barbara</i> ^{T▪}	0.173 (0.410)	0.166 (0.413)	-0.509 (0.503)	0.924 (0.496)
<i>S. cochlear</i> ^T	0.048 (0.463)	0.161 (0.587)	-0.569 (0.335)	-1.649 (0.139)
<i>S. longicosta</i> ^{T•}	0.070 (0.265)	0.227 (0.497)	0.221 (0.675)	0.702 (0.314)
<i>S. longicosta</i> ^{T▼}	0.183 (0.060)	0.389 (0.290)	-0.122 (0.500)	2.555 (0.880)
<i>S. argenvillei</i> ^{NT}	0.050 (0.472)	0.280 (0.577)	-0.737 (0.278)	-1.439 (0.067)
<i>S. granularis</i> ^{NT▪}	0.103 (0.141)	0.250 (0.297)	0.441 (0.789)	0.677 (0.426)
<i>S. granularis</i> ^{NT▼}	0.091 (0.070)	0.087 (0.175)	1.179 (1.000)	3.627 (0.993)
<i>S. miliaris</i> ^{NT}	0.015 (0.710)	0.131 (0.630)	-0.902 (0.211)	-2.235 (0.020*)
<i>S. natalensis</i> ^{NT}	0.030 (0.655)	0.150 (0.765)	0.049 (0.605)	-0.475 (0.207)
<i>Cymbula</i>				
<i>C. compressa</i> ^T	0.000 (-)	0.000 (-)	0.000 (-)	0.000 (-)
<i>C. miniata</i> ^T	0.038 (0.730)	0.125 (0.847)	-0.505 (0.325)	-0.640 (0.208)
<i>C. granatina</i> ^{NT}	0.025 (0.347)	0.178 (0.372)	-0.080 (0.518)	-0.888 (0.239)
<i>C. oculus</i> ^{NT}	0.117 (0.336)	0.308 (0.591)	-0.152 (0.521)	-0.176 (0.299)

3.3.7 Mismatch Distribution

3.3.7.1 Mismatch distribution amongst *Scutellastra* species

A unimodal mismatch distribution was observed amongst populations of *Scutellastra argenvillei* (Figure 3.4a), *S. cochlear* (Figure 3.4c), *S. longicosta* (Southern lineage, Figure 3.4d), *S. granularis* (Southwestern lineage, Figure 3.4f), *S. miliaris* (Figure 3.4h) and *S. natalensis* (Figure 3.4i). All these species revealed non-significant Φ_{ST} genetic differentiation, Tajima's D, Fu and Li's D and Fu's Fs tests ($p > 0.05$), suggesting spatial population expansion rather than recent demographic expansion. Multimodal mismatch distributions was observed within the southwestern lineage of *S. barbara* (Figure 3.4b), the eastern lineage of *S. longicosta* (Figure 3.4e), and the southeastern lineage of *S. granularis* (Figure 3.4g). The multimodal mismatch distributions and non-significant Tajima's D and Fu's Fs ($p > 0.05$) suggest these species are at demographic equilibrium. However, these lineages were characterised by non-significant SSD values and Raggedness index ($p > 0.05$), suggesting spatial population expansion.

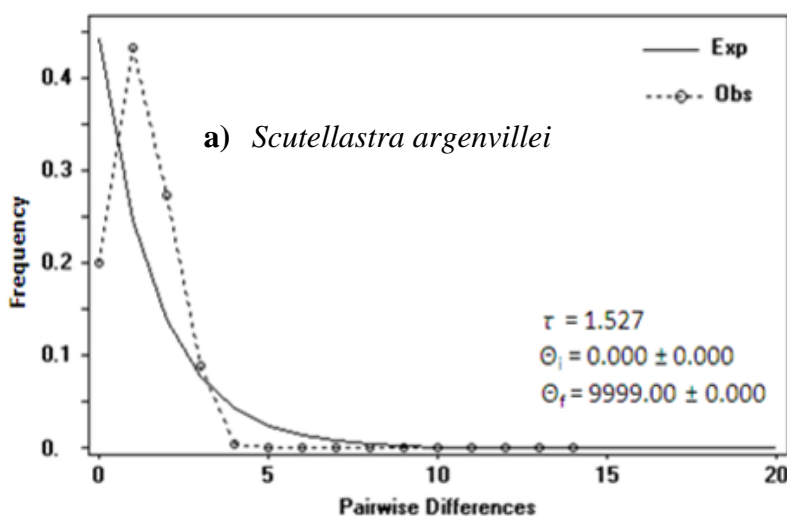
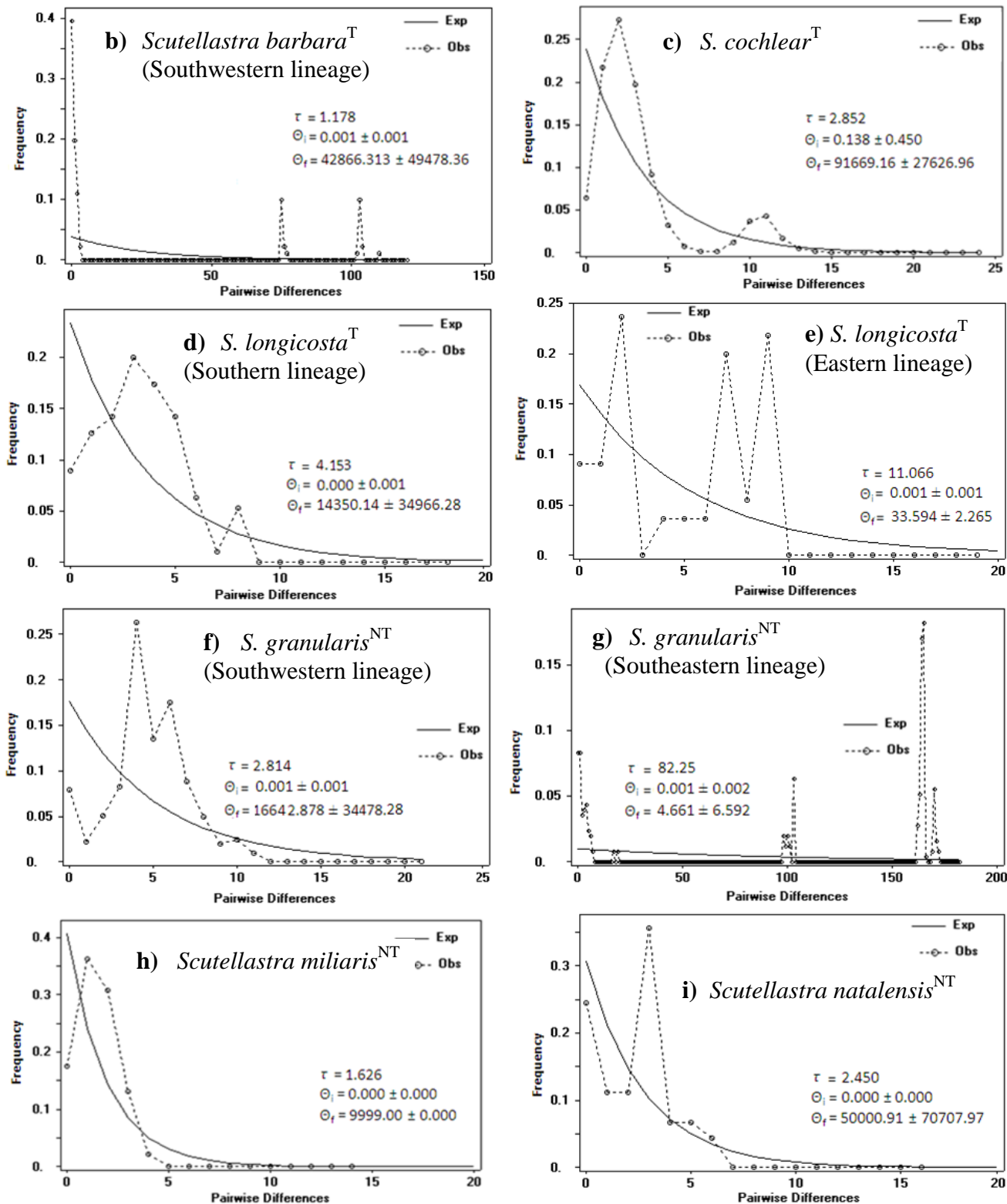


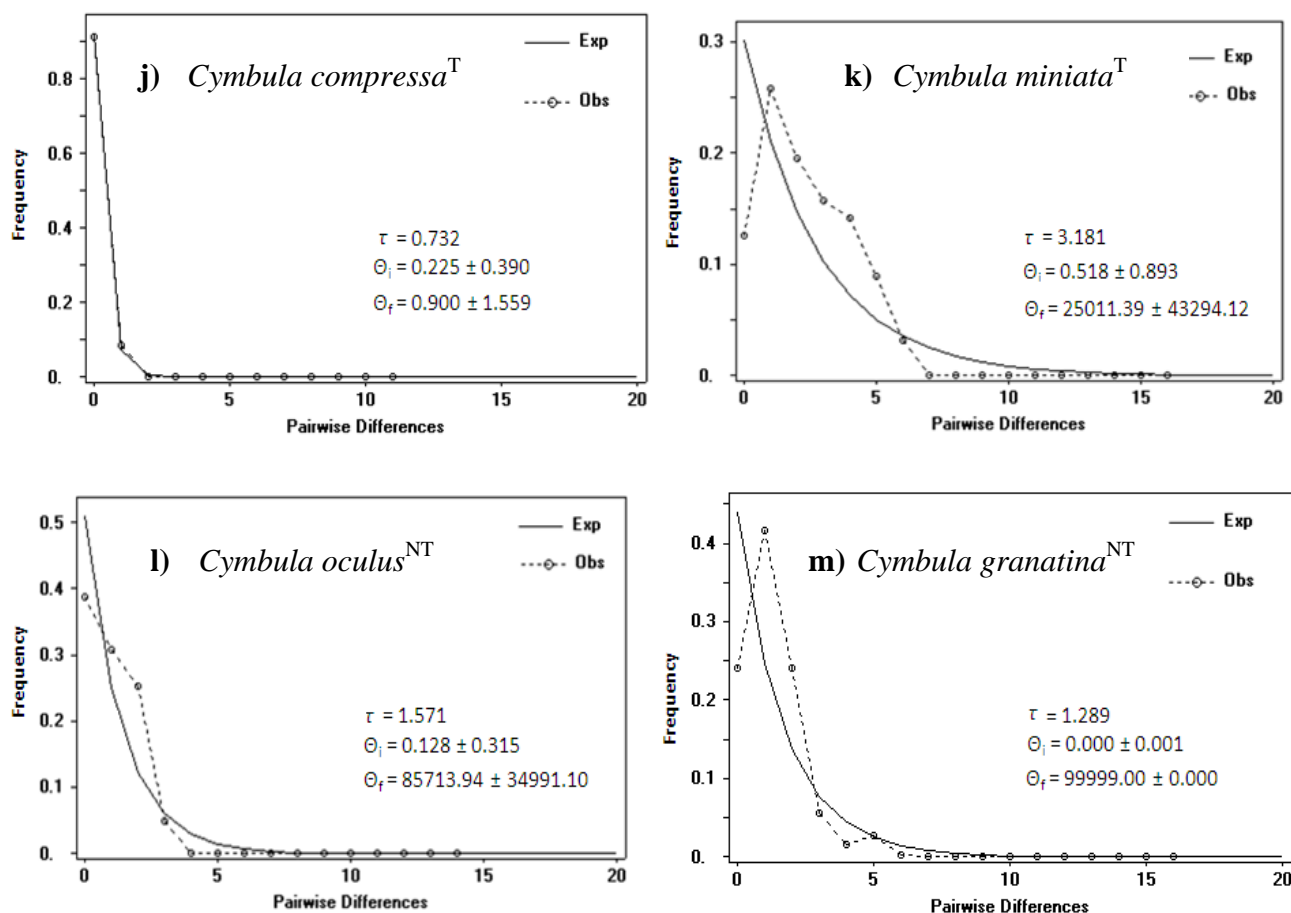
Figure 3.4a: The plot of mismatch distributions amongst populations of the non-territorial *Scutellastra argenvillei*.



Figures 3.4b - i: The plots of mismatch distributions amongst populations of different *Scutellastra* species. ^T = Territorial foragers, ^{NT} = Non-territorial foragers.

3.3.7.2 Mismatch distribution amongst *Cymbula* species

Cymbula compressa was characterized by almost uniform genetic structure and an L-shaped mismatch distribution, suggesting a recent spatial population expansion (Figure 3.4j). A unimodal mismatch distribution was observed in *C. miniata* (Figure 3.4k), *C. oculus* (Figure 3.4i) and *C. granatina* (Figure 3.4m). All these species revealed non-significant Φ_{ST} genetic differentiation, Tajima's D , F_u and Li's D and F_s tests ($p > 0.05$), suggesting spatial population expansion rather than recent demographic expansion.



Figures 3.4j - m: The plots of mismatch distributions amongst populations of different *Cymbula* species. ^T = Territorial foragers, ^{NT} = Non-territorial foragers.

3.3.8 Estimated times of spatial expansion

The non-significant SSD and Raggedness index values ($p > 0.005$) and multimodal mismatch distributions supported spatial range expansion in these patellid limpets. The estimated times of expansion are presented below (Table 3.10) and were mostly in the mid- or late-Pleistocene. Population expansion of all species is estimated to have started 0.538 - 0.053 million years ago (Mya), around the early to late Pleistocene.

Table 3.10: The estimated time since spatial expansion calibrated using a mutational rate of 1.0% sequence divergence per million years per site as estimated for *Cellana* spp. (González-Wevar et al. 2010, 2011a). τ is the time since expansion measured in mutational time units and t_e is the absolute time (Mya) since spatial expansion. ^T = Territorial foragers, ^{NT} = Non-territorial foragers. [▼] = Southwestern lineage and [•] = Southern lineage.

Species	τ (Mean \pm SD)	t_e (95% confidence intervals)	Epoch
<i>Scutellastra</i>			
<i>S. barbara</i> ^{T▼}	1.178 (\pm 1.328)	0.110 (0.011 - 0.122) Mya	mid-Pleistocene
<i>S. cochlear</i> ^T	2.852 (\pm 2.847)	0.270 (0.040 - 0.437) Mya	mid-Pleistocene
<i>S. longicosta</i> ^{T•}	5.873 (\pm 3.799)	0.380 (0.109 - 0.506) Mya	early-Pleistocene
<i>S. argenvillei</i> ^{NT}	1.527 (\pm 0.198)	0.140 (0.014 - 0.288) Mya	mid-Pleistocene
<i>S. granularis</i> ^{NT▼}	3.826 (\pm 2.819)	0.210 (0.088 - 0.417) Mya	mid-Pleistocene
<i>S. miliaris</i> ^{NT}	1.626 (\pm 0.015)	0.130 (0.015 - 0.233) Mya	mid-Pleistocene
<i>S. natalensis</i> ^{NT}	2.450 (\pm 0.545)	0.230 (0.021 - 0.406) Mya	mid-Pleistocene
<i>Cymbula</i>			
<i>C. compressa</i> ^T	0.732 (\pm 1.268)	0.050 (0.007 - 1.595) Mya	late-Pleistocene
<i>C. miniata</i> ^T	3.181 (\pm 1.350)	0.220 (0.026 - 0.464) Mya	mid-Pleistocene
<i>C. granatina</i> ^{NT}	1.289 (\pm 0.281)	0.090 (0.017 - 0.168) Mya	late-Pleistocene
<i>C. oculus</i> ^{NT}	1.571 (\pm 0.950)	0.110 (0.015 - 1.071) Mya	mid-Pleistocene

3.4 Discussion

3.4.1 Molecular diversity amongst territorial and non-territorial foragers

There were no obvious trends or patterns of variation in haplotype (h) and nucleotide diversity (π) between territorial and non-territorial foragers within phylogeographic (Table 3.4) and biogeographic regions (Table 3.5). Furthermore, there was no consistent difference between territorial and non-territorial foragers in nucleotide diversity (π) and various theta parameters (θ_π , θ_S and θ_K) at the intrasite (within sites) scale (Tables 3.6a - l). However, territorial species revealed significantly higher haplotype diversity than non-territorial species ($P < 0.05$) within sites with the exception of one site (Kenton-on-Sea). Strikingly, this trend was observed only amongst sympatric *Scutellastra* spp. (Tables 3.6a - l).

In *Cymbula*, the non-territorial *C. granatina* revealed greater haplotype diversity than the sympatric territorial *C. compressa* (Tables 3.6i - l). The territorial *Cymbula miniata* was characterized by a higher level of haplotype diversity than the congeneric territorial *C. compressa*, which almost displayed genetic homogeneity across its range. *C. compressa* lives exclusively on the stipes of the kelps, which undergo high levels of biomass loss each year through storm damage (Koop & Field 1980). As such, high levels of gene flow via rafting kelp are possible (Powell 1973) and could lead to genetic homogeneity, obscuring any possible effects of territoriality.

The correlation between foraging traits (territoriality) and molecular diversity (haplotype diversity) was observed only at the intrasite scale. The profoundly territorial species (*Scutellastra barbara*, *S. cochlear* and *S. longicosta*) demonstrated the greatest haplotype diversity within site scale and at phylogeographic regions. However, an exception to this was the non-territorial *Scutellastra granularis* which revealed haplotype diversity that was almost equivalent to that of the congeneric territorial species. This could possibly be due to the presence of different lineages since *Scutellastra granularis* revealed a phylogeographic break along the mid south coast.

3.4.2 *Haplotype distribution between territorial and non-territorial foragers*

The territorial and non-territorial limpets have similar larval development, thus the contrasting intrasite haplotype diversity inferred for the two groups from their genetic structure cannot be explained by differences in their life histories. The observed trends in haplotype diversity could be attributed either to the ecological adaptations of territorial and non-territorial foraging or chance effects due to limited sampling. In advancing the former rationale, territorial and non-territorial grazers display substantial differences in habitat requirements during settlement and this has the potential to affect larval recruitment. Non-territorial grazers show ontogenetic variation in habitat requirements, larvae settle and feed low on the shore and after two years they progressively migrate to the high shore (Branch 1971 and 1985b). Thus, non-territorial larvae could disperse over extensive distances after settlement, and they are relatively unrestricted in their choice of settlement site since they do not require special habitats or scars on which to settle. This has the potential to increase and sustain gene flow amongst distant populations.

In contrast, the larvae of territorial grazers settle permanently on the low shore either on a fixed scar or on the shells of adult molluscs. Once these limpets occupy a territory, they remain there until they die. Therefore, following settlement, territorial species show virtually no dispersal. Patellogastropods are presumed to have lecithotrophic larvae, which have energy reserves and do not acquire energy through feeding (Thorson 1961, Lucas et al. 1979, Hadfield et al. 1997, Kay & Emler 2002 and Paulay & Meyer 2006). They have a brief veliger stage (\approx 3-11 days) after which they metamorphose into a juvenile phase (Goldstein et al. 2006, Bird et al. 2007, González-Wevar et al. 2010, 2011a). This may influence settlement in territorial grazers since the juveniles have more specialized settlement requirements, and the requirement for a fixed home scar or territory may also result in reduced recruitment and minimal dispersal before the larva depletes its energy reserves. This could contribute to diminished gene flow amongst distant populations and higher genetic heterogeneity within a species.

The occurrence of many private (site-restricted) haplotypes and the existence of few or no haplotypes that are dominant amongst sites further suggest minimal larval dispersal in the territorial grazers. For example, in *Scutellastra barbara*, a total of 14 haplotypes were private and only one site amongst seven (Groenriviermond), had no private haplotypes.

Scutellastra cochlear revealed the greatest number of private haplotypes of all the territorial species analysed. A total of 36 haplotypes were private, while only six haplotypes were shared amongst sites. Almost all the 12 localities were characterized by private haplotypes, the sole exception being Muizenberg. At least one private haplotype was sampled from each population and the greatest numbers of private haplotypes were sampled from populations within bays. For example, four and seven private haplotypes were sampled from Doring Bay and Sardinia Bay respectively whereas two private haplotypes were sampled from Camps Bay and Mossel Bay.

Correspondingly, a total of 13 haplotypes were private and only four haplotypes occurred at more than one site in the territorial *Scutellastra longicosta*. With the exception of the most dominant haplotypes, the other common haplotypes were mostly sampled from the two most adjacent sites (approximately <300km apart). Similarly, populations within bays (i.e. Mossel Bay and Sardinia Bay) had a greater number of private haplotypes than populations on the open coast. Yet again, almost all eight localities were characterized by private haplotypes, again with the exception of Muizenberg. The lack of private haplotypes from Muizenberg in *S. cochlear*, *S. longicosta* and *S. granularis* is intriguing. This appears to be linked to extrinsic rather than species-specific factors. Muizenberg is located at the western overlap between the cool-temperate and the warm-temperate regions. These species and all other patellid limpets distributed across this western overlap did not reveal phylogeographic breaks here (see chapter two), implying high gene flow across this region. This is in striking contrast to several studies which discovered a phylogeographic boundary across this western overlap region for various estuarine and marine taxa including crustaceans (Norton 2005, Teske et al. 2006, 2007a, 2007c), clinid fish (von der Heyden et al. 2008) and the marine gastropod *Haliotis midae* (Evans et al. 2004 and van der Merwe 2009).

3.4.3 Gene flow within territorial and non-territorial foragers

The analyses of gene flow indexes in DnaSP revealed lower values of N_m (number of migrants) for the territorial *Scutellastra barbara* and *S. longicosta* than for congeneric non-territorial grazers (Table 3.11). The only exception was the territorial *S. cochlear* which had a higher N_m (1.15) than the non-territorial *S. granularis* ($N_m = 0.19 - 0.25$). The former species revealed no genetic homogeneity (in spite of high gene flow) but the highest number of private haplotypes from site to site, further supporting the probability of minimal larval dispersal. The southwestern lineages of the territorial *S. barbara* ($N_m = 0.22$) and non-territorial *S. granularis* ($N_m = 0.25$) had almost equivalent gene flow. Overall, there were no obvious trends of gene flow variation within territorial and non-territorial species of either *Scutellastra* and *Cymbula* (Table 3.11).

Table 3.11: The results of gene flow analyses based on sequence data for all the species within phylogeographic and biogeographic regions. ^T = Territorial foragers, ^{NT} = Non-territorial foragers. [■] = Southwestern lineage, [•] = Southern lineage and [▼] = Southeastern lineage.

Species	F _{ST}	N _m	Species	F _{ST}	N _m
<i>Scutellastra</i>			<i>Cymbula</i>		
<i>S. barbara</i> ^{T▼}	0.534	0.22	<i>C. compressa</i> ^T	0.000	3.29
<i>S. cochlear</i> ^T	0.178	1.15	<i>C. miniata</i> ^T	0.096	2.84
<i>S. longicosta</i> ^{T•}	0.643	0.14	<i>C. granatina</i> ^{NT}	0.085	2.70
<i>S. argenvillei</i> ^{NT}	0.018	13.39	<i>C. oculus</i> ^{NT}	0.025	10.23
<i>S. natalensis</i> ^{NT}	0.111	2.50	<i>S. granularis</i> ^{NT■}	0.521	0.25
<i>S. miliaris</i> ^{NT}	0.019	13.56	<i>S. granularis</i> ^{NT▼}	0.572	0.19

3.4.4 Historical spatial expansion within territorial and non-territorial patellid limpets.

Most species revealed evidence of spatial population expansion (non-significant SSD, Raggedness indices, Tajima's D and Fu's F_s statistics and unimodal mismatch distribution), the exceptions being *Scutellastra miliaris*, *S. barbara* (southwestern lineage), *S. longicosta* (eastern lineage) and *S. granularis* (southeastern lineage).

Scutellastra miliaris revealed significant negative Fu's F_s statistics (though Tajima's D was non-significant) and unimodal mismatch distribution, indicating recent demographic expansion. The mismatch analyses of SSD and Raggedness indices were also non-significant ($p > 0.005$), thus the non-significant Tajima's D has stronger overall support than the significant Fu's F_s test. The contrast between Tajima's D and Fu's F_s statistics could be attributed to the different criteria employed by the two tests in computing test statistics or their power to detect population growth (Ramos-Onsins & Rozas 2002 and Ribeiro et al. 2010).

When tested within phylogeographic and biogeographic regions, the Tajima's D and Fu's F_s statistics were significantly negative for *Scutellastra barbara*, *S. longicosta* and *S. granularis*. However, the lineages of these species were characterized by multimodal mismatch distribution, suggesting their populations are at demographic equilibrium. The effect of lumping of multiple lineages on the observed multiple mismatch distribution is ruled out since each lineage was analysed separately. For *Scutellastra longicosta* and *S. granularis*, it is entirely possible that these species have a younger lineage that shows a clear signature of spatial expansion (Figures 3.4d and 3.4f) and an older lineage in the southeast that is at demographic equilibrium (Figures 3.4e and 3.4g). This is further supported by the fact that the estimated time since demographic equilibrium was far older for both the southeastern lineages of *S. longicosta* (1.01 Mya) and the southeastern lineage of *S. granularis* (6.05 Mya). This suggests a possible westward spatial expansion of the southern lineage (*S. longicosta*) and the southwestern lineage (*S. granularis*) with subsequent phylogeographic disjunctions within these species.

The spatial expansion time amongst most of these patellid limpets (*Scutellastra barbara*, *S. cochlear*, *S. argenvillei*, *S. granularis*, *S. miliaris*, *S. natalensis*, *Cymbula miniata* and *C. oculus*) was estimated to be around the mid Pleistocene (0.287 - 0.109 Mya). The congruent dating of mid-Pleistocene spatial expansion suggests a common effect of oceanographic oscillation on spatial expansion amongst these species. The major rise in sea-level and formation of most of the South African shoreline is dated at 0.200 - 0.080 Mya (Roberts & Berger 1997 and Ramsay & Cooper 2002), corresponding with the estimated times of expansion for most of these species (early to mid Pleistocene).

Post-glacial spatial range expansion amongst these patellid limpets started to take place in the late- (*S. granularis*) to mid-Pleistocene (most species). Mid to late Pleistocene sea-levels increased gradually following the ice-ages (Ramsay & Cooper 2002), covering previously ice-covered areas and allowing these species to spread southwestward and colonise new habitats. Thus, these species managed to expand their range during dynamic oceanographic oscillations and dramatic sea-level changes in the late to mid Pleistocene (Fisher et al. 2010). The west coast restricted species, the territorial *Cymbula compressa* and non-territorial *C. granatina*, inhabited the cold Benguela region relatively recently, during the early Pleistocene (0.053 and 0.0935 Mya respectively). There is no difference in demographic history between territorial and non-territorial foragers, both *Scutellastra* and *Cymbula* species revealed evidence of post-glacial spatial expansion around the Pleistocene.

Pleistocene population expansions have been documented before for various animal taxa along the South African marine realm (Teske et al. 2003, 2011b, 2013b; von der Heyden et al. 2010, 2011, 2013, Reynold 2011 and Muller et al. 2012). Similar Pleistocene population spatial expansions following interglacial fluctuations have been discovered worldwide for various marine taxa including patellogastropods (Sá-Pinto et al. 2005, Espinosa et al. 2011, Ribeiro et al. 2010, González-Wevar et al. 2011a, 2011b); fishes (Gysels et al. 2004, Domingues et al. 2005, Larmuseau et al. 2009); seaweeds (Hoarau et al. 2007); shrimps (Teixeira et al. 2011); nemertean

worms (Andrade et al. 2011) and barnacles (Derycke et al. 2008, Zakas et al. 2009, Marko et al. 2010 and Flight et al. 2012). Holocene spatial population expansions have also been documented for South African spiny lobsters (Gopal et al. 2006, von der Heyden et al. 2007c) and Cape hake (von der Heyden et al. 2007a).

It is clear that dramatic Pleistocene glacial cycles affected demographic patterns of various marine taxa differently (Marko et al. 2010). The demographic distribution of these limpets was affected by the Last Glacial Maximum (LGM: ~ 18,000 – 21, 000 years ago), unlike other South African marine animal taxa, which show post-LGM population expansion (Tolley 2005, Matthee et al. 2006, Gopal 2007, von der Heyden et al. 2007a, 2007c, 2010a, Neethling 2008, Teske et al. 2011a). The evidence of Pleistocene spatial expansion implies these limpets were at population equilibrium during the dramatic LGM sea temperatures, a pattern also discovered along the South African rocky shores for barnacles (Reynold 2011), sea urchins (Muller et al. 2012) and clinid fish (von der Heyden et al. 2011, 2013). The most fitting explanation for this was probably the existence of multiple refugial habitats within species` ranges and the high numbers of private haplotypes discovered within sites strongly support this explanation (Hewitt 1996, Waltari et al. 2007 and Reynold 2011).

3.4.5 Evolutionary adaptation of foraging behaviour in patellid limpets

Haplotype diversity (h) was higher for territorial *Scutellastra* spp. than non-territorial species only at the smallest, intrasite scale. *Scutellastra granularis* revealed southwestern and southeastern lineages with a boundary between Mossel Bay and Tsitsikamma. The high haplotype diversity observed within *S. granularis* within south coast sites may be attributed to the overlapping of these two lineages. Similarly, when values for *S. granularis* from sites near phylogeographic boundaries (Mossel Bay, Tsitsikamma, Sardinia Bay and Kenton-on-Sea) were removed, territorial grazers consistently displayed higher values of $\theta\pi$ (nucleotide diversity) and θ_s (segregating sites) than congeneric non-territorial grazers. The specialist-generalist model does not always explain genetic variability between various ecological specialists and generalists (Haynie et al. 2009). However, the outcomes of this study are concordant with the specialist-generalist model dependent on the genus in question (*Scutellastra*) and the scale of analysis (intrasite scale).

Interestingly, similarly high levels of genetic diversity uncovered in the territorial *Scutellastra* spp. were also discovered in the southern African intertidal mussel *Perna perna* (Zardi et al. 2007). It is feasible that similar patterns might also prevail in other sessile/sedentary or mobile intertidal southern African invertebrates, although this requires further investigation. For example, high shore species of *Afrolittorina* snails, which have larval settlement similar to the non-territorial spp., also displayed relatively little genetic heterogeneity (Matumba 2013). The profoundly territorial *S. cochlear* and *S. longicosta* had the greatest number of private haplotypes from within bay populations. It is proposed that empirical studies with site-focused sampling be conducted to investigate if coastal topography affects haplotype distribution of these limpets similarly to intertidal mussels (Nicastro et al. 2008 and Teske et al. 2013a). The present study is concordant with other studies which have highlighted the hazards of making general conclusions on genetic structure of congeneric species with similar life histories (Sá-Pinto et al. 2005, Goldstein et al. 2006, Bird et al. 2007, 2011, Aranzamendi et al. 2009 and Ribeiro et al. 2010).

Territorial and non-territorial foragers in *Scutellastra* display different levels of genetic diversity at the smallest within-site scales. However, at the largest biogeographic scales, there were no differences in demographic history between territorial and non-territorial species in either *Cymbula* or *Scutellastra*. These patellid limpets underwent historical population expansion from the early to the late Pleistocene, probably following dramatic sea-level fluctuations which exposed suitable rocky shore habitats (Ramsay & Cooper 2002, Marko et al. 2010, Teske et al. 2007d, 2011a and von der Heyden et al. 2011). The west-coast restricted species (*Cymbula compressa* and *C. granatina*), were only able to colonise the cold temperatures of the Benguela region relatively recently (early to late Holocene).

Whether there were significant differences in haplotype diversity between territorial and non-territorial species depended on the genus in question. There were noteworthy intrasite differences in the haplotype diversity between territorial and non-territorial *Scutellastra* but not *Cymbula* species. Overall, haplotype diversity of these patellid limpets seems to be linked to species-specific foraging ecology rather than the prevailing biogeographic limits. This was further supported by the fact that the correlation between genetic diversity and foraging behaviour was discernible only within-sites scale but not within phylogeographic or biogeographic regions. The sympatric intertidal southern African patellid limpets display contrasting genetic diversity that is correlated with their foraging ecology. The territorial *Scutellastra* species exhibited greater haplotype diversity than congeneric non-territorial species at the intrasite scale. The ecological adaptations of territorial foraging (i.e. special algal food and fixed home range) are correlated with greater haplotype diversity compared to the less costly ecological adaptation of non-territorial foraging (i.e. general foraging and high mobility).

CHAPTER FOUR

*Stable isotope signatures of sympatric
intertidal patellid limpets
(Gastropoda:Patellogastropoda) with
different foraging behaviours along the
South African shoreline*



4.1 Introduction

The southern African coastline is dominated by two major oceanographic currents characterized by different physical and chemical properties (Shannon 1985 and Lutjeharms 2004). The southern coast is dominated by the oligotrophic Agulhas Current flowing southward from the east coast and the western coast is dominated by the eutrophic Benguela Current flowing northward from the tip of the Cape Peninsula (Figure 4.1). The Agulhas current follows the edge of the continental shelf and as it moves southward from the eastern coast it retroreflects off-shore when approaching the Agulhas Bank (Lutjeharms 2004). The discrepancy in chemical composition between the two current systems influences primary production along the coast (Bustamante et al. 1995 and Bustamante & Branch 1996b). The cool temperate west coast is very productive and nutrient rich due to the Benguela upwelling which bring nutrients from the bottom of the ocean up to the surface inshore waters (Andrews & Hutchings 1980, Bustamante et al. 1995 and Bustamante & Branch 1996a).

Recently, large spatial-scale ecological studies have identified four biogeographic clusters based on the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of suspended particulate matter (SPM), macroalgae, filter feeders (Hill et al. 2006 and Hill & McQuaid 2008) and birds (Jaquemet & McQuaid 2008, Kohler et al. 2011). The four stable isotopes clusters (West coast cluster, South-western coast cluster, South-eastern coast cluster and East coast cluster have been delineated by Hill & McQuaid (2008) based on isotope signals of mussels. Interestingly, the western coast cluster was found to have high signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in almost all of the studies (Hill et al. 2006, Hill & McQuaid 2008 and Jaquemet & McQuaid 2008). This has mainly been attributed to the intensity of Benguela upwelling along the western coast (Jaquemet & McQuaid 2008). The upwelled waters along the Benguela result in high abundances of phytoplankton, which increases isotope signatures (Nakatsuka et al. 1992). The upwelled surface water is enriched in nitrates and dissolved inorganic carbon which is assimilated by primary producers yielding high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures (Altabet 2001 and Peeters et al. 2002).

These previous studies were primarily focused on either filter feeders or top predators (birds) and this study shifts the focus to the analysis of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of intertidal grazers along the same coastline. The intertidal grazers in question are patellid limpets with two different foraging traits, most species being either territorial or non-territorial grazers. Considering that territorial grazers will have a more restricted diet than the, presumably, broad diet of non-territorial grazers, it is plausible that the two types of grazers will be characterized by subtle differences in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures.

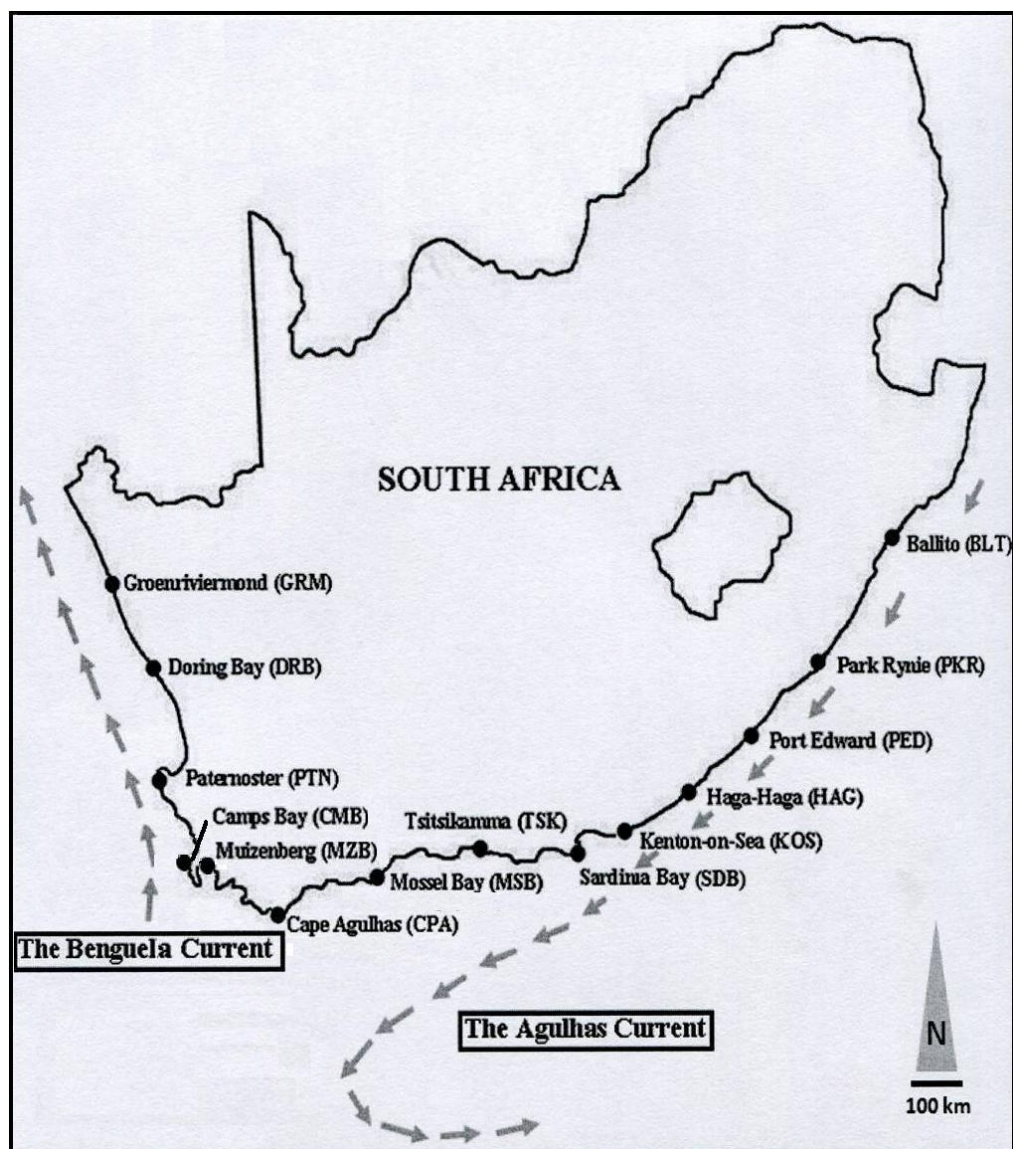


Figure 4.1: A map of South African coastline showing the sampling sites and the two major oceanographic currents.

The territorial species *Scutellastra cochlear* and *S. longicosta* forage primarily on the encrusting alga *Spongites yendoi* (Foslie) and *Ralfsia verrucosa* or *R. expansa* respectively (Branch 1980). These limpets have similar distributional ranges to their symbiotic algae. The picture below depicts the territories of *Scutellastra cochlear* and *S. longicosta* with their associated encrusting algae (Figure 4.2). The territorial kelp limpet *Cymbula compressa* forages primarily on the sea bamboo *Ecklonia maxima*. The adult limpets are found on the stipes of the kelp where they feed on the kelp and its epiphytes (Branch 1971). The territorial pink-rayed limpet *Cymbula miniata* forages primarily on the garden of the coralline encrusting alga *Spongites yendoi*. The symbiosis between *C. compressa* and *E. maxima* is only found along the western coast due to the restricted range of both the limpet and kelp.

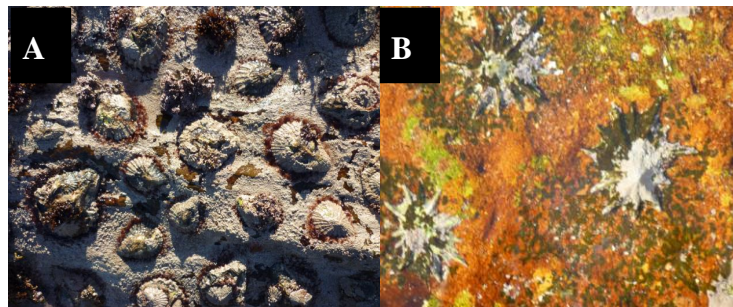


Figure 4.2: A picture showing the territories of (A) *Scutellastra cochlear* and (B) *S. longicosta* with their symbiotic encrusting *Spongites yendoi* and *Ralfsia verrucosa* respectively.

The non-territorial *Scutellastra granularis* is one of the most widely distributed species occurring from the Namibian coast to as far as Haga-Haga (Figure 4.1) on the eastern coast (Ridgway et al. 1998b). Its closely related sister taxon, *S. natalensis*, is largely restricted to the eastern coast from Port St. Johns to as far as Ballito (Figure 4.1) in northern Kwazulu-Natal (Personal observation). The non-territorial *Cymbula oculus* is distributed only along the eastern and southern coasts, while the non-territorial *C. granatina* is restricted to the west coast (Branch et al. 1994). The juveniles of these non-territorial species settle low on the shore and progressively migrate upwards as they age and inhabit the high shore as adults. However, once settled high on the shore, they do not occupy a fixed feeding area, but rather move around in search of algal food (Branch 1971, 1974 and 1975c). Thus, the non-territorial grazers are likely to be characterized by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios that are more variable around the mean than those of the territorial grazers.

The symbiosis between territorial grazers and their associated encrusting algae is mutualistic in most aspects including ecology, anatomy, physiology and nutrient recycling (Branch 1981). Thus, it is probable that over time these territorial grazers have evolved and adapted to primarily or exclusively forage on and sustain their associated encrusting algae or gardens of filamentous red algae. For example, McQuaid & Froneman (1993) found that the grazing pattern of the territorial *Scutellastra longicosta* is adapted to maximize productivity of the associated alga *Ralfsia verrucosa* and eliminate other competitive algae. Removal of *S. longicosta* from their territories resulted in rapid removal of *R. verrucosa* through destructive over-grazing by non-territorial limpets. The foraging pattern of *S. cochlear* on the associated alga *Spongites yendoi* reduces the algal thallus thickness and this increases algal attachment as thinner thalli have greater attachment strength than thicker thalli (Keats et al. 1994 and Maneveldt 1995). The ammonium in the excreta of the territorial *Scutellastra cochlear* is taken-up and reused by the garden of the filamentous red algae *Gelidium micropterum* and *Herposiphonia* spp. (Plaganyi & Branch 2000). The dissolved recycled inorganic nitrogen is in the form of ammonia and urea (Michener & Schell 1994). Thus it is plausible that indirectly or directly, this intimacy in nitrogen recycling might positively affect the $\delta^{15}\text{N}$ signature of the associated encrusting alga.

The encrusting algae *Spongites yendoi* and *R. verrucosa* comprise inorganic calcium carbonate (CaCO_3) which has different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios compared to the organic carbon incorporated in animal tissues (Rau et al. 1992 and Cloern et al. 2002). This could provide a positive bias in $\delta^{13}\text{C}$ and a negative bias in $\delta^{15}\text{N}$ ratios of the algae. It is recommended that any inorganic carbon in CaCO_3 be removed through acidification prior to stable isotopes analysis, although it is unclear how and to what extent acidification alters $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios amongst different taxa (Bunn et al. 1995, Pinnegar & Polunin 1999 and McCutchan et al. 2003). Empirical studies showed that algal acidification reduces $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios (Jacob et al. 2005 and Ng et al. 2007). On average, algal acidification significantly decreases $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios by $\approx 0.117\text{‰}$ and $\approx 0.320\text{‰}$ respectively (Jacob et al. 2005). Thus, algal acidification decreases $\delta^{15}\text{N}$ ratios more markedly than $\delta^{13}\text{C}$ ratios, resulting in higher C/N ratios in decalcified samples (Ng et al. 2007). The quality of the diet can also affect stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of the consumers (Webb et al. 1998a). Theoretically, it is expected that high quality diet would positively affect $\delta^{15}\text{N}$ ratio

and negatively affect the $\delta^{13}\text{C}$ ratio of the consumers (DeNiro & Epstein 1977, Focker & Becker 1998, Rau et al. 1992, Rothe & Gleixner 2000, McCutchan et al. 2003 and Haubert et al. 2005). However, several empirical studies have indicated that food quality affects stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios differently amongst various taxa including locusts (Webb et al. 1998a and 1998b), spiders (Oelbermann & Scheu 2002), collembolans (Haubert et al. 2005), polychaetes (Olive et al. 2003), fish (Gaye-Siessegger et al. 2003) and crustaceans (Adams & Sterner 2000).

Several *in situ* studies have already documented significant differences between the diets of territorial and non-territorial grazers (Branch 1975c, Branch & Newell 1978, Maneveldt et al. 2006 and Maneveldt & Keats 2008). These studies were exclusively based on observing foraging patterns in the field and performing gut content analyses. The present study applies stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses to investigate fractionational variation between the diets of territorial and non-territorial grazers. Stable isotope signatures of carbon and nitrogen give an estimation of an animal's diet over a long period of time and thus reflect long-term foraging behaviour (Peterson & Fry 1987 and Schmidt et al. 1998).

The $\delta^{13}\text{C}$ ratio of consumers generally reflects the $\delta^{13}\text{C}$ signature of their diet, while the $\delta^{15}\text{N}$ ratio reflects their trophic level (DeNiro & Epstein 1978, DeNiro & Epstein 1981, Wada et al. 1993 and Post 2002). These stable elemental isotopes are assimilated or fractionated at a relatively small and constant rate from diet source to the consumers (DeNiro & Epstein 1981 and Peterson & Fry 1987). The minute neutron-based isotopic variations occurring during fractionation are measured and amplified into parts per thousands (‰), so that even small isotopic variations can be detected (Fry 2008). The average fractionation rates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from one trophic level to the next are $\approx 1\text{‰}$ and $\approx 3\text{‰}$ respectively (DeNiro & Epstein 1978 and DeNiro & Epstein 1981). However, estimates of fractionation rates can differ considerably among taxa (Gannes et al. 1997, 1998 and Pearson et al. 2003) and this study will apply a fractionation rate of 2.4‰ for $\delta^{15}\text{N}$ as estimated for limpets (Dunton 2001). The fractionation rate for the $\delta^{13}\text{C}$ ratio might vary from as little as -1.2‰ to as large as +4.3‰ depending on

taxon and this study will assume a fractionation rate of -1.2‰ for limpets following DeNiro & Epstein (1976) and Pearson et al. (2003).

Stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures serve as appropriate trace elements to investigate diet variation within and amongst species assimilating different food sources (Michener & Schell 1994). However, territorial and non-territorial grazers forage on intertidal algae from the same trophic level and should putatively have equivalent stable $\delta^{15}\text{N}$ ratios. In effect, it is anticipated that if there are variations in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios between territorial and non-territorial grazers, they would be minute but ecologically significant. The dual-inlet gas isotope ratio mass spectrometer has a great capability for measuring such differences with high precision and extreme accuracy (Boutton 1991), allowing the detection of such tiny variations.

Territorial and non-territorial grazers generally forage on macroalgae from the same trophic level with similar carbon and nitrogen sources. Intertidal mussels are filter feeder that include nearshore algal detritus in their diets (Hill et al. 2006), which may thus be expected to show similar large-scale geographic patterns to those of sympatric limpets. The central hypothesis of the study was that non-territorial grazers would exhibit higher variability around the mean in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures compared to territorial grazers because they forage on multiple species of algae (see Bearhop et al. 2004, Matthews & Mazumder 2004). The study investigated if non-territorial grazers are characterized on average by higher means or $\pm\text{SD}$ values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios than territorial grazers.

In particular, the study investigated the following three hypotheses: 1) There will be no significant difference in mean values of carbon and nitrogen signatures between territorial and non-territorial grazers. 2) Non-territorial grazers will be characterized by higher variation around mean values of carbon and nitrogen stable isotope ratios than territorial grazers. 3) Algal grazers will show large-scale (biogeographic) patterns in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures that resemble those shown by intertidal mussels, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment along the west coast because of greater productivity there.

4.2 Materials and Methods

4.2.1 Study species

This study investigated intra- and inter-specific variation in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of selected patellid limpets along the southern African coastline. The model species were selected based on differences in their foraging behaviour (Table 4.1).

Table 4.1: The study species and their foraging behaviour.

Foraging behaviour	<i>Scutellastra</i> spp.	<i>Cymbula</i> spp.
Territorial grazers	<i>S. barbara</i> <i>S. cochlear</i> <i>S. longicosta</i>	<i>C. miniata</i> <i>C. compressa</i>
Non-territorial grazers	<i>S. granularis</i> <i>S. natalensis</i> <i>S. argenvillei</i>	<i>C. granatina</i> <i>C. oculus</i>

4.2.2 Sampling procedure

Samples of both territorial and non-territorial grazers were collected from 14 sites along the South African coast (Figure 4.1). From each site, at least five individuals of each species present were collected and immediately frozen in ice. Individual samples were collected randomly at least 5m apart from each other. The most abundant or frequently encountered algae within each site were also collected. Individual algal samples were also collected randomly at least 5m apart, at least three individual algal samples were collected for each species. For territorial grazers, their associated encrusting algae were collected by scraping the encrusting layer with a small scraper. All samples were immediately stored in ice upon collection.

4.2.3 Sample preparation

The foot muscle tissue from each limpet was removed, rinsed in distilled water (dH₂O) and oven dried at 60 °C for 48 hrs. The macro-algae were thoroughly rinsed in dH₂O and any visible epiphytes removed before oven drying at 60 °C for 48 hrs. The encrusting algae were treated with hydrochloric acid (HCL) to remove the inorganic carbon in CaCO₃. The samples were treated with 1M HCL drop-by-drop until no more CO₂ bubbles were observed. Then, the acidified samples were oven dried in 60 °C for 48 hrs without rinsing to minimize loss of dissolved organic matter (DOM) following Jacobs et al. (2005). The dried materials were then ground into a homogeneous powder using a sterilized pestle and mortar. The powdered samples were weighed and loaded into tin cups prior to isotope analysis. The limpet samples were about 1mg and the macroalgae about 2mg.

4.2.4 Stable isotopes analysis

The stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios were determined using a continuous flow Isotope Ratio Mass Spectrometer (IRMS) at the IsoEnvironmental Lab, Rhodes University, South Africa. The samples were combusted in on-line Carlo-Erba preparation units calibrated relative to the international standards of the Cretaceous PeeDee Belemite (PDB) marine limestone fossil formation for $\delta^{13}\text{C}$ and atmospheric nitrogen (Air) for $\delta^{15}\text{N}$ (Boutton 1991). The results are expressed in the standard delta notation $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where X is the element in question and R is the ratio of heavy to light isotope. The final δ values measured in ‰ show that the samples can either be enriched or depleted in heavy isotopes relative to the standard materials (Fry & Sherr 1984 and Peterson & Fry 1987). Precision of replicate determinations was $\pm 0.05\text{‰}$ for both carbon and nitrogen.

4.2.5 Data analysis

The data analyses were performed using both Microsoft Excel 2010 and Primer v. 6.1.11 (Anderson et al. 2008). All the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ graphs were produced using SigmaPlot v.10.0 (Systat 2004). One-way ANOVA was performed to test for significant differences in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios amongst observed isotopic clusters identified from large biogeographic scale collections. Non-parametric, permutational multivariate analyses of variance (PERMANOVA) with 9999 permutations were used to determine the effect of territoriality on stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures amongst all limpet species. Site was selected as a random factor while territoriality and non-territoriality were selected as fixed factors. The effect of territoriality was investigated in two separate tests using different species and sites due differences in species` distribution.

Firstly, the interaction between territoriality and sites was investigated in two territorial species (*Scutellastra cochlear* and *S. longicosta*) and two non-territorial species (*S. granularis* and *Cymbula oculus*) from six sites along the southeastern coast (Haga-Haga, Kenton-on-Sea, Sardinia Bay, Tsitsikamma, Mossel Bay and Cape Agulhas) where all four species occurred. Secondly, the interaction between territoriality and sites was investigated in two territorial species (*Scutellastra cochlear* and *Cymbula compressa*) and two non-territorial species (*Scutellastra granularis* and *Cymbula granatina*) from two west coast sites (Groenriviermond and Doring Bay). The PERMANOVA test for the west coast included only two sites owing to the sampling limitations (*Cymbula compressa* was not sampled from Muizenberg, Camps Bay or Paternoster).

It is important to note that the PERMANOVA tests on the effect of territoriality on stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios were confounded by species. Along the south coast, the data were robust, with two territorial and two non-territorial species from each of six sites. However, due to sampling limitations along the west coast, the PERMANOVA test comprised two territorial and two non-territorials species from each of only two sites (Groenriviermond and Doring Bay).

4.3 Results

4.3.1 Stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratio correlation between algae and patellid limpets

The encrusting algae associated with the territorial grazers, *Spongites yendoi* and *Ralfsia verrucosa* were significantly enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios compared to the non-encrusting algae. The encrusting alga *R. verrucosa* was significantly enriched in stable $\delta^{13}\text{C}$ compared to all other non-encrusting algae and limpets (Figures 4.3a - 4.3d). *Scutellastra longicosta* and *R. verrucosa* both had almost equivalent $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios (Figures 4.3a - 4.3d) with a difference of only $< 0.5\text{‰}$ in both elemental isotopes.

The encrusting alga *Spongites yendoi* was more enriched in stable $\delta^{15}\text{N}$ ratio than its territorial consumer *Scutellastra cochlear* (Figures 4.3e and 4.3h) and other non-encrusting algae (Figures 2.3e - 2.3h). The stable $\delta^{15}\text{N}$ ratios of *Spongites yendoi* were almost equivalent to that of its sympatric primary consumers (Figures 4.3e - 4.3h). The similar pattern observed between *Scutellastra longicosta* and *R. verrucosa* was also observed between *Cymbula compressa* and the kelp. The kelp was more enriched in $\delta^{13}\text{C}$ (by 2 - 3‰) than its symbiotic limpet *C. compressa* (Figures 4.3g and 4.3h). The $\delta^{15}\text{N}$ ratios of *C. compressa* and the kelp were almost equivalent, ranging from 6 - 6.5‰ between the two shores analysed (Figures 4.3g and 4.3h).

The non-territorial limpets *S. granularis* and *C. oculus* showed expected trophic enrichment compared to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of two algae, *Ulva* sp. and *Nothogenia erinacea* (Figure 2.3a). The stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of *S. granularis* and two red algae (*Gelidium pristoides* and *Hypnea spicifera*) revealed the expected trophic fractionation in Sardinia Bay (Figure 4.3c) and Cape Agulhas (Figure 4.3d). The plots of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios did not show the theoretically expected isotopic enrichment of $\approx 1.2\text{‰}$ in $\delta^{13}\text{C}$ and $\approx 2.4\text{‰}$ in $\delta^{15}\text{N}$ between the territorial grazers and their associated encrusting algae (*Scutellastra* spp.) and non-encrusting algae (*Cymbula* spp.). However, this trophic fractionation was partially observed between non-territorial grazers and non-encrusting algae (Figures 4.3a, 4.3c and 4.3d).

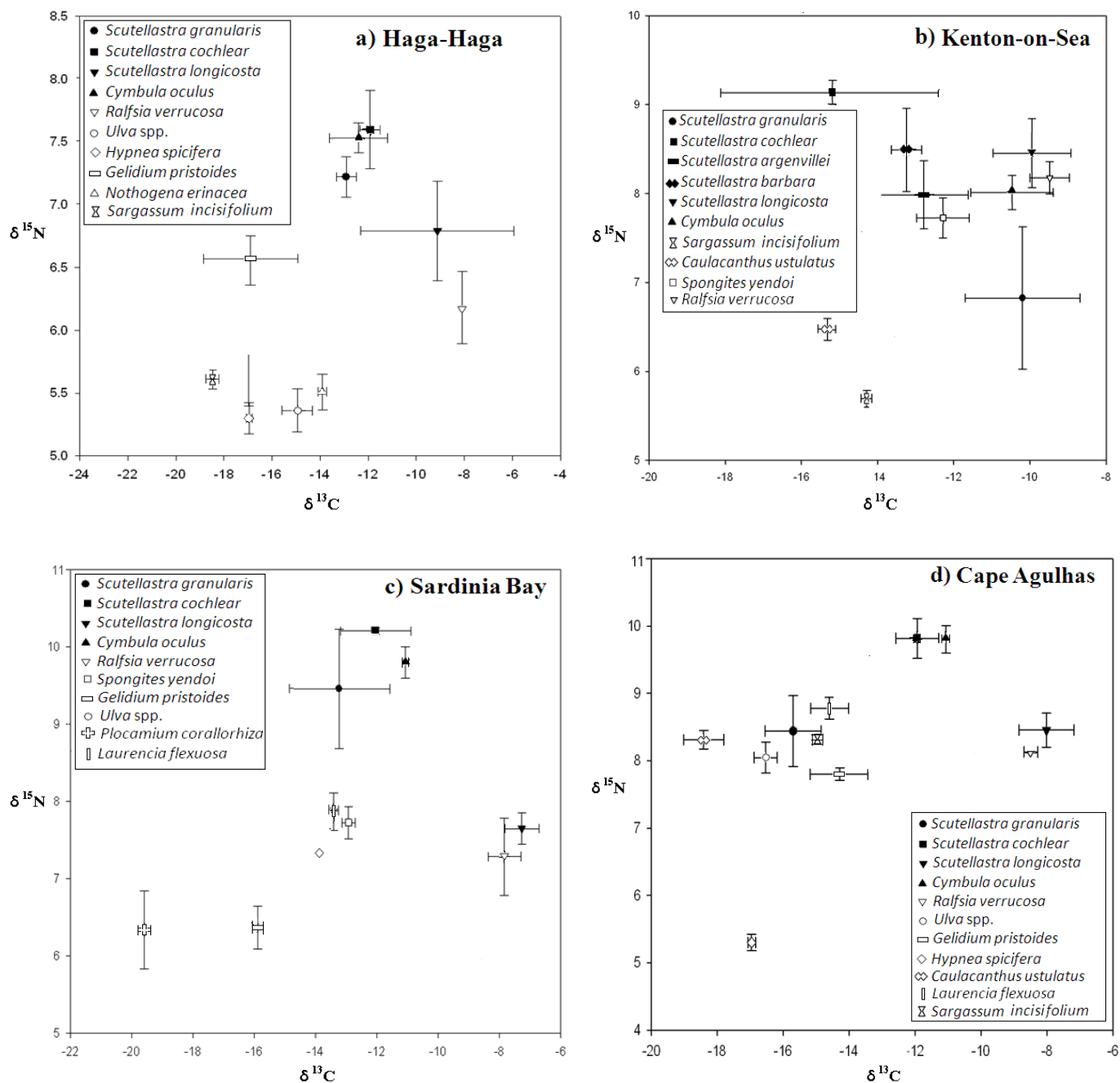


Figure 4.3: Plots of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of the algae and limpets from different sites. The limpets are coded with solid shapes and the algae are coded with empty shapes.

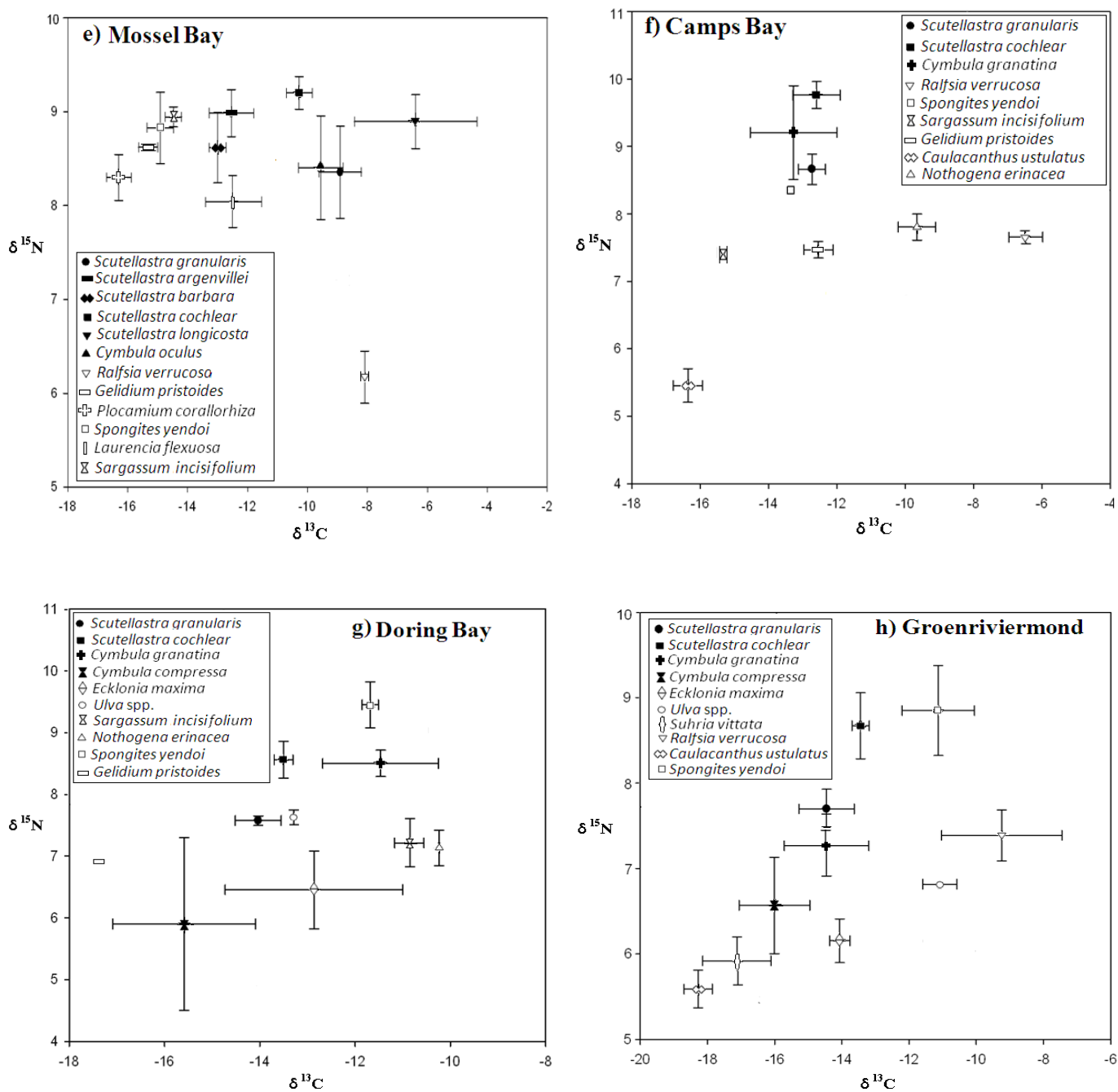


Figure 4.3: Plots of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of the algae and limpets from different sites. The limpets are coded with solid shapes and the algae are coded with empty shapes.

4.3.2 Stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of patellid limpets within sites

The mean \pm SDEV values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of all the limpets used in this analysis are presented in Tables 4.2 and 4.3 respectively. The territorial and non-territorial grazers generally forage on macroalgae from the same trophic level with similar carbon and nitrogen sources. The intra-site PERMANOVA test revealed no significant effect of foraging trait on mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of these limpets (Tables 4.4 and 4.5). However, the analysis revealed a significant interaction effect between territoriality and sites in both $\delta^{13}\text{C}$ ($p = 0.0007$) and $\delta^{15}\text{N}$ ($p = 0.0002$) ratios of limpets from six sites along the Agulhas region. Interestingly, the PERMANOVA intra-site pair-wise test further revealed the effect of foraging trait to be more pronounced in mean $\delta^{13}\text{C}$ but not mean $\delta^{15}\text{N}$ ratios of the limpets. The territorial grazers from four sites (HAG, KOS, SDB and TSK) were more enriched in mean $\delta^{13}\text{C}$ ratios (1-2‰) than non-territorial grazers (Table 4.6). However, there was a significant effect of territoriality on mean $\delta^{15}\text{N}$ ratios between the territorial and non-territorial grazers only at Kenton-on-Sea (Table 4.7).

Table 4.2: Mean (\pm SDEV) intra-site $\delta^{13}\text{C}$ values for the limpet species.

^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Limpets	HAG	KOS	SDB	TSK	MSB	CPA	MZB	CMB	PTN	DRB	GRM
<i>S. granularis</i> ^{NT}	-12.91 ± 0.41	-10.26 ± 1.68	-13.23 ± 2.76	-11.85 ± 0.01	-8.98 ± 0.27	-14.94 ± 0.13	-11.54 ± 0.40	-12.73 ± 0.40	-16.02 ± 0.47	-14.22 ± 1.90	-14.03 ± 0.48
<i>S. cochlear</i> ^T	-11.92 ± 0.41	-15.21 ± 2.94	-12.05 ± 1.15	-10.42 ± 0.32	-10.28 ± 0.43	-11.93 ± 0.64	-11.51 ± 0.52	-12.60 ± 0.69	-12.98 ± 0.66	-11.28 ± 0.57	-13.51 ± 0.20
<i>S. longicosta</i> ^T	-9.12 ± 3.18	-9.94 ± 1.02	-7.27 ± 0.55	-10.52 ± 0.35	-6.39 ± 0.80	-8.01 ± 0.84					
<i>C. oculus</i> ^{NT}	-12.40 ± 1.21	-10.06 ± 1.23	-12.71 ± 1.32	-11.32 ± 1.30	-9.55 ± 0.75	-11.07 ± 0.11					
<i>C. granatina</i> ^{NT}							-10.54 ± 1.30	-13.27 ± 1.27	-14.11 ± 0.84	-11.47 ± 1.21	-15.06 ± 1.05
<i>C. compressa</i> ^T										-15.72 ± 1.64	-16.28 ± 1.01

Table 4.3: Mean (\pm SDEV) intra-site $\delta^{15}\text{N}$ values for the limpet species.^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Limpets	HAG	KOS	SDB	TSK	MSB	CPA	MZB	CMB	PTN	DRB	GRM
<i>S. granularis</i> ^{NT}	7.22 ± 0.16	6.79 ± 0.89	9.46 ± 0.77	9.18 ± 0.11	8.54 ± 0.36	8.34 ± 0.07	10.52 ± 0.17	8.66 ± 0.22	9.03 ± 0.70	7.93 ± 0.40	7.58 ± 0.01
<i>S. cochlear</i> ^T	7.60 ± 0.31	9.12 ± 0.17	10.21 ± 0.04	8.70 ± 0.14	9.20 ± 0.17	9.82 ± 0.30	10.37 ± 0.44	9.76 ± 0.20	10.11 ± 0.02	8.79 ± 0.56	8.56 ± 0.30
<i>S. longicosta</i> ^T	6.79 ± 0.40	8.45 ± 0.39	7.65 ± 0.20	9.38 ± 0.50	8.78 ± 0.19	8.45 ± 0.25					
<i>C. oculus</i> ^{NT}	7.53 ± 0.12	7.96 ± 0.25	10.64 ± 0.26	9.25 ± 0.24	8.40 ± 0.55	9.80 ± 0.20					
<i>C. granatina</i> ^{NT}							10.46 ± 0.21	9.21 ± 0.69	9.32 ± 0.33	8.50 ± 0.21	7.30 ± 0.45
<i>C. compressa</i> ^T										5.77 ± 1.52	6.49 ± 0.57

Table 4.4: Table showing PERMANOVA results for the effects of territoriality based on mean $\delta^{13}\text{C}$ ratios of *Cymbula oculus*^{NT}, *Scutellastra granularis*^{NT}, *S. cochlear*^T and *S. longicosta*^T amongst six shores. Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Shores = Sh	5	160.27	32.053	7.8465	9960	0.0001	0.0001
F. trait = Ft	1	44.991	44.991	2.1111	9846	0.2018	0.204
Sh x Ft	5	108.98	21.796	5.3356	9937	0.0002	0.0007
Residual	97	396.25	4.085				
Total	108	697.18					

Table 4.5: Table showing PERMANOVA results for the effects of territoriality based on mean $\delta^{15}\text{N}$ ratios of *Cymbula oculus*^{NT}, *Scutellastra granularis*^{NT}, *S. cochlear*^T and *S. longicosta*^T amongst six shores. Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Shores = Sh	5	55.738	11.148	30.506	9943	0.0001	0.0001
F. trait = Ft	1	0.12585	0.12585	5.9906E-2	9700	0.8101	0.7591
Sh x Ft	5	10.748	2.1497	5.8826	9942	0.0002	0.0002
Residual	97	35.447	0.36543				
Total	108	102.54					

Table 4.6: Table showing PERMANOVA results for the effects of foraging trait based on mean $\delta^{13}\text{C}$ ratios of *Cymbula oculus*^{NT}, *Scutellastra granularis*^{NT}, *S. cochlear*^T and *S. longicosta*^T within six shores. Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Shores	Average distance between traits	Unique Permutations	Permutations (MC)	P value Permanova
Haga-Haga (HAG)	2.2334	9306	0.0278	0.0117
Kenton-on-Sea (KOS)	3.1017	9352	0.0354	0.0272
Sardinia Bay (SDB)	3.8533	462	0.0342	0.0410
Tsitsikamma (TSK)	0.96854	9297	0.0015	0.0014
Mossel Bay (MSB)	2.6012	9345	0.1762	0.1744
Cape Agulhas (CPA)	3.6316	9294	0.0093	0.0133

Table 4.7: Table showing PERMANOVA results for the effects of foraging trait based on mean $\delta^{15}\text{N}$ ratios of *Cymbula oculus*^{NT}, *Scutellastra granularis*^{NT}, *S. cochlear*^T and *S. longicosta*^T within six shores. Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Shores	Average distance between traits	Unique Permutations	Permutations (MC)	P value Permanova
Haga-Haga (HAG)	0.46075	9359	0.4717	0.4743
Kenton-on-Sea (KOS)	1.2012	9312	0.0007	0.0003
Sardinia Bay (SDB)	1.4851	462	0.1259	0.1246
Tsitsikamma (TSK)	0.45462	9309	0.7049	0.7089
Mossel Bay (MSB)	0.39729	9344	0.1551	0.1546
Cape Agulhas (CPA)	0.79418	9344	0.3995	0.387

In contrast to the south coast, the PERMANOVA analysis of interaction between territoriality and sites revealed no significant effect of territoriality on mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios amongst limpets from two sites along the west coast (Tables 4.8 and 4.9).

Table 4.8: Table showing PERMANOVA results for the effects of territoriality based on mean $\delta^{13}\text{C}$ ratios of *Cymbula granatina*^{NT}, *Scutellastra granularis*^{NT}, *C. compressa*^T and *S. cochlear*^T from two shores along the west coast (Groenriviermond and Doring Bay).

Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Shores = Sh	1	24	24	7.2987	9840	0.0098	0.0088
F. trait = Ft	1	8.0297	8.0297	3.7372	6	0.3058	0.5029
Sh x Ft	1	2.1486	2.1486	0.65341	9855	0.4242	0.4368
Residual	37	121.67	3.2883				
Total	40	152.97					

Table 4.9: Table showing PERMANOVA results for the effects of territoriality based on mean $\delta^{15}\text{N}$ ratios of *Cymbula granatina*^{NT}, *Scutellastra granularis*^{NT}, *C. compressa*^T and *S. cochlear*^T from two shores along the west coast (Groenriviermond and Doring Bay).

Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Shores = Sh	1	0.79434	0.79434	0.60135	9850	0.4335	0.4442
F. trait = Ft	1	3.5273	3.5273	1.1095	6	0.4874	0.5008
Sh x Ft	1	3.1793	3.1793	2.4068	9827	0.1317	0.1252
Residual	37	48.875	1.3209				
Total	40	55.45					

4.3.3 Stable isotope signatures of patellid limpets among sites

The average \pm SDEV values for $\delta^{13}\text{C}$ ratios and $\delta^{15}\text{N}$ ratios are presented in Tables 4.10 and 4.11 respectively for all the limpets species used in this analysis. The non-territorial grazers were expected to be characterized by higher variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios around the mean than the territorial grazers. Strikingly, the results of PERMANOVA analysis for the effect of territoriality revealed no significant difference in standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios between the territorial and non-territorial grazers. The Permanova p values were 0.4951 for $\delta^{13}\text{C}$ ratios (Table 4.12) and 0.1904 for $\delta^{15}\text{N}$ ratios (Table 4.13) based on four patellid species from six shores along the south-eastern coast. Additionally, the Permanova p values were 0.7885 for $\delta^{13}\text{C}$ ratios (Table 2.14) and 0.7978 for $\delta^{15}\text{N}$ ratios (Table 4.15) based on four patellid species from two shores along the west coast (Groenriviermond and Doring Bay).

Table 4.10: The mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ standard deviations for *Scutellastra* spp. amongst all the sites.

Territorial grazers	STDEV $\delta^{13}\text{C}$	STDEV $\delta^{15}\text{N}$
<i>S. cochlear</i>	± 0.88	± 0.30
<i>S. longicosta</i>	± 1.28	± 0.41
Non-territorial grazers		
<i>S. granularis</i>	± 0.89	± 0.40
<i>S. natalensis</i>	± 0.68	± 0.38
Intermediate grazers		
<i>S. argenvillei</i>	± 0.91	± 0.36
<i>S. barbara</i>	± 0.79	± 0.34

Table 4.11: The mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ standard deviations for *Cymbula* spp. amongst all the sites.

Territorial grazers	STDEV $\delta^{13}\text{C}$	STDEV $\delta^{15}\text{N}$
<i>C. compressa</i>	± 1.33	± 0.44
<i>C. miniata</i>	± 0.95	± 0.68
Non-territorial grazers		
<i>C. oculus</i>	± 1.27	± 0.37
<i>C. granatina</i>	± 1.19	± 0.38

Table 4.12: Table showing PERMANOVA results for the effects of territoriality based on standard deviations of $\delta^{13}\text{C}$ ratios of *Cymbula oculus*^{NT}, *Scutellastra granularis*^{NT}, *S. cochlear*^T and *S. longicosta*^T amongst 6 shores (HAG, KOS, SDB, TSK, MSB and CPA). Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Sites = Si	5	6.2223	1.2445	1.819	9959	0.1835	0.1816
F. trait = Ft	1	7.6439E-2	7.6439E-2	0.12297	9330	0.7389	0.7332
Si x Ft	5	3.1081	0.62162	0.90864	9959	0.5145	0.4951
Residual	12	8.2095	0.68412				
Total	23	17.616					

Table 4.13: Table showing PERMANOVA results for the effects of territoriality based on standard deviations of $\delta^{15}\text{N}$ ratios of *Cymbula oculus*^{NT}, *Scutellastra granularis*^{NT}, *S. cochlear*^T and *S. longicosta*^T amongst 6 shores (HAG, KOS, SDB, TSK, MSB and CPA). Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Sites = Si	5	0.12154	2.4309E-2	0.60248	9947	0.6957	0.7075
F. trait = Ft	1	3.5308E-2	3.5308E-2	0.48175	9300	0.5141	0.523
Si x Ft	5	0.36646	7.3292E-2	1.8165	9954	0.186	0.1904
Residual	12	0.48418	4.0348E-2				
Total	23	1.0075					

Table 4.14: Table showing PERMANOVA results for the effects of territoriality based on standard deviations of $\delta^{13}\text{C}$ ratios of *Cymbula granatina*^{NT}, *Scutellastra granularis*^{NT}, *C. compressa*^T and *S. cochlear*^T from two shores along the west coast (Groenriviermond and Doring). Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Sites = Si	1	2.4457E-2	2.4457E-2	6.7378E-2	310	0.8103	0.8075
F. trait = Ft	1	9.5044E-2	9.5044E-2	2.7436	6	0.3492	0.5079
Si x Ft	1	3.4642E-2	3.4642E-2	9.5438E-2	312	0.7788	0.7885
Residual	3	1.0889	0.36298				
Total	6	1.2612					

Table 4.15: Table showing PERMANOVA results for the effects of territoriality based on standard deviations of $\delta^{15}\text{N}$ ratios of *Cymbula granatina*^{NT}, *Scutellastra granularis*^{NT}, *C. compressa*^T and *S. cochlear*^T from two shores along the west coast (Groenriviermond and Doring). Foraging traits (Ft): ^T = Territorial grazers and ^{NT} = Non-territorial grazers.

Source	Degree of Freedom	Sum of Squares	Mean Squares	F-ratios	Unique Permutations	Permutation (MC)	P value (Permanova)
Sites = Si	1	2.4457E-2	2.4457E-2	6.7378E-2	310	0.8215	0.8121
F. trait = Ft	1	9.5044E-2	9.5044E-2	2.7436	6	0.3434	0.4944
Si x Ft	1	3.4642E-2	3.4642E-2	9.5438E-2	312	0.7786	0.7978
Residual	3	1.0889	0.36298				
Total	6	1.2612					

4.3.4 Stable isotope signatures of patellid limpets at large biogeographic scales

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures revealed similar biogeographical patterns in isotopic signatures for all the limpets (Figures 4.4 and 4.5). The $\delta^{13}\text{C}$ signatures of the limpets were most depleted along the west coast, most enriched along the south coast and intermediate along the eastern coast (Table 4.16). In contrast, the $\delta^{15}\text{N}$ signatures of the limpets were highest along the south coast and then lowest towards the east (KOS - BLT) and intermediate along the west (CMB - GRM) coasts (Table 4.17). The highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios were recorded along the south coast at SDB, TSK, MSB, CPA and MZB (Tables 4.18 and 4.19). The isotopic signatures of *Cymbula granatina* also revealed a northward depletion in $\delta^{15}\text{N}$ ratios along the west coast and enrichment in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at one south coast site, MZB (Figure 4.6). *Scutellastra natalensis* has a restricted range (Figure 1f) and was only sampled from three sites (BLT, PKR and PED).

Table 4.16: The range of $\delta^{13}\text{C}$ values of all the limpets from different regions of the coast.

East coast	$\delta^{13}\text{C}$	South coast	$\delta^{13}\text{C}$	West coast	$\delta^{13}\text{C}$
BLT	$\pm 13.58 - 9.87\text{‰}$	SDB	$\pm 13.23 - 7.27\text{‰}$	CMB	$\pm 13.27 - 12.60\text{‰}$
PKR	$\pm 14.66 - 11.75\text{‰}$	TSK	$\pm 14.80 - 10.52\text{‰}$	PTN	$\pm 16.02 - 12.98\text{‰}$
PED	$\pm 13.13 - 9.74\text{‰}$	MSB	$\pm 10.28 - 8.91\text{‰}$	DRB	$\pm 15.72 - 11.28 \text{‰}$
HAG	$\pm 13.03 - 9.12\text{‰}$	CPA	$\pm 15.03 - 8.06\text{‰}$	GRM	$\pm 16.28 - 13.51\text{‰}$
KOS	$\pm 15.21 - 9.24\text{‰}$	MZB	$\pm 11.64 - 10.46\text{‰}$		

Table 4.17: The range of $\delta^{15}\text{N}$ values of all the limpets from different regions of the coasts.

East coast	$\delta^{15}\text{N}$	South coast	$\delta^{15}\text{N}$	West coast	$\delta^{15}\text{N}$
BLT	$\pm 5.94 - 7.26\text{‰}$	SDB	$\pm 7.65 - 10.46\text{‰}$	CMB	$\pm 8.66 - 9.76\text{‰}$
PKR	$\pm 6.41 - 7.11\text{‰}$	TSK	$\pm 8.24 - 9.18\text{‰}$	PTN	$\pm 9.03 - 10.11\text{‰}$
PED	$\pm 5.77 - 7.05\text{‰}$	MSB	$\pm 8.36 - 9.20\text{‰}$	DRB	$\pm 5.77 - 8.79\text{‰}$
HAG	$\pm 6.79 - 7.63\text{‰}$	CPA	$\pm 8.43 - 9.83\text{‰}$	GRM	$\pm 6.57 - 8.67\text{‰}$
KOS	$\pm 6.79 - 7.96\text{‰}$	MZB	$\pm 10.37 - 10.54\text{‰}$		

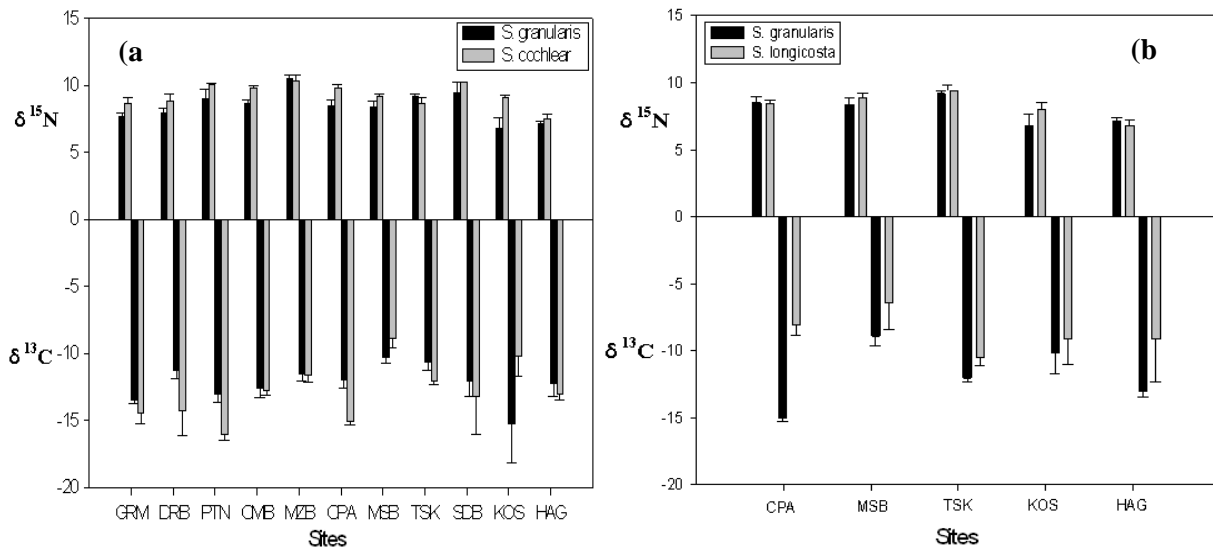


Figure 4.4: Relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and sites for: (a) the non-territorial *S. granularis* and territorials *S. cochlear* and (b) the non-territorial *S. granularis* and the territorial *S. longicosta*. Sites are sampled from closest to Namibia to closest to Mozambique.

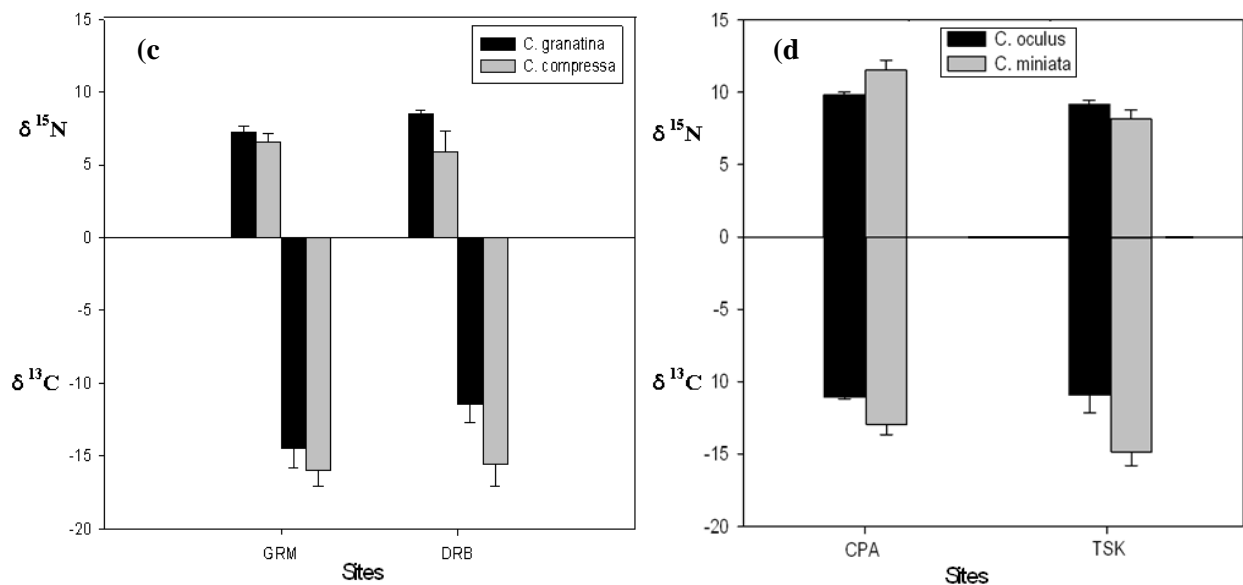


Figure 4.5: Relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and sites for: (c) the territorial *Cymbula compressa* and the non-territorial *C. granatina* and (d) the territorial *C. miniata* and the non-territorial *C. oculus*.

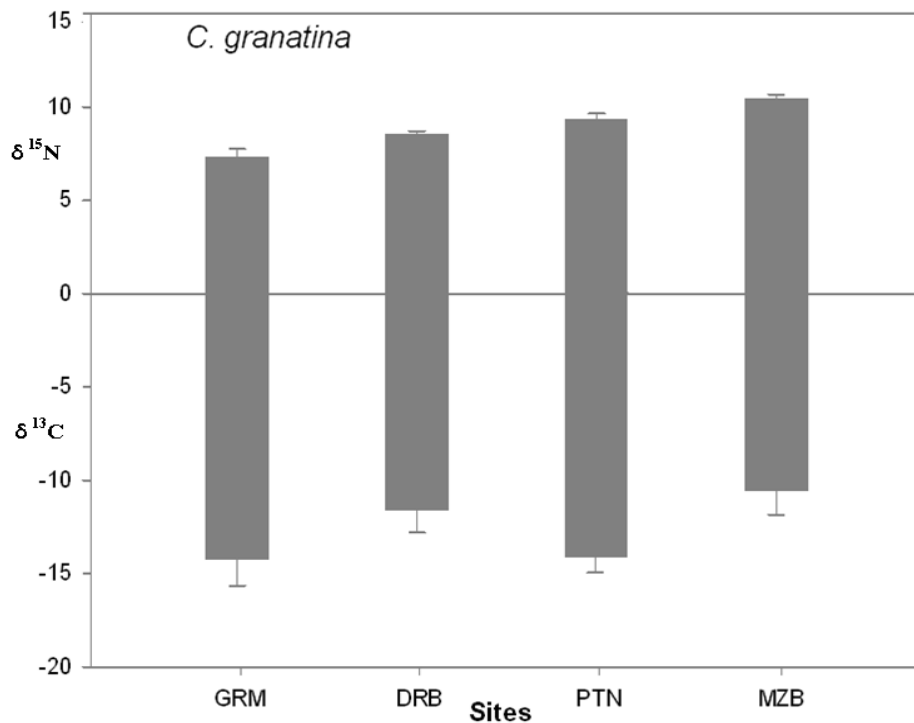


Figure 4.6: Graph showing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *Cymbula granatina* amongst sites.

4.3.5 Biogeographic clusters in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of patellid limpets

The SigmaPlot analysis of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *Scutellastra granularis*, *S. longicosta*, *S. cochlear* and *C. oculus* revealed four biogeographic clusters. *S. granularis* and *S. cochlear* grouped into Western, South-western and Eastern clusters (Figures 4.7 and 4.8). *S. longicosta* and *C. oculus* grouped into South-western and South-eastern clusters (Figures 4.9 and 4.10). However, there were a few sites that clustered differently depending on the species. For example, Camps Bay (CMB) was resolved into the western cluster for *S. cochlear* (Figure 4.8) but resolved into the south-western cluster for *S. granularis* (Figure 4.7) and *C. oculus* (Figure 4.10). For *S. cochlear*, Doring Bay (DRB) grouped with the south-western cluster while Muizenberg (MZB) and Sardinia Bay (SDB) grouped into the western cluster. Two sites, Kenton-on-Sea (KOS) and Mossel Bay (MSB) were grouped into the south-western cluster for *S. longicosta* (Figure 4.9), however they clustered together as the only south-eastern cluster for *C. oculus* (Figure 4.10).

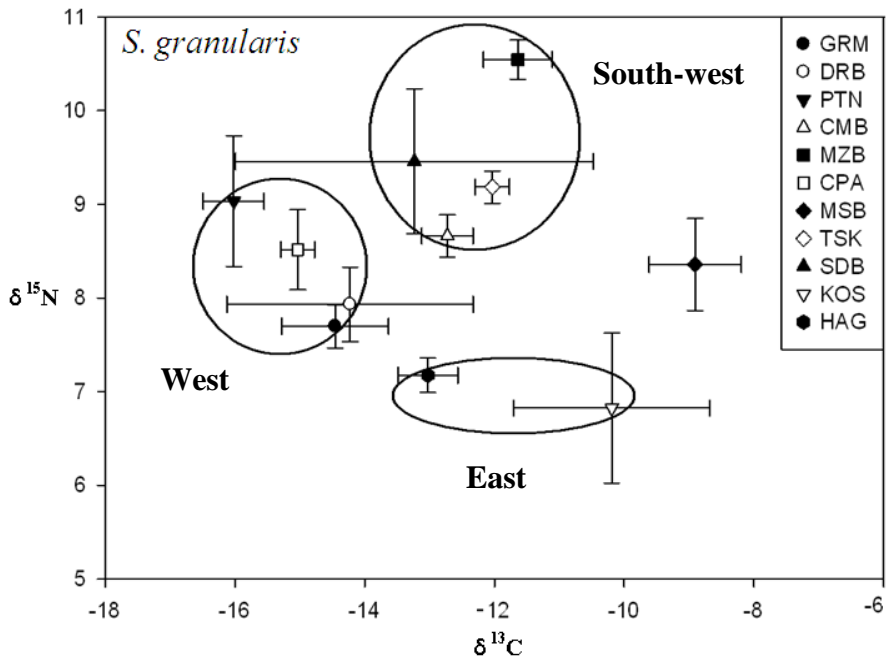


Figure 4.7: Graph showing plot of $\delta^{13}C$ and $\delta^{15}N$ values of *Scutellastra granularis* from all sites.

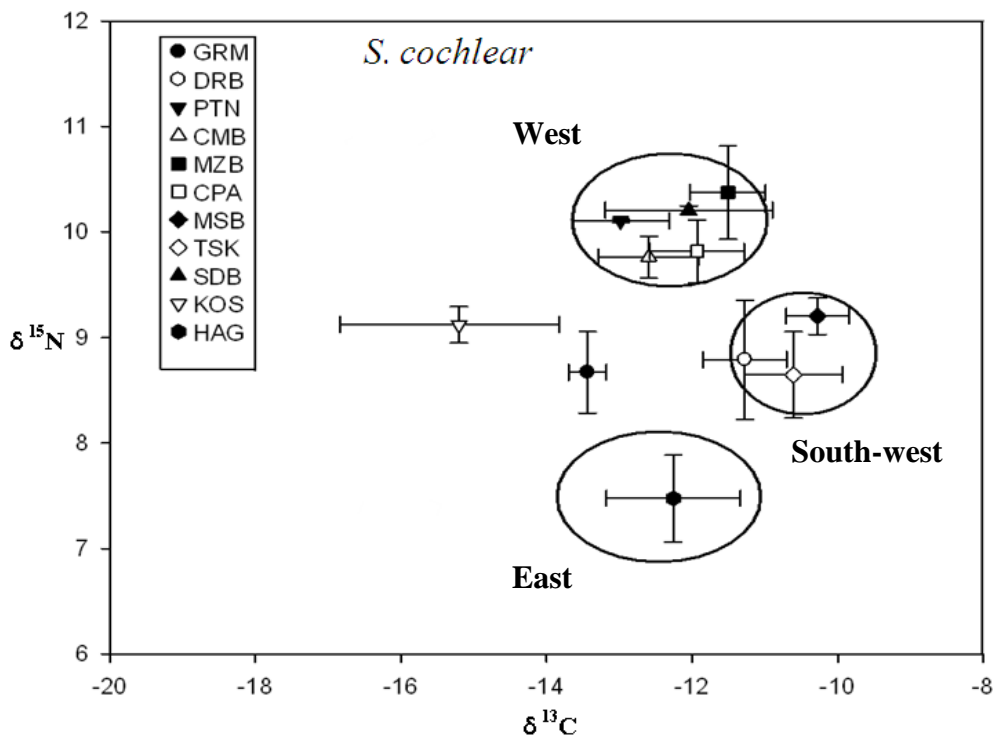


Figure 4.8: Graph showing plot of $\delta^{13}C$ and $\delta^{15}N$ values of *Scutellastra cochlear* from all sites.

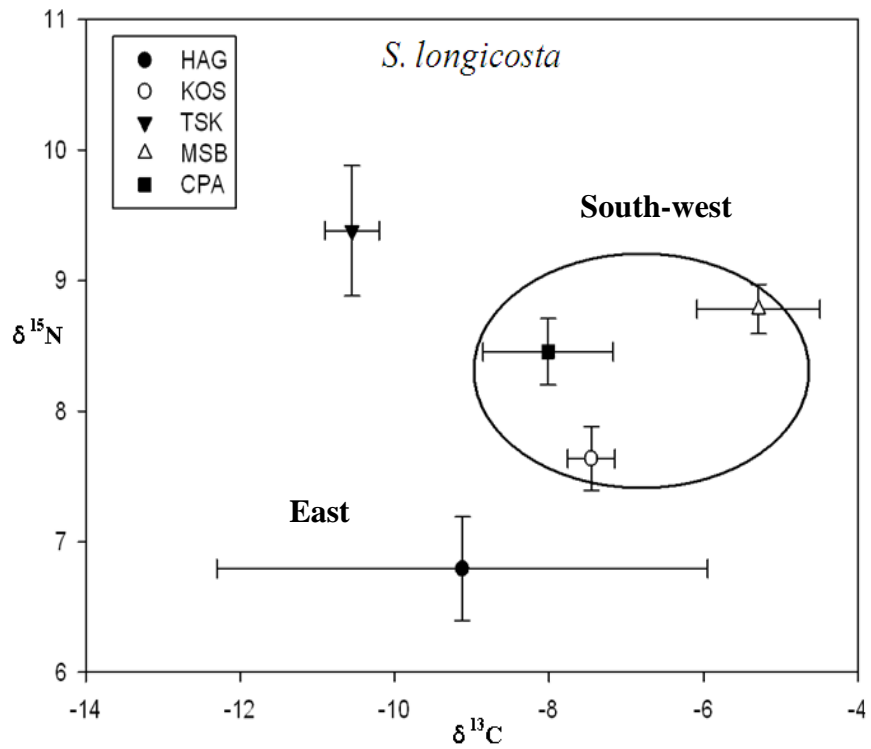


Figure 4.9: Graph showing plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Scutellastra longicosta* from all sites.

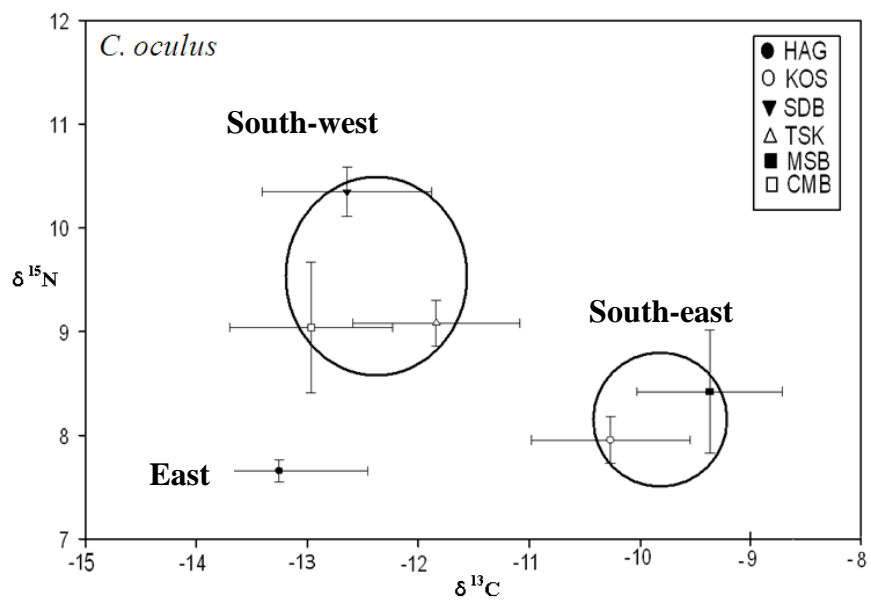


Figure 4.10: Graph showing plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Cymbula oculus* from all sites.

4.4 Discussion

The plots of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios did not reveal the expected trophic fractionation between encrusting algae and their territorial limpets. However, expected isotopic enrichment between producers and consumers was observed between non-encrusting algae and the non-territorial grazers. The lack of trophic fractionation between territorial limpets and their associated encrusting algae is not surprising. The diet of territorial grazers can comprise other algae from their territorial garden as well as the associated encrusting alga (Branch 1971, 1975a, 1980 and Maneveldt & Keats 2008). Similarly, Hill & McQuaid (2008) also found no trophic fractionation between the territorial *S. longicosta* and its associated encrusting alga *Ralfsia verrucosa*. The two encrusting algae, *Spongites yendoi* and *R. verrucosa* were respectively enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios compared to other non-encrusting algae. This suggests variation in nutritional content between the encrusting and non-encrusting algae. The observed enrichment in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in encrusting coralline algae is likely due to their high nutritional content compared to non-encrusting algae. The encrusting coralline algae are more nutritious than non-encrusting coralline algae (Maneveldt & Keats 2008) and this seems to be reflected even at the level of the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of these algae.

High quality food items are expected to be depleted in $\delta^{13}\text{C}$ ratios (DeNiro & Epstein 1977, Focker & Becker 1998 and Rau et al. 1992), however in this study encrusting algae were significantly enriched in $\delta^{13}\text{C}$ compared to non-encrusting algae and even limpets. This could possibly be attributed to the high natural content of inorganic carbon in encrusting coralline algae. Despite algal acidification prior to isotope analysis, this acid treatment could have at worst been minimal or inefficient at degrading all traces of inorganic carbon. In contrast to the expected negative effect of algal acidification, acid-treated encrusting algae were significantly enriched in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. These results suggest the negative effects of algal acidification on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios were minimal or insignificant. Thus, the primary explanations for the enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in encrusting coralline algae is their high nutritional content or the inefficiency of algal acidification prior to analyses.

At large spatial scales, the limpets revealed similar biogeographic distributions of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures along the coastline. However, at small, local scales, there was intriguing variation in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios between the territorial and non-territorial grazers in both genera. The PERMANOVA analyses of the effect of foraging trait on mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios revealed significant interactions between foraging trait and sites. These results were intriguing in three aspects which will be addressed below. Firstly, there was significant interaction between site and territoriality for mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios but not their respective standard deviations. Secondly, mean $\delta^{13}\text{C}$ ratios were significantly different between territorial and non-territorial species at all but one site, while mean $\delta^{15}\text{N}$ ratios differed at only one site. Thirdly, the effects of territoriality were discovered only for *Scutellastra* spp. but not *Cymbula*.

The lack of variation in the standard deviations of the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios suggests the non-territorial grazers seem to predominantly forage on a particular alga out of the multiple algae available. The plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios between algae and limpets show that the non-territorial grazers (*Scutellastra granularis* and *Cymbula oculus*) primarily forage either on *Ulva* spp., *Gelidium pristoides*, *Hypnea spicifera* or *Nothogena erinacea*. Thus, the non-territorial grazers are not necessarily generalist foragers but tend to display algal preferences or forage on the most ubiquitous algae. *G. pristoides* and *Ulva* spp. are the most dominant intertidal high shore algae across their distributional range.

The $\delta^{13}\text{C}$ ratios reflect the signature of the source diet while the $\delta^{15}\text{N}$ ratios provide information on the signature of the whole ecosystem. Thus, it is not surprising that the $\delta^{15}\text{N}$ ratios of the territorial and non-territorial grazers were not significantly different since both have the same nitrogen source. However, the variation in $\delta^{13}\text{C}$ ratios ($\approx 1\text{-}2\%$) reflects the differences in the diet source between the territorial and non-territorial grazers. The territorial grazers forage either on their associated encrusting algae or their algal garden while non-territorial grazers forage on different algal species. The enrichment in $\delta^{13}\text{C}$ ratios of territorial grazers corresponds with the enriched $\delta^{13}\text{C}$ ratios of encrusting non-coralline and coralline algae. This indicates the territorial grazers forage primarily on the garden of the encrusting non-coralline and coralline algae.

It is worth noting that there were two important limitations in the analyses of the data. Firstly, the analyses were confounded in terms of geography and species, with *Cymbula* largely restricted to the west coast. This inevitably hindered robust comparison of the same species from different geographic regions. Secondly, only two sites were analysed along the west coast. Thus, the effects of foraging traits were confounded with the genus, with *Scutellastra* mostly on the south coast and *Cymbula* on the west coast.

Although species of both *Scutellastra* and *Cymbula* were territorial grazers, their associated algae have different chemical compositions. The territorial *S. cochlear* forages primarily on a carbon-enriched encrusting coralline alga, *Spongites yendoi*, while the territorial *C. compressa* forages on kelp and its epiphytes (Branch 1975c). Thus the territorial grazers in *Scutellastra*, *S. cochlear* and *S. longicosta* are exclusively dependent on a diet rich in carbon and nitrogen unlike the non-territorial grazers, *S. granularis* and *S. natalensis*. Territoriality culminated in enriched $\delta^{13}\text{C}$ ratios in the territorial *Scutellastra* spp. but not in the territorial *C. compressa*.

At large biogeographic scales, the limpets exhibited depletion in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios along the eastern coast, enrichment along the southern coast and then moderate depletion along the western coast (Figure 4.11). Interestingly, SPM and filter feeders and top predators revealed similar pattern but with even more enrichment along the west coast (Hill et al. 2006, Hill & McQuaid 2008, Jaquemet & McQuaid 2008 and Kohler et al. 2011). The sites most strongly affected by the Agulhas current system (BLT - CPA) showed east-south enrichment in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, a pattern also found in nearshore SPM and mussels (Hill et al. 2006). Intertidal mussels filter feed primarily on phytoplankton and nearshore algal detritus (Hill et al. 2006), thus their diet almost matches that of their sympatric limpets. Nearshore and offshore waters have different carbon and nitrogen sources, with the onshore water influenced by macroalgal-derived carbon and the offshore water reflecting a phytoplankton signature (Hill et al. 2006). This east-south enrichment in isotopic ratios is due to the mixing differences between onshore and offshore waters as the Agulhas current moves from east to south (Hill et al. 2008). Similarly, the drop in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of patellid limpets along the west coast can be attributed to the mixing effect between the onshore and offshore waters.

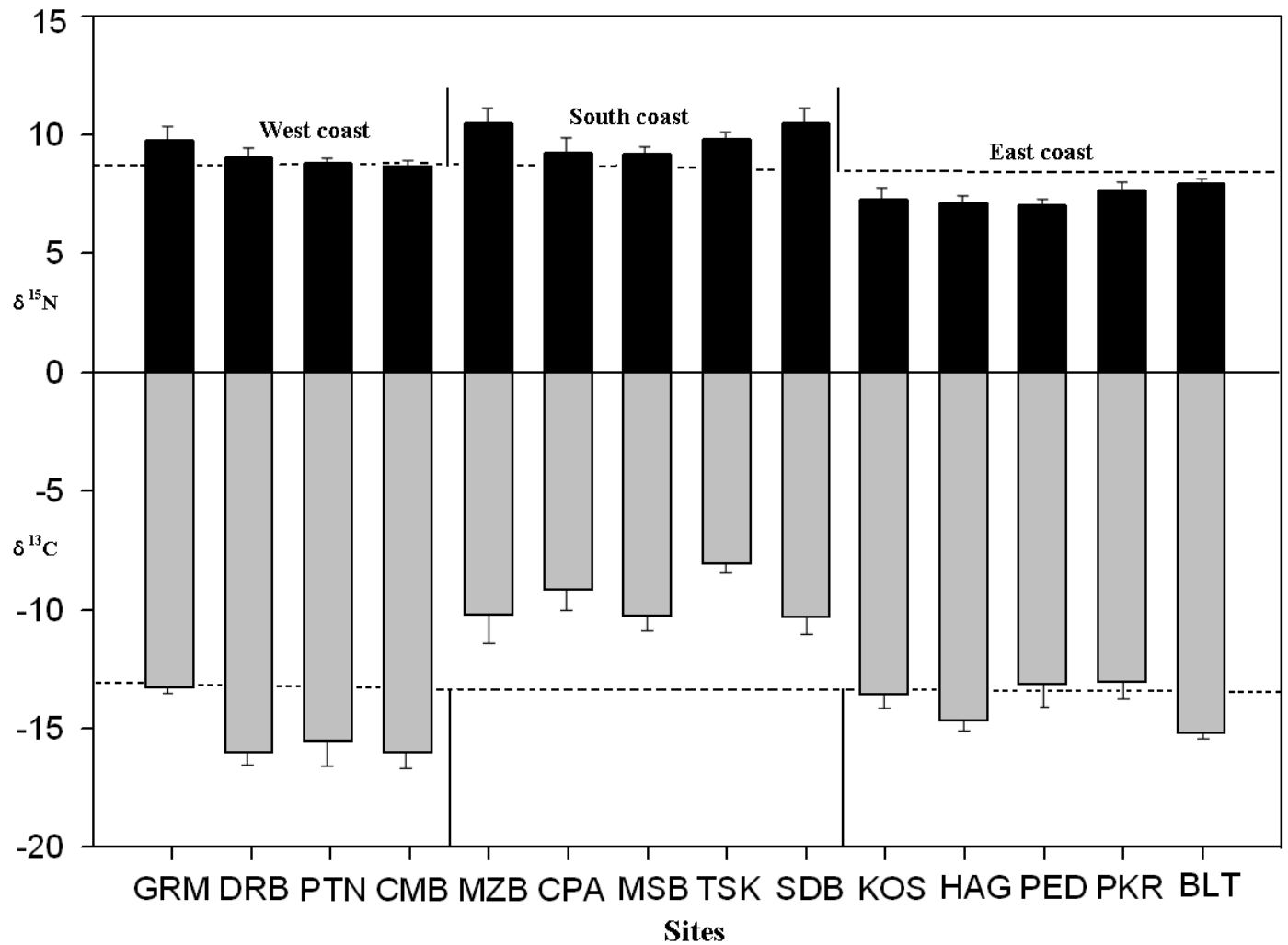


Figure 4.11: Graph illustrating large-scale biographic trends in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of all the limpets species collected from each site across the coastline. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios are the average isotopic value for all patellid limpets collected from each site. The dotted lines represent the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all the sites.

One-way ANOVA revealed significant differences ($p < 0.05$) in $\delta^{15}\text{N}$ ratios for all the limpets species at the large biogeographic scale (Table 4.18). The limpets along the south coast were more enriched in $\delta^{15}\text{N}$ ratios (9.20 – 10.46‰) followed by the west coast (8.67– 9.76‰) then the east coast (7.05 – 7.96‰). However, one-way ANOVA revealed that differences in $\delta^{13}\text{C}$ ratios for all the limpets species along large biogeographic scale were non-significant ($p > 0.05$, Table 4.19).

Table 4.18: The results of one-way ANOVA of stable $\delta^{15}\text{N}$ ratios for all the limpets species along large biogeographic scale.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	15.29884	2	7.64942	31.02793	<0.0001	3.885293835
Within Groups	2.9584	12	0.246533			
Total	18.25724	14				

Table 4.19: The results of one-way ANOVA of stable $\delta^{13}\text{C}$ ratios for all the limpets species along large biogeographic scale.

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	89.68428	2	44.84214	40.10781	0.4856	3.885294
Within Groups	13.41648	12	1.11804			
Total	103.1008	14				

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of patellid limpets (all species from each site) revealed three biogeographic clusters (West, South and East clusters) which are illustrated on the map in Figure 4.12. The western cluster included sites from Groenriviermond to Cape Agulhas, the southern cluster included sites from Muizenberg to Sardinia Bay and the eastern cluster included sites from Kenton-on-Sea to Ballito (Figure 4.12). The western and southern clusters overlapped

along the region between Muizenberg and Cape Agulhas. It is important to note that for the eastern cluster, two northeastern sites, Park Rynie (PKR) and Balito (BLT) were only represented by one species, the non-territorial *Scutellastra natalensis* which is restricted to this region.

These three biogeographic clusters are similar to the biogeographic clusters discovered in stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of SPM and filter feeders (Hill et al. 2006 and Hill & McQuaid 2008). However, these previous studies further delineated the South coast cluster into south-western and south-eastern clusters.

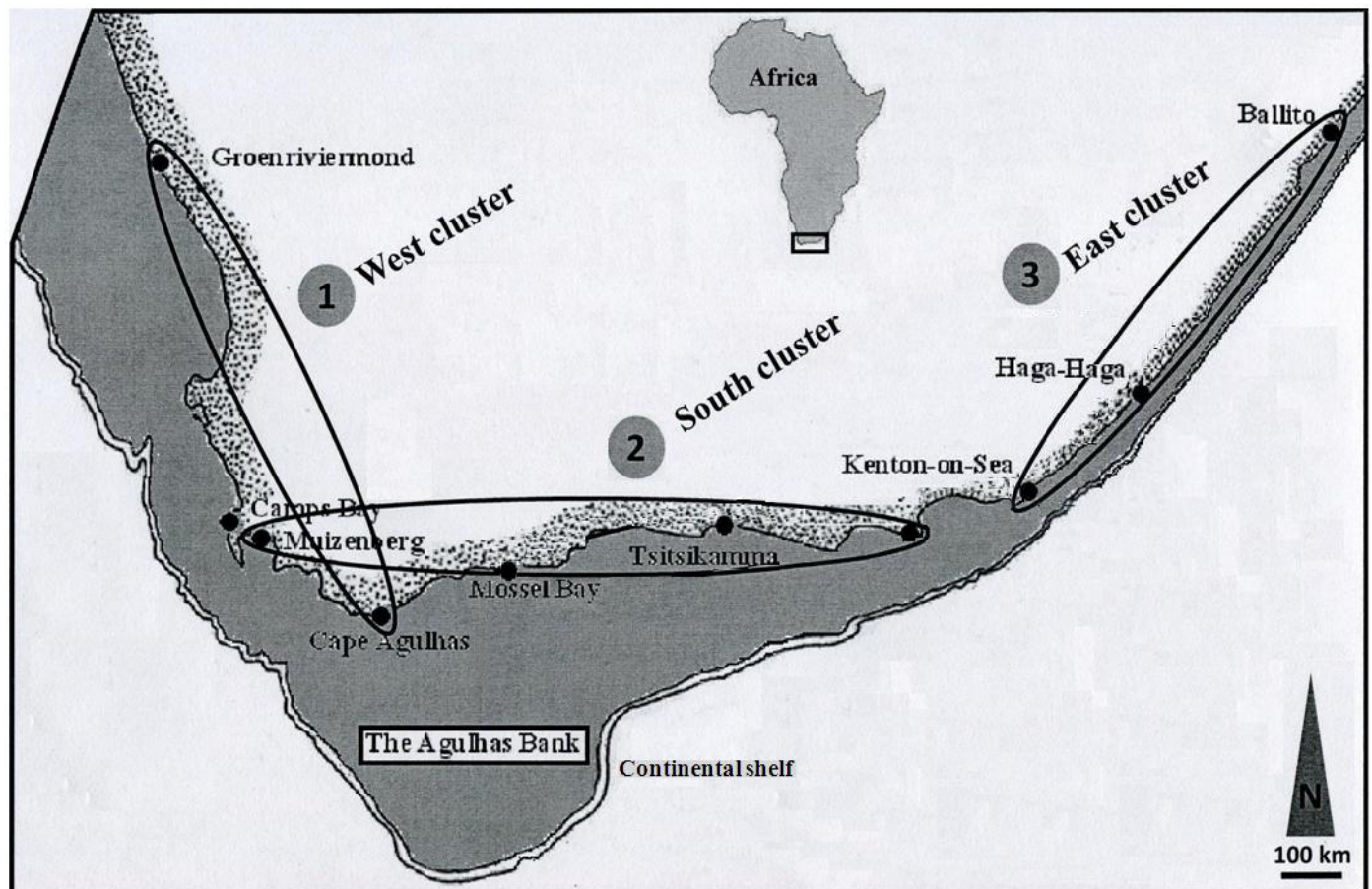


Figure 4.12: Map of the South African coastline illustrating the breadth of the continental shelf and the three isotopic biogeographic clusters discovered in this study.

The Agulhas current follows the edge of the continental shelf along the eastern and southern coast of South Africa (Lutjeharms 2004). Along the eastern coast, the continental shelf is narrow (Figure 4.12) and the Agulhas current flows close to the shore, resulting in strong mixture between onshore and offshore waters (Goschen & Schumann 1990 and 1994). However, the continental shelf becomes broad moving southward (Figure 4.12) and the Agulhas current moves further offshore resulting in weaker mixing between onshore and offshore waters (Roberts 2005). The continental shelf progressively becomes broader along the Agulhas bank, resulting in no mixture at all between inshore and offshore waters (Figure 4.12).

Thus, it is not surprising that the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of limpets were recorded along the south coast from either the sites where the Agulhas current flows further from the coast or from the sites inshore of the Agulhas Bank (Figure 4.12). The continental shelf is moderately broad along the west coast compared to the east coast and the Benguela current flows closer inshore; resulting in partial mixture between onshore and offshore waters (Shannon 1985 and Bustamante & Branch 1996a). Thus the limpets revealed moderate enrichment in $\delta^{15}\text{N}$ signatures along the western coast compared to the eastern coast.

At large biogeographic scales, the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of these limpets are correlated with the prevailing biogeographic and oceanographic conditions rather than their foraging behaviour. The difference in nutrient composition between the biogeographic regions is so intense it is even reflected in the stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of different but closely related species irrespective of their foraging behaviour. For example, species from different genera with different foraging behaviour along the same coastline show similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. On the other hand, closely related species (of the same genus) with the same foraging behaviour from different coastlines showed different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. This illustrates a strong link between isotope signatures and oceanographic conditions along the southern African coastline.

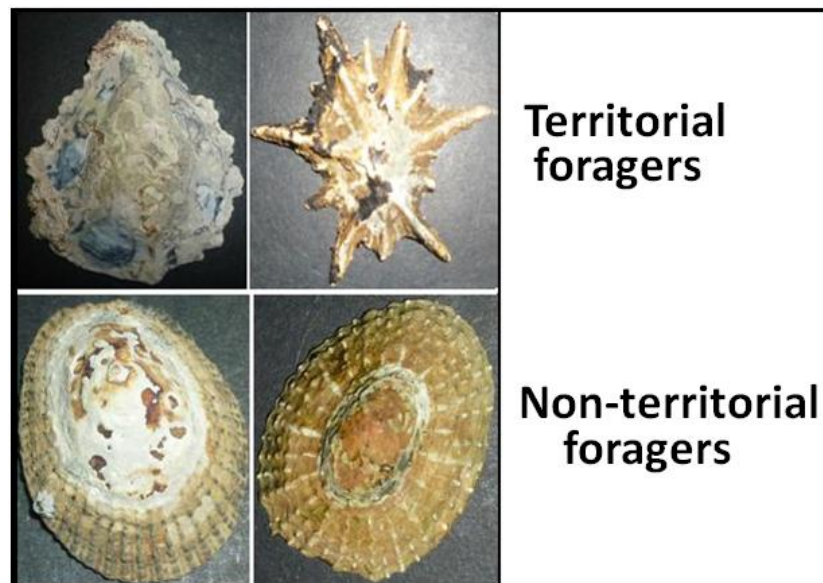
Although both filter feeders and intertidal grazers revealed similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic clusters, there was biogeographic-dependent variation in isotopic ratios between these two types of primary consumers. The intertidal grazers displayed most isotopic enrichment along the south coast and moderate depletion long along the west coast (this study). Contrarily, the filter feeders revealed most isotopic enrichment along the west coast (Hill et al. 2006 and Hill & McQuaid 2008). This suggests that upwelling along the west coast does not affect the stable isotope signatures of the intertidal algae in the same way as for phytoplankton. A plausible explanation for this is that upwelled waters along the west coast result in greater phytoplankton blooms in offshore waters than in inshore waters.

In conclusion, the large-scale biogeographic distribution of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in primary consumers along the southern African coastline is dependent on the type of the feeding mechanism in question (i.e. filter feeders or macro-algal grazers). The biogeographic distribution of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in sympatric patellid limpets is largely determined by primary production within their distributional range and the mixing intensity between the onshore and offshore waters. However, at smaller, local scales, there were significant differences in carbon signatures between territorial and non territorial grazers only along the south coast (sites inshore of the Agulhas Bank or strongly influenced by the Agulhas current). The fact that an effect of territoriality on the stable $\delta^{13}\text{C}$ ratios of limpets was only observed from the sites within the Agulhas current system further indicates the strong influence of mixing between offshore and inshore waters.

The evolution of resource partitioning (territoriality and non-territoriality) in patellid limpets is so ecologically stable that it is reflected in the baseline stable $\delta^{13}\text{C}$ signatures of these limpets, though this was only identified along the south coast. Territoriality does have an influence on the stable isotope signatures of patellid limpets; however this effect is variable not only geographically, but amongst taxa depending on the nutritional composition of their diets.

SYNTHESIS

Evolutionary adaptation of foraging behaviour in sympatric intertidal southern African patellid limpets: deep evolutionary divergence between territorial and non-territorial foragers



SYNTHESIS

This study adopted a multifaceted approach to investigate evolutionary adaptations of foraging behaviour amongst sympatric intertidal southern African patellid limpets at different scales. An integrative approach using genetic and stable isotope data has proved useful in clarifying the factors driving population connectivity and differentiation (Cleggs et al. 2003, Millet et al. 2005, Charles et al. 2006 and Cook et al. 2007). The ecological and evolutionary signals of territoriality were correspondingly detectable at the elemental isotopic level and the molecular diversity level. The partitioning of ecological resources corresponded with different phylogenetic structure between territorial and non-territorial species. At the interspecific phylogeographic level, both territorial and non-territorial grazers displayed similar phylogeographic structure corresponding with recognised biogeographic limits. At the large biogeographic scale, both territorial and non-territorial grazers were characterised by similar demographic history with Pleistocene spatial expansion. At the intraspecific level and within-sites scales, the territorial grazers exhibited significantly greater haplotype diversity than non-territorial grazers. Thus, at the smallest local (within-sites) scale, the genetic structure of these limpets reflects species-specific foraging behaviour.

Territorial and non-territorial grazers displayed significant differences in both genetic diversity and foraging ecology at two different spatial scales. At large, biogeographic scales, both types of grazers revealed similar isotopic and phylogeographic clusters. At the smallest, local scale, territorial grazers were characterized by isotopic enrichment and greater genetic diversity than non-territorial grazers, but this pattern was discovered only along the south coast. The reason for territorial/non-territorial differences being observed in only one biogeographic region is unclear. The most obvious environmental difference among the three coastal regions is that the south coast is less affected by powerful oceanographic currents than the Benguela dominated west coast and the Agulhas dominated east coast, though how this could be linked to differences among limpets with different foraging strategies is not obvious. This east-south enrichment in

isotopic ratios can be attributed to the lack of mixing intensity between onshore and offshore waters as the Agulhas current moves from north-east to southwest (Hill et al. 2008).

The correlations between foraging trait and stable isotope ratios and genealogy of these limpets were only discernible at the smallest, local (within sites) scales. Large scale extrinsic variables (e.g. biogeography, regional upwelling, oceanography and population connectivity) concealed the subtle within-site isotopic and genetic differences between territorial and non-territorial grazers. Genetic analyses of these limpets indicated greatest genetic heterogeneity to be either an adaptive strategy or an evolutionary response linked to territorial foraging. The evolution of territorial foraging corresponds with greater haplotype diversity and extraordinary conchological shape. Contrarily, the evolution of non-territorial foraging corresponds with less haplotype diversity and non-specialised conchological shape. The differences in conchological shape between territorial (more specialised) and non-territorial (less specialised) foragers is probably due to the differences in ecological adaptations to wave exposure between low shore (territorial foragers) and high shore (non-territorial foragers) species. The differences in stable isotope ratios between territorial and non-territorial grazers reflect the foraging behaviour of these limpets.

The observed genetic and isotopic differences between territorial and non-territorial grazers were confounded with genus. For example, *Cymbula* spp. revealed no significant differences in either genetic diversity or stable isotope signatures between territorial and non-territorial grazers. In contrast, the scutellastrid species revealed deep evolutionary and conchological divergence, suggesting the need to recognise this at the generic level. The remarkable anatomical differences in tooth radula between territorial and non-territorial species (Maneveldt et al. 2006) convincingly support the need for generic recognition of these scutellastrid clades. This tooth structure has been used effectively as a morphological character to distinguish taxa at both the species (Ridgway et al. 1998b, 1999, 2000, Nakano & Spencer 2007 and Nakano et al. 2009) and generic levels (Dall 1871, Pilsbry 1891, Koch 1949, Lindberg & McLean 1981 and Simison & Lindberg 1999). Furthermore, the estimated 10% mitochondrial CO1 divergence between the

territorial *Scutellastra A* and the non-territorial *Scutellastra B* clades is consistent with previous estimation of CO1 divergence between recognised clades of patellid limpets (Sá-Pinto et al. 2005, Aranzamendi et al. 2009 and González-Wevar et al. 2010).

Territorial foraging independently evolved twice within the southern African limpets as a result of ecological needs (habitat and algal-diet) during the ice-cold Oligocene climate. The two limpet genera evolved similar, but not identical, resource partitioning strategies based on the habitats and algae available. The Oligocene abundance of intertidal algae (Steneck 1986, Aquirre et al 2000, 2010), coupled with limited rocky shore substratum possibly shaped the evolution of resource specialization (habitat and algal-diet) amongst these sympatric southern African patellid limpets. Thus, the territorial and non-territorial species are distinguishable at the phylogenetic level, molecular index level (CO1 diversity) and even at the baseline stable isotope level. All of these strongly support the taxonomic re-consideration of the scutellastrid species complex into two monophyletic sister genera characterized by their foraging behaviour.

The outcomes of this study yielded novel insights which are crucial in advancing knowledge on the evolution of patellid limpets. Subsequent to their spread into the southern African shoreline from the southern Tethys Sea, these limpets underwent selective evolutionary mutations to partition ecological resources. These selective mutations occurred over many generations whereby the ancestral taxa evolved into a diversity of congeneric territorial and non-territorial species. The evolution of these differences was not only essential in partitioning ecological resources, but taxonomically critical at the phylogenetic level. The integrated and interrelated approaches of this study revealed interesting patterns in stable isotope signatures and genetic diversity of these true limpets associated with their foraging behaviour. The observed patterns presumably result in isotopic enrichment and genetic heterogeneity as consequences of territorial foraging.

This study highlighted the necessity for small within-site (10m scale) or among-site (10s of kilometers) intraspecific genetic studies amongst coastal taxa. The biogeographic limits seem to confound small-scale genetic patterns in most coastal invertebrates and thus, studies focused on small-scale factors or ecological traits would be necessary to unravel cryptic genetic heterogeneity. The present study pinpointed the pivotal role of scale when interpreting empirical ecological and genealogical findings. The stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios and genetic structure of these limpets differ significantly between territorial and non-territorial foragers but this was discernible only in the context of scale. It has similarly been previously established that the interpretation of ecological findings is scale-dependent along a dynamic continuum like the South African shoreline (Nicastro et al. 2008, Mmonwa 2009, Cole & McQuaid 2011, Cole et al. 2012, Teske et al. 2013a and von der Heyden et al. 2013). It is thus, appropriate and important to investigate and compare evolutionary hypotheses at various spatial scales to yield better insight into evolutionary processes and patterns within and amongst species. Exhaustive examination of the small-scale intraspecific genetic variations between opposite sexes and species with different life history strategies can provide insight on such genetic heterogeneity (Teske et al. 2013a and von der Heyden et al. 2013).

The minimally explored small-scale genetic analyses provide stimulating research avenues with the potential to yield novel insights into intraspecific microevolutionary processes and patterns. The application of different ecological approaches to investigate small-scale evolutionary hypotheses can further enhance our understanding of such microevolutionary patterns. As well as providing novel insights into the evolutionary ecology of patellogastropods, this study should highlight the hazards of neglecting scale when investigating ecological and evolutionary hypotheses. The parallel patterns between stable isotope signatures and haplotype diversity in territorial and non-territorial foragers presumably stem from foraging behaviour as an evolutionary adaptation or response to interspecific competition. This study demonstrated the importance of genetic diversity as a crucial adaptive response to cope with limited ecological resources (i.e. space and algal food) in the dynamic intertidal zone.

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APPENDICES

1. Species with non-significant Φ_{ST} indices and lack of phylogeographic structure

A. *Scutellastra argenvillei*

Non-significant Φ_{ST} genetic differentiation

The species was collected from only four sites representing each region of the coast: Haga Haga (east coast), Mossel Bay (South coast), Lamberts Bay and Cape Columbine (west coast).

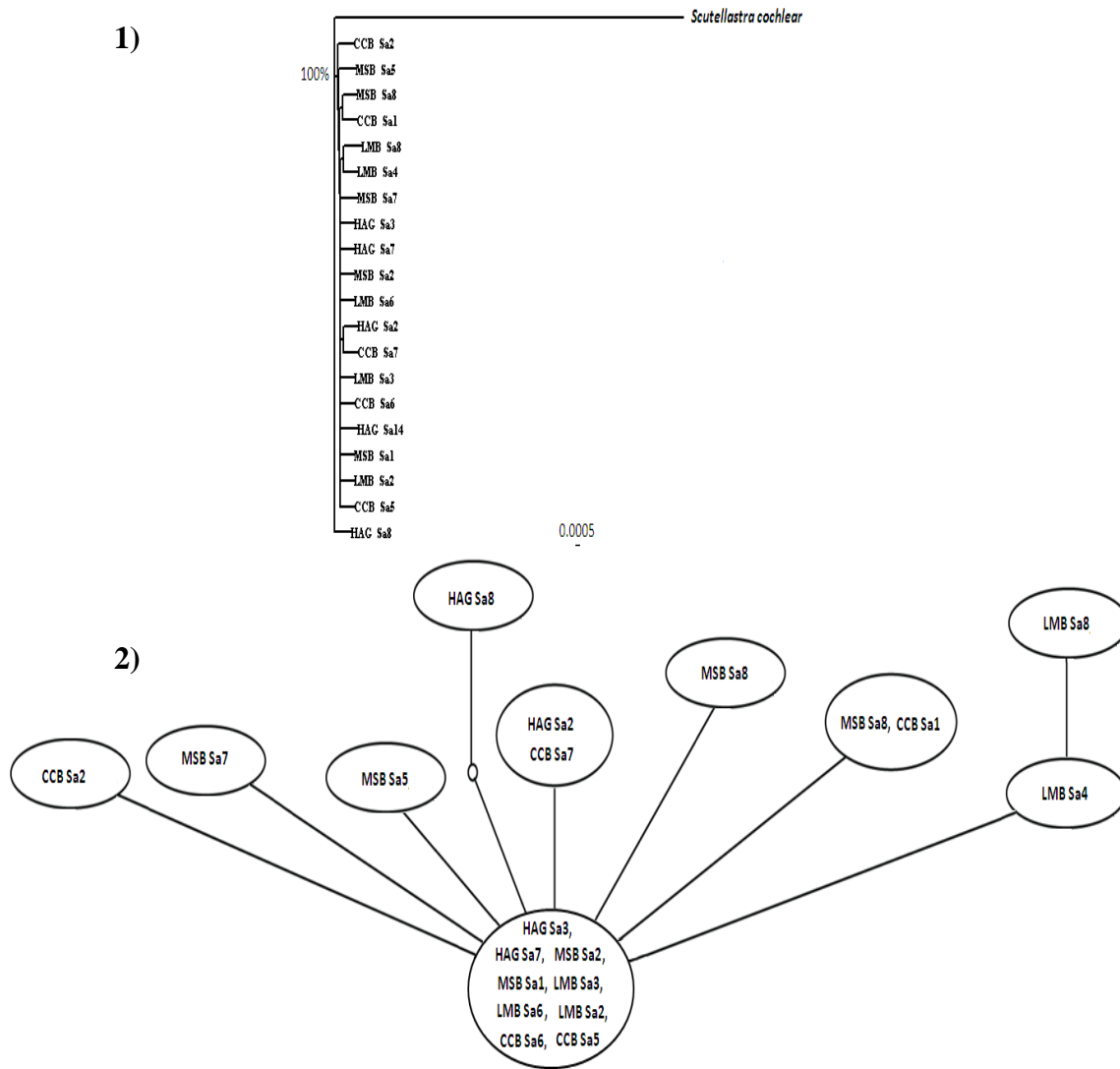
Table A: The results of Φ_{ST} values (lower diagonal) and statistical significance of p values (upper diagonal) amongst populations of the non territorial *Scutellastra argenvillei*.

* = significant at $p < 0.0500$ and ns = not significant.

	Haga Haga	Mossel Bay	Lamberts Bay	Cape Columbine
Haga Haga		ns	ns	ns
Mossel Bay	1.000		ns	ns
Lamberts Bay	1.000	1.000		ns
Cape Columbine	1.000	1.000	1.000	

A. *Scutellastra argenvillei*

No phylogeographic structure



Figures A1 and A2: A1) The CO1 Neighbor Joining tree and A2) haplotype network of the non-territorial *Scutellastra argenvillei*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations: Haga-Haga (HAG), Mossel Bay (MSB), Lamberts Bay (LBM) and Cape Columbine (CCB).

B. *Scutellastra miliaris*

Non-significant Φ_{ST} genetic differentiation

Table B: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) between populations of the non-territorial *Scutellastra miliaris*.

* = significant at $p < 0.0500$ and ns = not significant.

Scutellastra miliaris

	Baia de Bengo	Lobito
Baia de Bengo		ns
Lobito	0.857	

C. *Scutellastra natalensis*

Non-significant Φ_{ST} genetic differentiation

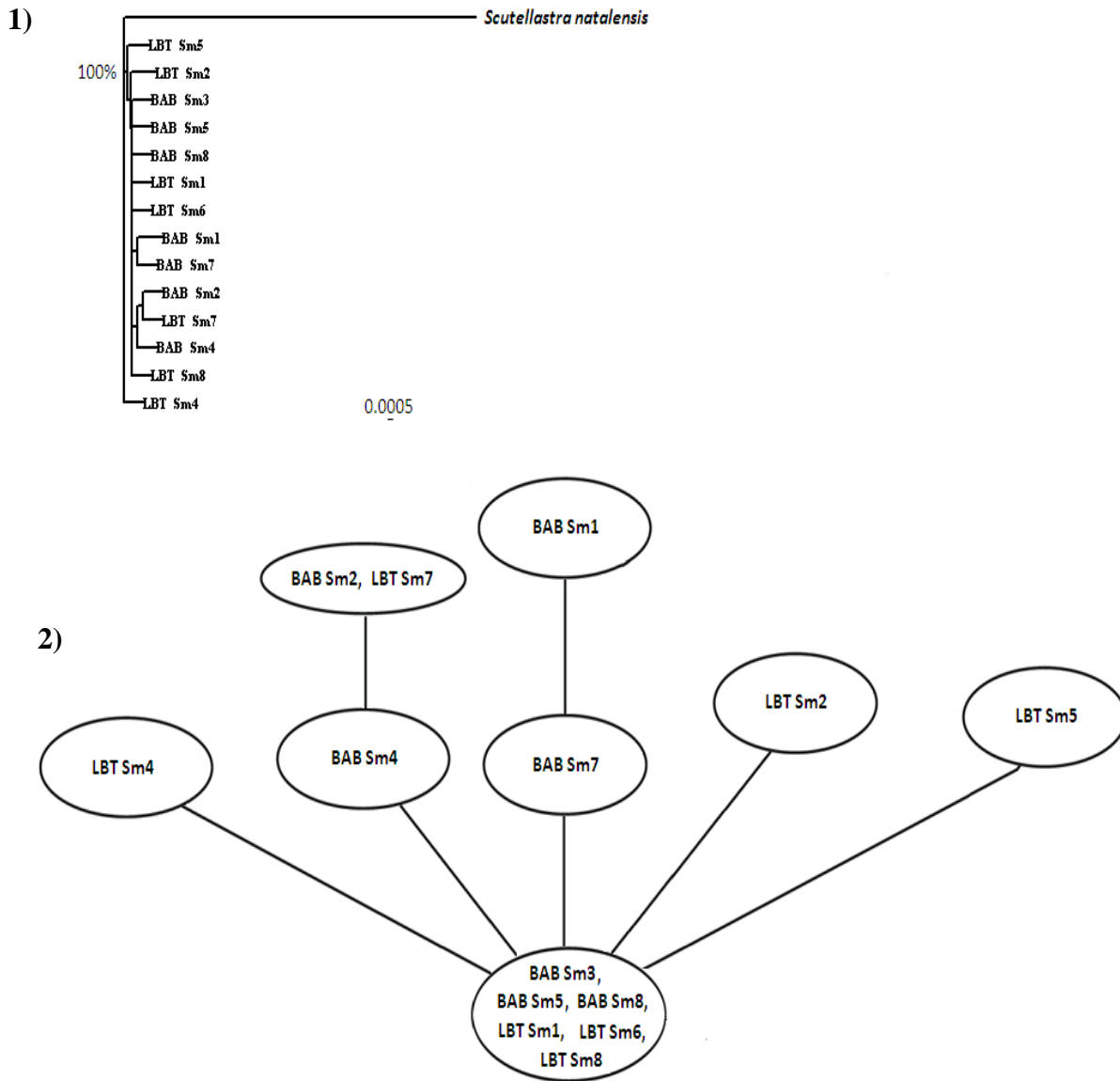
Table C: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) between populations of the non-territorial *Scutellastra natalensis*. * = significant at $p < 0.0500$ and ns = not significant.

Scutellastra natalensis

	Ballito	Port Edward
Ballito		ns
Port Edward	0.991	

B. *Scutellastra miliaris*

No phylogeographic structure

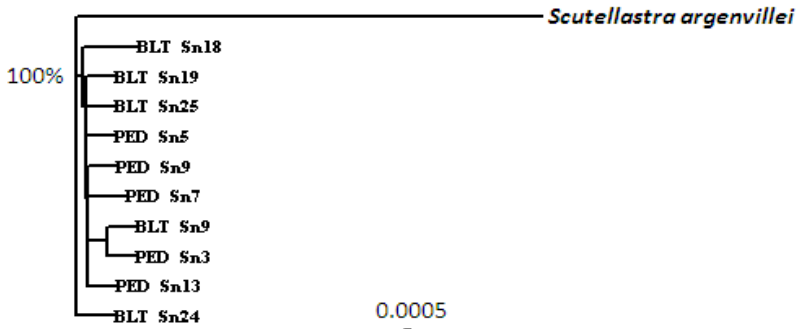


Figures B1 and B2: B1) The COI Neighbor Joining tree and **B2)** haplotype network of the non-territorial *Scutellastra miliaris*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations: Baia de Bengo (BAB) and Lobito (LBT).

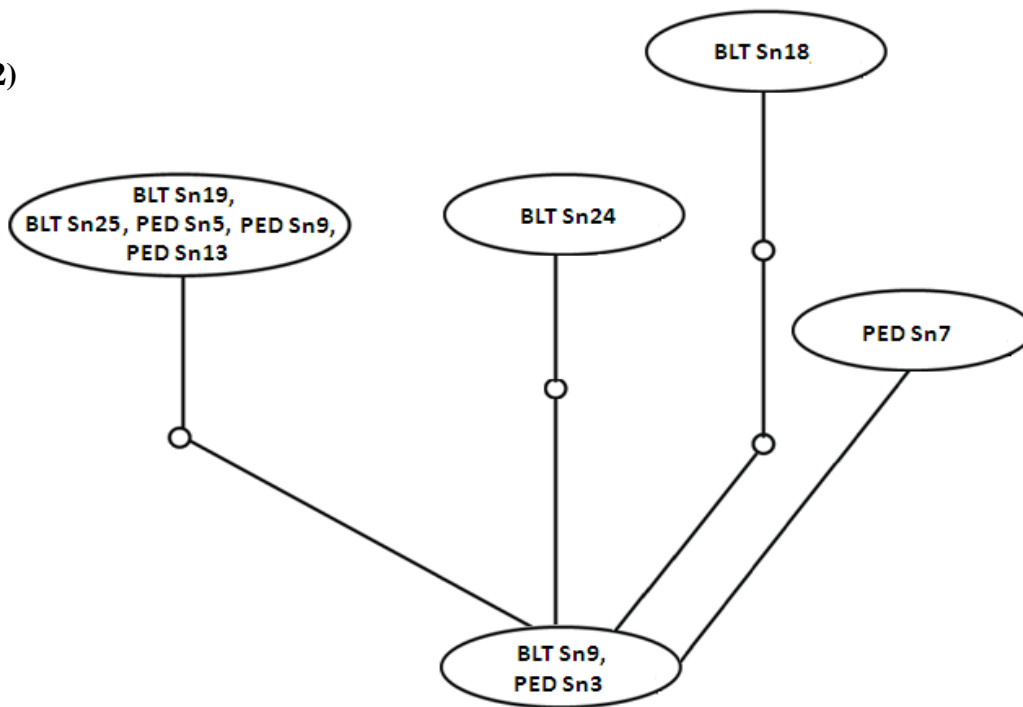
C. *Scutellastra natalensis*

No phylogeographic structure

1)



2)



Figures C1 and C2: C1) The CO1 Neighbor Joining tree and C2) haplotype network of the non-territorial *Scutellastra natalensis*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations: Balito (BLT Sn9) and PED (PED Sn3).

D. *Cymbula compressa*

Non-significant Φ_{ST} genetic differentiation

Table D: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) amongst populations of the non-territorial *Cymbula compressa*.

* = significant at $p < 0.0500$ and ns = not significant.

	Camps Bay	Paternoster	Doring Bay	Groenriviermond
Camps Bay		ns	ns	ns
Paternoster	1.00		ns	ns
Doring Bay	1.00	1.00		ns
Groenriviermond	1.00	1.00	1.00	

E. *Cymbula miniata*

Non-significant Φ_{ST} genetic differentiation

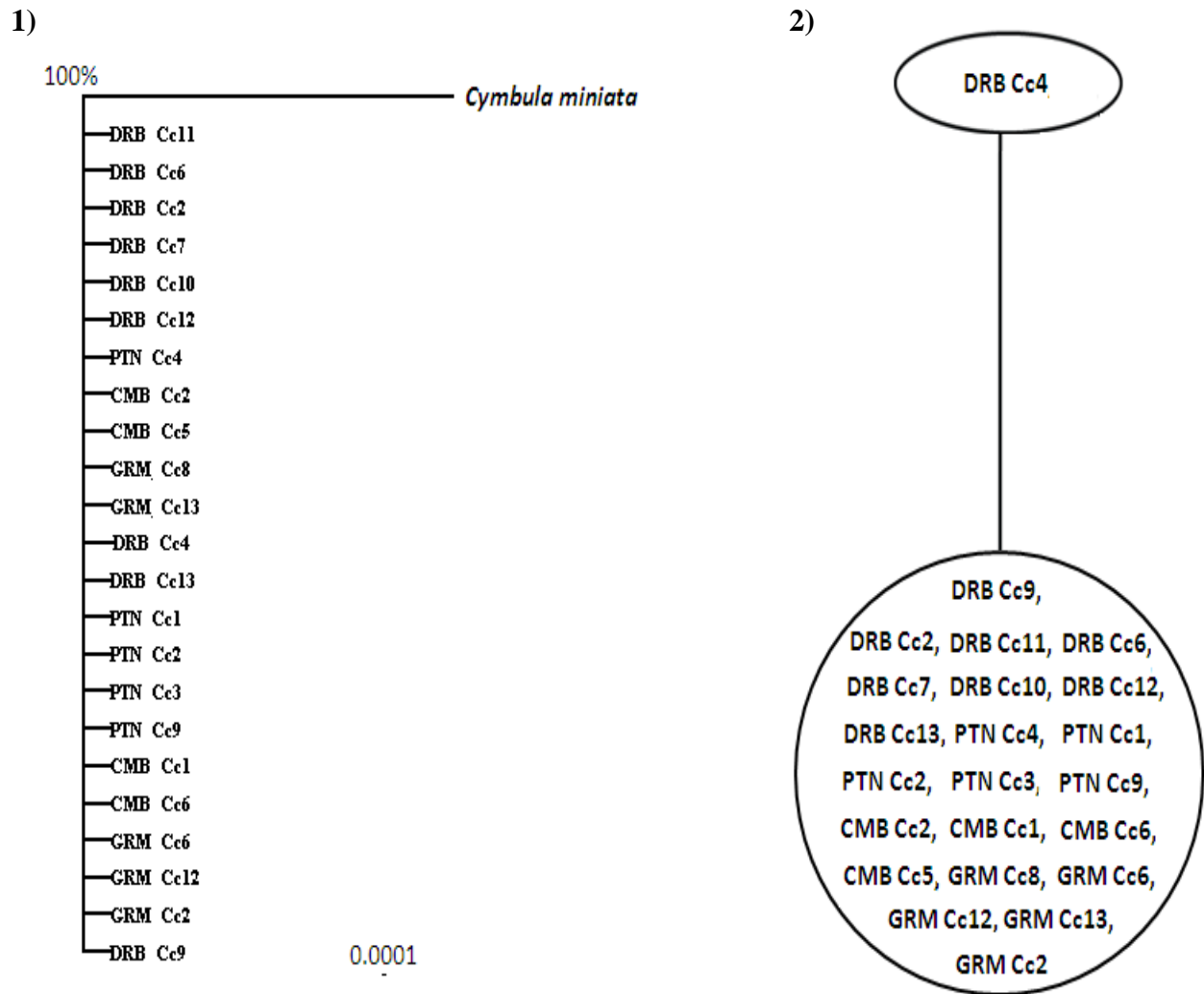
Table E: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) amongst populations of the non-territorial *Cymbula miniata*.

* = significant at $p < 0.0500$ and ns = not significant.

	Lamberts Bay	Mossel Bay	Haga Haga	Port St. Johns
Lamberts Bay		ns	ns	ns
Mossel Bay	0.736		ns	ns
Haga Haga	0.736	0.709		ns
Port St. Johns	0.736	0.545	1.00	

D. *Cymbula compressa*

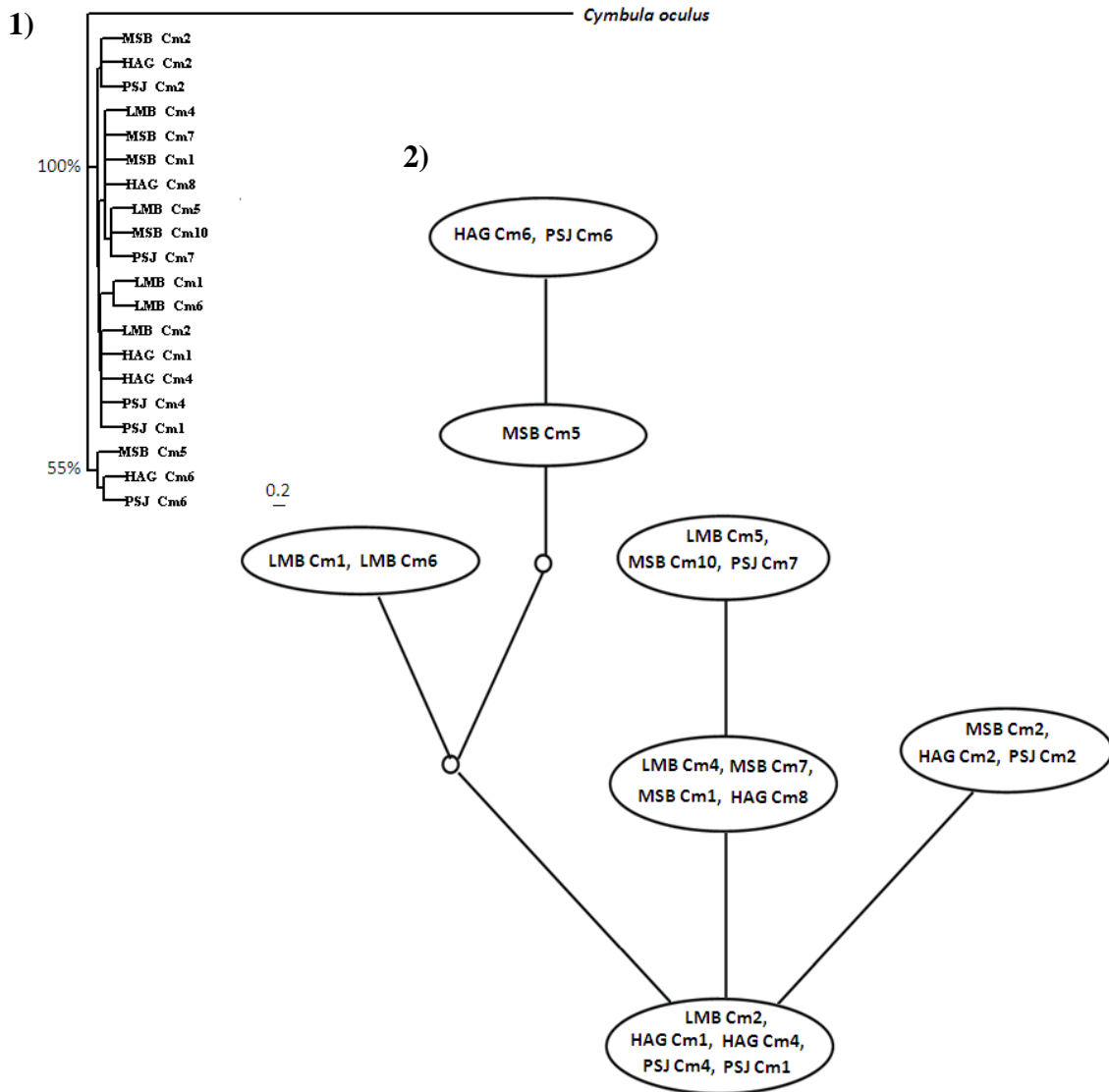
No phylogeographic structure



Figures D1 and D2: D1) The CO1 Neighbor Joining tree and D2) haplotype network of the territorial *Cymbula compressa*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations: Camps Bay (CMB), Paternoster (PTN), Doring Bay (DRB) and Groenriviermond (GRM).

E. *Cymbula miniata*

No phylogeographic structure



Figures E1 and E1: E1) The CO1 Neighbor Joining tree and E2) haplotype network of the non-territorial *Cymbula miniata*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations: Port St. Johns (PSJ), Haga Haga (HAG), Mossel Bay (MSB) and Lamberts Bay (LMB).

F. *Cymbula granatina*

Non-significant Φ_{ST} genetic differentiation

Table F: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) amongst populations of the non-territorial *Cymbula granatina*.

* = significant at $p < 0.0500$ and ns = not significant.

	Camps Bay	Paternoster	Doring Bay	Groenriviermond
Camps Bay		ns	ns	ns
Paternoster	0.227		ns	ns
Doring Bay	0.390	0.345		ns
Groenriviermond	0.900	0.573	1.00	

G. *Cymbula oculus*

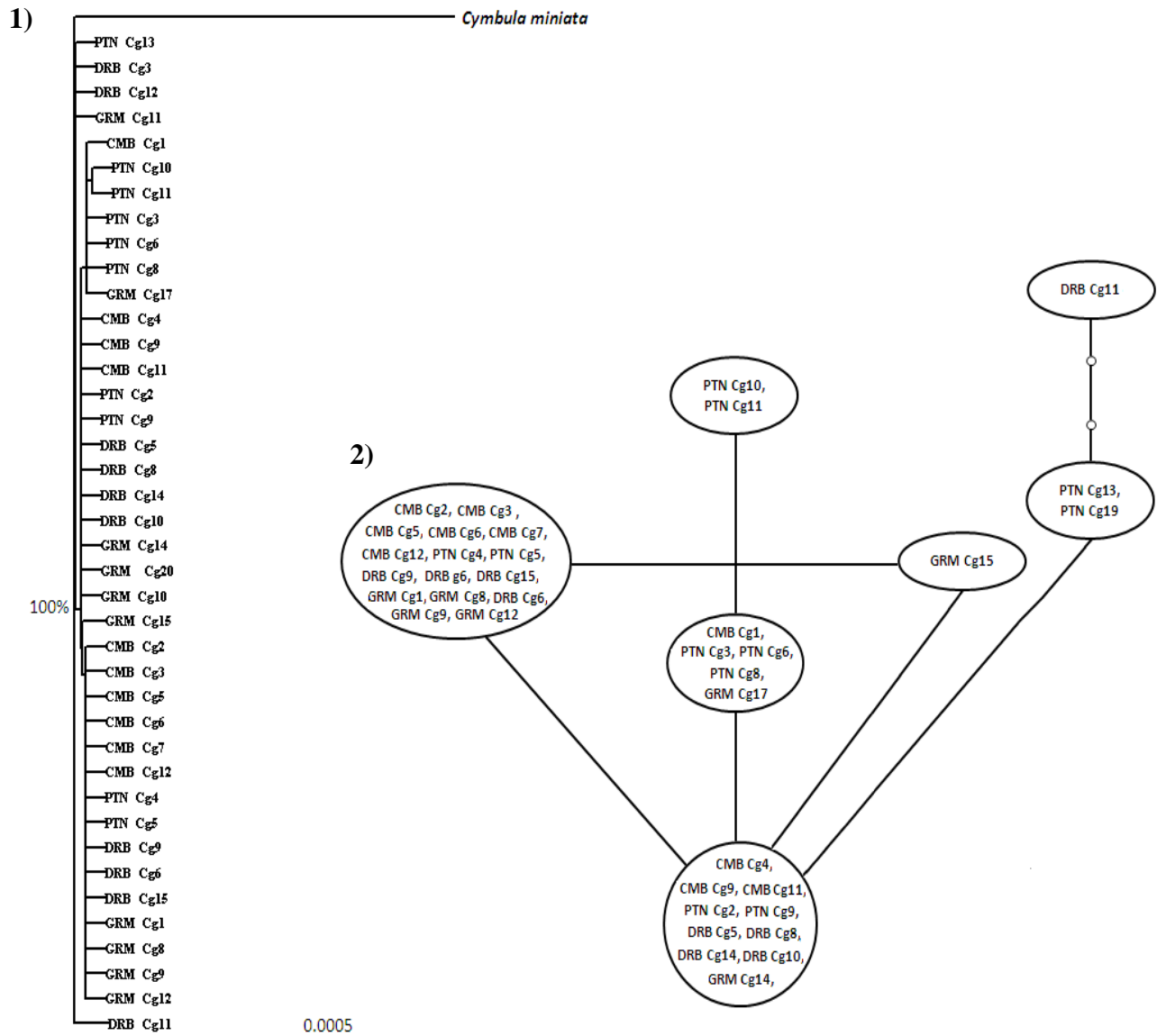
Table G: The results of Φ_{ST} values (lower diagonal) and statistical significance of population differentiation (upper diagonal) amongst populations of the non-territorial *Cymbula oculus*.

* = significant at $p < 0.0500$ and ns = not significant.

	KOS	SDB	TSK	MSB	CPA	MZB	CMB
Kenton-on-Sea (KOS)		ns	ns	*	ns	ns	ns
Sardinia Bay (SDB)	0.318		ns	ns	ns	ns	ns
Tsitsikamma (TSK)	0.600	1.000		ns	ns	ns	ns
Mossel Bay (MSB)	0.045	0.181	0.145		ns	ns	ns
Cape Agulhas (CPA)	0.300	0.691	0.463	0.518		ns	ns
Muizenberg (MZB)	0.672	1.000	1.000	0.082	0.736		ns
Camps Bay (CMB)	0.409	1.000	1.000	0.301	1.000	1.000	

F. *Cymbula granatina*

No phylogeographic structure

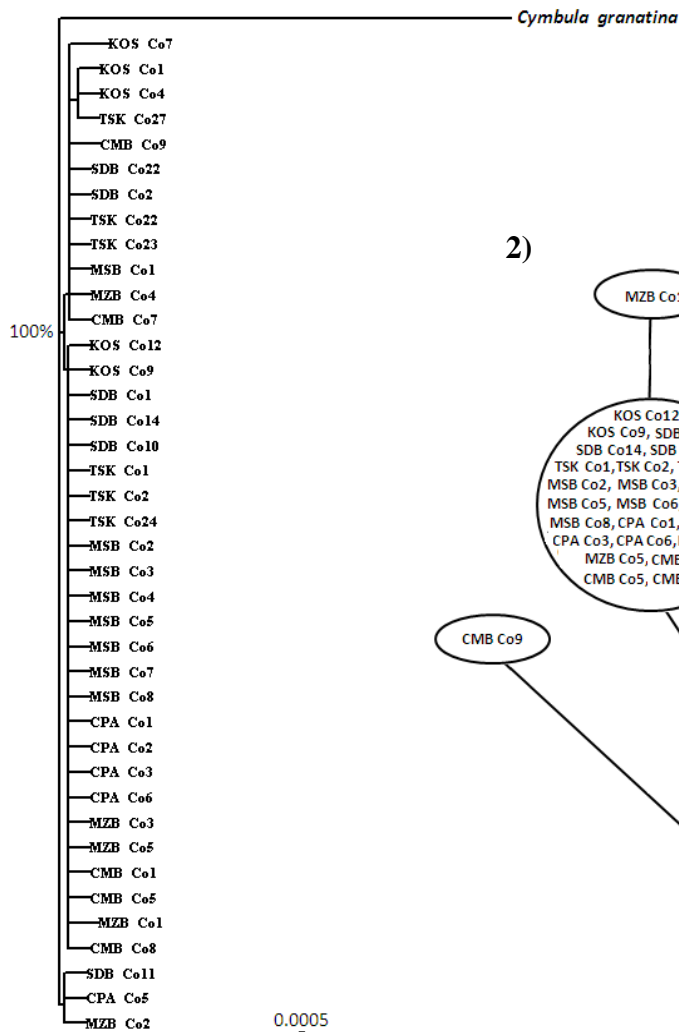


Figures F1 and F2: F1) The CO1 Neighbor Joining tree and F2) haplotype network of the non-territorial *Cymbula granatina*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotypes names are site abbreviation followed by sample number. Sites abbreviations: Camps Bay (CMB), Paternoster (PTN), Doring Bay (DRB), and Groenriviermond (GRM).

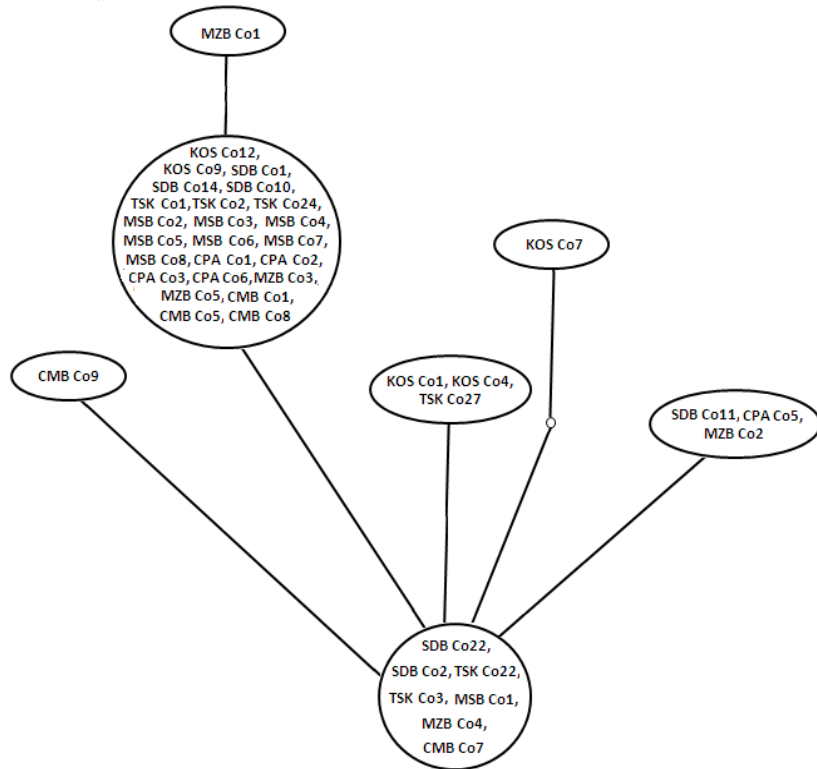
G. *Cymbula oculus*

No phylogeographic structure

1)



2)



Figures G1 and G2: G1) The CO1 Neighbor Joining tree and G2) haplotype network of the non-territorial *Cymbula oculus*. Open circles indicate mutations and samples are represented as site abbreviation followed by specimen number. Haplotype names are site abbreviation followed by sample number. Sites abbreviations: Kenton-on-Sea (KOS), Sardinia Bay (SDB), Tsitsikamma (TSK), Mossel Bay (MSB), Cape Agulhas (CPA), Muizenberg (MZB) and Camps Bay (CMB).

2. Concatenated data set alignment (12S rRNA, 16S rRNA and CO1)

62 Taxa, 1507 characters

BAB Sm8

TGCCAGGGCACTACGAACGCATGTTTAAAACCCAAAGGACTTGCCGGTGCTATAATCCAACCTAGGGGAAGCTGTCCCTTAATTCGATAACCCACGAAAATCTTAC
 TTGCCCTAG-----TAATCAG-CTTGATACCGTCGTCT-----AGCCGGCCTTAGCGAGGGGATAAAGCTGGC-AAGAGAGG-----
 TCTTCCCTAGAAAAGACAGATAAAGGTGCAGCTAATGGGTAAAGGGA-AGGATGTGTACAATTGATAATTTGCT---AGTGAATCTTA-ATGAAAA---TTGAG-
 AGGAAAGAGGACTTAGAAGTAATCTT-----ACAATCAAAAACATGGCTCTTTGT-AC-A-TAAAAGATAGGGAGTCTGGCCTGCTCAATGATGAT----
 -----TTTCATTAATAGCCGCAGTATCTGACTGCGTG-----AAAGTAGCATAATAATTTGCCTTTAATTTGGTGGCTGGTATG-
 AATGGTACT-----
 ATGAGGGTGAAGCTGTCTAGCATATTCTTTGAAGTTACCTATTAGGTGAAAAGGCCTAAATAGTTTTATAAGACAAGAAGACCCTGTCAAGCTTT-----
 ATAGCGG-GCAGGAGGT-TTAAA-ATCCTGTTTTGG-----TATTTGATTGGGGCAATCGGGGAGCAAGAAGAA-TCTCCCTTTTTTTCCTT-CC-
 TTCTAGGAATGACCCG-----
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 TTCAAAGTGAACGAGTCCCTTTTGTGTGGTCAAGTAAATCACTGCTATCTTACTCCTTTCTCTCTGCTGCTAGCCGGAGCCATTACTATGCTATTATG
 CGACCGTAACCTTAATACGTCCTTTTTGACCCAAGAGGTGGTGGTACCCTGTCTGTACCAGCACCTGTT-----

BLT Sn9

TGCCAGGGTAGTACGAATGCATGTTTAAAACCCAAAGGACTTGCCGGTGCTATAATCCAACCTAGGGGAAGCTGTCCCTTAATTCGATAACCCACGAAAATCTTAC
 TTATCCTAG-----TAATCAG-CTTGATACCGTCGTCT-----AGCCGGCCTTAGCGAGGGAGAAAAAGCTGGC-AAAAAAGG-----
 TCTTCTAGAAAAGACAGATAAAGGTGCAGCTAATGGGTAAAGGGA-AGGATGTGTACAATTAATAATTTGCT---AGTGAATCTTA-ATGAAAA---TT-----
 -----AGGAGGAAAAGAGGACTTAGAAGTAATCTTTACATTCAAAAACATGGCTCTTTGT--G-----
 TGTAAGAAGATAAAGGAGTCTGGCCTGCTCAATGATGATTTTTCATTAATAAGCCGCGTATTCTGACCCGCTG-----
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CCB Sa7

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CCB Sb2

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CMB Co8

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CMB Sc9

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CPA Sc9

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CPA Sg1

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CPA Sl10

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DRB Cc5

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GRM Cc11

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GRM Cc14

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GRM Cc6

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GRM Cg11

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GRM Cg7

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GRM Cm5

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GRM Sa2

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GRM Sb1

TGCCAGGGTACTACGAATACATATTTAAAACCTCAAAGGACTTGGCGGTGCTATAATCTAACTAGGGGAACCTGTTCTTAATTCGATGACCCACGAGAATCTTAC
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GRM Sc6

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GRM Sg9

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HAG Cm1

TGCCAGGGTACTACGAATACATATTTAAAACCAAAGGACTTGGCGGTGCTATAATCCAAGTGGGAACTGTCCCTGATTGCGATAATCCACGAAAACTTTAC
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HAG Sa1

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HAG Si9

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KOS Co7

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KOS Sa2

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KOS Sc2

TGCCAGGGTACTACGAACACATGTTTAAAACCCAAAGGAATTGGCGGTACTATAATCCAAGTGGGAACTTGTCCCTAATTTCGATAACCCACGAAAATCTTAC
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KOS Sc4

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KOS Sg4

TGCCAGGGTACTACGAACGCATGTTTAAAACCCAAAGGACTTGGCGGTGCTATAATCCAAGTGGGAACTTGTCCCTAATTGATTACCCACGAAAATCTTAC
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KOS Sl6

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LBT Sm2

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LBT Sm7

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LMB Cm1

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LMB Sa6

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LMB Sb3

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MSB Cm1

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MSB Co14

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 TTTTCCCTAATAAGACAGATAAAGGTGTAGCCAATAGGTAAAGGGA-AGGATGTGTTACAATTAATAATTTGAT---AATGGAATCTA-ATGAAA-----
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 AAAAAAGGGAGTCTGGCCTGCTCAGTGATGAGATTTTCAATAATAGCCGAGTATCCTGACTGCGTG-----
 AAAGTAGCATAATAATTTGCCTTTAATTGGTGGCTGGTATC-AACGGTA-----
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 AGGTA-AAAACAAGTT-----AAAGTCTTTATTTTATTTTGTGTTGATTGGGGCAATCGGGGAGTAAGAAAA-----
 TCTCCTCATTGATCTTGCCTGTCAAGGCATGACCCACTATTA-----

GTGATCATGGGAAGATTACTGCAGGATAACAGCGTAATTTTTTTGTGAGTCTTATTTAAAAAAGTTTGGCAGCTCGATGTTGGATTAGGGTATCCTGA
 AGGTGCAGAAGCTTTCAAGGGTTGGTTTGTCAACCATAAAACCAACTTTATATATTTTAGGGATGTGATCTGGTTTAGTTGGAACAGGTTAAGTATACT
 GATTCGAGCAGAGTAGGCCAACCCGGATCTCTTTAGGGGACGACCAGTTATATAATGTAATTGTAACAGCCCATGCTTTTCGTCATAATCTTTTTTATGTTATA
 CCCATGATAAATCGTGGATTGGTAATGACTAGTCCCCCTTATACTAGGAGCCCCAGATATAGCTTTCCCCGATTAAATAACATAAGATTCTGACTCCTACCAC
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MSB Co15

TGCCGGGGCACTACGAACACATGTTTAAACCCAAAGGACTTGGCGGTGCTATAATCCAACCTAGGGGAACCTGTCCCTAATTGATAACCCACGAAAATCTTAC
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 TTTTCCCTAATAAGACAGATAAAGGTGTAGCCAATAGGTAAAGGGA-AGGATGTGTTACAATTAATAATTTGAT---AATGGAATCTA-ATGAAA-----
 -----TTTTAGGAGAAAGAGGACTTAGAAGTAATCTTGTAGTTCAAAAACATGGCTCCCTGTCTT-TT-----
 AAAAAAGGGAGTCTGGCCTGCTCAGTGATGAGATTTTCAATAATAGCCGAGTATCCTGACTGCGTG-----
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MSB Sa2

TGCCAGGGTACTACGAACGCATGTTTAAAACCCAAAGGACTTGGCGGTGCTGTAATCCAAGTGGGAACTTGTCCCTAATTCGATGACCCACGAAAAATCTTAC
TTACCTTAGC-----A-ATCAG-CTTATATACCGTCGTCT-----AGCCGGCCTTAGCGAGGAAAAAAGCTGGC-AAAAAAG-----
TTTTCCCTAGGAAGACAGATAAAGGTGCAGCTAATGGGTAAGGGA-----AGGATGTGTTACAATTAATAATTTGTTCAAGTGAATCTTA-
ATGAAA-----TTTAGGAGGAAAGAGGACTTAGAAGTAATTCTTATAATTCAAAAACATGGCTCTCTGT-A-----
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AAAGTAGCATAAATAATTTGCCTTTAATTGGTGGCTGGTATC-AATGGTATT-----
ATGAGGGTGAAGCTGTCTTTCGCTATTCTTTGAAGTTACCTATTAGGTGAAAAGGCCTAAATGGTTTTATAAGACAAGAAGACCCTGTCAAGCTTT-----
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TTCTAGGAATGACCCG-----
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CAACTAGAGCGGGTCCACTCTTTGTATGATCAGTAAAAATTACCGTATCTTACTACTTCTTCTACCCGCTCCTAGCTGGAGCCATTACTATGTATTATGCGA
CCGTAACCTTAATACGTCCTTTTTGACCAAGAGGAGGTGGGGACCCTGTCTTATACGACACTTATT-----

MSB Sb4

TGCCAGGGTACTACGAATACATATTTAAAACCCAAAGGACTTGGCGGTGCTATAATCTAAGTGGGAACTGTTCTTAATTCGATGACCCACGAGAATCTTAC
CTATTTTAG-----T-TTATCAGATTTATATACCGTCGTT-AA-----CTAACCTC-----
TTAAGAGTAAAAAGTTAGTAAGAAAAGGCCACTTTCTAATAAAAACAGATAAAGGTGTAGCTAATAAATAAGGGGAAGAAATGTTTACAATTAATAACTTGT
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ACA-AAG---TT-AAGA-TTAT-CTAATATATT-T-----TGTTTGGTTGGGGCAACCGGGGGCAAATAAAA-
TCCCTCCTTCTATTTCCCTTTCTAGGAACGACCCG-----ATTA-----
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MSB Sc22

TGCCAGGGTACTACGAACACATGTTTAAAACCCAAAGGAATTGGCGGTACTATAATCCAAGTGGGAACTGTTCTTAATTCGATAACCCACGAAAAATCTTAC
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AAAAAAGGTTTTTCCCTAATAAAAACAGATAAAGGTGTAGCCAACGAGTGA-GGG-----AGAATTTGTTACAATTAACAATTTGTT-AATGGA-
CCAAAAATGAAA-TTTTTTGGGA-----GAAAGAGGACTTAGAAGTAATTTTTTAAATTCAAAAACATGGCTCTCTGTGTT-----
AAAGAGATAGGGAGTCTCGCTGCTCAATGATG-T-TCTCATTAAATAGCCGAGTATCCTGACTGCGTG-----
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TGCTTTCTAGGGATGATCCG-ATTA-
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MSB Si3

TGCCAGGGTACTACGAACACATGTTTAAAACCCAAAGGAATTGGCGGTACTATAATCCAAGTGGGGAACCTGTCCCTAATTCGATAACCCACGAAAATCTTAC
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 CCAAAAATGAAA--TTTTTTGGG-----GAAAGAGGACTTAGAAGTAAATTTTAAATCAAAAACATGGCTCTGTGTCT-----
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 TACCTTTCTAGGGATGATCCGC-ATTA-
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PED Co1

TGCCGGGCACTACGAACACATGTTTAAAACCCAAAGGACTTGGCGGTGCTATAATCCAAGTGGGGAACCTGTCCCTAATTCGATAACCCACGAAAATCTTAC
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PKR Sn7

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PSJ Hc1

TGCCAGGGTACTACGAATACATGTTTAAAACCCAAAGGACTGGCGGTGCTATAATCCAAGTGGGGAACCTGTCCCTAATTCGATAACCCACGAAAATCTTAC
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TGATCCCTAACAGACAGATAAAGGTGTAGCCGATGGATAAAGGGA-AGGATGTGTACAATTAATAAATCGAT--ATTGGAACCTTA-ATGAAA-----
 -----GTTTAGGGGGAAAGAGGACTTAGAAGTAATCCCCTAGTTCAAAAACATGGCTCCCTGTGT-----
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 AAAGTAGCATAAATAATTTGCCTTTAATTGGTGGCTGGTATC-AACGGTA-----
 TGATGAGAGTGGGGCTGTCTCATGTATTTTCTTGAATTACCTATTAGGTGAAAAGGCTAAATAATTTTATAAGACAAGAAGACCCTGTCAAGCTTTACAGC
 GGG-TGGAAGCA-----GATGATAACTATTTAATCTGACTTTGTTGTTGATTGGGGCAATCGGGGTCAAAAAAAA-TCTCCCC-----
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PSJ Hc2

TGCCAGGGTACTACGAATACATGTTTAAACCCAAAGGACTGGGCGGTGCTATAATCCAAGTGGGAACTGTCCTTAATTCGATAACCCACGAAAATCTTAC
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PSJ Sb4

TGCCAGGGTACTACGAATACATATTTAAACTCAAAGGACTGGGCGGTGCTATAATCTAACTAGGGGAACTGTCCTTAATTCGATGACCCACGAGAATCTTAC
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 AATGGACTC-AAGATGAAA-----TTTCTTGAAGAAAAGAGGACTTAGAAGTAATTTCTTTAATTCAAAAACATGGCTCTCTGTGGT-----
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 TTCCCTTACCAGGGACGACCCGC-----ATTA-----
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PSJ Sb5

TGCCAGGGTACTACGAATACATATTTAAACTCAAAGGACTGGGCGGTGCTATAATCTAACTAGGGGAACTGTCCTTAATTCGATGACCCACGAGAATCTTAC
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 AATGGACTC-AAGATGAAA-----TTTCTTGAAGAAAAGAGGACTTAGAAGTAATTTCTTTAATTCAAAAACATGGCTCTCTGTGGT-----
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PSJ Sn13

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TTCTAGGAATGACCCG-----
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PTN Cg11

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PTN Cg3 PTN Cg6

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Patella aspera

TGCCAGGGTACTACGAACACATGTTTGAAGTCAAAGAAGCTTGGCGGTGCTTTAAGCCAGCTAGGGGAACCTGTCCTTTAATTCGATAGTCCACGAAAATCTTAC
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Patella depressa

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Patella vulgata

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SDB Cm1

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SDB Sb5

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TSK Co1

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TSK Sc1

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TSK Sg5

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 CTAAGGCGATCTGGGGAAAAAGTTACTGCAGGGATAACAGCGTAATTTCTCTGTGAGTCTTATTTAAGAGAAAGTTTGCACCTCGATGTTGGATTAGGGTA
 TCCTGAAGGTGCAGAAGCTTTCAAGGGTTGGTTTGTCAACCATTAAAACCAACCTTATATATTATTTAGGTATGTGGTCTGGTCTAGTTGGAAACCGGCTTAAAG
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TSK S12

TGCCAGGGTACTACGAACACATGTTTAAAACCAAAGGAATTGGCGGTACTATAATCCAAGTGGGAACTGTTCTTAATTCGATAACCCACGAAAAATCTTAC
 TCACTCTAGC---T---AATCAG-CTTATATACCGTCTGTT-----AGCTAACCTTT-CTAGAGAAAAGAAAGTTAGC-AAAAAAGG-----
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 AAAAA---T-AAAA-TTTATTTT-ATGTCTT-T-----GTTTGGTTGGGGCAACCCGGGGGCACATAAAA-TCCCTCCTTTTTTCC-
 TACCTTTCTAGGGATGATCCGC-ATTA-
 GCGATCTAAGGAAAAAGCTACTGCAGGGATAACAGCGTAATTTCTTTGTGAGTCTTATTTTAAAGAAAGTTTGCACCTCGATGTTGGATTAGGGTATCCTGA
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END;

3. APTSβ alignment

90 Taxa, 1507 characters

>PSJ Sb4

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 AAATGGCCAAATATTTCCCATATGAAGTATGTTGAAAGCTAAAGCAT-GCTTTAATAGGGAAC-----TCCC GTT-TTGATCCCAA-CATAAACTAA-
 ATGTTTTGCTCC--C--G-TTTGAA-GTTTCTACCATCATATAAG
 AAATAACAAAATCAGCAGACTCT-----

>PSJ Sb5 SDB Sb5

CTAAGCTAG-GT-----
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 ATGTTTTGCTCC--C--G-TTTGAA-GTTTCTAC-ATCATATAAG
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>MSB Sb4

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>LMB Sb3

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 CCCGCTGGCCGAAATGT-ATTGGGCCATATAAG----
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>CCB Sb2 GRM Sb1

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 CCCGCTGGCCGAAATGT-ATTGGGCCATATAAG----
 GGCTAACAAAATCAGCAGTTTCT-----

>MSB Sa2

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 TATTTGGAGAA--T--GATCTCCA-CTCGCCTG-A---TGTTGAAATGGCAAAGATTTTCTAACAT-----

>HAG Sa1 KOS Sa2 CCB Sa7 LMB Sa6 GRM Sa2

CTAAGCTAG-GT-TGATGAAACCT-CAAAGGGA-TTGTTAACTG--GGAACCT-CCTGGATTCTTCTCTT-----GCACCCAGTGT-GATGATTTTAGATAAGT-G-
 AACCT-GT-CGTGTCTGGACAGCGTGTA-----ACTAAATTTAACTATTCTAAATCATACTAAATGCTTGCTTGGCTTAACTAA-TATT-
 TATTTGGAGAA--T--GATCTCCA-CTCGCCTG-A---TGTTGAAATGGCAAAGATTTTCTAACAT-----

>HAG Sa7

CTAAGCTAG-GT-TGATGAAACCT-CAAAGGGA-TGTTTAACTGG-GCAACT-CCTGGATTCTTCTCTT-----GCACCCAGTGTGATGATTTTAGATAAGT-G-
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 TATTTGGAGAA--T--GATCTCCA-CTCGCCTG-A---TGTTGAAATGGCAAAGATTTTCTAACAT-----

>SDB Sa6

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>KOS Sc2

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TTAACTGGAACTCC-ATTCTGATCCAACACAAAATAAT-TATTTTGCACCC-C----AATCGGAA-GTT-
 TCTACAATCATGTTAAAATGGCAAATATTTCCAATAT-----
>KOS Sc4
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>TSK Sc1
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>MSB Sc22
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>CMB Sc9
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>CPA Sc9
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>GRM Sc6
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 TCTACAATCATGTTAAAATGGCAAATATTTCCAATAT-----

>CPA Sc6
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>CPA Sc13
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>TSK Sl2
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 CAGTAAGGAGTATTATAAACCTAAGGAACGCTTAACTGGAACTCCTGTTTTGATCCAACACAAAATAA-ATATTTTACTCCC-CT--CTTTGAA-GTTTTTAC-
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>KOS Sl6
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>HAG S19

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 AATGTTTCCAATAAGGAGTATTA-----

>MSB S13

CCTCTGAAG-GTATG-----
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 GGGCCCGTGCCCGA-GAAATCTAAGGAACGCTTAACTGGAACTCC-ATTCTGATCTAACACAAAATAAT-TATTTTCCACCC-CA--ATCGGAA-
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>CMB S11 CPA S10 SDB S14

CCTCTGAAG-GTATG-----
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 AAT-TGGTAA-----
 GAAGTTTCCAATGTGGAATATTT-----

>CPA Sg1

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 GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG--TATTTTGCCCC-CA-GTTTTACA-CAAGTT-
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>GRM Sg9

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-A-TTCC-----
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 GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG--TATTTACTCCCC-CA-CTTTTCTA-CAAGTT-
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>TSK Sg5 DRB Sg4

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-A-TGCC-----
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>CPA Sg9

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 GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACATAAAAA-TCAG--TATTTTGCCCC-CA-GTTTTACA-CAAGTT-
 GAATTGGC-AGAGAT-TCCCATATGAAATAAATGG-----

>MSB Sg7

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-A-TGCC-----
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>CMB Sg13

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 GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG--TATTTTGCCCC--ACGTTTTACA-CAAGTT-
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>DRB Sg2 CMB Sg1

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-A-TGCC-----
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 GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG--TATTTTGCCCC--ACGTTTTACA-CAAGTT-
 GAATTGGC-AGAGAT-TCCCATATGAAATAAATGG-----

>SDB Sg3 MSB Sg1 HAG Sg11

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-A-TGTC-----
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GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG--TATTTTGCCCC-CA-GTTTTACA-CAAGTT-GAATTGGC-AGAGAT-TCCCATATGAAATAAATGG-----

>KOS Sg4 SDB Sg10 MSB Sg10

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-A-TGCC-----
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GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG-- TATTTTGCCCC-CA-GTTTTACA-CAAGTT-GAATTGGC-AGAGAT-TCCCATATGAAATAAATGG-----

>LBT Sm2

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAA-ATGGCC-----
TTTTAGAGCCAAACACATAAGTAAACATTTTGCAACCCAGTTTGAAGTTTCTAC-ACCAT-----
GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG-- TATTTTGCCCC--ACGTTTTACA-CAAGTT-GAATTGGC-AGAGAT-TCCCATATGAAATAAATGG-----

>BAB Sm8

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAAA—TGCC-----
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>FMG Sm1

AAAGTCATCAGCTTGA-CTGA-CG--AAACCTCAAAGGTATGCTTAACTGGAAA—TGCC-----
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GTTGAAAGAGTAAACTTTCCTATGATGAAACCTCTTGGGTATGCTGAACTGG-AAATGCCAAACACAAAA-TCAG-- TATTTTGCCCC--ACGTTTTACA-CAAGTT-GAATTGGC-AGAGAT-TCCCATATGAAATAAATGG-----

>LBT Sm7

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>BAB Sm1

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>BAB Sm5

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>BLT Sn9

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>PKR Sn7 PSJ Sn13

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>PED Sn1

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>HAG Cm1

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 GACAATAGATATCTAAAGCTAATTT-TATTTTCGATT-C--AGGTATCTCT-----GGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>SDB Cm1

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 GACAATAGATATCTAAAGCTAATTT-----TATTTTGATT-C--AGGTATCTCT--GGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>LMB Cm1

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 CAGAATAAATATTTTGATTTTTTCTCAATGTTGAATTGGTAAGAAGTTTCCAATGTGGAATATTTGACAATAGATATCTAAAGCTAATTT-TATTTTGATT-C--
 AGGTATCTCT-----GGGATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>GRM Cm6

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 CAGAATAAATATTTTGATTTTTTCTCAATGTTGAATTGGTAAGAAGTTTCCAATGTGGAATATTTGACAATAGATATCTAAAGCTAATTT-TATTTTGATT-C--
 -----AGGTATCTCTGGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>GRM Cc6 GRM Cc11 GRM Cc14 FSB Cc1 FSB Cc2 DRB Cc5 DRB Cc12 MSB Cm1 HAG Cm5

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 CAGAATAAATATTTTGATTTTT-----
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>PTN Cg3 PTN Cg6

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>PTN Cg11

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>DRB Cg6 GRM Cg7 GRM Cg11

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 GGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>PSJ Cs1

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 GGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>KOS Co7 CMB Co1

TTTACCATGAGA-TGA--TCACC-TCCAAGGTCATCAGCTTGACTGA-TG-----
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 GGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>PED Co1 TSK Co1 MSB Co14 MSB Co15 CMB Co8 MSB Co3 MZB Co1 MSB Co6 CPA Co11

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 GGTATACGGACAGATGAACGAACCCCCGGGGCCCCGTGCC-----

>PSJ Hc1 PSJ Hc2

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 GGTATACGGACAGATGAACGAACCCCGGGGCCCGTGCC-----

>PSJ *Cellana capensis*

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 GCACCA-----
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 CT-GGTATACGGACAGATGAACGAACCCCTGGGGCCCGTGCC--

END;

4. Mitochondrial CO1 alignments of all the species**a) *Scutellastra barbara***

44 taxa 539 characters

PSJ Sb4

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PSJ Sb3

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PSJ Sb2

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PSJ Sb8

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HAG Sb7

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HAG Sb2

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HAG Sb9

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HAG Sb4

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HAG Sb13

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SDB Sb9

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SDB Sb7

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SDB Sb4

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SDB Sb3

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MSB Sb6

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MSB Sb5

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TGCT

MSB Sb4

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TGCT

MSB Sb2

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TGCT

MSB Sb1

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TGCT

MSB Sb3

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TGCT

MSB Sb7

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TGCT

MSB Sb8

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TGCT

CCB Sb3

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TGCT

CCB Sb6

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TGCT

CCB Sb1

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TGCT

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TGCT

CCB Sb5

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CCB Sb8

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CCB Sb4

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CCB Sb2

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LMB Sb5

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LMB Sb4

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LMB Sb2

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LMB Sb6

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LMB Sb3

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LMB Sb1

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GRM Sb1

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GRM Sb6

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GRM Sb5

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GRM Sb2

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GRM Sb4

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TGCT

PED Sc6

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b) *Scutellastra cochlear*

82 taxa 538 characters

PED Sc6

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PED Sc8

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PED Sc4

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PED Sc3

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PED Sc2

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PED Sc14

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HAG Sc3

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HAG Sc2

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HAG Sc7

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HAG Sc6

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HAG Sc11

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HAG Sc1

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HAG Sc9

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HAG Sc5

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HAG Sc4

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HAG Sc10

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HAG Sc8

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KOS Sc19

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KOS Sc13

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KOS Sc10

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KOS Sc12

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KOS Sc9

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SDB Sc8

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SDB Sc7

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SDB Sc6

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SDB Sc12

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SDB Sc11

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SDB Sc9

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SDB Sc3

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SDB Sc14

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SDB Sc10

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SDB Sc5

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TSK Sc4

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TSK Sc2

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TSK Sc7

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TSK Sc5

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TSK Sc1

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MSB Sc2

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MSB Sc10

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MSB Sc12

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MSB Sc1

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CPA Sc5

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CPA Sc2

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CPA Sc9

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CPA Sc1

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CPA Sc8

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CPA Sc7

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MZB Sc15

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MZB Sc4

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MZB Sc8

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MZB Sc4

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MZB Sc19

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MZB Sc18

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CMB Sc3

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CMB Sc7

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CMB Sc2

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CMB Sc11

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CMB Sc9

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PTN Sc17

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PTN Sc15

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PTN Sc9

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PTN Sc5

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PTN Sc3

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DRB Sc11

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DRB Sc12

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DRB Sc6

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DRB Sc10

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DRB Sc5

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GRM Sc4

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GRM Sc2

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GRM Sc6

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GRM Sc9

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GRM Sc8

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GRM Sc12

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GRM Sc1

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GRM Sc5

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GRM Sc10

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GRM Sc11

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GRM Sc7

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MSB S13

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c) *Scutellastra longicosta*

42 taxa 539 characters

PSJ S15

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PSJ S14

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PSJ S12

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PSJ S13

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PSJ S11

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HAG S17

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HAG SI4

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ATGCT

HAG SI3

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HAG SI11

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ATGCT

HAG SI1

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ATGCT

HAG SI10

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AT--

KOS SI5

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TATGCT

KOS SI4

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ATGCT

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CTATGCT

KOS SI10

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KOS SI8

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KOS SI2

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SDB SI5

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TATGCT

SDB SI11

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TATGCT

SDB SI4

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SDB SI14

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CTATGCT

SDB SI1

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TSK SI3

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ATGCT

TSK SI11

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ATGCT

TSK SI8

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ATGCT

TSK SI5

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ATGCT

TSK SI4

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ATGCT

MSB SI5

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MSB SI2

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TATGCT

MSB SI3

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MSB SI24

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MSB SI10

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ATGCT

CPA SI11

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ATGCT

CPA SI9

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CPA SI8

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TATGCT

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ATGCT

CPA SI2

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ATGCT

CPA SI7

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ATGCT

MZB SI3

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MZB SI2

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ATGCT

MZB SI1

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ATGCT

MZB SI12

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ATGCT

MZB SI10

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ATGCT

MSB Sb5

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d) *Scutellastra granularis*

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KOS Sg27

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KOS Sg28

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SDB Sg3

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SDB Sg12

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SDB Sg2

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SDB Sg20

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HAG Sg8

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HAG Sg6

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HAG Sg13

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HAG Sg11

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HAG Sg10

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KOS Sg20

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KOS Sg13

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KOS Sg26

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KOS Sg19

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SDB Sg5

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SDB Sg9

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SDB Sg10

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TSK Sg27

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TSK Sg30

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TSK Sg2

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TSK Sg11

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TSK Sg5

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MSB Sg9

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MSB Sg7

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MSB Sg5

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MSB Sg4

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MSB Sg3

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MSB Sg10

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MSB Sg1

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CPA Sg9

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CPA Sg3

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CPA Sg17

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CPA Sg10

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CPA Sg1

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MZB Sg6

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MZB Sg12

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MZB Sg2

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MZB Sg11

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MZB Sg3

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CMB Sg13

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CMB Sg10

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CMB Sg8

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CMB Sg1

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CMB Sg12

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PTN Sg7

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PTN Sg23

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PTN Sg12

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PTN Sg8

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PTN Sg11

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DRB Sg9

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DRB Sg12

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DRB Sg11

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DRB Sg7

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DRB Sg5

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GRM Sg9

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GRM Sg13

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GRM Sg10

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GRM Sg12

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GRM Sg11

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BAB Sm3

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e) *Scutellastra natalensis*

11 taxa 537 characters

BLT Sn18

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BLT Sn19

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BLT Sn9

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PED Sn7

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PED Sn5

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PED Sn9

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PED Sn3

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HAG Sa7

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ATGCT

f) *Scutellastra miliaris*

15 taxa 603 characters

BAB Sm1

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BAB Sm2

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BAB Sm3

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BAB Sm4

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BAB Sm5

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BAB Sm7

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BAB Sm8

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LBT Sm1

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LBT Sm8

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LBT Sm7

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BLT Sn9

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g) *Scutellastra argenvillei*

21 taxa 541 characters

HAG Sa2

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HAG Sa3

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MSB Sa2

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MSB Sa5

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LMB Sa8

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LMB Sa2

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CCB Sa7

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CCB Sa2

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CCB Sa6

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CCB Sa1

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CCB Sa5

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PED Sc6

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h) *Cymbula miniata*

21 taxa 711 characters

LMB Cm1

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LMB Cm5

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MSB Cm5

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MSB Cm1

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MSB Cm2

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MSB Cm10

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HAG Cm1

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HAG Cm4

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HAG Cm6

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HAG Cm2

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HAG Cm8

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PSJ Cm4

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PSJ Cm6

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PSJ Cm2

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PSJ Cm1

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PSJ Cm7

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SDB Co2

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i) *Cymbula oculus*

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KOS Co7

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KOS Co1

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KOS Co4

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KOS Co12

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KOS Co9

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SDB Co1

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SDB Co22

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SDB Co2

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SDB Co14

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SDB Co10

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SDB Co11

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TSK Co1

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TSK Co2

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TSK Co22

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TSK Co27

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TSK Co23

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TSK Co24

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MSB Co1

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MSB Co2

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MSB Co3

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MSB Co4

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MSB Co5

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MSB Co6

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MSB Co7

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MSB Co8

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CPA Co1

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CPA Co2

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CPA Co3

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CPA Co5

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CPA Co6

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MZB Co1

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MZB Co2

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MZB Co3

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MZB Co4

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MZB Co5

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CMB Co1

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CMB Co5

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CMB Co7

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CMB Co9

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CMB Co8

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HAG Cm4

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j) *Cymbula compressa*

24 taxa 689 characters

DRB Cc9

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DRB Cc4

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DRB Cc11

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DRB Cc6

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DRB Cc2

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DRB Cc7

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DRB Cc10

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DRB Cc12

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DRB Cc13

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PTN Cc4

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PTN Cc1

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PTN Cc2

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PTN Cc3

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PTN Cc9

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CMB Cc2

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CMB Cc1

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CMB Cc6

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CMB Cc5

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GRM Cc8

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GRM Cc6

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GRM Cc12

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GRM Cc13

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GRM Cc2

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PSJ Cm4

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k) *Cymbula granatina*

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CMB Cg1

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CMB Cg2

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CMB Cg3

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CMB Cg4

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CMB Cg5

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CMB Cg6

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CMB Cg7

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CMB Cg9

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CMB Cg11

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CMB Cg12

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PTN Cg2

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PTN Cg4

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PTN Cg5

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PTN Cg9

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PTN Cg10

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PTN Cg11

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PTN Cg13

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DRB Cg5

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DRB Cg8

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DRB Cg14

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DRB Cg9

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DRB Cg6

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DRB Cg3

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DRB Cg10

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DRB Cg11

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DRB Cg12

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DRB Cg15

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GRM Cg14

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GRM Cg15

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GRM Cg1

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GRM Cg8

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GRM Cg9

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GRM Cg20

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GRM Cg11

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GRM Cg12

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GRM Cg17

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GRM Cg10

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LMB Cm2

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END;

5. Stable isotope data

5.1 Raw $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios of all samples from all the sites

Sample	$\delta^{15}\text{N}$ ratio	$\delta^{13}\text{C}$ ratio	C:N	Sample	$\delta^{15}\text{N}$ ratio	$\delta^{13}\text{C}$ ratio	C:N
Hagsc1	6.86	-12.43	3.53	SDBsa1	7.95	-13.77	3.31
Hagsc2	7.82	-13.98	3.50	SDBsa2	7.25	-13.73	3.32
Hagsc3	7.80	-11.89	3.39	SDBsa3	8.55	-11.90	3.51
Hagsc4	7.36	-12.16	3.38	SDBsa4	7.63	-14.11	3.36
Hagsc5	7.17	-11.35	3.45	SDBsa5	7.67	-13.66	3.51
Hagsc6	7.84	-11.75	3.43	SDBsa6	7.38	-12.13	3.33
Hagco1	7.68	-11.48	3.71	SDBsa7	8.05	-12.28	3.38
Hagco2	7.60	-13.24	3.55	SDBsa8	7.99	-12.71	3.36
Hagco3	7.52	-10.89	3.61	SDBsa9	8.21	-11.42	3.36
Hagco4	7.49	-12.57	3.58	SDBsa10	7.55	-13.72	3.46
Hagco5	7.37	-14.36	3.66	KOSsa5	7.83	-12.51	3.36
Hagco6	8.12	-13.82	3.57	KOSsa6	7.41	-11.21	3.58
Hagsl1	6.34	-6.31	3.65	KOSsa7	7.80	-13.69	3.52
Hagsl2	7.09	-10.76	3.67	SDBsb1	8.25	-12.46	3.38
Hagsl3	6.57	-6.63	3.51	SDBsb2	8.04	-11.54	3.28
Hagsl4	7.16	-12.80	3.66	SDBsb3	8.89	-12.07	3.45
Hagsg4	7.40	-12.50	3.54	MSBsb1	8.40	-12.70	3.41
Hagsg2	7.28	-12.91	3.59	MSBsb2	8.82	-13.35	3.56
Hagsg3	6.94	-12.67	3.63	MSBsb3	9.03	-12.89	3.54
Hagsg1	7.04	-12.89	3.67	MSBsb4	8.22	-13.04	3.56
Hagsg6	7.07	-13.59	3.56	KOSsb1	8.82	-12.96	3.51
Hagsg8	7.32	-13.59	3.62	KOSsb2	8.16	-13.52	3.44
GRMcg1	7.27	-15.00	3.37	TSKsb6	7.73	-12.18	3.43
GRMcg3	7.17	-14.70	3.54	TSKsb8	7.98	-13.13	3.34
GRMcg6	6.79	-12.92	3.55	TSKco1	8.19	-9.45	3.60
GRMcg7	8.02	-12.99	3.45	KOSco2	7.95	-9.05	3.53
GRMsc1	9.35	-12.98	3.27	KOSco4	8.17	-9.68	3.52
GRMsc4	8.26	-13.76	3.39	KOSco5	7.58	-9.94	3.52
GRMsc5	8.98	-13.25	3.37	KOSco6	8.15	-11.00	3.60
GRMsc6	8.73	-13.51	3.29	KOSco7	8.03	-11.89	3.48
GRMsc8	8.34	-13.62	3.31	KOSco8	7.97	-9.64	3.57
GRMcC2	6.20	-17.08	3.51	KOSco9	8.22	-11.24	3.45
GRMcC5	6.42	-15.15	3.49	KOSsl3	8.05	-7.34	3.51
GRMcC6	6.52	-16.20	3.67	KOSsl4	7.33	-7.19	3.46
GRMsg1	7.67	-14.05	3.64	KOSsl6	7.69	-13.54	3.55

GRMmsg5	7.47	-14.28	3.58	KOSsl7	7.97	-11.64	3.52
GRMmsg7	7.63	-13.25	3.56	KOSsl8	7.48	-7.96	3.62
GRMmsg9	7.54	-15.65	3.80	KOSsl9	8.26	-9.69	3.54
HagSP2	5.79	-13.83	13.35	KOSsl11	8.21	-7.28	3.52
HagHs1	5.21	-17.04	8.41	KOSsl12	8.05	-9.19	3.50
HagHs2	5.39	-16.88	8.78	SDBsl1	7.49	-6.43	3.52
HagRv1	6.46	-8.13	15.16	TSKcm1	7.89	-14.78	3.47
HagRv2	6.20	-8.13	15.27	TSKcm2	7.68	-15.76	3.47
HagRv3	5.89	-8.01	15.03	TSKcm3	8.87	-13.86	3.30
GRMK2	6.24	-14.40	14.63	CPAcm1	11.02	-12.44	3.47
GRMRv1	7.68	-8.18	17.20	GRMcc3	6.29	-16.11	3.65
GRMRv2	7.09	-8.24	17.12	GRMcc9	7.26	-14.54	3.58
GRMCu1	5.75	-18.06	8.37	GRMmsg4	8.15	-14.05	3.80
GRMCu2	5.68	-18.02	8.33	GRMmsg6	7.85	-15.36	3.73
GRMCu3	5.34	-18.76	8.37	GRMsc2	8.51	-13.39	3.52
GRMGv1	8.00	-11.69	8.30	GRMsc1	8.53	-13.57	3.39
GRMRv2	7.40	-11.31	15.31	GRMcg8	7.26	-15.82	3.52
HagU1	5.24	-14.50	7.74	GRMcg9	7.10	-13.53	3.72
HagU3	5.48	-15.39	8.71	HAGsy1	5.19	-16.04	13.25
HagLF1	5.86	-15.88	10.94	HAGsy2	5.09	-16.33	14.17
HagEv1	5.41	-14.03	12.81	KOSsy1	7.15	-13.16	7.57
HagEv2	5.61	-13.79	13.08	CMBsy4	8.36	-13.38	7.07
HagP1	5.58	-18.64	15.31	SDBsy3	6.82	-13.08	4.31
MSBsg1	8.82	-9.02	3.45	SDBco2	10.77	-12.94	3.52
MSBsg2	8.44	-8.91	3.61	SDBco1	10.82	-13.90	3.51
MSBsg3	8.61	-8.64	3.58	SDBco3	10.35	-11.28	3.56
MSBsg4	7.98	-8.94	3.40	SDBsc1	10.25	-10.74	3.44
MSBsg5	8.85	-9.38	3.43	SDBsc2	10.19	-12.87	3.41
MSBsg6	8.04	-7.90	3.59	SDBsc3	10.17	-12.53	3.35
MSBsg7	7.45	-8.24	3.51	SDBsg1	10.34	-10.41	3.45
MSBsg8	8.66	-10.23	3.36	SDBsg2	9.13	-13.36	3.47
MSBsl1	8.52	-4.14	3.62	SDBsg3	8.90	-15.93	3.50
MSBsl2	8.71	-6.15	3.43	CMBco1	9.86	-11.45	3.43
MSBsl3	8.96	-5.72	3.50	CMBco2	9.37	-13.53	3.64
MSBsl4	8.75	-5.58	3.59	CMBco3	9.37	-13.69	3.64
MSBsl5	8.96	-4.85	3.56	CMBco4	8.22	-14.40	3.85
MSBsl6	9.34	-7.10	3.62	CMBsc1	9.68	-13.07	3.37
MSBsl7	8.68	-6.68	3.55	CMBsc2	10.00	-12.31	3.42
MSBsl8	9.24	-10.89	3.48	CMBsc3	9.52	-11.53	3.31
MSBco1	9.31	-7.90	3.52	CMBsc4	9.93	-13.25	3.48
MSBco2	7.87	-9.87	3.61	CMBsc5	9.68	-12.82	3.29
MSBco3	8.32	-8.70	3.72	CMBsg1	8.55	-12.94	3.51

MSBco4	8.97	-6.96	3.51	CMBsg2	8.46	-12.83	3.56
MSBco5	7.88	-9.17	3.60	CMBsg3	9.04	-12.02	3.54
MSBco6	9.03	-10.66	3.55	CMBsg4	8.64	-12.95	3.51
MSBco7	8.98	-9.36	3.58	CMBsg5	8.62	-12.89	3.40
MSBsc1	9.36	-10.91	3.44	DRBsc1	8.51	-11.46	3.49
MSBsc3	9.02	-10.00	3.40	DRBsc2	7.99	-11.09	3.49
MSBsc4	9.08	-10.21	3.47	DRBsc3	9.37	-10.61	3.40
MSBsc5	9.34	-9.99	3.45	DRBsc4	8.84	-12.15	3.47
PTNsg1	9.32	-15.88	3.67	DRBsc5	9.25	-11.07	3.48
PTNsg2	8.71	-15.76	3.55	DRBsg1	7.87	-14.18	3.82
PTNsg3	8.25	-15.72	3.59	DRBsg2	8.48	-11.56	3.64
PTNsg4	9.85	-16.71	4.05	DRBsg3	7.84	-15.51	3.69
PTNsc1	10.12	-13.45	3.41	DRBsg4	7.54	-15.65	3.65
PTNsc2	10.09	-12.51	3.37	DRBcg1	8.24	-12.64	3.72
PTNcg1	9.37	-13.91	3.73	DRBcg2	8.58	-11.91	3.48
PTNcg2	8.96	-15.04	3.72	DRBcg3	8.74	-9.78	3.59
PTNcg3	9.62	-13.40	3.58	DRBcg4	8.45	-11.54	3.53
PTNlf1	8.52	-14.36	8.75	DRBcc1	4.09	-17.52	3.61
PTNlf2	8.82	-12.04	9.49	DRBcc2	4.16	-17.46	3.56
PTNu1	7.49	-15.33	8.63	DRBcc3	7.17	-14.10	3.61
PTNu2	7.53	-14.43	9.23	DRBcc4	6.92	-14.65	3.57
PTNer2	8.61	-14.72	9.43	DRBcc5	6.49	-14.87	3.67
PTNp1	7.77	-15.17	12.65	DRBcc6	6.59	-14.94	3.61
PTNp2	7.39	-14.64	12.07	DRBh1	7.71	-13.31	8.07
MSBp2	9.02	-14.28	14.09	DRBh2	7.51	-13.27	9.94
MSBrv2	8.81	-7.19	14.13	DRBg1	6.91	-17.37	5.47
MSBrv3	9.06	-7.07	14.65	DRBer1	6.93	-10.23	13.57
MSBpc1	8.13	-16.59	7.01	DRBp1	7.47	-10.51	12.99
MSBpc2	8.47	-16.00	6.82	DRBer2	7.34	-10.25	13.20
MSBgp1	8.59	-14.98	14.35	DRBk1	6.90	-11.54	21.50
MSBgp3	8.65	-15.28	15.46	CMBg1	7.52	-12.07	10.54
MSBlf1	7.84	-13.13	8.17	CMBg2	7.56	-12.88	9.88
MSBlf2	8.24	-11.80	7.83	CMBg3	7.33	-12.68	10.57
MSBrv1	9.06	-6.77	16.22	CMBu1	5.18	-16.53	9.08
KOSrv1	8.31	-9.84	11.67	CMBu2	5.67	-15.87	8.86
KOSrv2	8.05	-9.12	11.98	CMBu3	5.51	-16.67	8.81
CMBsy2	7.71	-5.44	17.93	CMBrv1	7.59	-6.82	15.85
GRMsy2	8.48	-10.37	10.38	CMBrv2	7.72	-6.12	15.29
MSBsy1	8.66	-11.30	11.03	CMBrv3	7.28	-7.84	13.37
CPAsl1	8.30	-8.79	3.72	CMBp1	6.52	-16.67	8.33
CPAsl2	8.56	-7.34	3.60	CMBp2	7.39	-15.25	10.00
CPAsl3	8.84	-8.94	3.65	CMBp3	7.47	-15.44	9.58

CPAsI5	8.19	-7.06	3.62	PEDcu2	6.32	-15.45	10.80
CPAsI6	8.31	-8.27	3.71	PEDHs2	6.93	-14.62	9.53
CPAsc1	9.71	-10.98	3.27	PEDgp2	6.54	-15.52	15.37
CPAsc2	9.79	-12.56	3.46	PEDu1	6.12	-12.71	11.81
CPAsc3	9.39	-11.74	3.41	PEDu2	6.02	-11.91	11.75
CPAsc4	10.13	-12.50	3.51	PEDs1	6.29	-12.93	13.24
CPAsc5	10.06	-11.88	3.49	KOSp1	5.66	-14.36	10.45
CPAsg1	9.38	-15.51	3.74	KOSp2	5.72	-14.23	10.47
CPAsg2	8.38	-14.81	3.71	KOScp2	6.98	-16.11	8.76
CPAsg3	8.25	-14.90	3.60	KOScp3	6.70	-16.16	8.93
CPAsg4	8.33	-14.96	3.51	KOScu1	6.86	-15.22	8.61
CPAsg5	8.32	-15.15	3.59	GRMsv2	6.12	-17.84	12.01
CPAsg6	8.43	-14.87	3.64	GRMer1	7.39	-12.76	17.06
CPAco1	9.95	-10.99	3.61	GRMu2	6.82	-11.51	12.57
CPAco2	9.66	-11.14	3.62	GRMu3	6.81	-10.74	10.73
PEDsn1	6.19	-12.07	3.39	GRMsv3	5.72	-16.40	12.90
PEDsn2	7.05	-12.69	3.48	GRMk1	6.01	-14.18	14.34
PEDsn3	6.40	-12.54	3.44	GRMk3	6.47	-13.96	14.10
PEDsn4	6.12	-12.24	3.43	MZBsc1	10.53	-11.56	3.28
PEDsn5	6.89	-13.13	3.58	MZBsc2	9.61	-12.25	3.43
PEDsn6	5.77	-9.74	3.43	MZBsc3	10.44	-10.91	3.41
PEDsn7	6.50	-11.55	3.64	MZBsc4	10.76	-11.68	3.29
PEDsn8	6.19	-10.06	3.56	MZBsc5	10.52	-11.16	3.38
PEDsn9	5.90	-10.00	3.47	MZBsg1	10.50	-11.89	3.46
PEDsn10	6.11	-10.23	3.62	MZBsg2	10.45	-12.43	3.60
CPAHs1	8.70	-16.68	9.32	MZBsg3	10.80	-11.89	3.53
CPAHs2	8.29	-16.74	10.41	MZBsg4	10.46	-11.01	3.55
CPAcu1	8.41	-18.85	8.84	MZBsg5	10.37	-11.66	3.60
CPAcu2	8.21	-17.98	8.91	MZBsg6	10.81	-10.94	3.61
CPArv1	8.11	-8.64	11.63	MZBsg7	10.23	-12.05	3.54
CPArv2	7.65	-8.11	15.76	MZBsg8	10.71	-11.25	3.62
CPArv3	8.15	-8.34	14.00	MZBcg1	10.56	-11.83	3.68
CPAgp1	7.75	-14.93	15.26	MZBcg2	10.60	-10.56	3.80
CPAgp2	7.85	-13.69	18.52	MZBcg3	10.21	-9.23	3.78
CPAgp3	8.09	-17.47	14.82	KOSsa1	8.01	-13.56	3.26
CPAlf1	8.84	-14.18	10.28	KOSsa2	7.99	-11.18	3.41
CPAlf3	8.71	-15.00	9.24	KOSsa3	8.65	-13.70	3.56
CPAu2	7.89	-16.78	9.46	KOSsa4	8.20	-13.64	3.41
CPAu3	8.21	-16.28	9.22	KOSsc2	9.23	-17.95	3.49
PEDct1	5.48	-15.24	13.87	KOSsc3	8.96	-18.21	3.27
KOSsg1	5.75	-9.24	3.46	KOSsc4	8.95	-15.40	3.67
KOSsg2	7.24	-9.00	3.42	KOSsc5	9.11	-11.89	3.66

PKRsn7	6.54	-12.83	3.47	SDBrv1	7.64	-7.46	18.14
PKRsn8	6.43	-12.40	3.54	SDBrv2	6.93	-8.22	17.93
PKRsn9	6.61	-13.34	3.45	SDBp1	7.90	-13.91	19.33
PKRsn10	6.41	-14.22	3.48	SDBu1	7.33	-13.89	7.70
PKRsc1	8.63	-14.22	3.23	SDBpc2	6.69	-19.68	9.19
BLTsn1	6.59	-10.36	3.40	BLTgp1	6.95	-15.32	13.91
BLTsn2	5.94	-11.01	3.50	SDBsy1	7.88	-12.78	6.69
BLTsn3	6.98	-10.62	3.38	SDBsy2	7.57	-11.80	7.23
BLTsn4	5.83	-10.17	3.40	GRMSy2	9.22	-11.89	6.72
BLTsn5	6.36	-9.87	3.36	DRBsy1	9.06	-11.71	7.34
BLTsn6	7.17	-12.72	3.42	DRBsy2	9.49	-11.50	6.92
BLTsn7	6.14	-13.58	3.46	DRBsy3	9.81	-11.84	7.12
BLTsn9	7.26	-11.38	3.39	MSBsa2	9.24	-11.66	3.44
BLTsn10	6.39	-10.60	3.41	MSBsa3	9.04	-12.83	3.46
PEDsc6	9.22	-16.90	3.47	MSBsa4	8.67	-11.52	3.40
BLThs1	5.34	-18.72	8.22	MSBsa5	9.30	-13.09	3.44
BLThs2	6.51	-17.10	8.11	MSBsa6	8.85	-12.99	3.40
BLTct1	7.19	-14.50	15.39	MSBsa7	8.82	-13.14	3.48
BLTct2	7.16	-14.34	15.40	TSKsb1	8.42	-13.91	3.34
BLTpc1	6.05	-19.73	7.81	TSKsb2	8.31	-12.50	3.28
BLTpc2	6.03	-18.83	8.58	TSKsb3	8.22	-13.01	3.28
BLTcu1	6.63	-16.93	8.85	TSKsb4	8.20	-11.75	3.30
PKRhs2	4.86	-18.13	8.92	TSKsb5	8.60	-12.94	3.33
PKRpc3	5.58	-19.74	8.23	TSKsb7	8.12	-13.54	3.34
PKRpc1	5.35	-18.18	8.35	TSKsb9	8.03	-13.26	3.29
PKRs1	5.58	-14.89	15.23	TSKsb10	8.80	-12.90	3.26
PKRs2	5.56	-14.79	16.76	TSKsc1	8.75	-10.26	3.20
PKRhs1	5.16	-14.27	9.70	TSKsc2	9.16	-9.72	3.23
PKRhs3	5.48	-15.03	9.60	TSKsc3	8.50	-10.68	3.32
PKRbf1	4.17	-15.11	10.95	TSKsc4	8.85	-10.35	3.29
PKRbf3	3.35	-15.86	11.14	TSKsc5	7.75	-11.82	3.31
PKRgp3	5.87	-14.40	14.17	TSKsc6	8.65	-10.03	3.20
PKRgp2	6.12	-13.92	14.98	TSKsc7	8.77	-11.23	3.28
GRMk3	5.89	-13.70	14.81	TSKsc8	8.73	-10.81	3.41
BLTu2	6.47	-14.24	13.15	TSKsg1	9.08	-11.77	3.32
BLTcr1	4.15	-19.04	8.44	TSKsg2	9.09	-12.28	3.38
SDBlf1	7.79	-13.31	11.26	TSKsg3	9.32	-12.37	3.43
SDBlf2	7.68	-13.60	9.48	TSKsg4	9.15	-12.36	3.39
SDBlf3	8.14	-13.34	10.35	TSKsg5	9.27	-11.91	3.25
SDBgp1	6.47	-16.01	14.97	TSKsg6	9.19	-11.71	3.40

SDBgp2	6.58	-13.06	13.12	TSKsg7	8.9	-11.91	3.29
SDBgp3	6.06	-15.79	15.37	KOSsg4	7.25	-9.59	3.61
TSKsg8	9.47	-11.93	3.44	TSKco7	9.42	-10.84	3.59
TSKsl1	9.86	-10.33	3.45	TSKco8	8.84	-10.07	3.61
TSKsl2	9.56	-10.45	3.31	TSKsy1	8.56	-15.22	7.62
TSKsl3	9.62	-10.46	3.4	TSKsy2	9.1	-14.6	7.49
TSKsl4	8.56	-10.35	3.38	TSKrv2	7.55	-8.18	17.04
TSKsl5	9.31	-11.17	3.41	TSKwr1	6.73	-14.22	12.47
TSKsl6	9.66	-9.99	3.43	TSKer3	6.75	-13.87	11.88
TSKsl7	9.23	-11.57	3.5	TSKlf1	7.47	-13.72	10.46
TSKsl8	9.58	-9.81	3.38	TSKlf2	7.67	-12.62	13.04
TSKco1	8.9	-11.2	3.49	TSKpc1	6.11	-15.5	10.55
TSKco2	9.56	-11.47	3.62	TSKpc2	5.98	-16.49	9.44
TSKco3	9.32	-13.36	3.52	TSKgp1	5.12	-20.6	12.04
TSKco4	9.17	-9.82	3.57	TSKgp3	5.39	-18.94	12.86
TSKco5	9.3	-10.73	3.55	TSKu1	6.66	-14.57	7.59
TSKco6	8.77	-9.47	3.56	TSKu2	6.87	-14.02	7.62
TSKp2	6.15	-17.23	13.52	TSKp1	6.87	-16.64	11.94
KOSgfd	7.13	-13.92	14.81	KOSpc1	5.89	-20.78	10.37
KOSgt1	6.94	-16.03	14.78	KOSpc2	6.09	-19.69	10.98
KOSht1	6.38	-9.83	13.01	KOSu2	6.49	-13.75	10.88
KOSlf1	7.37	-14.83	11.53	KOSu3	6.41	-13.52	11.24
KOShtb	6.76	-15.22	10.27	KOSu1	6.51	-13.73	10.90

5.2 Standard deviations of stable $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios for selected sites and species

Sites	Species	Foraging trait	ST DEV $\delta^{15}\text{N}$	ST DEV $\delta^{13}\text{C}$
Haga-Haga (HAG)	<i>C. oculus</i>	Non-territorial	0.119687823	1.213164885
	<i>S. granularis</i>	Non-territorial	0.159237896	0.412464967
	<i>S. cochlear</i>	Territorial	0.312471365	0.411977195
	<i>S. longicosta</i>	Territorial	0.397967890	3.177217088
Kenton-on-Sea (KOS)	<i>C. oculus</i>	Non-territorial	0.246525317	1.234061433
	<i>S. granularis</i>	Non-territorial	0.890507454	1.679506382
	<i>S. argenvillei</i>	Non-territorial	0.318799523	1.085558477
	<i>S. cochlear</i>	Territorial	0.170896533	2.936135431
Sardinia Bay (SDB)	<i>S. longicosta</i>	Territorial	0.388277245	1.022214237
	<i>C. oculus</i>	Non-territorial	0.259882381	1.321026304
	<i>S. granularis</i>	Non-territorial	0.773975293	2.758562118
	<i>S. argenvillei</i>	Non-territorial	0.484772833	0.873323955
Tsitsikamma (TSK)	<i>S. cochlear</i>	Territorial	0.041772808	1.146617527
	<i>S. longicosta</i>	Territorial	0.198590117	0.555623521
	<i>C. oculus</i>	Non-territorial	0.241878266	1.303799657
	<i>S. granularis</i>	Non-territorial	0.107519643	0.099307414
Mossel Bay (MSB)	<i>S. cochlear</i>	Territorial	0.136961063	0.315209463
	<i>S. longicosta</i>	Territorial	0.499445165	0.350391028
	<i>S. argenvillei</i>	Non-territorial	0.264448916	0.765108314
	<i>S. granularis</i>	Non-territorial	0.355476399	0.265521253
Cape Agulhas (CPA)	<i>C. oculus</i>	Non-territorial	0.553047391	0.747726218
	<i>S. cochlear</i>	Territorial	0.174156140	0.434178139
	<i>S. longicosta</i>	Territorial	0.188748727	0.795687414
	<i>S. granularis</i>	Non-territorial	0.068657101	0.129378648
Doring Bay (DRB)	<i>C. oculus</i>	Non-territorial	0.203012058	0.110981956
	<i>S. cochlear</i>	Territorial	0.296477826	0.644333174
	<i>S. longicosta</i>	Territorial	0.253098916	0.840365214
	<i>S. granularis</i>	Non-territorial	0.396738087	1.897792635
Groenriviermond (GRM)	<i>C. granatina</i>	Non-territorial	0.213287506	1.214847831
	<i>S. cochlear</i>	Territorial	0.564694631	0.572917591
	<i>C. compressa</i>	Territorial	1.399688501	1.499864532
	<i>S. granularis</i>	Non-territorial	0.077132580	0.481066257
Groenriviermond (GRM)	<i>C. granatina</i>	Non-territorial	0.446436099	1.049678760
	<i>S. cochlear</i>	Territorial	0.296894280	0.196527533
	<i>C. compressa</i>	Territorial	0.573558512	1.013974004