

**SYSTEMATICS OF THE PHASIANELLOIDEA IN
SOUTHERN AFRICA
(MOLLUSCA: GASTROPODA: VETIGASTROPODA)**

By

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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy
in the discipline of Zoology,
School of Biological and Conservation Sciences,
University of KwaZulu–Natal, Pietermaritzburg

October, 2010

As the candidate's Supervisor I agree/do not agree to the submission of this thesis.

Signed: _____ Name: _____ Date: _____



T. adusta



T. africana



T. bicarinata



T. capensis



T. elongata



T. formosa



T. insignis



T. ios



T. kochii



T. kraussi



T. neritina



T. retrolineata



T. saxatilis



T. striolata



H. variabilis



P. solida

The southern African pheasant shell species.

GENERAL ABSTRACT

The taxonomy and biogeography of the southern African pheasant shell fauna are poorly known. Thirty-one nominal taxa referable to Phasianelloidea have been described or recorded in this region, but no systematic revision of these has ever been undertaken. Morphological evidence suggests that 16 taxa represent valid species, 13 are synonyms and two represent incorrect identifications. DNA sequence data from mitochondrial COI and 16S markers are used to assess the validity of the described nominal southern African *Tricolia* species. Phylogenetic analyses recovered seven distinct clades. *Tricolia adusta*, *T. elongata*, *T. formosa*, *T. kochii*, *T. saxatilis* and *T. neritina* were recovered as distinct species. *Tricolia africana* and *T. capensis* are genetically indistinguishable. However, morphological characters of the shell are clearly diagnosable. This could be due to incomplete sorting (ancestral polymorphism) reflecting recent speciation with rapid morphological and ecological divergence co-incident with geographical separation. Similarly, there is little genetic differentiation between *T. bicarinata*, *T. insignis* and *T. kraussi*. In this case the similarity is also supported by morphological data as the three species are conchologically close with intergrading shell characters, and might even be one species exhibiting ecogeographic variation in shell form. Monophyly of the southern African *Tricolia* species is not supported as well as the relationship between these and the European *Tricolia pullus*. In the last chapter a molecular phylogeny based on sequence data from mtDNA (COI and 16S), nuclear (18S and 28S) and the combined data (COI, 16S, 18S and 28S) is presented for the Phasianelloidea. Bayesian inference analyses performed on the combined data support the monophyly of *Tricolia sensu stricto*, *Eulithidium* and *Phasianella*. *Tricolia sensu lato* is not monophyletic, as its southern Australian and Indo-West Pacific species do not cluster with its southern African and Eastern Atlantic representatives. The position of *Hilola* and *Gabrielona* within the Phasianelloidea is unresolved. Phylogenetic reconstructions using bayesian inference support monophyly of the Phasianelloidea.

PREFACE

The work described in this thesis was carried out in the School of Biological and Conservation Sciences, University of KwaZulu–Natal, Pietermaritzburg Campus, together with the Natal Museum, Pietermaritzburg, from January 2004 to June 2010, under the supervision of Dr David Herbert (Natal Museum) and co–supervision of Dr Rauri Bowie (Museum of Vertebrate Zoology and University of California, Berkeley), Dr Peter Teske (Rhodes University, Grahamstown), and Professor Denis Brothers (University of KwaZulu–Natal).

This thesis, unless specifically indicated to the contrary in the text, represents original work by the author and has not been submitted in any form to another University. Where other work has been used, it has been acknowledged.

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DECLARATION – PLAGIARISM

I, TSHIFHIWA CONSTANCE NANGAMMBI, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
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DECLARATION – PUBLICATIONS

Publication 1 (attached)

Nangammbi, T.C. & Herbert, D.G. 2006. Two new species of *Tricolia* Risso, 1826 from South Africa (Mollusca: Gastropoda: Phasianellidae). *African Invertebrates* **47**: 11-22.

Publication 2 (attached)

Nangammbi, T.C. & Herbert, D.G. 2008. A new species of pheasant shell from the south-western Indian Ocean (Mollusca: Gastropoda: Vetigastropoda: Phasianellidae: *Tricolia*). *African Invertebrates* **49**(2): 13-19.

The contribution of the authors of the above publications was the same. These papers represent the results of my study with input from Dr Herbert and which included presentation of the manuscripts, editing and guidance through the publication process.

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DISCLAIMER

NOTE: This thesis, except for the attached publications, is not intended to form part of the permanent scientific record; it is itself therefore not a valid publication for the purposes of zoological nomenclature.

DEDICATION

To my late mother

Vho–Tshithudivha Maria Nangammbi

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LIST OF ABBREVIATIONS

A/L	Aperture: Length ratio.
AMSA	Australian Museum, Sydney, Australia.
ANSP	The Academy of Natural Sciences, Philadelphia, USA.
BMNH	The Natural History Museum, London, UK.
CSIR	Council for Scientific and Industrial Research, South Africa.
EM	East London Museum, South Africa.
EKZNW	Ezemvelo KwaZulu-Natal Wildlife, South Africa.
FMNH	The Field Museum of Natural History, Chicago, USA.
ICZN	International Code of Zoological Nomenclature.
L/W	Length: Width ratio.
LACM	Los Angeles County Museum of Natural History, California, USA.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MNHV	Museum of Natural History of Vienna, Austria.
NEC	The Ndlambe Environmental Conservation, Port Alfred, South Africa.
NMDP	Natal Museum Dredging Programme, Pietermaritzburg, South Africa.
NMSA	Natal Museum, Pietermaritzburg, South Africa.
NHMW	National History Museum of Wales, Cardiff, UK.
NPB	Natal Parks Board (now Ezemvelo KZN Wildlife), South Africa.
ORI	Oceanographic Research Institute, South Africa.
OUMNH	Oxford University Museum of Natural History, Oxford, UK.
PFAO	Percy FitzPatrick Institute of African Ornithology.
RU	Rhodes University, Grahamstown, South Africa.
SAMC	South African Museum, Cape Town [now Iziko Museum], South Africa.
SBMNH	Santa Barbara Museum of Natural History, California, USA.
UCT	University of Cape Town, South Africa.
UKZN	University of KwaZulu–Natal, South Africa.
USNM	National Museum of Natural History, Washington D.C., USA.
WAM	Western Australian Museum, Perth, Australia.
ZMHB	Museum für Naturkunde der Humboldt–Universität, Berlin, Germany.

GENERAL INTRODUCTION

The primary intent of this dissertation is to address three areas of systematic biology looking at the small marine gastropod Phasianellidae (*sensu* Williams & Ozawa 2006, Williams *et al.* 2008) in southern Africa. The first aim is to resolve the alpha taxonomic problems associated with the number of valid and endemic species within the southern African malacofauna. The second aim is to assess the validity of identified taxonomic names within the southern African pheasant shell species based on the mitochondrial protein-coding COI gene and ribosomal RNA 16S marker. The third aim is to investigate unresolved phylogenetic relationships between *Tricolia*, *Phasianella* and *Gabrielona* including two more genera namely *Hilola* and *Eulithidium* based on the mitochondrial and nuclear DNA sequences data.

In chapter 1 of this thesis, I document the historical review of pheasant shell classification by nineteenth and early twentieth century authors. This chapter also discusses characters (morphology, DNA sequences etc.) used by these scholars in their placement of pheasant shell within different classification hierarchy. The current classification of pheasant shell subfamilies together with the number of genera within each subfamily is discussed. Furthermore, the fossil record, age, time of origin and the distribution of pheasant shell species are discussed.

The southern African pheasant shell fauna has never been critically revised. To date, only *Tricolia* is recorded in the southern African malacological literature. Despite being well represented in samples from near-shore, subtidal reef habitats in eastern South Africa, members of *Phasianella* have up until now not been identified as elements of the southern African marine biota. In chapter 2, I undertake a detailed taxonomic revision of all the described and recorded southern African pheasant shell species on the basis of morphological features of the operculum, protoconch, radula, and external anatomy (much to date is unknown with regard to the southern African shell fauna). For the completion of this chapter, recently described species of *Tricolia* in southern Africa namely, *T. adusta*, *T. retrolineata* and *T. saxatilis* Nangammbi & Herbert (2006, 2008) have been included.

To date, no studies have ever been done to investigate the validity of the described subgenera and nominal species based on molecular sequence data. In chapter 3, I assess the validity of the described subgenera and nominal species within the southern African *Tricolia* species based on molecular sequence data from the mitochondrial COI and 16S rRNA markers.

Students of vetigastropod systematics have to date failed to resolve the relationships between the three pheasant shell genera, and their higher taxonomic status and placement within the Trochoidea has long been a matter of conjecture. Furthermore, the diversity, affinities and origin of various pheasant shell faunas around the globe have received little attention. Consequently, the historical biogeographical processes underlying the present day distribution patterns are largely unknown. In chapter 4, I explore unresolved phylogenetic relationships between *Eulithidium*, *Hilola*, *Tricolia*, *Phasianella* and *Gabrielona* based on the mitochondrial COI and 16S rRNA markers and nuclear 18S and 28S rRNA markers. The final section summarises the main findings of the study and outlines future directions and recommendations.

The aim of this study is to shed light on the following aspects:

1. To unravel the alpha-taxonomy of the southern African *Tricolia* fauna.
2. To investigate the phylogenetic relationships within the southern African representatives of *Tricolia*, specifically to investigate whether the taxa concerned represent a monophyletic entity and thus a single evolutionary radiation.
3. To investigate phylogenetic relationships between southern Africa taxa and representative taxa from other regions (i.e., East Africa, Eastern Atlantic/Mediterranean, southern Australia and Indo-West Pacific).
4. To evaluate the validity of the available subgeneric names within *Tricolia*, in particular *Chromotis* and *Hilola*, and establish to which of these subgenera the southern African species belong.
5. To explore the unresolved phylogenetic relationship between *Eulithidium*, *Tricolia*, *Phasianella*, and *Gabrielona*.

CHAPTER 1: LITERATURE REVIEW

1.1. HISTORICAL REVIEW OF PHEASANT SHELL CLASSIFICATION (PHASIANELLIDAE *SENSU LATO*)

The common name “pheasant shell” is presently used to refer to three vetigastropod subfamilies (Tricoliinae, Phasianellinae and Gabrieloninae Hickman & McLean 1990 and Hickman 1996). Vermeij & Lindberg (2000) treated the three phasianellid genera as separate families. Williams *et al.* (2008) and Williams *et al.* (2010) suggested *Phasianella*, *Gabrielona* and *Tricolia* be treated as separate families within a new superfamily Phasianelloidea. Typical features of the family include a shell that is glossy (and usually smooth), with a variegated colour pattern, a lack of interior nacre and a calcareous, paucispiral operculum. In addition the rachidian tooth of the radula is commonly reduced or absent (Hickman & McLean 1990). In southern Africa, these shells are easily identified by their small size, bright red colours and are very commonly found washed ashore along the beach–drift line.

The Tricoliinae Woodring, 1928 is the largest of the pheasant shells, containing approximately 61 described species that have been placed into two genera: *Tricolia* Risso, 1826 (45 species) and *Eulithidium* Pilsbry, 1898 (16 species). Species in *Tricolia* occur in southern Africa, subtropical East Africa, south–western Australia, tropical Indo–West Pacific, the Eastern Atlantic/Mediterranean, Amsterdam and St. Paul Islands and northern Japan. Species placed in *Eulithidium* are restricted to the Eastern Pacific and Western Atlantic. The bulk of *Tricolia* species occur in southern Africa (25, 11.25%) and the Eastern Atlantic/Mediterranean (11, 5%), and in *Eulithidium* endemism is highest in the Eastern Pacific (10, 1.6%). The Phasianellinae is comprised of approximately seven species that have been placed in one genus: *Phasianella* Lamarck, 1804. *Phasianella* is restricted to the tropical Indo–West Pacific including the subtropical east coast of southern Africa and south–western Australia. Gabrieloninae is almost exclusively tropical containing approximately six species that have been placed into two genera: *Gabrielona* Iredale, 1917 (tropical/temperate Indo–West Pacific and southern Australia) and *Eugabrielona* Hickman & McLean, 1990 (Caribbean).

The taxonomic classification of pheasant shells has long been controversial with some authors placing them within the Trochidae (i.e., Swainson 1840, Chenu 1859, Kobelt 1879), whereas others included them within the Turbinidae (i.e., Pilsbry 1888, Thiele 1929, Hickman & McLean 1990, Hickman 1998), and the Phasianellidae (i.e., Wenz 1938, Robertson 1958, Keen & Robertson 1960, Williams & Ozawa 2006, Williams *et al.* 2008).

More recently, pheasant shells have been treated as separate families within a new superfamily Phasianelloidea (*sensu* Vermeij & Lindberg 2000, Williams *et al.* 2010, Table 1.1).

The pheasant shells have been monographed by Philippi (1853), Reeve (1862), Kiener (1847) and Sowerby (1887). In the *Manual of Conchology*, Pilsbry (1888) discussed the taxonomic grouping of pheasant shells of the world within the Turbinidae. His monograph included species from southern Africa, the Eastern Atlantic, the Western Atlantic, the Eastern Pacific and the Indo–West Pacific regions and this work contributed to many global revisions and formed the basis for further regional taxonomic studies on the Western Atlantic, the Indo–West Pacific and the Eastern Atlantic/Mediterranean (Robertson 1958, 1973, 1985, Gofas 1982, 1986, 1993, Hickman & McLean 1990). Although Pilsbry (1888) placed the pheasant shells within the Turbinidae he treated them as a separate subfamily, the Phasianellinae. In Pilsbry's study, two distinct genera were recognized, *Phasianella* and *Alcyona* Adams, 1860: the latter genus is now considered to be part of the Trochidae because it possesses a corneous operculum. *Chromotis* H. & A. Adams, 1863, *Eucosmia* Carpenter, 1864, *Tricolia*, and *Orthomesus* Pilsbry, 1888 were treated as subgenera of *Phasianella*. In his subsequent studies, Pilsbry replaced *Eucosmia* with *Eulithidium* because *Eucosmia* was preoccupied in zoology for a group of moths established by Stephens (1831). *Orthomesus* was later treated by Robertson (1985) as a synonym of *Phasianella*.

Following Pilsbry (1888), Thiele (1929) revised the taxonomy of pheasant shells and recognized four distinct genera: *Eulithidium*, *Phasianella*, *Prisogaster* Mörch, 1850 and *Tricolia* placing them within the Turbinidae and Phasianellinae. In his "*Handbuch der Paläozoologie*", Wenz (1938) discussed the pheasant shells under Phasianellidae, and also recognized four recent genera: *Eulithidium*, *Phasianella*, *Prisogaster* and *Tricolia*, and two fossil genera *Aizyella* Cossmann, 1889 and *Pseudophasianus* Cossmann, 1918. In the same study, the two taxa *Steganomphalus* Harris & Burrows, 1891 and *Chromotis* were treated as subgenera of *Tricolia*, and *Hilola* Pilsbry, 1917 as a subgenus of *Eulithidium*. Unlike Thiele and Wenz, Hickman & McLean (1990) regarded *Prisogaster* as a distinct genus within the Prisogasterinae, separate from the pheasant shells.

Following Wenz, Robertson (1958) grouped the pheasant shells within the Phasianellidae, and recognized two subfamilies: Phasianellinae and Tricoliinae. The Phasianellinae included only *Phasianella*, with Tricoliinae comprised of two genera, *Tricolia* and *Gabrielona*. Robertson treated the following taxa as subgenera of *Tricolia*: *Aizyella*, *Phasianochilus* Cossmann, 1918 [fossil], *Hilola*, *Pellax* Finlay, 1926, and *Eotricolia* Kuroda & Habe, 1954.

However, *Pellax* has subsequently been shown to be a Caenogastropoda (Robertson 1985, Wilson 1993). Ponder (1965) ranked *Pellax* as a subgenus of *Eatoniella* Dall, 1876, which he placed in the Eatoniellidae and is referred to Caenogastropoda: Cingulopsoidea (*vide* Bouchet & Rocroi 2005).

Keen & Robertson (1960) followed Robertson (1958) and Wenz (1938) in placing the pheasant shells within the Phasianellidae, and recognized three genera: *Phasianella*, *Gabrielona* and *Tricolia*. Within *Tricolia*, three subgenera, *Hilola*, *Pellax* and *Eotricolia*, and three fossil subgenera, *Aizyella*, *Phasianochilus* and *Pseudophasianus* were recognized. These authors listed *Chromotis* and *Eulithidium* as synonyms of *Tricolia*. In a break from tradition, Robertson (1985) re-defined *Tricolia*, regarding them as a separate family, the Tricoliidae, distinct from the Phasianellidae, and retained *Phasianella* within the Phasianellidae, and suggested that *Gabrielona* can be placed in the “Turbinidae *sensu lato*”, pending anatomical data on the group.

Later, Hickman & McLean (1990) and Hickman (1996) treated the pheasant shells as an informal group of three separate subfamilies, Phasianellinae, Tricoliinae and Gabrieloninae, within a broadly-interpreted family Turbinidae. Within the Tricoliinae, they recognized two genera: *Tricolia* and *Eulithidium*. The subgenera of *Tricolia* were not discussed in their work. Gabrieloninae was recognized as a new subfamily comprised of two genera: *Gabrielona* and *Eugabrielona*. The latter was described as a new genus, and *Gabrielona sulcifera* Robertson, 1973 was designated as the type species. Under this taxonomic arrangement the Phasianellinae is comprised only of *Phasianella*.

Although the referral of the pheasant shells to the Turbinidae was supported by phylogenetic analysis of morphological and behavioural characters (Hickman 1996), the relationship between the three subfamilies could not be resolved and remains unclear to this day. Species delimitation and taxonomy of the Eastern Atlantic/Mediterranean species of *Tricolia* was recently revised by Gofas (1982, 1986, 1993). In the 1982 revision Gofas followed Keen & Robertson (1960) by placing these taxa in the Phasianellidae, and in 1993, he published notes on some Ibero-Moroccan and Mediterranean *Tricolia* (Gastropoda, Tricoliidae), including the description of several new species.

Although the systematic studies of the Turbinidae by Williams & Ozawa (2006) broadly followed Hickman & McLean (1990), they recognized the pheasant shell as a distinct family, the Phasianellidae. This was the first molecular study to include the three pheasant shell subfamilies, and to test the monophyly of the group based on molecular sequence data. The

molecular data suggested that the three subfamilies form a well-resolved monophyletic assemblage based on the 18S rRNA, 28S rRNA, COI (no third position), and the combined (18S, 28S and COI) datasets. However, the Tricoliinae was not recovered as monophyletic and formed a paraphyletic entity including the Phasianellinae. In summary, the study by Williams & Ozawa (2006) emphasized that the subfamily relationships and systematics of the Phasianellidae are unresolved and require further study. The most recent systematics study by Williams *et al.* (2008) placed Phasianellidae and Colloniidae in a superfamily of their own, Phasianelloidea.

One of the primary objectives of this Ph.D. thesis is thus to clarify relationships within the *Eulithidium–Gabrielona–Phasianella–Tricolia* complex and to evaluate the status and ranking of associated supraspecific taxa. This aspect of the study will dovetail with the larger and more broadly sampled molecular analysis of the Turbinidae *sensu lato* conducted by Williams & Ozawa (2006). It is intended that the present, more focused study will complement this family-level analysis by providing detailed data relating to the pheasant shell component. At a local level, this expanded dataset will be used to investigate phylogenetic relationships within the southern African *Tricolia* radiation, specifically to investigate whether the taxa concerned represent a monophyletic entity and radiation. At a slightly higher taxonomic level, the data will be used to evaluate subgeneric groupings within *Tricolia*, in particular *Chromotis* and *Hiloa*.

In this study I present a phylogenetic analysis of the pheasant shell genera *Eulithidium*, *Gabrielona*, *Phasianella* and *Tricolia* based on morphology, mitochondrial COI and 16S rRNA, and nuclear 28S and 18S rRNA markers, as well as detailed discussion of the morphology and ecology of these molluscs with particular reference to the *Tricolia* radiation in southern Africa.

Table 1.1. Summary of the taxonomic treatment of pheasant shells by various authors.

Author	Family placement	Subfamily placement	Genera treated
Risso (1826)	“Les Ellipsostomes”		<i>Tricolia</i>
Swainson (1840)	Trochidae	Phasianellinae	<i>Phasianella</i>
Philippi (1853)	Trochacea		<i>Phasianella</i> (<i>Tricolia</i> as synonym of <i>Phasianella</i>)
H. & A. Adams (1854)	Trochidae	Eutropiinae [=Phasianellinae]	<i>Eutropia</i> (<i>Tricolia</i> as synonym of <i>Eutropia</i>)
Kobelt (1879)	Trochidae	Phasianellinae	<i>Phasianella</i> (<i>Tricolia</i> as synonym of <i>Phasianella</i>)
Tryon (1883)	Phasianellidae		<i>Phasianella</i> (<i>Tricolia</i> as synonym of <i>Phasianella</i>)
Fischer (1885)	Turbinidae	Phasianellinae	<i>Phasianella</i> (<i>Tricolia</i> as synonym of <i>Phasianella</i>)
Pilsbry (1888)	Turbinidae	Phasianellinae	<i>Phasianella</i> (<i>Tricolia</i> as subgenus of <i>Phasianella</i>)
Simroth (1907)	Turbinidae	Phasianellinae	<i>Phasianella</i> (<i>Tricolia</i> as subgenus of <i>Phasianella</i>)
Iredale (1917)	Phasianellidae		<i>Gabrielona</i>
Woodring (1928)	Tricoliidae		<i>Tricolia</i>
Thiele (1929)	Turbinidae	Phasianellinae	<i>Tricolia</i> , <i>Eulithidium</i> , <i>Phasianella</i> and <i>Gabrielona</i>
Wenz (1938)	Phasianellidae		<i>Tricolia</i> , <i>Eulithidium</i> , <i>Phasianella</i> and <i>Gabrielona</i>
Woodring (1957)	Phasianellidae		<i>Tricolia</i>
Robertson (1958)	Phasianellidae	Phasianellinae	<i>Phasianella</i>
Robertson (1958)	Phasianellidae	Tricoliinae	<i>Tricolia</i> and <i>Gabrielona</i>
Keen & Robertson (1960)	Phasianellidae	Phasianellinae, Tricoliinae	<i>Tricolia</i> , <i>Phasianella</i> and <i>Gabrielona</i>
Marcus & Marcus (1960)	Phasianellidae		<i>Tricolia</i>
Fretter & Graham (1962)	Turbinidae		<i>Tricolia</i>
Franc (1968)	Phasianellidae		<i>Tricolia</i>
Fretter & Graham (1977)	Phasianellidae		<i>Tricolia</i>

Author	Family placement	Subfamily placement	Genera treated
Robertson (1973)	Phasianellidae		<i>Gabrielona</i>
Robertson (1985)	Phasianellidae		<i>Phasianella</i>
Robertson (1985)	Tricoliidae		<i>Tricolia</i>
Robertson (1985)	Turbinidae		<i>Gabrielona</i>
Gofas (1982)	Phasianellidae		<i>Tricolia</i>
Gofas (1993)	Tricoliidae		<i>Tricolia</i>
Moolenbeek & Dekker (1993)	Turbinidae	Phasianellinae, Tricoliinae and Gabrieloninae	<i>Phasianella</i> , <i>Tricolia</i> and <i>Gabrielona</i>
Hickman & McLean (1990)	Turbinidae	Phasianellinae	<i>Phasianella</i>
Hickman & McLean (1990)	Turbinidae	Tricoliinae	<i>Tricolia</i> and <i>Eulithidium</i>
Hickman & McLean (1990)	Turbinidae	Gabrieloninae	<i>Gabrielona</i> and <i>Eugabrielona</i>
Hickman (1996)	Turbinidae	Phasianellinae, Tricoliinae and Gabrieloninae	
Williams & Ozawa (2006)	Phasianellidae	Phasianellinae, Tricoliinae and Gabrieloninae	<i>Phasianella</i> , <i>Tricolia</i> and <i>Gabrielona</i>
Williams <i>et al.</i> (2008)	Phasianellidae	Phasianellinae, Tricoliinae and Gabrieloninae	<i>Phasianella</i> , <i>Tricolia</i> and <i>Gabrielona</i>

1.2. CHARACTERS IDENTIFIED BY VARIOUS AUTHORS IN THEIR PLACEMENT OF PHEASANT SHELL GENERA

As outlined above, many authors have actively worked on the taxonomy of the pheasant shell genera over the last 150 years. Consequently, different characters have been used in the classification of these genera and their constituent species including: shell surface and/or sculpture, shell pigments, shell microstructure, the number of shell muscles, protoconch, operculum, radula, soft tissue, jaw, sperm morphology and most recently DNA sequences. Each of these characters will be discussed in the following section. A summary of characters used by various authors in the placement of pheasant shells is given in Table 1.2.

Table 1.2. Summary of characters used by various authors in their placement of pheasant shell genera.

Author	Family placement	Characters used
Pilsbry (1888)		Shell structure, operculum, protoconch, radula, external anatomy and habitat.
Thiele (1929)	Turbinidae	Shell structure, operculum and protoconch.
Robertson (1958)	Phasianellidae	Shell structure, operculum, shell muscles, radula, jaws and external anatomy.
Robertson (1973)	Phasianellidae	Shell structure, operculum, protoconch, radula and external anatomy.
Robertson (1985)	Tricoliidae	Shell structure, operculum, radula, jaws and external anatomy.
Gofas (1982, 1986)	Phasianellidae	Shell structure, polychromatism, radula and external anatomy.
Hickman & McLean (1990)	Turbinidae	Ctenidium and ability to calcify operculum.
Gofas (1993)	Tricoliidae	Shell structure and colouration, protoconch, radula and external anatomy.
Hickman (1996)	Turbinidae	Shell structure, operculum, radula, columella muscles, external anatomy and behavioural/functional.
Williams & Ozawa (2006)	Phasianellidae	Mitochondrial COI, nuclear 18S and 28S rRNA markers.
Williams <i>et al.</i> (2008)		Mitochondrial COI, nuclear 18S and 28S rRNA markers.

1.2.1. Shell surface or sculpture

Pilsbry (1888) described the general features of the pheasant shells to be: bulimiform or subglobose in shape, polished and without epidermis or nacre, and variegated with bright red colours. Thiele (1929) considered pheasant shell characteristics to be: elongate to roundish in shape, smooth or with fine spiral striations, usually with variegated colour patterns, lacking interior nacre, anomphalous and with oval aperture. Robertson (1958) described the pheasant shell features as bulimoid and smooth with the exception of several southern African (i.e., *Tricolia bicarinata* Dunker, 1846) and Western Atlantic species (i.e., *Eulithidium bellum* Smith, 1937), which have a strong spiral sculpture. He also described *Gabrielona* shell features as globose, although there are several *Tricolia* species (i.e., *T. neritina* Dunker, 1846, *T. saxatilis* Nangambi & Herbert, 2006, *T. deschampsii* and *T. entomocheila* Gofas, 1993) which are similar in shell size and or shape.

All *Phasianella* shells are much larger in size and generally have a higher spire than species of *Tricolia* and *Gabrielona*. Robertson (1958) further suggested that the periostracum was entirely absent in the Phasianellidae, but in his subsequent studies (Robertson 1985); periostracum was observed in some southern Australian endemics (i.e., *T. tomlini* Gatliff & Gabriel, 1921). Additionally, Robertson (1985) added several further characters that distinguish *Tricolia* from *Phasianella*. Firstly, he suggested that spiral capillary lines are present in *Phasianella* but absent in *Tricolia*. Secondly, he reported the presence of an umbilical chink in *Tricolia*, which is absent in *Phasianella*. Thirdly, he noted the presence of porphyrin shell pigmentation in *Tricolia*, which is lacking in *Phasianella*.

Robertson (1973) provided a detailed shell description of *Gabrielona*, of which many diagnostic characters (i.e., small size, globose outline, low spire and the presence of an umbilicus) had been described in his previous publications. Gofas (1982) described Eastern Atlantic/Mediterranean *Tricolia* species as being porcellanous to translucent, never nacreous, and the whorls more or less convex, smooth, or with delicate microsculpture, and with a trochoid to moderately high spire. Although Hickman & McLean (1990) highlighted a number of problems with previous taxonomic classifications in providing a true diagnosis of taxa, they diagnosed the pheasant shells by lack of interior, their smooth and glossy surface and complex variegated colour pattern. In the same study, they diagnosed Gabrieloninae by the presence of a distinct apertural ridge and a palatal sulcus on the interior of the shell. Tricolinae is the only trochoidean in which there are records of sexual dimorphism in the size of adult shells and in the number of radula teeth (Robertson 1985). Phasianellinae was diagnosed by the presence of a weak lamella that supports the operculum against the

parietal region as the animal emerges or retracts from the shell Hickman & McLean (1990). They also emphasized the presence of spiral capillary lines on the shell surface of this subfamily as previously discussed by Robertson (1985). Hickman & McLean (1990) further suggested that *Tricolia* and *Phasianella* share many morphological characters, making their shells superficially similar. These include similar shell and aperture shape, lack of interior nacre and a variegated colour pattern. However, the presence of fluorescing porphyrins in the shell, absence of spiral capillary lines and the presence of an umbilical chink distinguish *Tricolia* from *Phasianella*. The Tricoliinae lack the palatal sulcus characteristic of the Gabrieloninae and also the parietal lamella characteristic of the Phasianellinae.

1.2.2. Shell pigments

The presence of porphyrin shell pigments, which fluoresce under ultraviolet light was recorded in the Tricoliinae and such pigments were found to be absent in all *Phasianella* and *Gabrielona* species (Robertson 1985).

1.2.3. Shell microstructure

The Phasianellidae has been described as having a plesiomorphic crossed lamellar shell structure, and lack apomorphic nacreous structure of the Turbinidae (Böggild 1930, Hedegaard 1997). A crossed lamellar shell structure is considered plesiomorphic in the class Gastropoda and in the order Vetigastropoda in particular (Hedegaard 1997).

1.2.4. The number of shell muscles

The number of shell muscles present in *Tricolia* has been discussed by Fretter (1955), Marcus & Marcus (1960), Fretter & Graham (1962) and Haszprunar (1985, 1988). Most Trochoidea that have been studied so far have one shell muscle (including the Turbinidae, Robertson 1958). Fretter (1955), however, discovered two shell muscles in *Tricolia pullus* (Linnaeus, 1758), whereas Geiger *et al.* (2008) commented on the double shell muscles in *Tricolia* and its potential ramification for higher classification. Robertson (1958) questioned whether these paired muscles are characteristic of the entire Phasianellidae or not, and recommended further investigation. Marcus & Marcus (1960) also recorded two shell muscles in *Eulithidium affine cruenta* (Robertson, 1958). Hickman & McLean (1990) mentioned the presence of one shell muscle in *Phasianella*. The number of shell muscles in *Gabrielona* is unknown and warrants investigation. A study detailing the number of shell muscles for the whole family is required.

1.2.5. Protoconch

Many early revisions studied the protoconch of the pheasant shells and described it as being typical of vetigastropod (i.e., 1.25 whorls). Robertson (1985) discussed and illustrated the protoconch of the southern Australian *Tricolia rosea* (Angas, 1867) as having strong spiral threads. Such spiral threads are absent in other pheasant shell species.

1.2.6. Operculum

Within the Vetigastropoda, a calcareous operculum has traditionally been considered a unique synapomorphy that unites all the turbinids *sensu lato* (Williams & Ozawa 2006); however, this character is no longer considered to be valid because the Turbinidae *sensu lato* is not monophyletic (Williams *et al.* 2008). Like many other characters, the opercular features of the pheasant shells have become a standard reference among vetigastropod taxonomists. The pheasant shell operculum is calcareous, white, thick, externally convex and smooth, internally slightly concave, and paucispiral with an eccentric nucleus (Pilsbry 1888, Thiele 1929, Robertson 1958, 1973, 1985, Gofas 1982, Hickman & McLean 1990).

The operculum has also been used to distinguish between Trochoidea families i.e., Phasianellidae and Turbinidae have a calcareous, paucispiral operculum, whereas Trochidae and Skeneidae have a corneous, multispiral operculum (Robertson 1958, Hickman & McLean 1990, Williams & Ozawa 2006). There are also reported differences in the operculum structure that separate the Phasianellidae from the Turbinidae, but such differences are not clearly defined (Vovelle 1969). Robertson (1958, 1973) discussed differences in the external opercular surface of *Tricolia*, *Phasianella* and *Gabrielona*. These include the convex and smooth external surface of *Tricolia* and *Phasianella*, and concave external surface of *Gabrielona*. Robertson went on to distinguish how the pheasant shell operculum fits into the aperture when the animal is fully withdrawn. Further differences in the external surface of the *Tricolia* and *Eulithidium* operculum were observed and discussed by Hickman & McLean (1990). That of *Tricolia* is smooth, whereas in *Eulithidium* the operculum has radiating ridges near the labral margin (Robertson 1985, Marincovich 1973, Hickman & McLean 1990).

The fact that juvenile phasianellids possess a perforated or pitted operculum has been shown in *E. bellum* (Robertson 1958). In *Tricolia*, a pitted operculum, with a coarsely granular external surface, and a sub-circular shape has been observed in the adult specimens of *T. saxatilis* (Nangammbi & Herbert 2006). A similar pit has been reported on

the juvenile operculum of *T. (Hiloa) variabilis* (Robertson 1985) suggesting that this might be a juvenile trait, which is concordant with the small size of the species concerned. Robertson (1985) mentioned the absence of a pitted operculum in juvenile specimens of *Phasianella*, but mentioned the occurrence of a pitted operculum in some turbinids (i.e., Colloniinae).

1.2.7. Radula

As in other Trochoidea families, the pheasant shell radula is rhipidoglossate [meaning each row has very numerous marginal teeth (∞); five pairs of lateral teeth (5); and a broadly ovate rachidian tooth with a cusp (1)] and it has previously been suggested that it may present useful characters to discriminate between species (Thiele 1891). Many pheasant shell radulae depart from this basic plan and this is something that appears to have phylogenetic significance. The radula formula of each genus and subgenus is listed in Table 1.3.

Robertson (1958) identified and described four main kinds of pheasant shell radulae. In the first group (*Phasianella*), the rachidian tooth is absent, there are five pairs of laterals and each transverse row of teeth is more or less straight. In the second group (*Gabrielona*), the rachidian tooth is large with a cusp, there are five pairs of laterals and the transverse rows of teeth are also straight. However, Robertson's description of the radula of *Gabrielona* was based on *G. brevis* (non Orbigny) [= *Gabrielona sulcifera*] from the West Indies. Later, Hickman & McLean (1990) erected a new genus *Eugabrielona* and designated *G. sulcifera* as the type species. *Gabrielona sensu stricto*, from the Indo–West Pacific and southern Australia, based on *G. pisinna* has only three pairs of lateral teeth per transverse row and a cusped rachidian tooth (Robertson 1973). In contrast, however, Moolenbeek & Dekker (1993) described a new species, *G. roni* from Indo Arabia, Oman which possesses five pairs of lateral teeth per transverse row and a cusped rachidian tooth. Consequently, the radula structure of *Gabrielona* cannot be resolved until the radula structure of the type species, *G. nepeanensis* (Gatliff & Gabriel, 1908) from southern Australia is studied.

Robertson's third group comprised *Hiloa*, *Eotricolia* [= *Hiloa*] and *Pellax*. In this group, laterals are reduced in number to two or three pairs, each with a hood, and a cusped rachidian tooth. The taxonomic status of these three taxa (*Hiloa*, *Eotricolia* and *Pellax*) is discussed in the introductory section of this chapter. In the fourth and final group (*Tricolia*), the rachidian tooth is large, membranous and without a cusp. The transverse rows of teeth are M-shaped, with five pairs of laterals. Robertson regarded the marginal teeth as fairly similar in all four groups. He also reported four pairs of laterals in the American (Eastern Pacific and Western Atlantic) taxa of *Eulithidium*. More recently, similar observations were

made by other authors (i.e., Marcus & Marcus 1960, Marinovich 1973, Robertson 1985, Hickman & McLean 1990).

In his contribution to “*The Monographs of Marine Mollusca of the Indo–West Pacific*”, Robertson (1985) mentioned a greater radula variation in *Tricolia* and *Gabrielona* species and uniformity in all *Phasianella* species. He described the southern African, subtropical East Africa, Amsterdam and St. Paul Island, Eastern Atlantic/Mediterranean and south–western Australian species of *Tricolia* as having five pairs of laterals per transverse row. In contrast, the Indo–West Pacific species either have five pairs of laterals per transverse row (i.e., *T. fordiana* Pilsbry, 1888) or three pairs [i.e., *T. (Hiloa) variabilis*, *T. indica* Winckworth, 1940 and *T. tristis* Pilsbry, 1903]. He also confirmed that there are four pairs of laterals per transverse row in the Western Atlantic and Eastern Pacific species of *Eulithidium*, and suggested that radula characteristics may have a phylogenetic and zoogeographic significance. He concluded that all the American species may have been derived from one stock missing the outermost lateral tooth. Robertson also noted that the rachidian tooth of the three southern Australian endemic species (*T. tomlini*, *T. rosea* and *T. gabiniiana* Cotton & Godfrey, 1938) is reduced to a narrow vestige. Further observations were made with regard to the rachidian tooth of *T. (Hiloa) variabilis*, which he noted had either one or two central cusps.

Ontogenetic changes in the trochoidean radula were documented by Warén (1990), who examined juvenile specimens of 18 species belonging to the Turbinidae, Tricoliidae and Trochidae. Within the Tricoliidae, Warén studied the radula plan of the type species, *T. pullus*, and he showed that all juvenile specimens pass through profound radula changes before they become adult. In addition, Marcus & Marcus (1960) have shown that ontogenetic changes also happen in *E. affine cruenta*. In contrast, during ontogeny *T. tristis*, *T. (Hiloa) variabilis* and *T. indica* retain the cusped rachidian tooth throughout their life stages, whereas in many species the adult rachidian tooth becomes broadly ovate without a cusp (i.e., *T. pullus*). The M–shape of the rows of teeth, which is considered to be one of the diagnostic characteristics of the Tricoliidae, is considered lost in the following *Tricolia* species: *T. tristis*, *T. (Hiloa) variabilis*, *T. indica*, *T. rosea* and *T. tomlini* (Warén 1990). Warén described the above species as having a pedomorphic modification and that of *T. pullus* and other *Tricolia* species as unmodified. He questioned Robertson’s (1985) interpretation of the rachidian tooth of the Indo–West Pacific species, *T. tristis*, *T. (Hiloa) variabilis* and *T. indica* as a “pseudocentral” (formed by fusion of the innermost lateral teeth).

There are three main conclusions to be drawn from this discussion of pheasant shell radulae. Firstly, the structure of pheasant shells, radula plays a significant role in distinguishing the genera from each other. For example, in *Phasianella* there are five pairs of laterals per transverse row, whereas in *Eulithidium* the number of lateral teeth is four per transverse row, and in *Tricolia* and *Gabrielona*, the number of lateral teeth can be five or three. In terms of the rachidian tooth, this is lacking in *Phasianella*, whereas in *Eulithidium*, *Tricolia* and *Gabrielona* the rachidian tooth is present. There is also great diversity within the *Tricolia* radula. For example, the southern Australian species have a rachidian tooth reduced to a narrow vestige, whereas in some of the Indo–West Pacific species (i.e., *T. (Hiloa) variabilis*), the rachidian tooth is broadly ovate with a cusp, whereas in the type species and the southern African species, the rachidian tooth is broadly ovate without a cusp (Nangammbi & Herbert 2006). Detailed study on the radula of the southern African *Tricolia* species has never been documented. Nonetheless, the radula of *T. adusta* and *T. saxatilis* has recently been described (Nangammbi & Herbert 2006). Finally, the structure of the juvenile radula is different from that of adult with some potentially paedomorphic species retaining the juvenile radula morphology in the adult.

Table 1.3. List of pheasant shell radula formulae for each genus.

Genera/subgenera	Origin	Formula	Transverse rows
<i>Tricolia</i>	Southern Africa	$\infty+5+1+5+\infty$	M-shaped
	Subtropical East Africa	$\infty+5+1+5+\infty$	M-shaped
	Eastern Atlantic/Mediterranean	$\infty+5+1+5+\infty$	M-shaped
	Amsterdam and St. Paul Islands	$\infty+5+1+5+\infty$	M-shaped
	Indo–West Pacific (<i>T. fordiana</i>)		
	southern Australia	$\infty+5+1+5+\infty$	M-shaped
	Northern Japan (<i>T. tristis</i>)	$\infty+5+1+5+\infty$	M-shaped
	Indo–West Pacific (<i>T. indica</i>)	$\infty+3+1+3+\infty$	M-shaped
		$\infty+3+1+3+\infty$	M-shaped
<i>Tricolia (Chromotis)</i>	Southern Africa	$\infty+5+1+5+\infty$	M-shaped
<i>Tricolia (Hiloa)</i>	Indo–West Pacific	$\infty+3+1+3+\infty$	M-shaped
<i>Eulithidium</i>	Eastern Pacific and Western Atlantic	$\infty+4+1+4+\infty$	M-shaped
<i>Phasianella</i>	Southern Africa	$\infty+5+0+5+\infty$	Straight
	Indo–West Pacific		Straight
	South–western Australia		Straight
<i>Gabrielona</i>	Indo–West Pacific (<i>G. pisinna</i>)	$\infty+3+1+3+\infty$	Straight
	Southern Australia (<i>G. nepeanensis</i>)	Unknown	Unknown
	Indo Arabia, Oman (<i>G. roni</i>)	$\infty+5+1+5+\infty$	Straight
<i>Eugabrielona</i>	Caribbean (<i>E. sulcifera</i>)	$\infty+5+1+5+\infty$	Straight

1.2.8. Soft tissue

Brief notes on the external anatomy of the pheasant shells in general were provided by Pilsbry (1888) and Thiele (1929). The anatomy of *Tricolia* has been studied by many authors (i.e., Forbes & Hanley 1849-1850, Clark 1855, Jeffreys 1865, Deshayes 1870, Pelseneer 1899, Fretter 1955, Fretter & Graham 1962, 1977). Pelseneer (1899) studied the anatomy of *T. pullus*, and recorded differences in the left and the right neck-lobes. Marcus & Marcus (1960) studied and drew in detail the anatomy of the Western Atlantic, *E. affine cruenta*. Brief notes on the anatomy of Western Atlantic and Indo-West Pacific species are included in Robertson (1958, 1985).

The first studies on the anatomy of *Phasianella* were those of Cuvier (1808), Quoy & Gaimard (1833-1834), Kiener (1847) and Risbec (1940). Robertson (1958) observed differences in the epipodial tentacles of *Tricolia* and *Phasianella*. Although he incorrectly concluded that neck-lobes were absent in *Phasianella*, he was correct in recording the presence of cephalic lappets, which are lacking in *Tricolia*. The absence of cephalic lappets in *Tricolia* was also reported by Pilsbry (1888). Subsequent to Robertson (1958), several studies have been made on the anatomy of *Tricolia* and *Phasianella*; these studies not only described the presence of neck-lobes in both genera, but also provided useful illustrations (Gofas 1982, 1986, 1993, Robertson 1985, Hickman & McLean 1990, Weidland *et al.* 1998).

Robertson's (1985) description and illustration of the anatomy of *T. pullus* were duplicated from Fretter & Graham (1962) with very few personal observations. Modern literature has added further comparative anatomical data (Gofas 1982, 1986, 1993, Hickman & McLean 1990, Weidland *et al.* 1998, Nangammbi & Herbert 2006). The external anatomy of *T. (Hiloa) variabilis*, *E. affine* (Adams, 1850), *E. pulloides* (Carpenter, 1865), *P. australis* (Gmelin, 1791) and *P. solida* (Born, 1778) were studied and illustrated by Hickman & McLean (1990). They also discussed differences in epipodial and neck-lobe structure between *Tricolia* and *Eulithidium*, recording three epipodial tentacles in *Tricolia* and two in *Eulithidium*. Furthermore, in *Eulithidium*, the left neck-lobe is digitated, while broad and finely fringed in *Tricolia*. They also recorded the presence of cephalic lappets in *Phasianella*, which are absent in *Tricolia* and *Eulithidium*, as noted previously by Robertson (1985).

Gofas (1986) discussed and illustrated the anatomy of the Eastern Atlantic species, *T. pullus* and *T. miniata* (Monterosato, 1884), and described the small Mediterranean species, *T. tingitana* Gofas, 1982 and *T. nordsiecki* (Talavera, 1978). Subsequent to this publication, Gofas (1993) described and illustrated the anatomy of a further small Mediterranean

species, *T. entomocheila*. Differences in the neck–lobes and number of epipodial tentacles of the Eastern Atlantic and the small Mediterranean species have been reported. The Eastern Atlantic species have three pairs of epipodial tentacles with both the right and left neck–lobes broad and finely fringed. Within the small Mediterranean species the neck–lobes and the number of epipodial tentacles are different, for example, in *T. tingitana* the right neck–lobe is broad and flat, whereas the left neck–lobe has 5-7 long digitations. In *T. entomocheila* the right neck–lobe is broad and flat, and the left neck–lobe is reduced to a single tentacle. Furthermore, *T. tingitana* has three pairs of epipodial tentacles, whereas *T. entomocheila* has two pairs.

More recently, Nangammbi & Herbert (2006) provided detailed descriptions of the anatomy of two new southern African species, *T. adusta* and *T. saxatilis*. Similarity in the external anatomy of *T. saxatilis* to the small Mediterranean species *T. tingitana* was also discussed. Despite efforts to restore dried bodies of *Gabrielona* (by rehydration), previous authors have failed to provide information on the external anatomy of this genus (Robertson 1973, Hickman & McLean 1990).

A few conclusions can be drawn from the discussion of external anatomy of pheasant shell genera. Firstly, the anatomy of *Gabrielona* is unknown and warrants investigation. Secondly, there are profound differences between the anatomy of *Eulithidium*, *Tricolia* and *Phasianella*, i.e., the presence of cephalic lappets in *Phasianella*. Thirdly, the anatomy of small (paedomorphic) species differs from that of larger ones.

1.2.9. Jaw

Very little attention has so far been given to the jaw of pheasant shells. Pilsbry (1888) described the jaw in the whole family as rhomboidal and covered with imbricating scales. He illustrated the jaw of *T. fordiana* from Singapore. Robertson (1958, 1985) discussed morphological differences between the *Phasianella* and *Tricolia* jaw. In *Tricolia*, each plate is more or less flat and consists of irregular polygons or slightly overlapping scales, whereas in *Phasianella*, each plate is internally concave, fibrous and not scaly. Robertson (1985) noted that his illustration of the *T. fordiana* jaw did not agree with that given by Pilsbry (1888), indicating a difference in their outlines. Robertson (1958) suggested that the jaw may be an important taxonomic character in this family but is variable and difficult to study. Marcus & Marcus (1960) described the jaw of *E. affine cruenta* as composed of flat lying rods that appear to be scaly on the surface. *Gabrielona* jaw has not yet being studied or recorded. Further detailed study on the jaws of pheasant shells is required.

1.2.10. Sperm morphology

In their examination of the spermatozoa of 11 species of South African vetigastropods from the superfamilies Haliotoidea, Fissurelloidea and Trochoidea, Hodgson & Foster (1992) suggested that within the Trochoidea, the most plesiomorphic sperm are found within the Trochidae and Phasianellidae, whereas the spermatozoa of the Turbinidae exhibit more apomorphic features. In the Trochidae and Phasianellidae, the nucleus has a relatively small U-shaped anterior invagination and the acrosome is undifferentiated and normally comprises $\leq 50\%$ of the total length of the sperm head. In the Turbinidae, the anterior nuclear invagination is wider, and the conical acrosome, the base of which lies within the nuclear invagination, is lengthened, comprising $> 50\%$ of the total head length. Hodgson (1995) has shown that sperm morphology can be used to differentiate between vetigastropod families. He referred to the Trochidae and Phasianellidae spermatozoa as having a barrel-shaped nucleus with a length to breadth ratio $< 4:1$ and a U-shaped anterior invagination. In many species within the two families, the contents of the broadly conical acrosome are uniformly electro-opaque, and the acrosome normally constitutes $\leq 50\%$ of the total head length and has a narrow posterior invagination.

In the Turbinidae, Hodgson (1995) described the spermatozoa as discussed in Hodgson & Foster (1992). To date, no studies have been done to investigate variation in sperm morphology in pheasant shell genera. The above mentioned studies investigated only a few species (i.e., *T. capensis*, *T. pullus*) in order to compare sperm morphology of the Phasianellidae with other trochoidean families. As a result, a study detailing sperm morphology of each genus within the pheasant shells is needed. Hodgson did not note any profound differences within the spermatozoa of Trochidae and Phasianellidae, but noted differences between these two families and Turbinidae.

1.3. PHEASANT SHELL SYSTEMATICS

1.3.1. Morphological data analyses

Robertson (1985) used both primitive and derived morphological characters of the shell, radula, jaws and others to infer phylogenetic relationships among the nine Indo–West Pacific species of *Tricolia*. His analyses identified four species groups as shown in figure 1.1. Clade 1 is composed of all the Eastern Atlantic, Western and South African *Tricolia* species. Clade 2 consists of *T. ios* Robertson, 1985 and *T. indica*. Clade 3 consists of three south–western

Australian species, *T. tomlini*, *T. gabiniana* and *T. rosea*. The final Clade 4 is composed of northern Japan, *T. tristis* and the Indo–West Pacific, *T. (Hilola) variabilis*.

Hickman & McLean (1990) and Hickman (1996) considered the pheasant shells to be the sister–group to the Turbininae and Prisogasterinae. This classification was based on shared teneidial characters as well as the ability to calcify an operculum partially covered by the metapodium. Hickman (1996) included the pheasant shells in her study of the phylogeny and patterns of evolutionary radiation in the Trochoidea based on 43 morphological and behavioural characters. Although the referral of the pheasant shells to the Turbinidae was supported by phylogenetic analysis, the relationship between the three subfamilies could not be resolved (Figs 1.2A, B). Although it was easy to enumerate derived characters that distinguish each of the subfamilies from other Turbinidae, it is difficult to find synapomorphic characters that unite the three subfamilies and distinguish them from the remaining Turbinidae (Hickman & McLean 1990). All three subfamilies are highly derived, but their relationships to the Turbinidae and to one another remain unresolved.

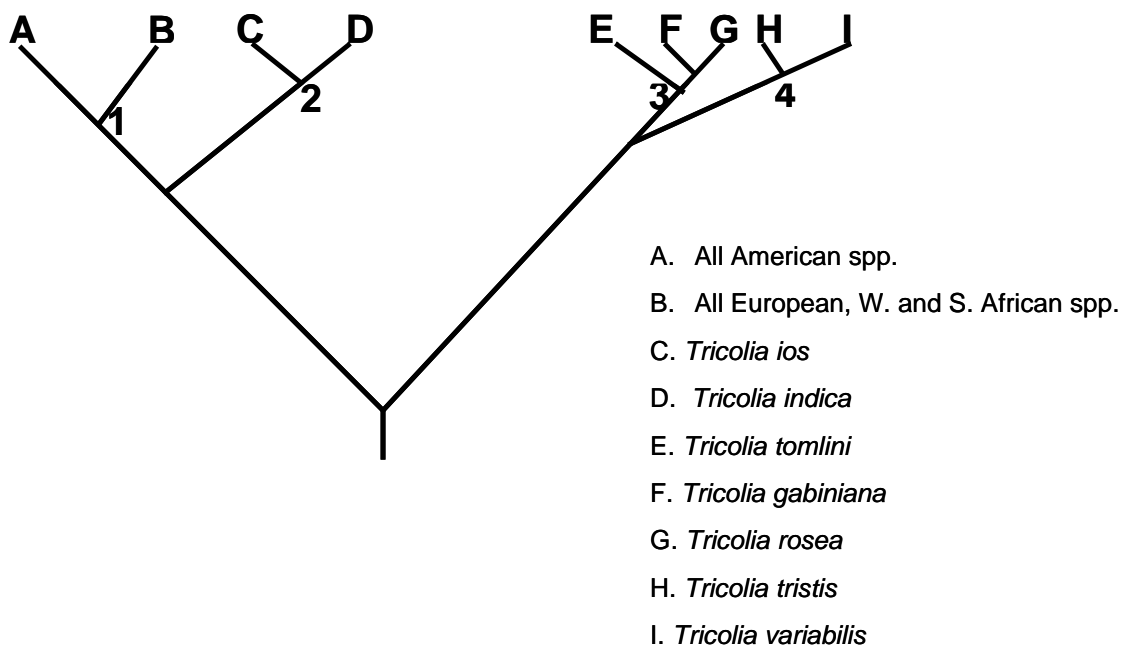


Figure 1.1. Cladogram showing inferred phylogeny and radiation within *Tricolia* by Robertson (1985).

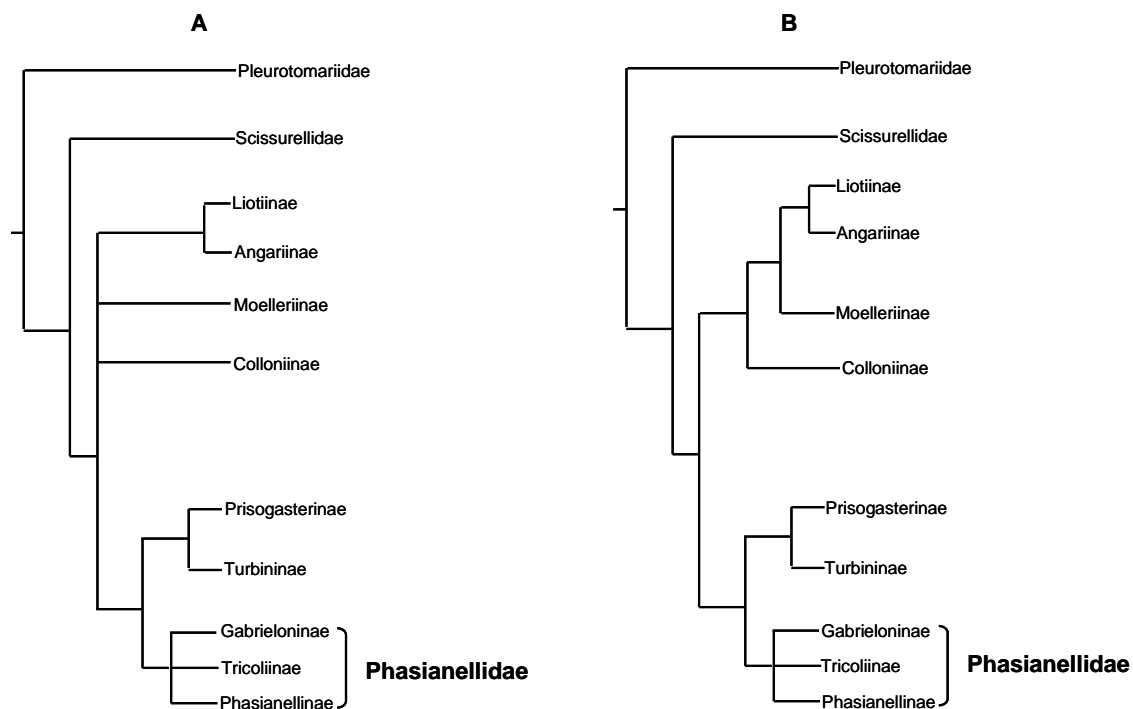


Figure 1.2. (A) Hickman's (1996) consensus of ten 43-step most-parsimonious trees (50% majority rule) for turbinid gastropods based on analysis of morphological and behavioural characters. (B) Hickman's (1996) consensus tree for turbinid gastropods showing the 43 steps and the autapomorphies of terminal groups.

1.3.2. DNA sequence analyses

In a molecular phylogenetic study of the turban shells, Williams & Ozawa (2006) (Figs 1.3, 1.4 herein) presented the first molecular phylogeny to be undertaken on the group, and their results regarding the grouping of the pheasant shells are discussed in section one of this chapter. Using evidence from 18S rRNA, 28S rRNA and the first and second codon positions of the COI gene, these authors proposed three families: Angariidae, Colloniidae and Phasianellidae. The Phasianellidae in their sense includes three turbinid *sensu lato* subfamilies: Phasianellinae, Tricoliinae, and Gabrieloninae. The Turbinidae *sensu stricto*, which traditionally includes the phasianellids, is now divided into Prisogasterinae, Turbininae and Liotiinae. The sister-group of the pheasant shell genera is the Colloniidae (comprising *Bothropoma* Thiele, 1921, *Collonista* Iredale, 1918 and *Homalopoma* Carpenter, 1864).

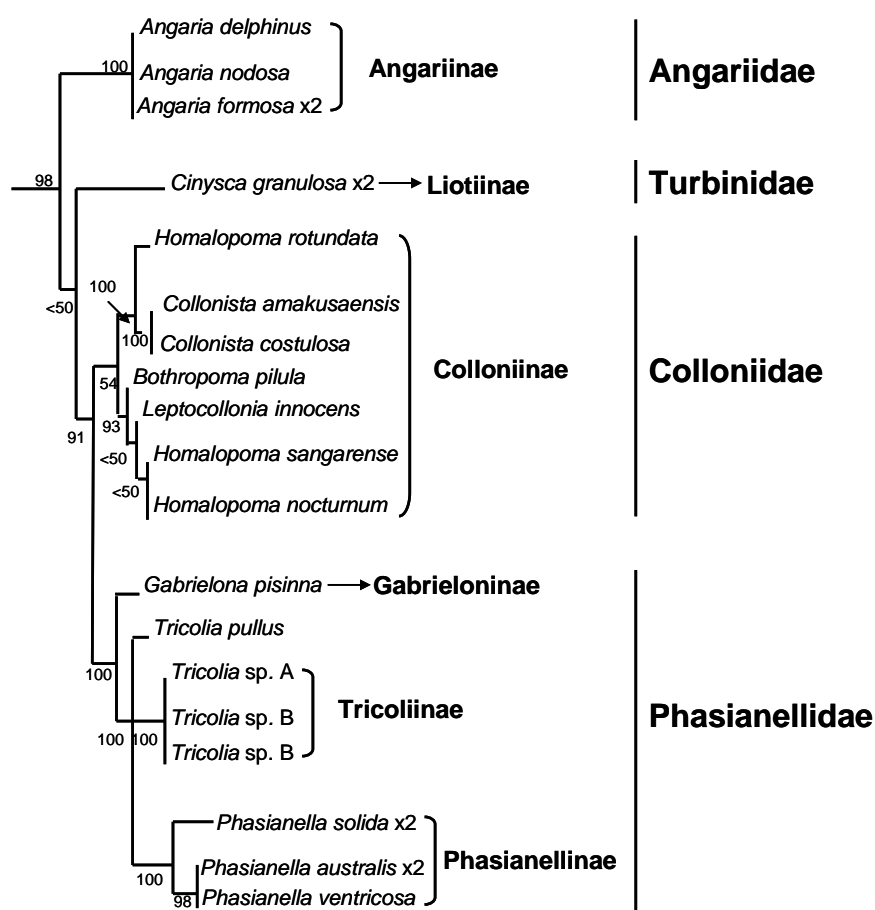


Figure 1.3. Williams & Ozawa's (2006) Bayesian phylogeny for pheasant shells based on 18S rRNA datasets with posterior probability values shown at nodes for each clade.

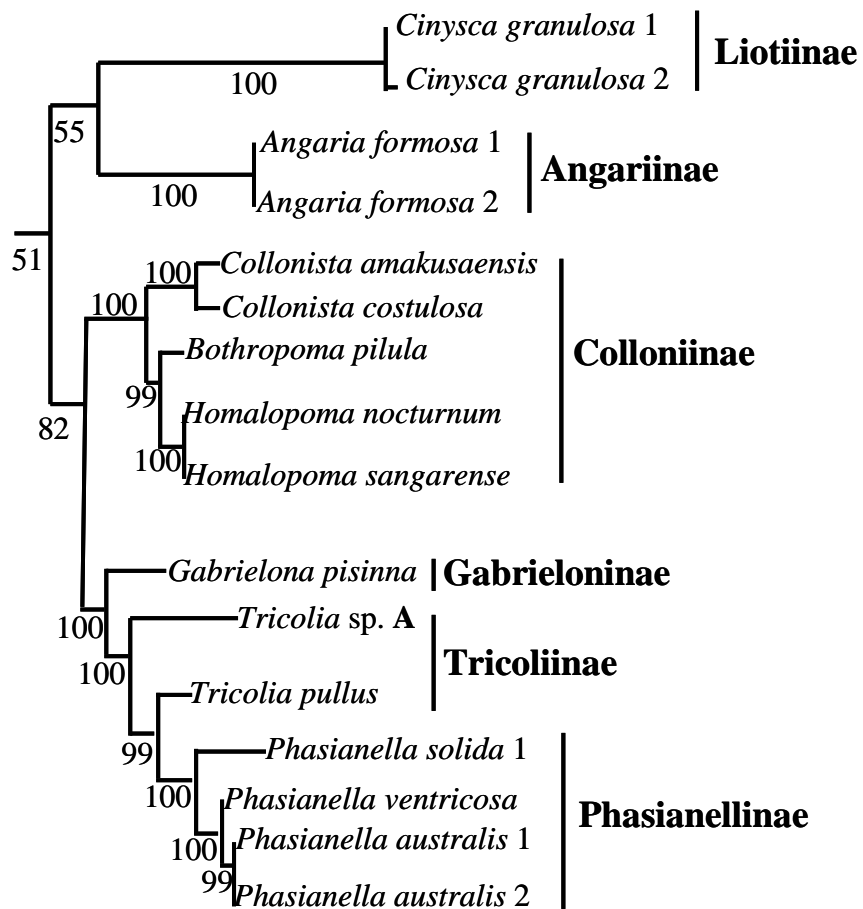


Figure 1.4. Williams & Ozawa's (2006) Bayesian phylogeny of pheasant shells based on combined datasets (18S rRNA + 28S rRNA + COI) with posterior probability values shown at nodes for each clade.

1.4. CURRENT CLASSIFICATION OF THE PHEASANT SHELL SUBFAMILIES

The superfamily Trochoidea Rafinesque, 1815 consists principally of the families Trochidae and Turbinidae. Hickman & McLean (1990) provisionally included, the Skeneidae. These authors further subdivided the Trochidae into 13 subfamilies and 11 tribes, whereas the Turbinidae was subdivided into nine subfamilies Angariinae, Colloniinae, Phasianellinae, Gabrieloninae, Tricoliinae, Prisogasterinae, Turbininae, Liotiinae and Moelleriinae which they further grouped into four informal groups: Angariinae and Colloniinae, Prisogasterinae and Turbininae, Liotiinae and Moelleriinae, Phasianellinae, Gabrieloninae and Tricoliinae. In the Southern Synthesis, Hickman (1998) used the family Turbinidae with the following subfamilies: Liotiinae; Angariinae; Turbininae, Gabrieloninae, Tricoliinae and Phasianellinae. Williams & Ozawa (2006) elevated Angariinae, Colloniinae, Phasianellinae, Gabrieloninae and Tricoliinae to family level within the superfamily Trochoidea, namely Angariidae, Colloniidae and Phasianellidae, leaving the Turbinidae *sensu stricto* to include Prisogasterinae, Turbininae and Liotiinae. In addition, Bouchet & Rocroi (2005) have recently raised Turbinidae to a superfamily level. However, Williams & Ozawa (2006) have shown that the Turbinidae is not monophyletic. Recently, Williams *et al.* (2008) placed Phasianellidae and Colloniidae into a new superfamily, Phasianelloidea.

The Turbinidae has traditionally been considered to be the most primitive family and the Trochidae the most derived (Hickman & McLean 1990). Turbinidae and Phasianellidae are diagnosed by the presence of a calcareous, paucispiral operculum. This character separates them from the Trochidae and the Skeneidae which have a corneous, multispiral operculum. Hickman & McLean (1990), however, differentiated the Turbinidae from the Trochidae on the basis of radula features (rachidian tooth with secondary cusp or attachment flap) and the presence of a long growing edge on the operculum, and from the Skeneidae on the basis of shell size and pigmentation. The monophyly of both the Turbinidae and the Trochidae has been tested, but most authors have failed to resolve relationships within these groups (Geiger & Thacker 2005, Donald *et al.* 2005, Williams & Ozawa 2006). However, Hickman (1996) suggested that there is a great deal of evidence for a monophyletic Turbinidae based on 19 synapomorphies in a parsimony analysis using 43 morphological characters. Although Hickman & McLean (1990) have argued that the pheasant shells should be considered part of the Turbinidae based on ctenidial characters shared with Turbininae and Prisogasterinae and the ability to calcify an operculum partly covered by the metapodium, nonetheless, Williams & Ozawa (2006) have recognized them as the distinct family Phasianellidae, based

on molecular sequence data. The next section will discuss current taxonomic classification of three pheasant shell subfamilies: Tricoliinae, Phasianellinae and Gabrieloninae.

1.4.1. The subfamily Tricoliinae

The Tricoliinae is presently considered to include two genera: *Tricolia* and *Eulithidium* (Hickman & McLean 1990). *Tricolia* has been divided into three subgenera: *Tricolia* (*Tricolia*) comprising approximately 31 species, *Tricolia* (*Hilola*) comprising a single species and *Tricolia* (*Chromotis*) also with a single species. The taxonomy of these subgenera is poorly understood. *Tricolia* (*Hilola*) is confined to the tropical Indo–West Pacific and is represented by *T. (Hilola) variabilis*, whereas *Chromotis* is confined to southern Africa and represented by *T. (Chromotis) neritina*. *Tricolia* is widely distributed in the Atlantic, Indian and Pacific Oceans with approximately 45 species that are found in southern Africa (25), subtropical East Africa (1), Amsterdam and St. Paul Islands (1), Eastern Atlantic/Mediterranean (11), south–western Australia (3), the tropical Indo–West Pacific (3), and northern Japan (1). Williams & Ozawa (2006) found considerable genetic differentiation between three individual specimens of *T. (Hilola) variabilis* from Japan, suggesting the possibility of cryptic species, and concluded that *T. (Hilola) variabilis* may represent at least two different species. This study will evaluate subgeneric names within *Tricolia*, in particular *Chromotis* and *Hilola*, and establish to which of these subgenera the southern African species belong.

1.4.2. The subfamily Phasianellinae

Phasianella (seven species) is to date the only extant genus within the Phasianellinae, and *Buccinum australe* Gmelin, 1791 was subsequently designated as the type species (ICZN 1962: Opinion 630).

1.4.3. The subfamily Gabrieloninae

Gabrieloninae Hickman & McLean (1990) is presently thought to include two extant genera: *Gabrielona* (five species) and *Eugabrielona* (one species) (Hickman & McLean 1990). *Eugabrielona* is monotypic and includes *Gabrielona sulcifera*, whereas *Gabrielona* is represented by several species of which *Phasianella nepeanensis* (Gatliff & Gabriel, 1908) is the type species. The relationship between *Gabrielona* and other supraspecific taxa within the Phasianellidae is not clear. Table 1.4 lists all the currently recognized pheasant shell genera, subgenera and species in the world.

Table 1.4. World list of the pheasant shells.

Subfamily	Genus	Species	Distribution
Tricoliinae	<i>Tricolia</i>	<i>T. adusta</i> Nangammbi & Herbert, 2006	Southern Africa
		<i>T. africana</i> (Bartsch, 1915)	Southern Africa
		<i>T. alfredensis</i> (Turton, 1932)	Southern Africa
		<i>T. bicarinata</i> (Dunker, 1846)	Southern Africa
		<i>T. capensis</i> (Dunker, 1846)	Southern Africa
		<i>T. carinata</i> (Turton, 1932)	Southern Africa
		<i>T. elongata</i> (Krauss, 1848)	Southern Africa
		<i>T. farquhari</i> (Turton, 1932)	Southern Africa
		<i>T. formosa</i> (Turton, 1932)	Southern Africa
		<i>T. fuscomaculata</i> (Turton, 1932)	Southern Africa
		<i>T. insignis</i> (Turton, 1932)	Southern Africa
		<i>T. pallida</i> (Turton, 1932)	Southern Africa
		<i>T. piperata</i> (Turton, 1932)	Southern Africa
		<i>T. kochii</i> (Philippi in Krauss, 1848)	Southern Africa
		<i>T. kochii maculata</i> (Turton, 1932)	Southern Africa
		<i>T. kochii nigra</i> (Turton, 1932)	Southern Africa
		<i>T. kochii viridis</i> (Turton, 1932)	Southern Africa
		<i>T. kraussi</i> (Smith, 1911)	Southern Africa
		<i>T. neritina</i> (Dunker, 1846)	Southern Africa
		<i>T. retrolineata</i> Nangammbi & Herbert, 2008	Southern Africa
<i>T. rufanensis</i> (Turton, 1932)	Southern Africa		
<i>T. rufanensis adjacens</i> (Turton, 1932)	Southern Africa		
<i>T. saxatilis</i> Nangammbi & Herbert, 2006	Southern Africa		

Subfamily	Genus	Species	Distribution
		<i>T. striolata</i> (Turton, 1932)	Southern Africa
		<i>T. tropidophora</i> (Tomlin, 1931)	Southern Africa
		<i>T. ios</i> Robertson, 1985	Southern Africa and subtropical East Africa
		<i>T. munieri</i> (Vélain, 1877)	Amsterdam and St. Paul Islands
		<i>T. gabiniana</i> (Cotton & Godfrey, 1938)	South–western Australia
		<i>T. rosea</i> (Angas, 1867)	South–western Australia
		<i>T. tomlini</i> (Gatliff & Gabriel, 1921)	South–western Australia
		<i>T. fordiana</i> (Pilsbry, 1888)	Tropical Indo–West Pacific
		<i>T. indica</i> (Winckworth, 1940)	Tropical Indo–West Pacific
		<i>T. (Hilola) variabilis</i> (Pease, 1861)	Tropical Indo–West Pacific
		<i>T. algoidea</i> (Pallary, 1920)	Mediterranean
		<i>T. deschampsi</i> Gofas, 1993	Mediterranean
		<i>T. entomocheila</i> Gofas, 1993	Eastern Atlantic
		<i>T. miniata</i> (Monterosato, 1884)	Mediterranean
		<i>T. nordsiecki</i> (Talavera, 1978)	Eastern Atlantic
		<i>T. petiti</i> (Craven, 1882)	Eastern Atlantic

Subfamily	Genus	Species	Distribution
		<i>T. pullus</i> (Linnaeus, 1758)	Eastern Atlantic
		<i>T. punctura</i> Gofas, 1993	Mediterranean
		<i>T. speciosa</i> (von Mühlfeldt, 1824)	Eastern Atlantic
		<i>T. tenuis</i> (Michaud, 1829)	Eastern Atlantic
		<i>T. tingitana</i> Gofas, 1982	Mediterranean
		<i>T. tristis</i> (Pilsbry, 1903)	Northern Japan
	<i>Eulithidium</i>	<i>E. affine</i> (Adams, 1850)	Western Atlantic
		<i>E. adamsi</i> (Philippi, 1852)	Western Atlantic
		<i>E. bellum</i> (Smith, 1937)	Western Atlantic
		<i>E. comptum</i> (Gould, 1855)	Western Atlantic
		<i>E. tessellatum</i> (Potiez & Michaud, 1838)	Western Atlantic
		<i>E. thalassicola</i> (Robertson, 1958)	Western Atlantic
		<i>E. cyclostomum</i> (Carpenter, 1864)	Eastern Pacific
		<i>E. dianthum</i> (McLean, 1970)	Eastern Pacific
		<i>E. macleani</i> (Marincovich, 1973)	Eastern Pacific
		<i>E. perforatum</i> (Philippi, 1848)	Eastern Pacific
		<i>E. phasianella</i> (Philippi, 1849)	Eastern Pacific
		<i>E. pulloides</i> (Carpenter, 1865)	Eastern Pacific
		<i>E. rubrilineatum</i> (Strong, 1928)	Eastern Pacific
		<i>E. substriatum</i> (Carpenter, 1864)	Eastern Pacific

Subfamily	Genus	Species	Distribution
		<i>E. umbilicatum</i> (Orbigny, 1840)	Eastern Pacific
		<i>E. variegatum</i> (Carpenter, 1864)	Eastern Pacific
Gabrieloninae	<i>Gabrielona</i>	<i>G. hadra</i> (Woodring, 1928)	Tropical Indo–West Pacific
		<i>G. nepeanensis</i> (Gatliff & Gabriel, 1908)	Temperate Indo–West Pacific and Australia
		<i>G. pisinna</i> Robertson, 1973	Tropical Indo–West Pacific
		<i>G. raunana</i> Ladd, 1966	Tropical Indo–West Pacific
		<i>G. roni</i> Moolenbeek & Dekker, 1993	Tropical Indo–West Pacific / Indo–Arabia: Oman
	<i>Eugabrielona</i>	<i>E. sulcifera</i> (Robertson, 1973)	Caribbean
Phasianellinae	<i>Phasianella</i>	<i>P. aethiopica</i> Philippi, 1853	Tropical Indo–West Pacific
		<i>P. australis</i> (Gmelin, 1791)	Western Australia
		<i>P. caloundra</i> Iredale, 1927	Tropical Indo–West Pacific / Australia
		<i>P. solida</i> (Born, 1778)	Indo–West Pacific, S. Western Australia, southern Africa
		<i>P. variegata</i> Lamarck, 1822	Western Australia
		<i>P. ventricosa</i> Swainson, 1822	Western Australia
		<i>P. wisemanni</i> Baird, 1873	Tropical Indo–West Pacific

1.5. BIOGEOGRAPHY AND FOSSIL RECORD

1.5.1. The fossil record and ages of pheasant shell genera

The oldest phasianellid fossil known occurs in European Paleocene deposits (Cossmann 1918). Robertson (1958) recorded a few fossil species in the Pliocene (5.332 to 1.806 mya) and Quaternary (1.806 mya to present) beds. *Tricolia* first appeared in the Paleocene (65.5 ± 0.3 to 55.8 ± 0.2 mya). *Hiloa*, *Chromotis* and *Eotricolia* are all Recent, whereas the extinct *Aizyella* and *Phasianochilus* are both well represented in the Eocene of the Paris Basin, with specimens preserving remnants of pigmentation pattern and including operculum (Robertson 1958, Hickman & McLean 1990). Phasianellinae first appeared in the Miocene (23.03 to 5.33 mya) of the Indian Ocean in Java and Australia (Hickman & McLean 1990). Robertson (1973) refigured specimens of “*Tricolia*” hadra Woodring (1928) from the Bowden Formation in Jamaica, West Indies and assigned it to *Gabrielona* (Hickman & McLean 1990). Although the operculum of Woodring’s species is not known, the shell clearly preserved the palatal sulcus that distinguishes it as member of the Gabrieloninae. *Gabrielona* was previously thought to have appeared during the Miocene in Jamaica, based on Woodring’s material. Donovan *et al.* (1998) stated that the Bowden Formation formed during the Pliocene and not the Miocene as previously thought. This Caribbean material, however, belongs to *Gabrielona* (*Eugabrielona*) Hickman & Mclean 1990, the Indo–West Pacific *Gabrielona sensu stricto* is only known from the Holocene. A summary of the age of pheasant shell genera is listed in Table 1.5.

1.5.2. Origin of pheasant shells

The origins of the various pheasant shell taxa around the globe have received very little attention, and consequently, the historical biogeography underlying the present day distribution is largely unknown. It was previously hypothesized that the Phasianellidae was derived from a trochoidean stock in Europe and spread around the world by way of the Tethys Sea, but no further information was provided (Robertson 1958). Previously, there have been suggestions of dispersal events to the northern Atlantic (Ridgeway *et al.* 1998) and Eastern Pacific (Powell 1973) through the Tethys Seaway, before its closure in the Middle Miocene (Koufopanou *et al.* 1999). The Phasianellidae origin predated the closure of the Tethys Sea.

Table 1.5. Estimated age of the origins of supraspecific taxa and their distribution based primarily on Keen & Robertson (1960), Robertson (1985) and Kensley (1972).

Genus/subgenus	Geological time	Distribution
<i>Tricolia</i>	Paleocene – Recent	Southern Africa East Africa Eastern Atlantic and Mediterranean Southern Australia Indo–West Pacific Amsterdam and St. Paul Islands Northern Japan
<i>T. (Chromotis)</i>	Pliocene – Recent	Southern Africa
<i>T. (Aizyella)</i>	Eocene (Paris Basin)	Europe
<i>T. (Phasianochilus)</i>	Eocene (Paris Basin) – Oligocene	France
<i>T. (Hiloa)</i>	Recent	Indo–West Pacific
<i>T. (Eotricolia)</i>	Recent	Japan
<i>Eulithidium</i>	Lower Miocene – Recent	Eastern Pacific and Western Atlantic
<i>Phasianella</i>	Miocene (Java, Australia) – Recent	Southern Australia and Indo–West Pacific
<i>Gabrielona</i>	Recent	Southern Australia and Indo–West Pacific
<i>Eugabrielona</i>	Pliocene (Jamaica) – Recent	Caribbean

1.6. DISTRIBUTION OF THE PHEASANT SHELLS

Tricolia is distributed widely in the Atlantic, Indian and Pacific Oceans with approximately 32 currently recognized species. The genus is represented by ca 13 valid and described species in southern Africa (discussed herein), one species in subtropical East Africa (Robertson 1985, Herbert 1991); 11 species in the Eastern Atlantic/Mediterranean (Gofas 1982, 1986, 1993, CLEMAM 2005); three species in southern Australia (Robertson 1980, 1985, Wilson 1993); one species in Amsterdam and St. Paul Islands (Robertson 1985), one species in northern Japan (Robertson 1985), and the entire tropical Indo–West Pacific with three species (Robertson 1974, 1985, Wilson 1993, Sasaki *in* Okutani 2000).

Eulithidium occurs in the Western Atlantic and Eastern Pacific oceans, with 10 species in the Eastern Pacific (Keen 1958, Abbott 1974, Turgeon *et al.* 1998), and six species in the Western Atlantic (Robertson 1958, Abbott 1974, Turgeon *et al.* 1998, Rosenberg 2005).

Phasianella and *Gabrielona* are found in the Indian Ocean with approximately seven species representing *Phasianella* and five species representing *Gabrielona* (Pilsbry 1888, Robertson 1973, Wilson 1993). *Eugabrielona* occurs in the western Atlantic Ocean (Caribbean) and comprises a single species (Hickman & McLean 1990). A list of all currently recognized genera, subgenera and species of the pheasant shell of the world is presented in Table 1.4.

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CHAPTER 2: A TAXONOMIC REVISION OF THE SOUTHERN AFRICAN PHEASANT SHELL FAUNA

ABSTRACT

All pheasant shells species known to occur in southern Africa are discussed based on their morphological characters. *Phasianella solida* is documented herein as an element of the southern African marine biota for the first time. Observations on the teleoconch, protoconch, operculum, radula and external anatomy are given for 14 of the 16 species discussed herein. For *T. retrolineata*, only the operculum data were available.

New synonyms: *Phasianella farquhari* Turton, 1932, *Phasianella rufanensis* Turton, 1932 and *Phasianella rufanensis adjacens* Turton, 1932 = *Tricolia africana* (Bartsch, 1915); *Phasianella alfredensis* Turton, 1932 = *Tricolia elongata* (Krauss, 1848); *Phasianella pallida* Turton, 1932 = *Tricolia formosa* (Turton, 1932); *Phasianella carinata* Turton, 1932, *Phasianella fuscomaculata* Turton, 1932, *Phasianella kochii maculata* Turton, 1932, *Phasianella kochii nigra* Turton, 1932 and *Phasianella kochii viridis* Turton, 1932 = *Tricolia kochii* (Philippi in Krauss, 1848); *Phasianella piperata* Turton, 1932 = *Tricolia striolata* (Turton, 1932).

Holotypes figured: *Gena lineata* Adams, 1850; *Phasianella africana* Bartsch, 1915; *Phasianella alfredensis* Turton, 1932; *Phasianella bicarinata* Dunker, 1846; *Phasianella carinata* Turton, 1932; *Phasianella elongata* Krauss, 1848; *Phasianella farquhari* Turton, 1932; *Phasianella formosa* Turton, 1932; *Phasianella rufanensis* Turton, 1932; *Phasianella rufanensis adjacens* Turton, 1932; *Phasianella fuscomaculata* Turton, 1932; *Phasianella pallida* Turton, 1932; *Phasianella piperata* Turton, 1932; *Phasianella insignis* Turton, 1932; *Phasianella striolata* Turton, 1932; *Tricolia adusta* Nangammbi & Herbert, 2006; *Tricolia retrolineata* Nangammbi & Herbert, 2008; *Tricolia saxatilis* Nangammbi & Herbert, 2006.

In terms of diversity and biogeography, a total number of 31 pheasant shell species has been described or recorded from this region of which 16 represent valid species or records, 13 are synonyms and two represent incorrect identifications. The following taxa are southern African endemics: *T. adusta*, *T. africana*, *T. bicarinata*, *T. capensis*, *T. elongata*, *T. formosa*, *T. insignis*, *T. kochii*, *T. kraussi*, *T. neritina*, *T. retrolineata*, *T. saxatilis* and *T. striolata*. *Hilola variabilis* and *P. solida* are tropical Indo–West Pacific species, while *T. ios* is a tropical East

African taxon. *Tricolia pullus* and *T. tenuis* are European taxa incorrectly recorded from South Africa.

The greatest diversity of pheasant shell species occurs between Durban and East London and between Cape Agulhas and Cape Town with both coastal intervals having 11 species. Between Kosi Bay and Durban and also East London and Port Elizabeth six species occur. The east (between Quirimba and Kosi Bay, three tropical species) and the west (between Cape Town and Benguela, three cold-temperate species) coastal regions have the lowest number of species. The geographic regions show increased faunal turnover at the subtropical-warm-temperate boundary, between the Mbashe River and East London, and also at the warm-temperate-cold-temperate boundary, between Cape Agulhas and Cape Town.

2.1. INTRODUCTION

Even though the southern African pheasant shell fauna contains many conspicuous and aesthetically appealing species, study of the group has remained in a state of neglect. To date, only *Tricolia* is discussed in the southern African malacological literature. Despite being well represented in samples from near-shore, subtidal reef habitats in eastern South Africa, members of *Phasianella* have up until now not been identified as elements of the southern African marine biota.

The southern African pheasant shell species were treated by Dunker (1846, as *Phasianella*), Krauss (1848, as *Phasianella*), Smith (1911, as *Phasianella*), Bartsch (1915, as *Phasianella*), Tomlin (1931, as *Phasianella*), Turton (1932, as *Phasianella*), and Barnard (1963, as *Tricolia*) (Table 2.1). In his revision of the local marine Mollusca, Barnard (1963) skirted the *Tricolia* issue, providing little clarity and the species-level taxonomy of local representatives of this genus remain chaotic. This is in no small part due to the endeavours of Turton (1932) who had little understanding of intraspecific variation and described most of his species based only upon beach-worn material.

No major systematic revision has been done on the southern African pheasant shells. There have been several subsequent studies discussing some of the commonly used names (i.e., Philippi 1853, Reeve 1862, Troschel 1878, Sowerby 1887, Pilsbry 1888, Sowerby 1892, Barnard 1951, Day 1969, Kensley 1972, 1973, 1977, Kilburn & Rippey 1982, Robertson 1985, Steyn & Lussi 1998, Herbert & Warén 1999), new regional records (Herbert 1991) and

new species (Nangammbi & Herbert 2006, 2008), but none of these have covered all of the local species and the described or recorded taxa have never been subjected to a critical review. Therefore, the pheasant shells are greatly in need of a modern revision. Globally, the most recent systematic studies on the group have included only the Eastern Pacific, Western Atlantic, Indo–West Pacific, southern Australian and Eastern Atlantic–Mediterranean species (i.e., Robertson 1958, 1973, 1974, 1977, 1980, 1985, Wilson 1993, Gofas 1982, 1986, 1993).

In addition, there is confusion regarding some of the 19th century names and which species they in fact represent. A further complication is the fact that shell form and colouration may be markedly influenced by the differing environmental conditions prevailing to the west and east of the Cape peninsula, resulting what might in reality be phenotypically diagnosable ecomorphs, rather than evolutionary distinct species.

A total of 31 nominal pheasant shell taxa have been described or recorded from this region, but perhaps as few as 50% of these represent genuinely distinct species. Resolution of these problems can only be addressed in the context of a thorough modern revision, using additional data from DNA sequences to shed light on morphologically difficult problems associated with environmental variability. However, even with acknowledgement of relatively high levels of synonymy, the southern African pheasant shell radiation is probably the most diverse phasianellid genus in this region.

Since there has been no major systematic revision published on the southern African pheasant shells and the existing information is scattered in the literature, this chapter aims to revise the southern African pheasant shells based on traditional morphological features of the shell, operculum, protoconch, radula and external anatomy (largely unknown to date with regard to the southern African fauna). Moreover, the results obtained from DNA studies have influenced decisions regarding generic referral, particularly in the taxon *Hiloa*.

Table 2.1. A list of the nominal pheasant shell species described or recorded in southern Africa. All taxa marked by an asterisk (*) represent southern African endemics.

Species	First record
<i>Hiloa variabilis</i> (Pease, 1861)	Herbert 1991
<i>Phasianella jaspidea</i> Reeve, 1862	Barnard 1963
<i>Phasianella solida</i> (Born, 1778)	This study
<i>Tricolia adusta</i> Nangammbi & Herbert, 2006*	Nangammbi & Herbert 2006
<i>Tricolia africana</i> (Bartsch, 1915)*	Bartsch 1915
<i>Tricolia alfredensis</i> (Turton, 1932)*	Turton 1932
<i>Tricolia bicarinata</i> (Dunker, 1846)*	Dunker 1846
<i>Tricolia capensis</i> (Dunker, 1846)*	Dunker 1846
<i>Tricolia carinata</i> (Turton, 1932)*	Turton 1932
<i>Tricolia elongata</i> (Krauss, 1848)*	Krauss 1848
<i>Tricolia farquhari</i> (Turton, 1932)*	Turton 1932
<i>Tricolia formosa</i> (Turton, 1932)*	Turton 1932
<i>Tricolia fuscomaculata</i> (Turton, 1932)*	Turton 1932
<i>Tricolia insignis</i> (Turton, 1932)*	Turton 1932
<i>Tricolia ios</i> Robertson, 1985	Herbert 1991
<i>Tricolia pallida</i> (Turton, 1932)*	Turton 1932
<i>Tricolia piperata</i> (Turton, 1932)*	Turton 1932
<i>Tricolia kochii</i> (Philippi <i>in</i> Krauss, 1848)*	Philippi <i>in</i> Krauss 1848
<i>Tricolia kochii maculata</i> (Turton, 1932)*	Turton 1932
<i>Tricolia kochii nigra</i> (Turton, 1932)*	Turton 1932
<i>Tricolia kochii viridis</i> (Turton, 1932)*	Turton 1932
<i>Tricolia kraussi</i> (Smith, 1911)*	Smith 1911
<i>Tricolia neritina</i> (Dunker, 1846)*	Dunker 1846
<i>Tricolia retrolineata</i> Nangammbi & Herbert, 2008*	Nangammbi & Herbert 2008
<i>Tricolia rufanensis</i> (Turton, 1932)*	Turton 1932
<i>Tricolia rufanensis adjacens</i> (Turton, 1932)*	Turton 1932
<i>Tricolia saxatilis</i> Nangammbi & Herbert, 2006*	Nangammbi & Herbert 2006
<i>Tricolia striolata</i> (Turton, 1932) *	Turton 1932
<i>Tricolia tropidophora</i> (Tomlin, 1931)*	Tomlin 1931
Incorrectly identified records	
<i>Tricolia pullus</i> (Linnaeus, 1758)	Turton 1932
<i>Tricolia tenuis</i> (Philippi, 1844)	Krauss 1848

2.2. MATERIALS AND METHODS

2.2.1. Source and reference material

Material in the Natal Museum collection formed the main resource for the morphology-based, species discrimination component of this study (approx. 460 lots with in excess of 5000 specimens). This was supplemented by material in the South African and East London Museums. Intertidal samples have been built up during the course of many years of institutional field-work. Dredging undertaken by the staff of the Natal Museum has provided much additional material including undescribed species and live-taken specimens of subtidal species previously known only from dead shells. The majority of specimens of tropical species have been collected during SCUBA diving field-work in Zululand. The valid names for these were determined by comparison with type specimens and original descriptions of the described nominal taxa loaned from Oxford University Museum of Natural History, Natural History Museum of London, Humboldt University Museum, Berlin and Muséum National d'Histoire Naturelle, Paris. Each valid species was then re-described and illustrated in detail. All material examined is listed under locality data of each species.

2.2.2. Field collection and study

This study involved collection of new material in the field. The main aims of collecting new specimens were: to obtain fresh material for DNA sequencing, to obtain more precise habitat data for each taxon, and to obtain material that could be studied and illustrated alive before preservation. Most of the available representative museum specimens are either dried shells or preserved in 70% ethanol. The field-work was done along the South African coastline, covering the three marine biogeographical provinces. Along the Atlantic Ocean, specimens were collected from: Cape Point, Scarborough (34.199°S:18.372°E), Kommetjie (34.140°S:18.320°E), Oudekraal (33.985°S:18.356°E), Camp's Bay (33.956°S:18.375°E), Sea Point (33.917°S:18.367°E), Three Anchor Bay (33.905°S:18.397°E), Mouille Point (33.899°S:18.404°E), Granger Bay (33.371°S:18.408°E), Yzerfontein (33.347°S:18.152°E), Robben Island (33.818°S:18.379°E) and Saldanha Bay (33.043°S:17.972°E). Along the South Western Cape, field-work was done at Hermanus (34.417°S:19.233°E), Hawston (34.401°S:19.122°E), Betty's Bay (34.371°S:18.893°E) and various localities in False Bay. In the southern Cape, specimens were collected from Jeffrey's Bay (34.050°S:24.917°E), Knysna (34.082°S:23.063°E), Buffel's Bay (34.083°S:22.958°E), Reebok Reef (34.079°S:22.171°E), Mossel Bay (34.183°S:22.133°E), Still Bay (34.383°S:21.450°E), Struis Bay (34.809°S:20.057°E) and Cape Agulhas (34.824°S:20.017°E). In KwaZulu-Natal, field-

work was done at Sodwana Bay (27.533°S:32.683°E), Shaka's Rock (29.517°S:31.233°E), Umdloti (29.683°S:31.113°E), Park Rynie (30.317°S:30.733°E) and Mtwalume (30.483°S:30.633°E).

Many species were collected on the intertidal rocky shores on foot, but others were collected by SCUBA diving on subtidal reef habitats. Stones covered with algal turf and other marine encrustations were collected at depths from 10-40 m and brought to the surface where they were scrubbed and cleaned thoroughly in a bucket of seawater. The debris accumulated in the bucket was then examined under the dissecting microscope and phaeotrichia specimens were extracted. Assistance in collecting subtidal reef specimens was obtained from colleagues listed under acknowledgements, who were surveying local subtidal reef biodiversity.

2.2.3. Laboratory study of living animals

Live collected animals were observed under a dissecting microscope in fresh seawater immediately after collection. A series of sketches and notes for each animal were made including body colouration, cephalic tentacles, cephalic lappets, number and size of the epipodial tentacles, neck-lobe size and digitations, and epipodial sense organs. Final line drawings presented in this chapter were made by L. Davis, Natal Museum.

2.2.4. Specimen preservation and preparation

For anatomical observations, living animals were preserved in 70% ethanol after relaxation for 12 hours in 7% MgCl₂ to prevent the head-foot retracting. For DNA sequencing material, the shells were firstly cracked to ensure rapid penetration of the ethanol, and were subsequently preserved in 100% ethanol without prior relaxation. The ethanol was replaced several times before long-term storage. For study of the protoconch, shells were cleaned with warm water and sonicated briefly. Radulae were dissected out, macerated in dilute 20% sodium hydroxide (NaOH) for ten minutes at room temperature, rinsed several times in clean water, sonicated briefly, air-dried via 70% alcohol and mounted on stubs using double-sided tape.

2.2.5. Scanning electron microscope and photography

Morphological features of the protoconch were observed with special reference to the number of whorls, apex shape, terminal lip and superficial sculpture as previously described by Herbert (1987) and Sasaki (1998). Morphological features of the operculum were observed with special reference to the shape, sculpture and presence of the exterior pit.

Radula features such as the rachidian tooth, number of lateral teeth, morphology of marginal teeth, cusps of innermost laterals and base plates were studied. Gold-coated specimens were observation at low accelerating voltage (5-10 kV) in a Hitachi S-570 scanning electron microscope. Photographs of shells were taken using a Nikon D70 camera with 55 mm AF Micro-Nikkor lens and extension tubes, or a Leica MZ16 stereomicroscope with automontage capacity [Syncroscopy].

2.3. RESULTS

In this chapter, morphological characters of the shell, protoconch, operculum, radula and external anatomy have been studied for each of the southern African pheasant shell species and representative sample from south-western Australia, America and the tropical Indo-West Pacific have been included (Table 2.2). A morphological character matrix and their coding are presented in Table 2.3.

Table 2.2. Morphological characters separating Phasianelloidea genera and species groups from each other.

Character	<i>Tricolia</i>	S. Australia <i>Tricolia</i>	<i>Eulithidium</i>	<i>Hiloa</i>	<i>Phasianella</i>	<i>Gabrielona</i>
Shell shape	turbiniform/bulimiform/globose	turbiniform/bulimiform	turbiniform	turbiniform	bulimiform	globose
Spiral capillary lines	absent	absent	absent	absent	present	absent
Umbilical chink	open	open	open	open	closed	open
Shell pigments porphyrins	present	present	present	present	absent	absent
Shell with apertural ridge and internal palatal sulcus	absent	absent	absent	absent	absent	present
Parietal region of shell with weak lamella that supports the operculum	absent	absent	absent	absent	present	absent
Operculum sculpture	smooth/distinctly granulate surface	smooth	with radiating ridges on labral margin	distinctly granulate surface	smooth	smooth
External surface of operculum	convex	convex	convex	convex	convex	concave
Marginal ridge of operculum	sunken	sunken	sunken	sunken	sunken	raised
Parietal edge of operculum	convex	convex	convex	convex	concave	concave
Protoconch shape	low	low/high	low	high	low	low

Character	<i>Tricolia</i>	S. Australia <i>Tricolia</i>	<i>Eulithidium</i>	<i>Hiloa</i>	<i>Phasianella</i>	<i>Gabrielona</i>
Protoconch sculpture	smooth/fine spiral lines	smooth/strong spiral cords	smooth/fine spiral lines	Smooth/fine spiral lines	smooth	granulated
Rachidian tooth of the radula	broadly ovate without a cusp	reduced to narrow vestige	broadly ovate without a cusp	Well developed with a prominent cusp	absent	broadly ovate with a cusp
Number of lateral teeth	5	5	4	3	5	3/5
Number of shell muscles	2	2	2	2	1	unknown
Cephalic lappets	absent	absent	absent	absent	present	absent
Number of epipodial tentacles	3	3	2	3	3	3
Neck-lobe digits	digitate on both sides/left-lobe digitate and right-lobe smooth	digitate on both sides	left-lobe digitate and right-lobe finely fringed	digitate on both sides	digitate on both sides	both lobes smooth

Morphological characters of pheasant shells and outgroups

Shell

1. Shell shape: 0 = globose, 1 = bulimoid, 2 = neritiform.
2. Spiral capillary lines: 0 = absent, 1 = present

Protoconch

3. Protoconch sculpture: 0 = smooth or with fine spiral lines, 1 = rough granulate surface.
4. Terminal lip of protoconch: 0 = straight, 1 = uniformly convex, 2 = sharply angular, ? = unknown.
5. Protoconch shape: 0 = protoconch low/depressed, apex bluntly rounded, 1 = protoconch exert, apex sharply rounded.

Operculum

6. Operculum shape: 0 = sub-circular, 1 = sub-ovate.
7. External surface of operculum: 0 = flat, 1 = convex, 2 = concave.
8. Operculum sculpture: 0 = distinctly granulate surface, 1 = smooth on the columella side and with radiating ridges on the labral side, 2 = more or less smooth or with fine spiral lines.
9. Marginal ridge of operculum: 0 = sunken, 1 = raised, 2 = absent.
10. Parietal edge of operculum: 0 = convex, 1 = concave.
11. Presence of an exterior pit on the operculum: 0 = present in adult, 1 = present in juvenile, 2 = absent.

External anatomy

12. Cephalic lappets: 0 = reduced or absent, 1 = present and well developed.
13. Number of epipodial tentacles: 0 = 4+ pairs, 1 = 3 pairs, 2 = 2 pairs.
14. Neck-lobe: 0 = poorly developed or present as individual digits, 1 = well developed.
15. Neck-lobe digits: 0 = digitated on both sides, 1 = one digitated and one smooth, 2 = both smooth, (-) inapplicable.
16. Neck-lobe size: 0 = equal, 1 = not equal, (-) inapplicable.
17. Middle epipodial tentacle: 0 = very small, 1 = slightly smaller, 2 = equal to others, (-) inapplicable.
18. Number of sense organs at the base of the first epipodial tentacle on left: 0 = one, 1 = two, ? = unknown.

Radula

19. Transverse rows of radula: 0 = M-shape, 1 = v-shape.

20. Central tooth: 0 = broadly ovate with cusp, 1 = broadly ovate without a cusp, 2 = reduced to a narrow vestige, cusp absent, 3 = absent.

21. Number of lateral teeth: 0 = 5 pairs, 1 = 4 pairs, 2 = 3 pairs.

22. Morphology of the marginal teeth: 0 = inner marginals with numerous ectocones and endocones ectocone, 1 = inner marginal bifid or notched interlocking with two notches on inner base of cusps of next outer tooth, 2 = inner marginal with one strong undivided ectocone.

23. Cusps of innermost three lateral teeth: 0 = multidentate/multicusped, 1 = mesocone with one or more endocone and one or more ectocone.

Table 2.3. Morphological character matrix of 23 characters for 22 Phasianelloidea taxa and for the outgroup taxa, *Collonista*, *Bothropoma* and *Homalopoma*.

Genus	Subgenus	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Tricolia</i>		<i>adusta</i>	1	0	0	2	0	1	1	2	0	0	2	0	1	1	0	0	1	0	0	1	0	2	0
<i>Tricolia</i>		<i>africana</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>bicarinata</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>capensis</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>elongata</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>formosa</i>	1	0	0	2	0	1	1	2	2	0	2	0	1	1	0	0	1	0	0	1	0	2	0
<i>Tricolia</i>		<i>insignis</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>kochii</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>kraussi</i>	1	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>saxatilis</i>	0	0	0	1	0	0	1	0	2	0	0	0	1	1	1	1	0	0	0	1	0	2	0
<i>Tricolia</i>	<i>Chromotis</i>	<i>neritina</i>	2	0	0	1	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Hilola</i>		<i>variabilis</i>	1	0	0	0	1	0	1	0	2	0	1	0	1	1	0	0	2	?	1	0	2	0	1
<i>Tricolia</i>		<i>ios</i>	1	0	0	2	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>fordiana</i>	1	0	0	2	0	1	1	2	2	0	2	0	1	1	0	0	1	?	0	1	0	2	0
<i>Tricolia</i>		<i>pullus</i>	1	0	1	2	0	1	1	2	2	0	2	0	1	1	0	0	1	1	0	1	0	1	0
<i>Tricolia</i>		<i>tingitana</i>	0	0	1	1	0	0	1	2	2	0	2	0	1	1	1	1	0	?	0	1	0	1	0
<i>Tricolia</i>		<i>tomlini</i>	1	0	0	?	1	0	1	0	2	0	2	0	1	1	0	0	2	?	1	2	0	2	0
<i>Eulithidium</i>		<i>affinis</i>	1	0	0	2	0	1	1	1	2	0	2	0	2	1	0	1	1	?	0	1	1	0	0
<i>Eulithidium</i>		<i>variegatum</i>	1	0	0	2	0	1	1	1	2	0	2	0	2	1	0	1	1	?	0	1	1	0	0
<i>Gabrielona</i>		<i>pisinna</i>	0	0	1	0	0	1	2	2	1	1	2	0	1	1	2	1	2	?	1	0	2	0	0
<i>Phasianella</i>		<i>australis</i>	1	1	0	2	0	1	1	2	2	1	1	1	1	1	0	0	1	0	1	3	0	1	1
<i>Phasianella</i>		<i>solida</i>	1	1	0	2	0	1	1	2	2	1	1	1	1	1	0	0	1	0	1	3	0	1	1
<i>Collonia</i>		outgroup	0	0	0	0	0	0	0	2	0	0	0	0	0	0	9	9	9	?	0	0	0	0	0
<i>Homalopoma</i>		outgroup	0	0	1	0	0	0	0	2	2	0	2	0	0	0	9	9	9	?	0	0	0	0	0
<i>Bothropoma</i>		outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	9	9	?	0	0	0	2	1

2.3.1. Shell shape, surface or sculpture

Species of pheasant shells generally have a turbiniform, globose or bulimiform shell shape (Fig. 2.1A, C, D). However, *T. neritina* has a neritiform shape similar to that of the species belonging to the Neritidae (Fig. 2.1B). Shell shape is intermediate between *Tricolia* since some species have a bulimiform shape of *Phasianella*, i.e., *T. elongata* and others have a globose shape of *Gabrielona*, i.e., *T. saxatilis*. This character is therefore not useful to distinguish among genera within the Phasianelloidea. *Gabrielona* species are globose and lower-spired, whereas *Phasianella* species are bulimiform with high spire. Spiral capillary lines are an autapomorphic character useful to distinguish *Phasianella* species from other members of the Phasianelloidea. Distinct spiral sculpture was observed in few of the southern African *Tricolia* species and these include: *T. bicarinata*, *T. insignis*, *T. striolata*, *T. kraussi* and *T. kochii*, but differs in the level of strength. The only American species with strong spiral cords is *E. bellum*.

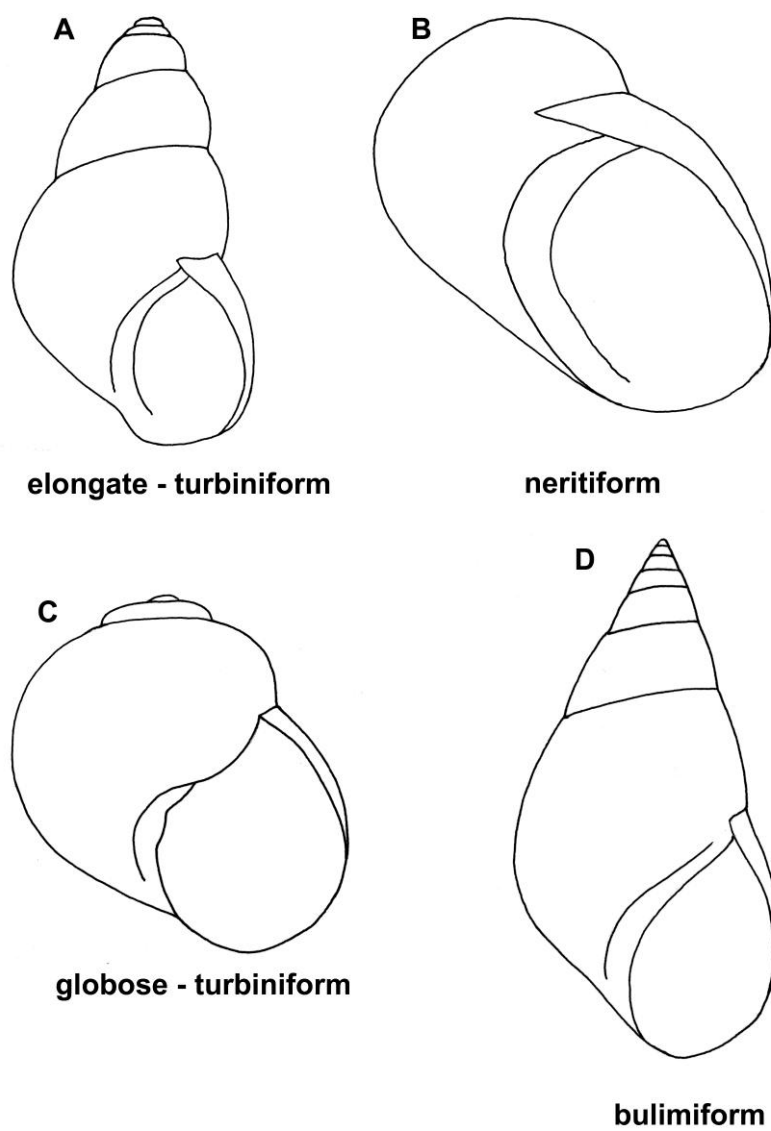


Figure 2.1. Phasianelloidea shell shape: (A) *T. africana*; (B) *T. neritina*; (C) *G. pisinna*; (D) *P. australis*. Illustrations by L. Davis 2006.

2.3.2. Protoconch shape or sculpture

A protoconch is an embryonic or larval shell of a mollusc. In many taxonomic descriptions, the protoconch is described as part of the shell. Within the Phasianelloidea, the protoconch is small and paucispiral (ca 1.25 whorls). The majority of species are smooth (Figs 2.2A, B) or have fine spiral lines (Fig. 2.2C), whereas others have a rough or granulate surface (Fig. 2.2D). However, the south-western Australian *Tricolia* species i.e., *T. rosea* has a strong spiral cord (Fig. 2.2E). A terminal lip is a point where the protoconch ends and the teleoconch begins. Teleoconch is defined as that part of the shell laid down by incremental growth after the formation of the protoconch. In many phasianellids taxa, the terminal lip shape is distinct. Some species are uniformly convex (Fig. 2.2E), whereas others are straight or have a distinct angle (Fig. 2.2A). Most species in the family have a low and bluntly rounded apex, exception being *Hilola variabilis* and *T. tomlini* with an exerted and narrowly rounded apex (Fig. 2.2F).

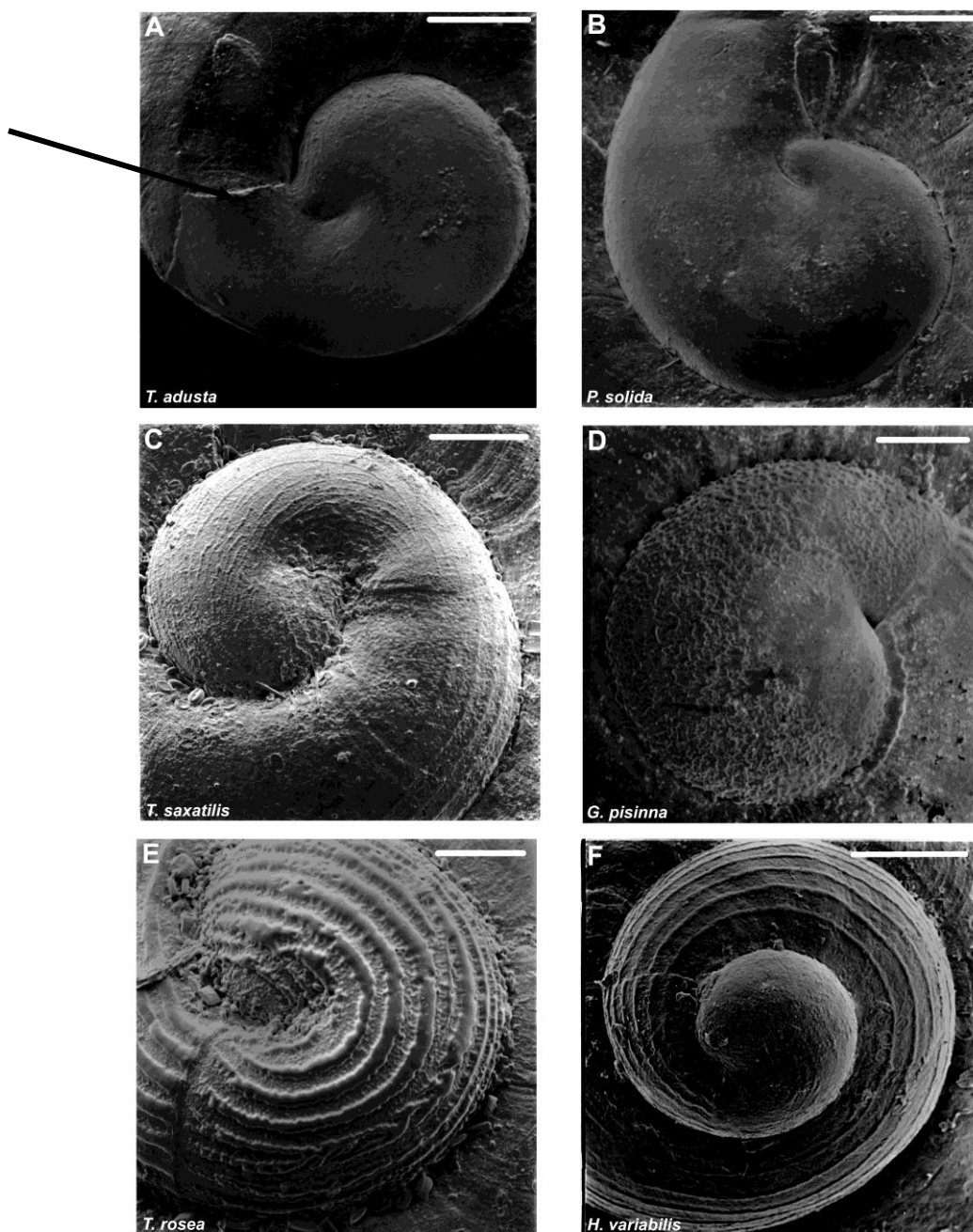


Figure 2.2. Scanning electron microscope of the external surface of protoconch of the Phasianelloidea: (A) *T. adusta*, Aliwal Shoal, Cracker Reef, KwaZulu–Natal, NMSA W2477, bar = 50 μm ; (B) *P. solida*, S.E. of Kosi River Mouth, KwaZulu–Natal, NMSA D6067, bar = 70 μm ; (C) *T. saxatilis*, Aliwal Shoal, KwaZulu–Natal, NMSA W2585, bar = 60 μm ; (D) *G. pisinna*, New Caledonia, MNHN, bar = 90 μm ; (E) *T. rosea*, Rottneest Island, Fish Hook Bay, WAM S16004, bar = 120 μm ; (F) *H. variabilis*, Between Bhanga Nek and Kosi Bay, KwaZulu–Natal, NMSA S2691, bar = 100 μm . The arrow indicates the terminal lip.

2.3.3. Operculum

Overall operculum morphology within the Phasianelloidea is calcareous, paucispiral with eccentric nucleus. The operculum shape of *Tricolia*, *Hilola*, *Eulithidium* and *Phasianella* is externally convex; whereas that of *Gabrielona* is externally concave (Fig. 2.3C). The external surface also varies between genera and species. The operculum sculpture of many *Tricolia*, *Phasianella* and *Gabrielona* species is more or less smooth (Figs 2.3A, B, C), whereas in *Eulithidium*, all species have radiating ridges on the labral margin (Fig. 2.3D). The operculum sculpture of *T. saxatilis*, *Hilola* and *T. tomlini* is granulated (Figs 2.3E-F, 2.4A). The labral margin of the operculum is diagnostic among Phasianelloidea genera. The labral marginal of *Gabrielona* is raised, whereas that of *Tricolia*, *Hilola*, *Eulithidium* and *Phasianella* lacks a distinct marginal ridge. The parietal edge shape of pheasant shell species is also distinct. This shape is formed as a result of the aperture shape. In *Tricolia*, *Hilola* and *Eulithidium* species, the parietal edge is convex, whereas in *Gabrielona* and *Phasianella* it is concave. The presence of an exterior pit on the juvenile operculum of *Hilola variabilis* and in adult specimens of *T. saxatilis* was previously reported by Robertson (1958) and Nangammbi & Herbert (2006). In this study, the exterior pit was also found in the juvenile operculum of *Phasianella* specimens (Fig. 2.4B). The occurrence of this character in juveniles of other pheasant shell genera needs further investigation since this could be one of the synapomorphic characters that unite the Phasianelloidea.

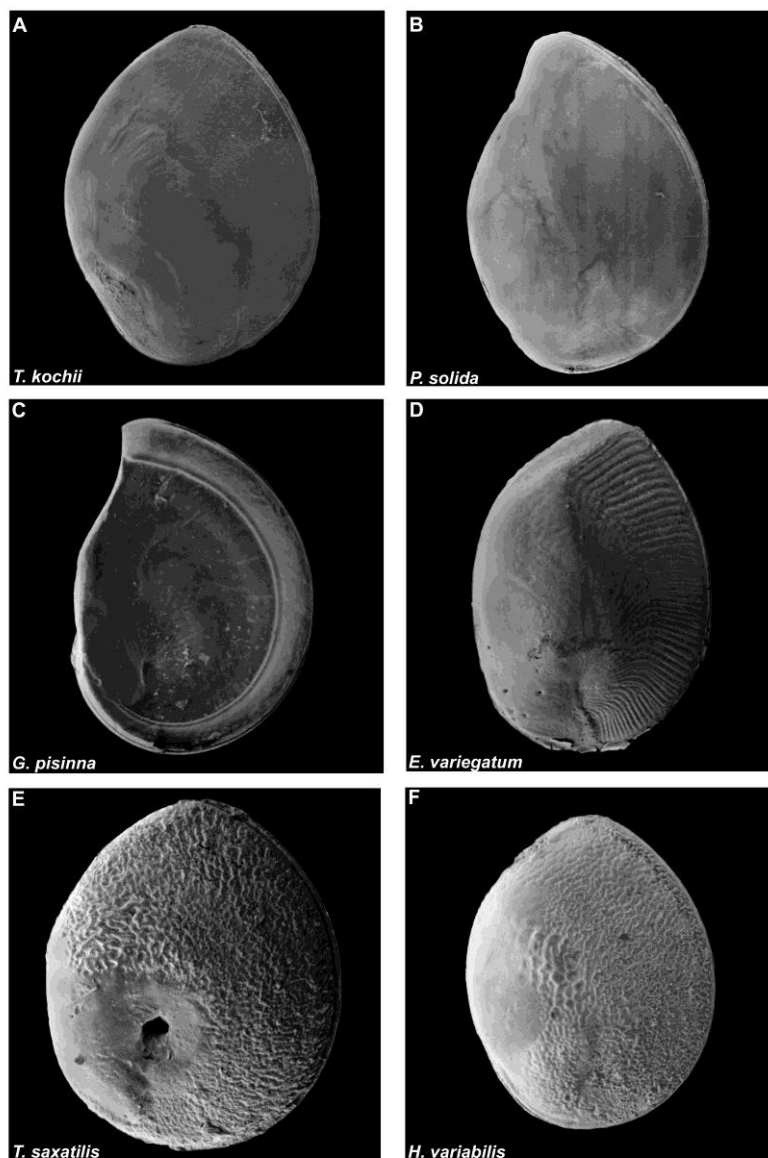


Figure 2.3. Scanning electron microscope of the external surface of operculum of the Phasianelloidea: (A) *T. kochii*, Three Sisters, Port Alfred, Eastern Cape, NMSA W1035, maximum diameter 1.6 mm; (B) *P. solida*, Kosi Bay, KwaZulu–Natal, NMSA S2254, maximum diameter 0.8 mm; (C) *G. pisinna*, Rottnest Island, Fish Hook Bay, Western Australia, WAM S16002, maximum diameter 0.9 mm; (D) *E. variegatum*, Bahia Cholla, Sonora, Mexico, LACM 148224, maximum diameter 2.1 mm; (E) *T. saxatilis*, Aliwal Shoal, KwaZulu–Natal, NMSA W2585, maximum diameter 0.6 mm; (F) *H. variabilis*, Dampier Archipelago, Kendrew Island, WAM S16003, maximum diameter 0.9 mm.

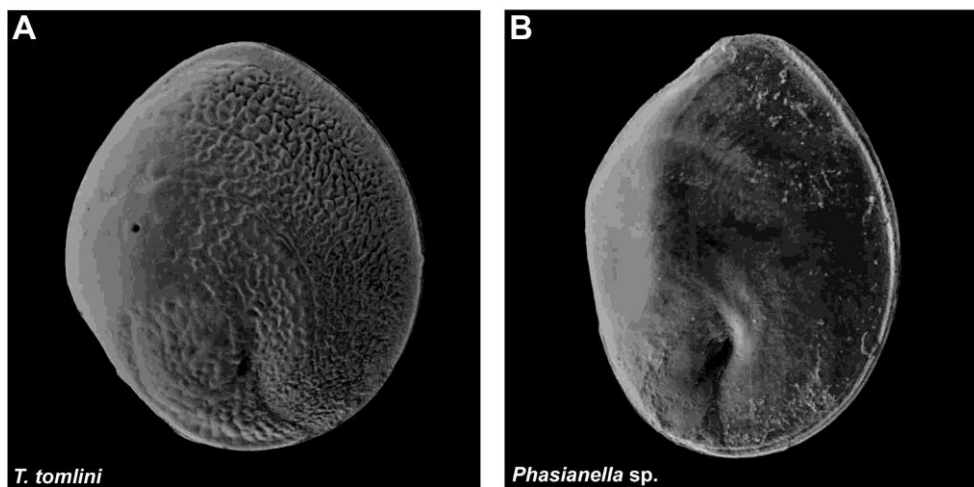


Figure 2.4. Scanning electron microscope of the external surface of operculum of the Phasianelloidea: (A) *T. tomlini*, Jurien Bay, Booka Valley Rocks, Western Australia, WAM S16028, maximum diameter 1.0 mm; (B) Juvenile *Phasianella* species, Jurien Bay, inside Favorite Island, Western Australia, WAM S15986, maximum diameter 0.6 mm.

2.3.4. Radula

A typical character of most Vetigastropoda families is having a rhipidoglossate radula (chapter 1, Table 1.3). All pheasant shell genera share a common ground plan with juvenile specimens having a cusped rachidian tooth i.e., *Tricolia* (*T. pullus*, Warén 1990), *Eulithidium* (*E. affine cruenta*, Marcus & Marcus 1960), *Phasianella* (this study, Fig. 2.5A), *Gabrielona* (*G. pisinna*, Hickman & McLean 1990), *Hilola* (*H. variabilis*, Hickman & McLean 1990) and *Eugabrielona* (*E. sulcifera*). In some genera the cusped rachidian tooth is retained to an adult stage i.e., *Hilola*, *Gabrielona*, *Eugabrielona* and some *Tricolia* species (i.e., *T. indica* and *T. tristis*), whereas in other genera the rachidian tooth is modified into the derived condition seen in the adult. The cusped rachidian tooth in the juvenile radula may represent a plesiomorphic character shared between trochoidean families (*sensu lato*) since this character was previously observed in other families such as Turbinidae and Trochidae (Warén 1990). However, this needs further investigation.

In *Phasianella*, the rachidian tooth is absent (Fig. 2.5F), whereas in *Tricolia* and *Eulithidium*, the rachidian tooth is broadly ovate without a cusp (Fig. 2.5D). In the south–western Australian *Tricolia* species, the rachidian tooth is reduced to a narrow vestige lying between the innermost pair of laterals (Fig. 2.5E). *Hilola* and *Gabrielona* have a cusped rachidian tooth (Figs 2.5B, 2.6C).

In *Phasianella*, *Hilola* and *Eulithidium*, the number of lateral teeth appears to be constant, but in *Tricolia* and *Gabrielona* there is evidence of variability. The southern African, Eastern Atlantic and the South Australian *Tricolia* species and *Phasianella* have five pairs of lateral teeth per transverse row (Figs 2.6A, Robertson 1985, Hickman & McLean 1990). The Indo–West Pacific *Tricolia* species and *Gabrielona* have either five (i.e., *T. fordiana*, *T. ios* and *G. roni*) or three (i.e., *T. indica*, *T. tristis* and *G. pisinna*) pairs of lateral teeth per transverse row (Robertson 1985). *Hilola* has three pairs of lateral teeth per transverse row (Fig. 2.6C). *Eulithidium* has four pairs of lateral teeth per transverse row (Fig. 2.6B).

Although Robertson (1958) found no difference in the morphology of marginal teeth within the Phasianelloidea, there does in fact seem to be some variation in the morphology of marginal teeth, even within species from the same region. Within southern Africa, Eastern Atlantic and the Indo–West Pacific *Tricolia* species, there are two forms of inner marginal dentition. In most species, the ectocone (ectocone refers to a cusp on the outer side of a

tooth) of the inner marginal teeth is bifid or notched, and interlocks with two notches at the base of the cusp of the adjacent outer tooth (Fig. 2.6E). In southern Africa, the other form only applies to *T. formosa*, *T. adusta* and *T. saxatilis*, whereas in the Eastern Atlantic it applies to the small Mediterranean *T. deschampsi*, *T. entomocheila*, *T. punctura* and *T. algoidea* with one strong undivided ectocone (Fig. 2.6F). In the southern Australian *Tricolia* species, two forms of marginal dentition occur. One strong undivided ectocone is found in *T. tomlini* and *T. gabiniana*, whereas *T. rosea* has numerous ectocones and endocones (endocone refers to a cusp on the medial side of a tooth, Robertson 1985). In the Indo–West Pacific *Tricolia* species, three forms of marginal dentition occur. The bifid or notched form is found in *T. ios*, whereas *T. fordiana* has one strong undivided ectocone, and *T. tristis* and *T. indica* have numerous ectocones and endocones (Robertson 1985). The inner marginal ectocone of *Phasianella* species is bifid or notched as in most *Tricolia* species. *Hilola*, *Eulithidium* and *Gabrielona* both have numerous ectocones and endocones, but in *Eulithidium* they are more distinct (Fig. 2.6D).

The cusps of the innermost three lateral teeth within the Phasianelloidea vary. In *Tricolia* and *Gabrielona* species, the innermost laterals have one large mesocone (mesocone refers to the middle cusp of a tooth) with several small ectocones and endocones (Figs 2.5B, D, E). In *Phasianella*, there is one lanceolate mesocone with a single ectocone and endocone (Fig. 2.5F). *Eugabrielona* is monocuspid and lacks ectocones and endocones (Robertson 1973, pl. 57).

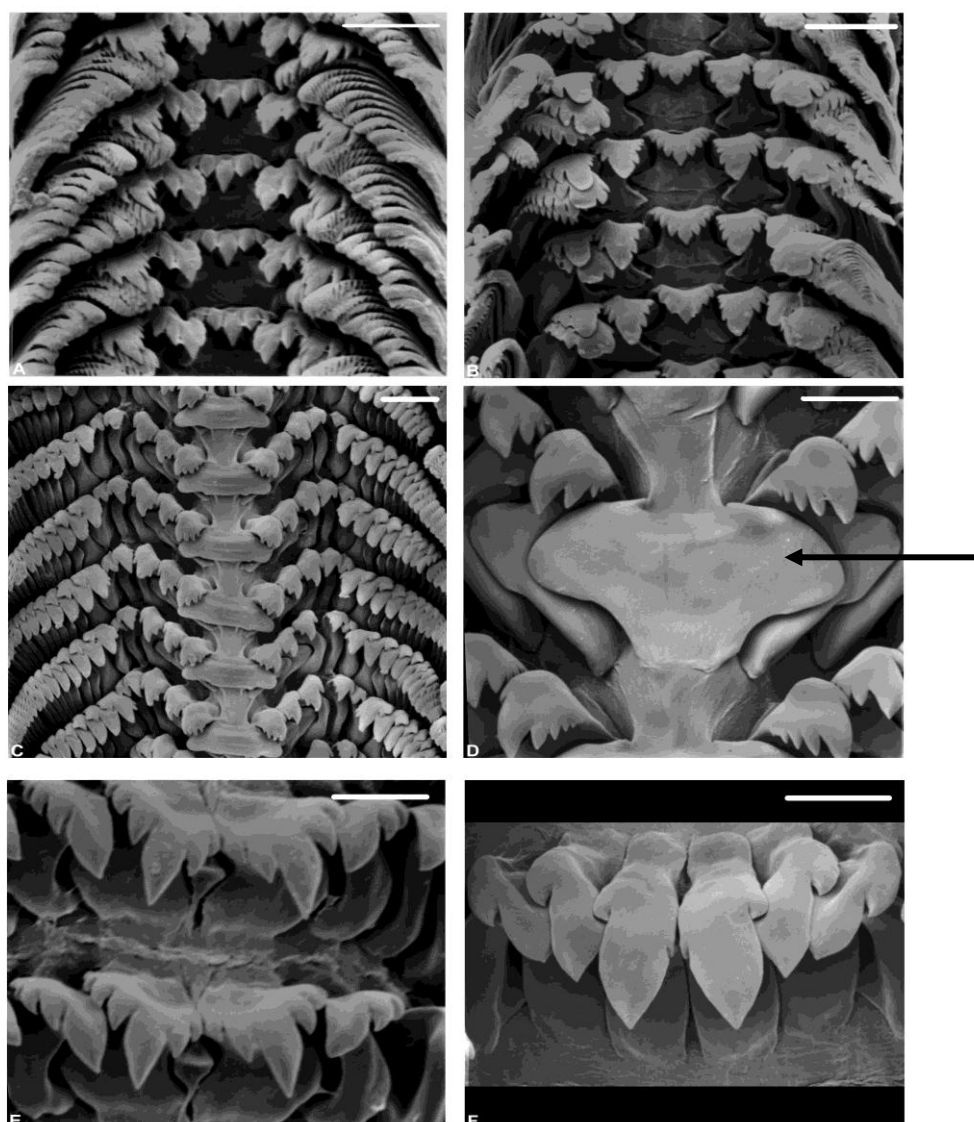


Figure 2.5. Transverse rows and rachidian tooth of radula of the Phasianelloidea: (A) Juvenile *Phasianella* species, Jurien Bay, inside Favorite Island, Western Australia, WAM S15986, bar = 80 μm ; (B) *G. pisinna*, Hamelin Bay, Western Australia, WAM S29216, bar = 50 μm ; (C) *T. capensis*, Sea Point, Atlantic Cape, NMSA W1524, bar = 120 μm ; (D) *T. kochii*, Three Sisters, Port Alfred, Eastern Cape, NMSA W1035, bar = 40 μm ; (E) *T. tomlini*, Jurien Bay, Booka Valley Rocks, Western Australia, WAM S16028, bar = 30 μm ; (F) *P. solida*, Pemba, Uimbe Beach, Mozambique, NMSA L6890, bar = 50 μm . The arrow indicates the rachidian tooth.

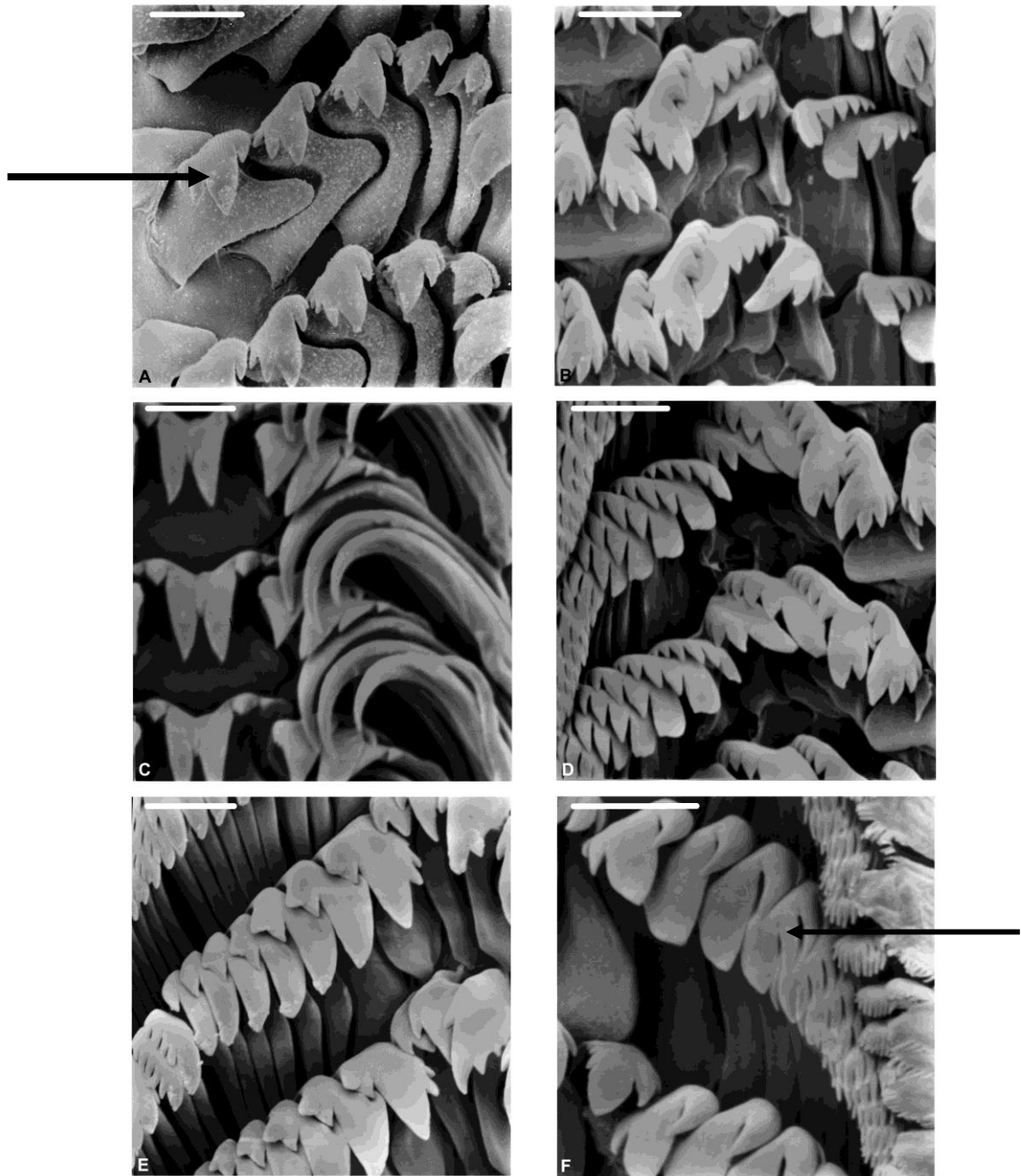


Figure 2.6. Number of lateral teeth and morphology of marginal teeth of the Phasianelloidea: (A) *T. capensis*, Camel Rock, Scarborough, Atlantic Cape, NMSA W2563, bar = 30 μm ; (B) *E. affine*, Puerto, Yofucoa, ANSP A18262, bar = 20 μm ; (C) *H. variabilis*, Dampier Archipelago, Kendrew Island, Western Australia, WAM S16003, bar = 10 μm ; (D) *E. affine*, Same specimen as Fig. 2.6B, bar = 30 μm ; (E) *T. capensis*, Sea Point, Atlantic Cape, NMSA W1524, bar = 30 μm ; (F) *T. adusta*, Off Phumula, KwaZulu–Natal, NMSA W2586, bar = 10 μm . The top arrow indicates the lateral teeth. The bottom arrow indicates the marginal teeth.

2.3.5. External anatomy

2.3.5.1. Neck-lobes

The neck-lobes are uniquely derived features of Trochoidea *sensu lato* (Hickman 1996). They vary from small flap of epipodial tissue with subdivided margins to broad, elaborate-fringed flaps capable of channeling water in and out of the mantle cavity. The digitations of both the left and right neck-lobes vary within the Phasianelloidea. In some genera the neck-lobe digits are somewhat asymmetrical, with longer digitations on the left than on the right or with no digitations on the right or on both sides. The size of the right and left neck-lobe also differs. In *Eulithidium*, the right-lobe is smaller than the left-lobe (Fig. 2.8B). In the south western Australian *Tricolia* species, the left and right lobes are similar in size (Fig. 2.8A). In some *Tricolia* species the left-lobe may have relatively few digits while the right-lobe is broad with a non-digitate margin, for example *T. saxatilis* (Fig. 2.7C). The number of neck-lobe digits appears to be a function of specimen size, but this has not been quantified. In most southern African *Tricolia* species, the left-lobe is broad and outspread with *ca* 20 digits and the right-lobe usually has smaller and fewer digits.

2.3.5.2. Cephalic lappets

Cephalic lappets are a pair of flap-like extensions located on the dorsal surface of the snout extending medially from the base of the cephalic tentacles, across the forehead, but usually not reaching the midline. The presence and absence of cephalic lappets is considered to be a useful character in trochoidean higher classification (Hickman & McLean 1990). Although, cephalic lappets are common within trochoidean taxa, they appear to be missing in the basal families (Hickman 1996). Within the Phasianelloidea, cephalic lappets only occur in *Phasianella* species (Fig. 2.8D), and are absent in other genera (Figs 2.7A–D, 2.8A–C).

2.3.5.3. Epipodial tentacles

Epipodial tentacles are found throughout the trochoidean taxa, but the number varies between genera. Pheasant shells have three pairs of papillate epipodial tentacles (Fig. 2.7A). However, Hickman & McLean (1990) recorded two pairs of papillate epipodial tentacles in *Eulithidium* (Fig. 2.8B). *Eulithidium* anatomy observed from this study indicates some features that might represent the third epipodial tentacles. The number of epipodial tentacles present in *Eulithidium* needs further investigation. In many *Tricolia* and *Phasianella*

species, the middle tentacle is very small (Fig. 2.7C) or slightly smaller (Fig. 2.7D). In *Gabrielona* and the southern Australian *Tricolia* species, the middle tentacles are more or less of the same size (Fig. 2.8C).

2.3.5.4. Epipodial sense organs, foot and head colour pattern

At the base of each epipodial tentacle there are epipodial sense organs. The number of epipodial sense organs at the base of the first epipodial tentacle on the left varies. In most southern African species and *T. pullus*, there are two sense organs at the base of the anterior epipodial tentacle on the right (Fig. 2.7A), whereas in *T. formosa*, *T. adusta* and *T. saxatilis* only one sense organ is present (Fig. 2.7B). Many taxa from other regions have their material preserved in ethanol and pose difficulty in observing the number of epipodial sense organs. Epipodial folds are usually pigmented, but colouration differs between species. The foot is longitudinally divided with a white sole. The head-foot colour pattern is variable, usually resembling that of shell; some species have turquoise spots on snout between and just in front of cephalic tentacles.

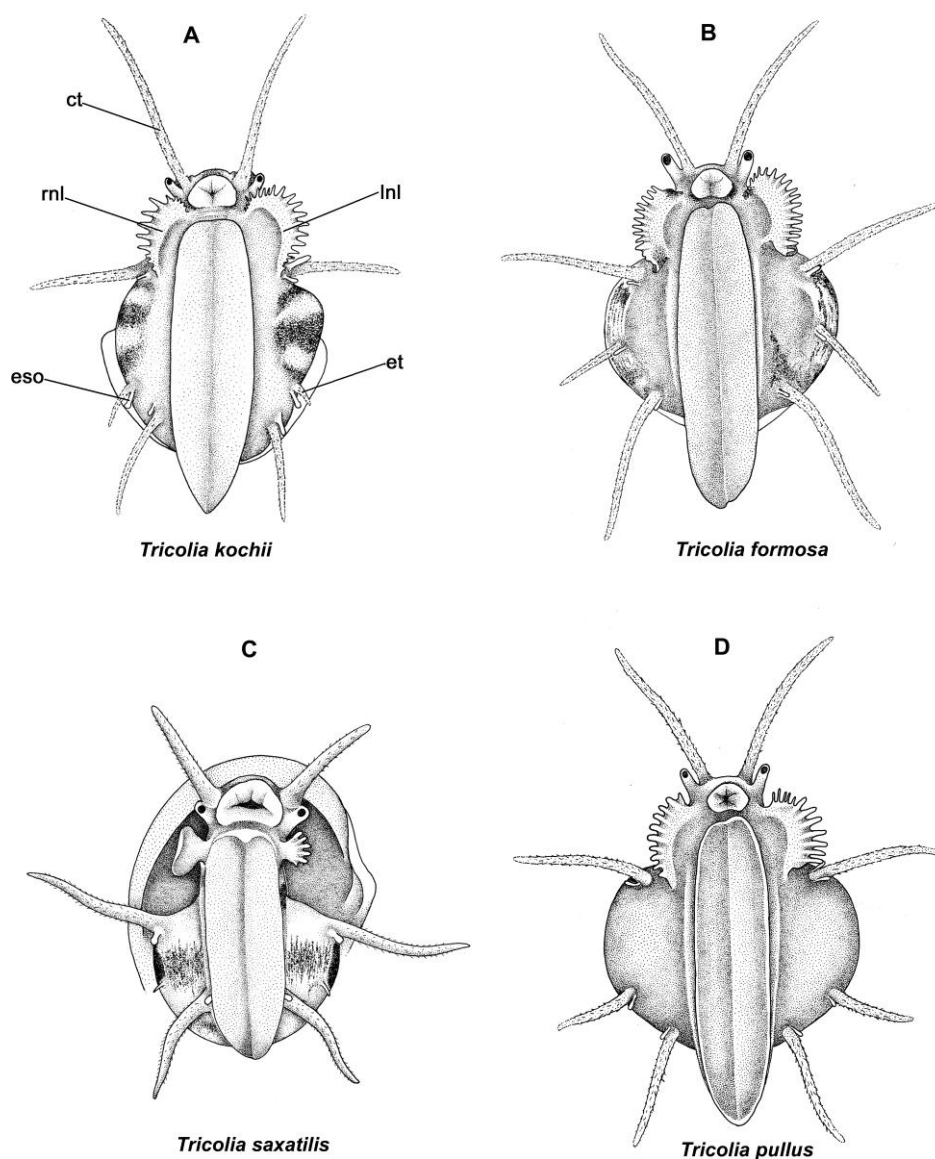


Figure 2.7. External anatomy of the Phasianelloidea: (A) *T. kochii*, Three Sisters, Port Alfred, Eastern Cape, NMSA W1035; ct – cephalic tentacles; eso – epipodial sense organ; et – epipodial tentacle; lnl – left neck-lobe ; rnl – right neck-lobe; (B) *T. formosa*, Off Macassar Beach, False Bay, NMSA W2581; (C) *T. saxatilis*, Aliwal Shoal, KwaZulu-Natal, NMSA W2585; (D) *T. pullus*, Gower Peninsula, Limeslade, United Kingdom, NMSA L6883. Illustrations by L. Davis 2006.

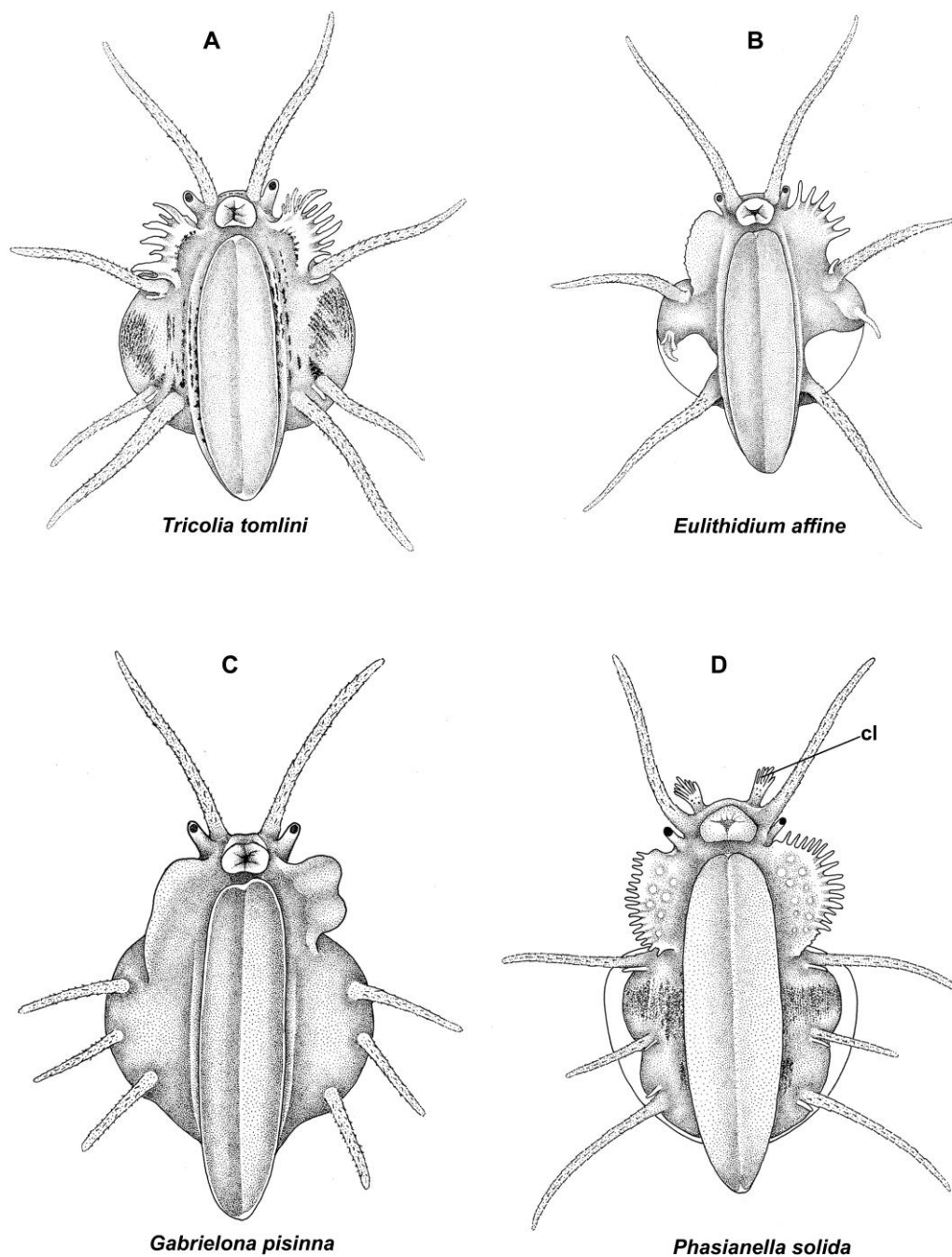


Figure 2.8. External anatomy of the Phasianelloidea: (A) *T. tomlini*, Hamelin Bay, Western Australia, WAM S29218; (B) *E. affine*, Oceanside of Snake Creek, Florida Keys, FMNH 308187; (C) *G. pisinna*, Rottnest Island, Fish Hook Bay, Western Australia, WAM S16002; (D) *P. solida*, Two-Mile Reef, Sodwana Bay, KwaZulu-Natal, NMSA W3388; cl – cephalic lappets. Illustrations by L. Davis 2006.

2.3.6. Biology

Southern African pheasant shells are predominately inhabitants of lower balanoid zone, and infratidal rocky shore (Branch & Branch 1981) areas where plant life is abundant. Some species only occur in the shallow subtidal zone along the southern African coastline (i.e., *T. formosa*, *T. adusta*, *T. saxatilis*, *T. ios* and *P. solida*). These species were collected alive through SCUBA diving and dredging.

Live collected specimens were found on the following algae genera: *Ulva* and *Codium* (green marine algae), *Gigartina* and *Ceramium* (red marine algae), and *Bifurcariopsis* (brown marine algae). Previous authors have also recorded them on *Porphyra* (Kilburn & Rippey 1982). The Eastern Atlantic species (i.e., *T. pullus*) were found on the following algae: *Gigartina*, *Plumaria*, *Nitophyllum*, *Ceramium*, *Chondrus*, *Rhodophyllis* and *Rhodymenia* in the Low Water Spring Tide and Laminarian zones on rocky shores extending sublittorally to 35 m (Fretter 1955, Robertson 1958, Fretter & Graham 1977). Some species have been sorted among gulleys and some were found in the stomachs of fish. Some of the American species have been dredged alive at 64 meters, but the majority of these species live on the intertidal rocky shores (Robertson 1958).

Pheasant shells are herbivores, feeding on marine algae, diatoms and detritus (Fretter & Graham 1977, Kilburn & Rippey 1982). Robertson (1974) claimed that *T. indica* has a carnivorous diet since it was recorded on a siliceous sand bottom without macroscopic plants and where the water was opaque with suspended detritus. The difference in colouration pattern among members of the same species may occur as a result of the food on which they feed i.e., Abalone species. The sexes are separate and fertilization is known to be external (Manly 1976, Fretter & Graham 1977, Kilburn & Rippey 1982). The eggs are shed into water, hatch into pelagic larvae and settle within few days.

2.4. TAXONOMY

Family Phasianellidae Swainson, 1840

Subfamily Phasianellinae Swainson, 1840

Phasianellinae [Trochidae] Swainson, 1840: 354; Chenu 1859: 342.

Eutropinae [Trochidae] Adams & Adams, 1854: 389 [genus *Eutropia* Swainson, 1840, is an objective synonym of *Phasianella*]

Eutropiidae; Finlay 1926: 373.

Phasianellinae [Turbinidae] Stoliczka, 1868: 352; Fischer 1885: 809; Pilsbry 1888: 162; Cossmann *in* Cossmann & Peyrot 1916: 321; Thiele 1924: 72; Thiele 1929: 70; Tomlin 1931: 420; Hickman & McLean 1990: 67-68; Herbert 1991: 308; Moolenbeek & Dekker 1993: 141; Herbert & Warén 1999: 222-224.

Phasianellidae; Bartsch 1915: 144; Pilsbry 1917: 207; Cossmann 1918: 156; Davies 1935: 228; Wenz 1938: 361; Robertson 1958: 254; Cotton 1959: 258; Keen & Robertson 1960: 1274; Iredale & McMichael 1962: 34; Barnard 1963: 206; McLean *in* Keen 1971: 356; Kensley 1973: 52; Kensley 1977: 190; Fretter & Graham 1977: 95; Gofas 1982: 48; Kilburn & Rippey 1982: 42; Hodgson & Foster 1992: 89-97; Hodgson 1995: 169, 172-175; Williams & Ozawa 2006: 37, 47-48; Nangammbi & Herbert 2006: 12.

Phasianellinae [Phasianellidae] Boss, 1982: 975.

Constituent genus: *Phasianella* Lamarck, 1804.

Diagnosis: Parietal region of shell with weak lamella supporting operculum as the animal emerges or retracts from the shell; shell surface with fine spiral capillary lines. Radula without functional rachidian tooth, lateral teeth with broad rectangular area of secondary attachment. Cephalic lappets present and well-developed. A single shell muscle present. Umbilicus closed.

Family Tricoliidae Vermeij & Lindberg, 2000

Subfamily Tricoliinae Woodring, 1928

Tricoliinae [Tricoliidae] Woodring, 1928: 418 [no diagnosis]; Robertson 1985: 39; Gofas 1993: 351.

Tricoliinae [Turbinidae] Hickman & McLean, 1990: 62-67; Moolenbeek & Dekker 1993: 141.

Tricoliinae [Phasianellidae] Robertson, 1958: 256; Boss 1982: 975; Williams & Ozawa 2006: 37, 47-48.

Constituent genera: *Tricolia* Risso, 1826, *Aizyella* Cossmann, 1889 and *Phasianochilus* Cossmann, 1918.

Diagnosis: Shell pigments (porphyrins–fluorescing under ultraviolet light), colour patterns variable within populations of a single species; sexual dimorphism in radula morphology and size of adult shell evident in some taxa (i.e., *Hilola*).

Family Gabrielonidae Vermeij & Lindberg, 2000
 Subfamily Gabrieloninae Hickman & McLean, 1990

Gabrieloninae Hickman & McLean, 1990: 59-62; Moolenbeek & Dekker 1993: 141; Williams & Ozawa 2006: 37, 47-48.

Gabrieloninae [Phasianellidae] Robertson, 1973: 41.

Constituent genera: *Gabrielona* Iredale, 1917 and *Eugabrielona* Hickman & McLean, 1990.

Diagnosis: Shell with distinct apertural ridge and internal palatal sulcus. External surface of operculum concave, with prominent bordering ridge except on sector fitting against columella, and a raised marginal ridge. Protoconch with granulated sculpture. Left and right neck-lobes smooth.

Phasianelloidea *incertae sedis*

The following taxa have traditionally been considered to be closely related to *Tricolia* (even subgenera thereof), but new molecular and morphological data indicate substantial differences and neither may in fact belong to the Tricoliinae. Their relationships within the Phasianelloidea are at present unclear.

Hiloa Pilsbry, 1917 (see page 76)

It is clear from morphological features and molecular data that *Hiloa* does not fit well within the Tricoliinae. As a result, this taxon will be treated as a separate genus. However, the subfamily in which it falls is still unknown.

Eulithidium Pilsbry, 1898

Constituent genus: *Eulithidium* Pilsbry, 1898.

Eucosmia Carpenter, 1864: 475. Type species, by subsequent designation, Pilsbry 1888:

177: *Eucosmia variegata* Carpenter, 1864.

Usatricolia Habe, 1956: 94-96, 98. Type species, by monotypy: *Phasianella compta* Gould, 1855.

Diagnosis: External surface of operculum with radiating ridges on the labral margin. Four pairs of lateral teeth on radula. Two pairs of epipodial tentacles on each side (needs confirmation).

The genus *Eulithidium* does not fit within the currently described subfamily Tricoliinae, particularly in the light of morphological evidence and thus it may need to be assigned to a subfamily of its own. However, since I do not wish to pre-empt formal proposal of a new subfamily in the thesis and thus risking confusion over dating of the name. I refrain proposing a new name in the thesis. Further to this, additional molecular markers will have to be screened and hopefully a supported phylogenetic placement of *Eulithidium* clade within the Phasianelloidea will be gained.

Discussion on the subfamilies

This study has followed Hickman & McLean (1990) who proposed the idea of an informal group comprising Phasianellinae, Tricoliinae and Gabrieloninae. Williams & Ozawa (2006) consistently treat them as belonging to one family, the Phasianellidae, rather than an informal group. In this study, the Tricoliinae includes two genera, *Tricolia* and *Hilooa*. For a long time, *Hilooa* has been treated as a subgenus of *Tricolia* (Robertson 1958, Keen & Robertson 1960) or as a synonym of *Tricolia* (Robertson 1985). This is due to the fact that these studies did not attach sufficient weight to the differences in morphology between *Hilooa* and *Tricolia*, which are distinct enough to warrant consideration as separate taxa. Based on morphological characters of the radula, operculum and apex shape as well as molecular results, *Hilooa* is herein considered a distinct genus and has been treated as such. Within Phasianellinae, a single genus *Phasianella* is recognized while Gabrieloninae includes *Gabrielona* and *Eugabrielona*. It has become evident that the New World radiation of *Tricolia*-like taxa are distinct, and as a result, a new subfamily is needed, which will include the Eastern Pacific and the Western Atlantic species of *Eulithidium*. Robertson (1958) and Hickman & McLean (1990) suggested that *Eulithidium* should be treated as a distinct genus from *Tricolia* based on morphological characters of the operculum, radula and external anatomy. Phylogenetic analyses (see chapter 4) placed *Eulithidium* outside Tricoliinae, Phasianellinae and Gabrieloninae and the inclusion of this genus within the Tricoliinae would have made the subfamily paraphyletic.

Key to genera of the Phasianelloidea

1. Colour pattern including spiral capillary lines; radula without rachidian tooth; cephalic lappets well developed.....***Phasianella***
 – Colour pattern lacking spiral capillary lines; rachidian tooth of radula present; cephalic lappets absent.....**2**
2. External surface of operculum with radiating ridges on labral margin; radula with four pairs of lateral teeth; two pairs of epipodial tentacles.....***Eulithidium***
 – External surface of operculum smooth or granulated, but lacking radiating ridges; radula with three or five pairs of lateral teeth; three pairs of epipodial tentacles.....**3**
3. External surface of operculum concave with raised marginal ridge.....**4**
 – External surface of operculum convex, labral edge often with a narrow marginal groove..**5**
4. Radula with three pairs of lateral teeth per transverse row, rachidian and laterals multicuspid.....***Gabrielona***
 – Radula with five pairs of lateral teeth per transverse row, rachidian and laterals monocuspid***Eugabrielona***
5. Protoconch exserted, apex narrowly rounded; rachidian tooth well developed with prominent cusp***Hiloa***
 – Protoconch usually low, apex bluntly rounded; rachidian tooth usually broadly ovate and lacking a cusp; if protoconch exserted then rachidian tooth reduced to a narrow vestige (*T. tomlini*)***Tricolia*¹**

¹ The generic affinities of a number of Indo–West Pacific and South Australian species traditionally referred to *Tricolia* are currently unclear. These exhibit atypical character states and may belong to undescribed genera.

Genus *Hiloa* Pilsbry, 1917

Hiloa Pilsbry, 1917: 207; Wenz 1938: 362; Robertson 1977 [1974]: 141-142; Robertson 1980: 259. Type species, by monotypy: *Phasianella thaanumi* Pilsbry, 1917: 209, pl. 15, figs 12-14 [= *Collonia variabilis* Pease, 1861]. Type loc.: Hawaii.

Eotricolia Kuroda & Habe, 1954: 86, 91, 93, 94. Type species, by original designation: *Phasianella megastoma* Pilsbry, 1895.

Diagnosis: External surface of operculum granulated, with juvenile having a distinct pit. Protoconch exerted, apex narrowly rounded. Radula with three pairs of lateral teeth per transverse row and rachidian tooth well-developed with prominent cusp, cusp retained in adult. Morphological and molecular data strongly suggest that *Hiloa* should be treated as a distinct genus separate from *Tricolia*.

Hiloa variabilis (Pease, 1861)

Figs 2.9-2.11

Collonia variabilis Pease, 1861: 436, pl. 61, figs 10, 11; Kay 1965: 61, pl. 7, figs 1, 2; Pease 1868: 234; Paetel 1887: 539. Type loc.: Sandwich Islands (Hawaii).

Eutropia (*Tricolia*) *virgo* Angas, 1867: 115, pl. 13, fig. 8. Type loc.: "Coogee" Bay, New South Wales [Australia].

Phasianella variabilis; Pilsbry 1888: 176, pl. 39a, figs 21, 22; Pilsbry 1917: 207-208; Edmondson 1933: 141, fig. 65b; Viader 1937: 54; Edmondson 1946: 163, fig. 77b.

Phasianella megastoma Pilsbry, 1895: 90, pl. 8, fig. 9. Type loc.: Nemoto "Boshiu" [Japan].

Phasianella oligomphala Pilsbry, 1895: 91, 196, pl. 8, fig. 8. Type loc.: Nemoto and Tokyo Harbor [Japan].

Phasianella bryani Pilsbry, 1917: 207-209, pl. 15, fig. 13. Type loc.: Haleiwa, west coast of Oahu [Hawaiian Islands].

Phasianella molokaiensis Pilsbry, 1917: 207-209, 230, pl. 15, fig. 10. Type loc.: Moomomi, on the north coast of western Molokai [Hawaiian Islands].

Phasianella thaanumi Pilsbry, 1917: 207, 209, 230, pl. 15, figs 12, 14. Type loc.: Hilo [Hawaii].

Phasianella variabilis kahoolawensis Pilsbry, 1917: 207-208, 230, pl. 15, fig. 11. Type loc.: north shore Kahoolawa [Hawaiian Islands].

Phasianella gregaria Laseron, 1955: 77, fig. 1. Type loc.: Long Reef, north of Sydney [Australia].

Tricolia variabilis; Iredale & McMichael 1962: 34; Ladd 1966: 54-55, pl. 10, figs 6, 7; Robertson 1974: 26; Kay 1979: 59-61, fig. 17; Robertson 1980: 259; 1985: 72-102, pls 55-96 (for full synonymy); Warén 1990: 186; Hickman & McLean 1990: 677-678, figs 15.59 a, b, d; Herbert 1991: 310, fig. 8; Moolenbeek & Dekker 1993: 145, 147, figs 13, 14; Wilson 1993: 103, un-numbered figure; Bosch *et al.* 1995: 100; Robertson 1997: 35; Dekker & Orlin 2000: 18.

Etymology: *variabilis* (Latin) – changeable or variable.

For a detailed description of the shell shape and colouration (Fig. 2.9); protoconch (Fig. 2.10A), operculum (Fig. 2.10B), radula (Figs 2.10C, D) and external anatomy, see Robertson (1985). For additional information on the external anatomy see Hickman & McLean (1990). Additional information on the South African distribution records, see Herbert (1991), and other geographical distribution records, see Robertson (1985) and Moolenbeek & Dekker (1993).

Geographical range (Fig. 2.11): Tropical Indo–West Pacific species, extending its distribution to the tropical waters of N.E. South Africa. Its distribution has been recorded from Red Sea and Indian Ocean Islands, Australia, Hawaiian Islands and Japan. The Natal Museum collection includes material from southern Mozambique, northern KwaZulu–Natal (from Kosi Bay to Leadsman Shoal) and from several extralimital localities listed in this thesis.

Type material: *Collonia variabilis*, lectotype (designated by Kay 1965, pl. 7, figs 1-2), BMNH 1963331, length 3.7 mm, diameter 2.9 mm. *Collonia variabilis*, 2 paralectotypes, BMNH 1963333, length 3.5 mm, diameter 2.8 mm; length 3.2 mm, diameter 2.6 mm (Kay 1965). *Eutropia (Tricolia) virgo*, lectotype (designated by Robertson 1985, pl. 59, figs 1-2), BMNH 1870.10.26.137. *Phasianella megastoma*, holotype, ANSP 70952. *Phasianella oligomphala*, holotype, ANSP 70951. *Phasianella variabilis kahoolawensis*, holotype, ANSP 116188. *Phasianella bryani*, holotype, ANSP 116320. *Phasianella molokaiensis*, holotype, ANSP 117054. *Phasianella thaanumi*, holotype, ANSP 117053. The synonymy given for this species is based on Robertson (1985); the type material listed has not been examined personally.

Material examined (all NMSA, unless indicated otherwise): MOZAMBIQUE CHANNEL: Bassas da India (21.500°S:39.833°E), coral sand from salvaged cannons, leg. D. Herbert (L476); same locality, India lagoon, coral sand on top of coral outcrop, 8-9 m, leg. ORI,

09.vii.1991 (K9400); same locality, interior of lagoon, sand sample, leg. J. Rozwadowski, vii.1991 (K9111).

SOUTH AFRICA: *KwaZulu–Natal*: between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), reef off marker 13 north, near pinnacles, 5-11 m, hand-dredged sand, dived D. Herbert 13.v.1990 (S9163); same locality, ca 8 m, underwater pump, dived D. Herbert & K. Bloem, 06.v.1990 (S2691); Kosi Bay (26.900°S:32.867°E), 1-4 km south of estuary mouth, 20-22 m, underwater pump, dived D. Herbert & K. Bloem, 05.v.1990 (S1975); same locality, stone surfaces, ca 15 m, dived D. Herbert, 04.v.1990 (S2883); same locality, sorted from stone washings, 9-7 m, dived D. Herbert *et al.* (D9830); Leadsman Shoal (27.800°S:32.617°E), 100 m, dredged A.D. Connell, iv.1980 (B4067).

Extralimital material examined: HAWAII: Hilo, ex D. Thaanum coll'n, H.C. Burnup coll'n, 1926 (F4230); same locality, ex D. Thaanum, ex Transvaal Museum (J2865); Oahu, Kahuku, xii.1969 (G3248); same locality, H. & M. Minzak, ix.1974 (G3229). AUSTRALIA: New South Wales, Sydney, Balmoral Bay, rocky shore, leg. D. Herbert, 08.ii.1997 (L4870). MALAYSIA: Terengganu, North of Kemamen, 8-20 m, fine sand, bottom grab, leg. R. Kilburn, 1994 (L6607). KENYA: Kilifi, lagoon inshore of coral reef, sand from base of coral outcrops, ca 4 m, leg. D. Herbert, 20.xii.1991 (K7969). MASCARENE ISLANDS: Mauritius: Point Radeau, South of Roches–Noires, shell debris, near reef gap, leg. R. Kilburn & D. Herbert, ix.1991 (K9492); Cap Malheureux, lagoon, algal mats in small bay, leg. R. Kilburn & D. Herbert, ix.1991 (K8325); Gris–gris, debris on surf beach opposite reef–break, leg. R. Kilburn & D. Herbert, ix.1991 (K8166); Riambel lagoon, beach–drift, leg. R. Kilburn & D. Herbert, ix.1991 (K9665); off Trou aux Biches, reef front, ca 10 m, fine sand, leg. D. Herbert, ix.1991 (K8535). RÉUNION ISLAND: L'Étang Salé les Bains, lagoon, volcanic sand, coral, leg. R. Kilburn & D. Herbert (K5145); Cap La Houssaye, 6-12 m, dived D. Herbert, 19.ix.1988 (K7343). RODRIGUES ISLAND: between Anse aux Anglais and Point Venus, beach–drift, leg. D. Herbert, ix.1991 (K7837); Grand Baie, beach–drift near stream, sheltered bay, leg. D. Herbert, ix.1991 (K9168).

Comparison: Robertson (1985) mentioned that the shells and radula of this species are sexually dimorphic, with mature males being smaller and having a flared outer lip and larger aperture. However, this requires confirmation because such sexual dimorphism has not yet been reported in any species of *Tricolia sensu stricto*. In comparison with other southern African pheasant shell species, *H. variabilis* differs from *Tricolia* species in terms of protoconch shape, operculum and radula features. The protoconch shape is exserted, with a

narrowly rounded apex. The operculum shape is sub-ovate and granulated on the external surface. The rachidian tooth of the radula (Figs 2.10C, D) is broadly ovate with either one or two prominent cusps (Robertson 1985). Furthermore, the number of lateral teeth per transverse row is three. Although *Hiloa variabilis* is monotypic, Williams & Ozawa (2006) had found considerable genetic differentiation between three individuals of *H. variabilis*, which suggested the possibility of cryptic species, and thus concluded that *H. variabilis* may represent at least two different species. This needs further investigation.



Figure 2.9. Shell shape and colouration of *H. variabilis*, length 5.4 mm, width 3.8 mm, NMSA S1975. Kosi Bay, KwaZulu–Natal.

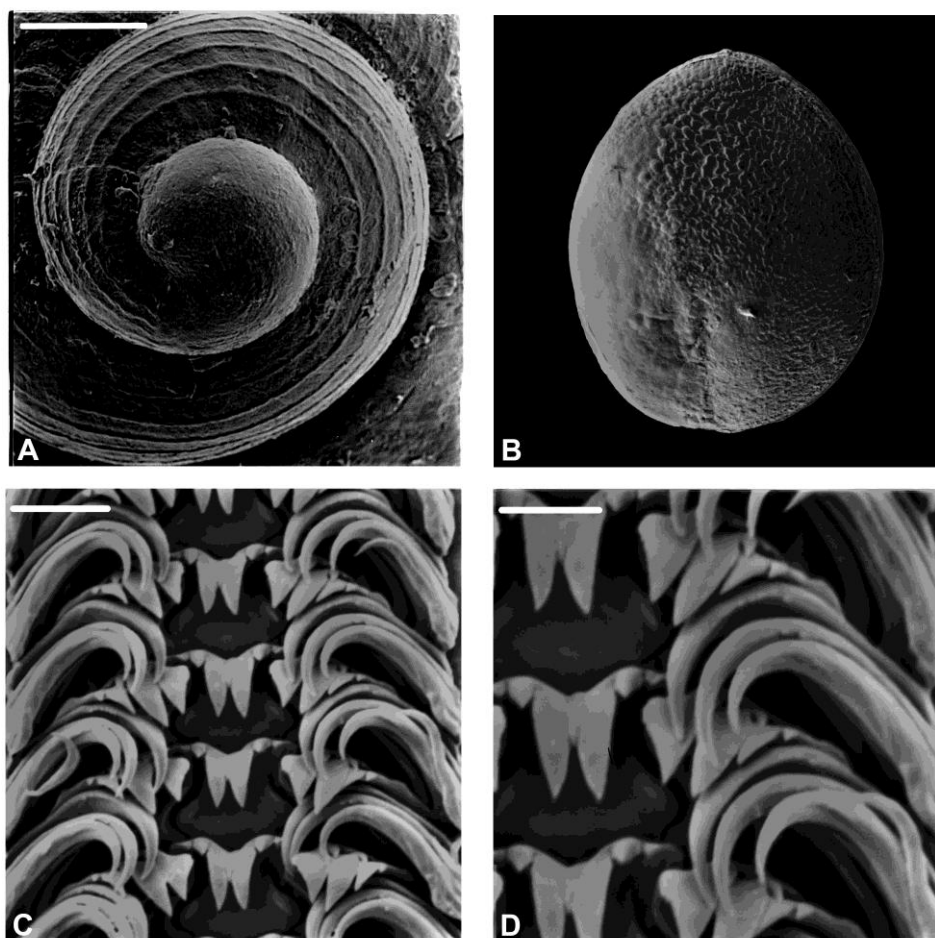


Figure 2.10. Scanning electron microscope of protoconch, operculum and radula of *H. variabilis*: (A) external surface of protoconch, showing exerted and narrowly rounded apex, NMSA S2691, bar = 100 μm ; (B) external surface of operculum, showing a granulate sculpture, WAM S16003, maximum diameter 0.9 mm; (C) central portion of radula, WAM S16003, bar = 30 μm ; (D) rachidian, laterals and marginal teeth, WAM S16003, bar = 5 μm .

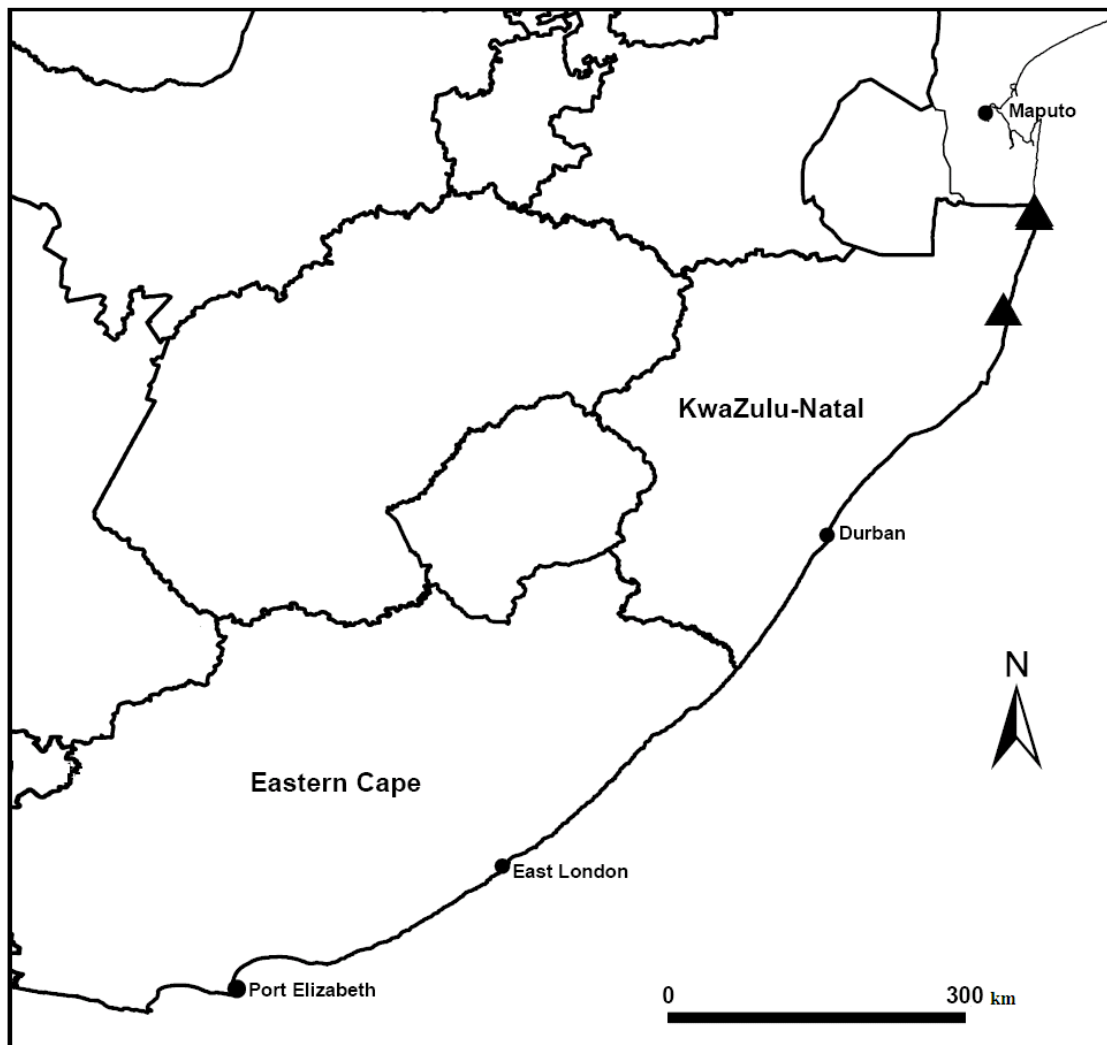


Figure 2.11. Distribution map of *H. variabilis*. Each black triangle represents one or more site records.

Genus *Phasianella* Lamarck, 1804

Phasianella Lamarck, 1804. Type species *Buccinum australe* Gmelin, 1791 (ICZN 1962: Opinion 630).

For full synonymy of this genus see Robertson (1958) and Keen & Robertson (1960).

Diagnosis: One shell muscle present². Presence of a weak lamella that supports the operculum against the parietal region as the animal emerges or retracts from the shell (Hickman & McLean 1990). Radula without rachidian tooth, lateral teeth with broad rectangular area of secondary attachment. Cephalic lappets present and well developed. Colour pattern including spiral capillary lines.

²The issue of one/two shell muscles in *Eulithidium/Phasianella/Tricolia* is pertinent and is a topic which needs further study .

Phasianella solida (Born, 1778)

Figs 2.12-2.15

Helix solida Born, 1778: 408. Type loc.: Not given.

Tricolia brongniartii Audouin, 1826: 41, pl. 5, fig. 23; Audouin 1828: 181; Viader 1937: 54; Bouchet & Danrigal 1982: 12-13, 16, 18, fig. 26. Type loc.: Red Sea coast, Egypt.

Tricolia brongniartii [sic]; Robertson 1985: 20.

Tricolia guerini Audouin, 1826: 41, pl. 5, fig. 24; Bouchet & Danrigal 1982: 13; Robertson 1985: 22. Type loc.: Red Sea coast, Egypt.

Phasianella broungniarti [sic]; Pilsbry 1888: 179, pl. 39, figs 63-66.

Phasianella solida; Kiener 1847: 4-5, pl. 3, figs 2-2a-2e; Philippi 1853: 24-25, pl. 2, figs 2, 3, 5; Sharabati 1984: pl. 2, fig. 19; Springsteen & Leobrera 1986: 37; Moolenbeek & Dekker 1993: 147-148, fig. 19; Wilson 1993: 102, pl. 11, figs 3a, b; Bosch *et al.* 1995: 97; Robertson 1997: 35; Dekker & Orlin 2000: 18; Hylleberg & Kilburn 2002: 23.

Phasianella modesta Gould, 1861: 157; Pilsbry 1888: 183; Yagura 1932: 26; Trew 1984: 82; Robertson 1985: 24; Springsteen & Leobrera 1986: 37. Type loc.: Loo Choo, Okinawa, Ryukyu Islands [Japan].

Phasianella histrio Reeve, 1862: pl. 4, sp. 15, figs a, b; Pilsbry 1888: 166, pl. 37, figs 34, 35; Springsteen & Leobrera 1986: 37. Type loc.: Islands of Masbate and Baclayon [Philippines].

Phasianella jaspidea Reeve, 1862: pl. 4, sp. 11; Von Martens 1879: 735; Sowerby 1887: 150, pl. 476, fig. 23; Pilsbry 1888: 179, figs 36, 44; Barnard 1963: 206, fig. 3a; Spry 1968: 8, sp. 20a; Kensley 1973: 52, fig. 141; Sawyer 1999: 14; Sawyer 2000: 10; Wronski 2007: 339. Type loc.: Zanzibar.

Phasianella variegata [non Lamarck, 1822]; Pilsbry 1888: 179, pl. 39, figs 97, 98.

Phasianella zigzag Odhner, 1919: 31, pl. 2, fig. 25; Dautzenberg 1929: 528; Robertson 1985: 25. Type loc.: Fénériver, N.W. Madagascar.

Eutropia modesta Johnson, 1964: 111.

Etymology, *solida* (Latin) – referring to solid form of the shell.

Diagnosis: Shell relatively large, bulimiform; smooth and glossy, lacking any spiral sculpture, marked only by fine growth-lines. Colouration extremely variable, ground colour reddish–

orange to reddish–brown with a mid brown band below suture; all specimens with spiral capillary lines.

Description (Figs 2.12, 2.13A-L):

Shell relatively large, bulimiform with high–spire; teleoconch of up to 4.5 whorls with moderately indented suture; whorls smoothly rounded, lacking any angulation; apex pointed. Sculpture weak, shell usually smooth and glossy; lacking any spiral sculpture, marked only by microscopic growth–lines. Aperture ovate–circular, with an incomplete peristome, outer lip thin; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed. Colouration enormously variable, ground colour reddish–orange to reddish–brown or white with a mid–brown band below the suture with patches of scattered white markings on the body whorl (Figs 2.13A, B); others with reddish shade of purple to brown background and with shades of brown to burnt reddish–brown bands below the suture (Figs 2.13C, D); some specimens with reddish–brown background and maroon spiral lines broken up by cream–coloured blocks and cream speckling with a mid–brown shoulder band (Figs 2.13E, F); some specimens with light, brownish–yellow to dark–brown background with or without reddish–orange–brown spiral markings and cream checkering (Figs 2.13G, H); others with cream–coloured background and buff, light, brownish–yellow, reddish–orange and reddish–brown feathering and an olive–green shoulder band (Figs 2.13I, J); some specimens with dark–reddish shades of purple to brown background with cream axial stripes and an olive–green or dark brown–grey shoulder band (Figs 2.13K, L); all specimens with spiral capillary lines, white markings and dark–brown to black chevron arrows on the body whorl.

Protoconch (Fig. 2.14A): Typically vetigastropod, comprising approx. 1.25 whorls; apical beak present but weak, terminal lip lacking a varix, but markedly angulate at mid–whorl, sculpture for the most part smooth.

Operculum (Fig. 2.14B): Typical of *Phasianella* (Hickman & McLean 1990), but clearly showing a narrow peripheral groove underlying labral margin, and with concave parietal ridge.

Radula (Figs 2.14C–F): Typical of *Phasianella* (Robertson 1958, Hickman & McLean 1990); Formula $\infty+5+0+5+\infty$.

External anatomy (Fig. 2.8D): Typical of *Phasianella*, in having well-developed cephalic lappets (Hickman & McLean 1990).

Measurements: Largest specimen examined – length 13.9 mm, width 3.8 mm.

Habitat: A subtidal species in South Africa inhabiting off-shore reefs; living specimens from shallow infratidal to 50 m, fossils and empty shells from beach-drift to 350 m.

Geographical range (Fig. 2.15): Tropical Indo-West Pacific species with its distribution extending into the tropical waters of N.E. South Africa. The Natal Museum collection includes samples ranging from Reunion Island (Possession Bay) to the Eastern Cape (Transkei, off Mbashe River).

Type material: *Phasianella solida*, syntypes, MNHV 14338 (Fig. 2.12). *Phasianella jaspidea*, three syntypes, BMNH 163319 (³K Way 2008, personal communication).

Material examined (all NMSA, unless indicated otherwise): MOZAMBIQUE: Quirimba Archipelago, Ibo Island (12.347°S:40.602°E), leg. R. Kilburn, 02.ix.1984 (K354, living); North West of Quisiva Island, leg. R. Kilburn, 27.ix.1984 (L6892, living); Pemba, Uimbe Beach (12.698°S:35.823°E), leg. R. Kilburn, 02.x.1984 (L6890, living); Sandbank, between Santa Carolina Island and mainland, in sand consolidated by worm-tubes, above low spring tide, 23.viii.1974 (L6891, living); Malongane (24.798°S:32.891°E), coral reef, hand dredged sand, 10–20 m, dived D. Herbert, 16.iv.1997 (L6900); Ponta do Ouro (26.850°S:32.917°E), subtidal, coral reef, hand-dredged sand, ca 20 m, dived D. Herbert, 14.iv.1997 (L5939).

SOUTH AFRICA: *KwaZulu-Natal*: between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), reef off marker 13 north, 9-14 m, dived D. Herbert *et al.*, 07-12.v.1990 (S1662); same locality, drop-off at outer edge, 12-20 m, dived D. Herbert *et al.*, 12-20.vii.1987 (D9432); same locality, algal portion, 5-9 m, underwater pump, dived D. Herbert & K. Bloem, 03.v.1990 (S2863, living); same locality, dived D. Herbert *et al.*, 03.v.1990 (S1472); same locality, near pinnacles, 10-12 m, hand-dredged sand, dived D. Herbert, 12.v.1990 (S2424); same locality, 5-11 m, dived D. Herbert *et al.*, 13.v.1990 (S3392); same locality, ca 13 m, hand-dredged sand, dived D. Herbert, 14.v.1990 (S3092); same locality, ca 8 m, underwater pump, dived D. Herbert & K. Bloem, 06.v.1990 (S2770); same locality, algal reef, 1.5 km south off marker number 13, 9-10 m, dived D. Herbert *et al.*, 18.vii.1987 (D9609); South East

³ K Way, Department of Zoology, Cromwell Road London, SW7 SBD, United Kingdom

of Kosi River mouth (26.913°S:32.917°E), 40-50 m, fine sand, algae, gorgonians, dredged R.V. *Meiring Naudé*, Stn. ZA22, 08.vi.1987 (D8857); same locality (26.923°S:32.918°E), 50 m, algae, shells, dredged R.V. *Meiring Naudé*, Stn. ZA20, 08.vi.1987 (D6067, living); Kosi Bay (26.900°S:32.867°E), main reef 1-4 km south of estuary mouth, ca 18 m, underwater pump, dived D. Herbert & K. Bloem, 06.v.1990 (S2254); same locality, ca 20 m, underwater pump, dived D. Herbert & R. Broker, 05.v.1990 (52509); same locality, 20-22 m, underwater pump, dived D. Herbert & K. Bloem, 05.v.1990 (S1991); same locality, off marker 17 north, 9-12 m, dived D. Herbert *et al.*, 04.v.1990 (S1898); same locality, marker 13 north, intertidal rocks and beach–drift, leg. D. Herbert & F. Wiercx, v.1990 (S1275); off Kosi Bay, 1-2 km, 9-17 m, sorted from stones washing, dived D. Herbert *et al.*, 12-20.vii.1987 (D9831); Mabibi–Hully Point (27.317°S:32.733°E), beach–drift, leg. D. Herbert, 09.x.1985 (D1896); Two–Mile Reef, Sodwana Bay (27.517°S:32.691°E), inner edge, 14-15 m, dived D. Herbert, 18-26.x.1986 (D4967); same locality, 10-15 m, dived D. Herbert, 18-26.x.1986 (D5118); same locality, 5-14.x.1985 (D1735); same locality, 10-15 m, hand–dredged sand, dived D. Herbert, 30.xii.1990 (S4315); same locality (27.517°S:32.691°E), rocky intertidal zone, 18 m, periphery of reef, loose boulders, dived ORI, 30.iii.2005 (W3388, living); Sodwana Bay (27.533°S:32.683°E), algal reef, 6-12 m, dived D. Herbert *et al.*, 13.ix.1987 (E571); North East of Gipsy Hill (27.778°S:32.653°E), 84-90 m, sand, dredged NMDP, Stn. ZK22, 09.vi.1990 (S7463); Leadsman Shoal, Raggie Reef (27.800°S:32.617°E), a mixed algal and coral reef 1-2 km north of Leven Point, 8-14 m, sorted from stone washings, dived D. Herbert & NPB, 13-15.v.1988 (E2723, E2724); same locality, 8-12 m, a mixed algal and coral reef, 1-2 km north of Leven Point, dived D. Herbert & NPB (E6807); same locality, main portion of coral reef, 7-11 m, dived D. Herbert & NPB, 14.vi.1988 (E6763); off Leven Point (27.925°S:32.608°E), 50-60 m, mud, dredged R.V. *Meiring Naudé*, 09.vi.1988 (E5867, E4134); Leven Point (27.917°S:32.583°E), sorted from stranded coralline algal debris washing ashore in bay immediately north of point, leg. D. Herbert, 15.v.1988 (E2785, E2787); off Park Rynie (30.385°S:30.833°E), 101 m, some sand, sponge rubble, dredged R.V. *Meiring Naudé*, Stn. X10, 19.viii.1981 (C1553).

Eastern Cape: off Port Grosvenor (29.967°S:31.419°E), 100-110 m, pebbles, some sand, dredged R.V. *Meiring Naudé*, Stn. D6, viii.1981 (C610); off Nthlonyane River (32.278°S:29.100°E), 300 m, medium sand, dredged R.V. *Meiring Naudé*, Stn. D9, 05.vii.1985 (C8718); same locality (32.292°S:29.090°E), 320-350 m, coarse sand, dredged R.V. *Meiring Naudé*, Stn. D9, 05.vii.1985 (C9151); off Mbashe River (32.353°S:29.023°E), 295–300 m, old shell rubble, dredged R.V. *Meiring Naudé*, Stn. Q15, 06.vii.1985 (C8890).

Extralimital material examined: RÉUNION ISLAND: Possession Bay, rounded boulders and stones below pebble beach, 3-6 m, dived D. Herbert, 22.ix.1988 (K5111, living).

Comparison: In comparison with other *Phasianella* species, *P. solida* differs in terms of the shell size and colouration. It is moderate in size and has a marking of white bands alternating with red below the suture and on the body whorl. Juvenile specimens of this species may be confused with adult *Tricolia* species, but may be distinguished from the latter by the spiral capillary lines, which is a typical character of *Phasianella* (Moolenbeek & Dekker 1993).

Hickman & McLean (1990) illustrated the shell and the anatomy of this species and that of *P. australis*. From these illustrations, the anatomy of *P. solida* differs from that of *P. australis* by having shorter cephalic lappets. In terms of the shell size, *P. solida* is moderate and *P. australis* is much larger. Hickman & McLean (1990) also illustrated the radula of other members of *Phasianella*. The radula of *P. solida* is illustrated herein for the first time.

Barnard (1963) and Kensley (1973) recorded *P. jaspidea* from Mozambique. The type locality for this species is Zanzibar. Pilsbry (1888) and Wronski (2007) treated *P. jaspidea* as a synonym of *P. variegata* Lamarck, 1822. However, Wilson (1993) showed that *P. variegata* is a western Australian endemic species and what Pilsbry (1888) considered to be the distribution of *P. variegata* is actually that of *P. solida*. Pilsbry (1888) also treated *P. brongnartii* as a synonym of *P. variegata*.

Additional notes: In view of the variability exhibited by *P. solida*, further potential synonyms of this species that need to be investigated are *Phasianella aethiopica* Philippi, 1853 and *Phasianella unifascialis* Kiener, 1847.



Figure 2.12. Syntype of *H. solida*, NHMW 14338, length = 25 mm (Copy of figure taken by A. Eschner 2008).

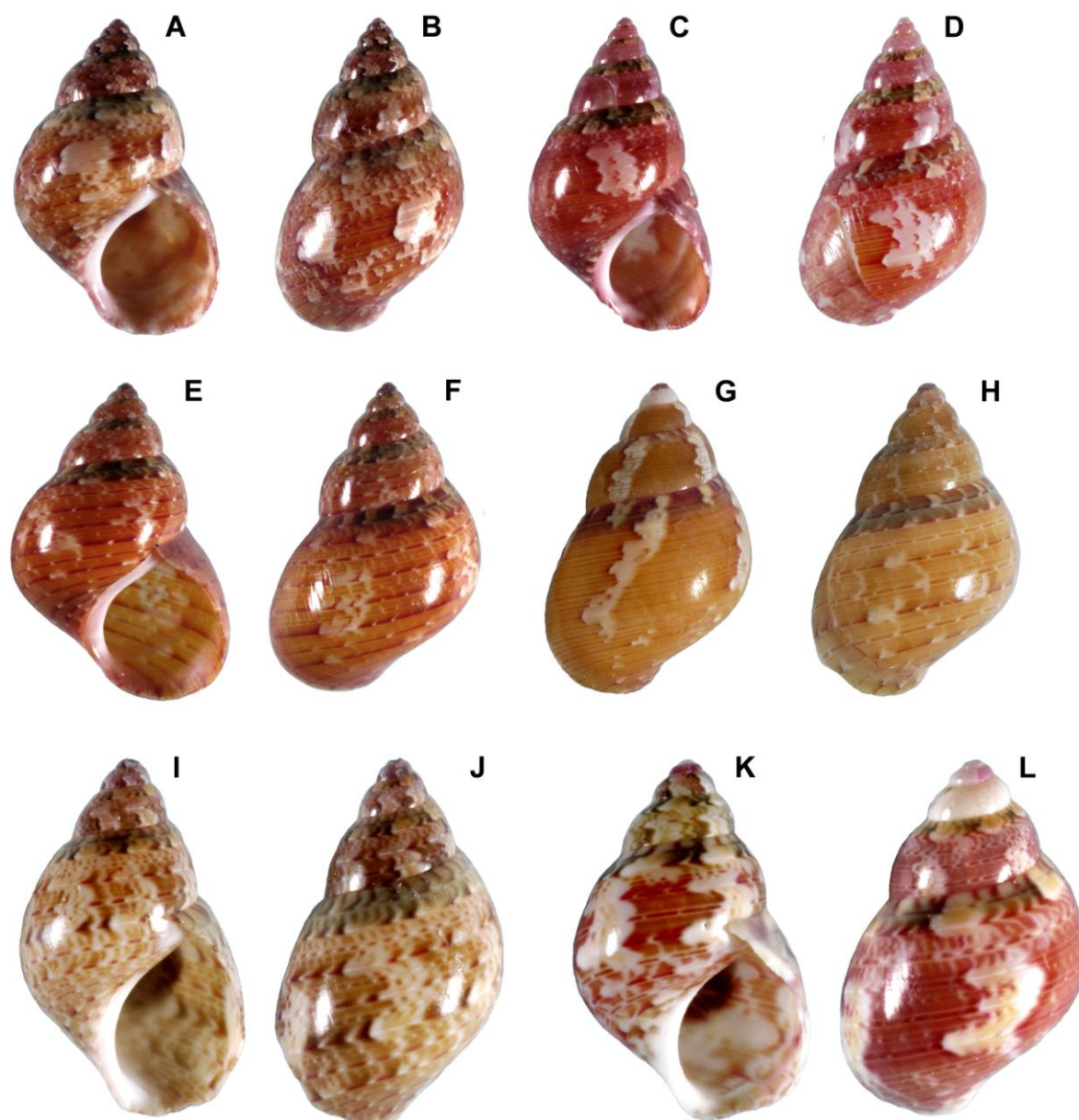


Figure 2.13. Variation in shell colouration of *P. solida*: (A, B) length 13.1 mm, width 7.0 mm, NMSA S2424. Between Bhanga Nek and Kosi Bay, KwaZulu–Natal; (C, D) length 12.0 mm, width 7.1 mm, NMSA S1662. Between Bhanga Nek and Kosi Bay, KwaZulu–Natal; (E, F) length 13.9 mm, width 7.0 mm, NMSA S1472. Between Bhanga Nek and Kosi Bay, KwaZulu–Natal; (G) length 10.1 mm, width 6.1 mm, NMSA D9432. Between Bhanga Nek and Kosi Bay, KwaZulu–Natal; (H) length 10.9 mm, width 5.4 mm, NMSA D9432. Between Bhanga Nek and Kosi Bay, KwaZulu–Natal; (I, J) length 7.3 mm, width 5.4 mm, NMSA L6900. Malongane, Mozambique; (K, L) length 6.0 mm, width 3.8 mm, NMSA L6900. Malongane, Mozambique.

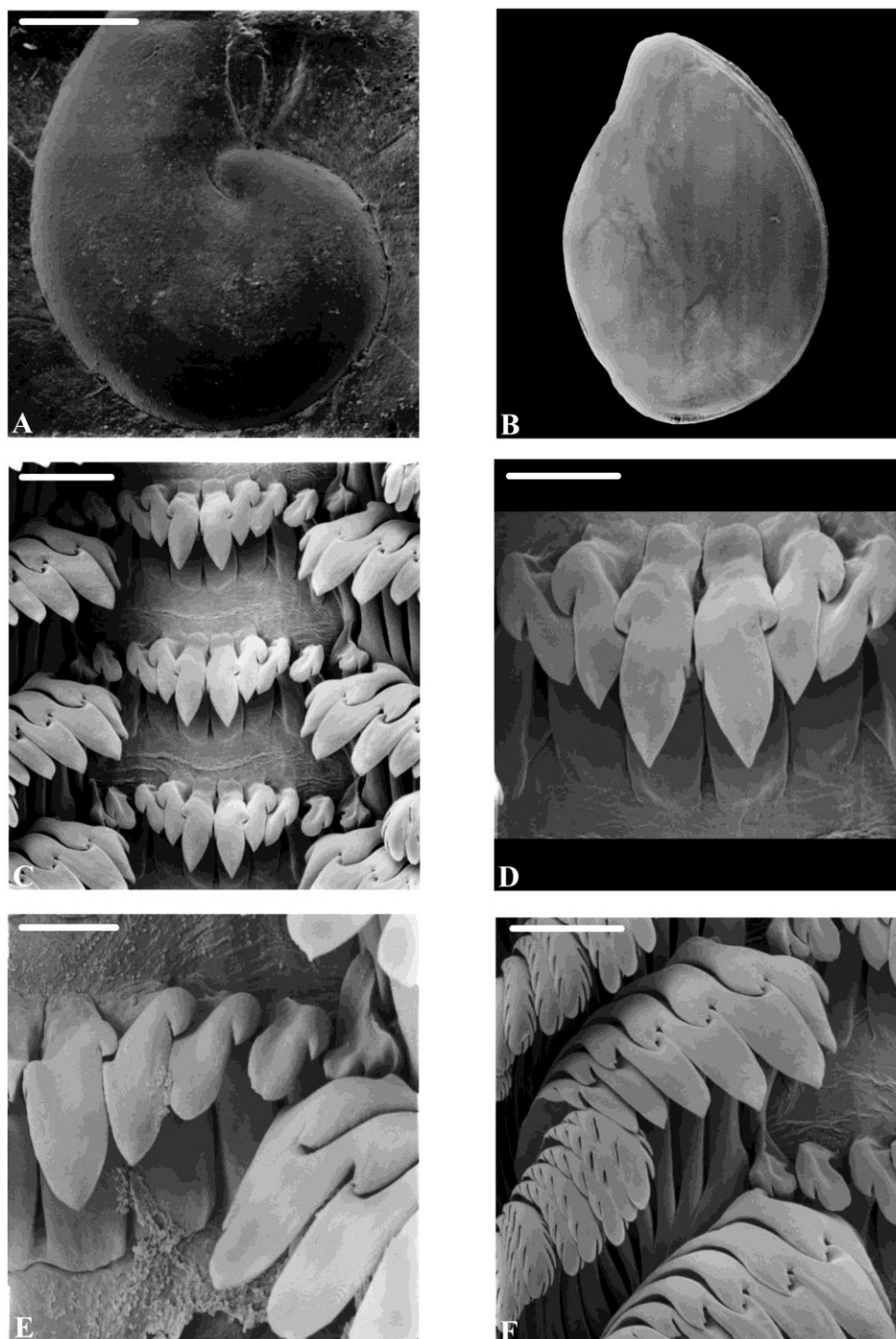


Figure 2.14. Scanning electron microscope of protoconch, operculum and radula of *P. solida*: (A) external surface of protoconch, showing smooth surface and angulate terminal lip, NMSA D6067, bar = 70 μm ; (B) external surface of operculum, showing smooth surface and a narrow peripheral groove underlying labral margin, NMSA S2254, maximum diameter 0.8 mm; (C) central portion of radula, NMSA L6890, bar = 150 μm ; (D) innermost lateral teeth, NMSA L6890, bar = 50 μm ; (E) lateral and innermost marginal teeth, NMSA S2254, bar = 90 μm ; (F) marginal teeth, NMSA L6890, bar = 80 μm .

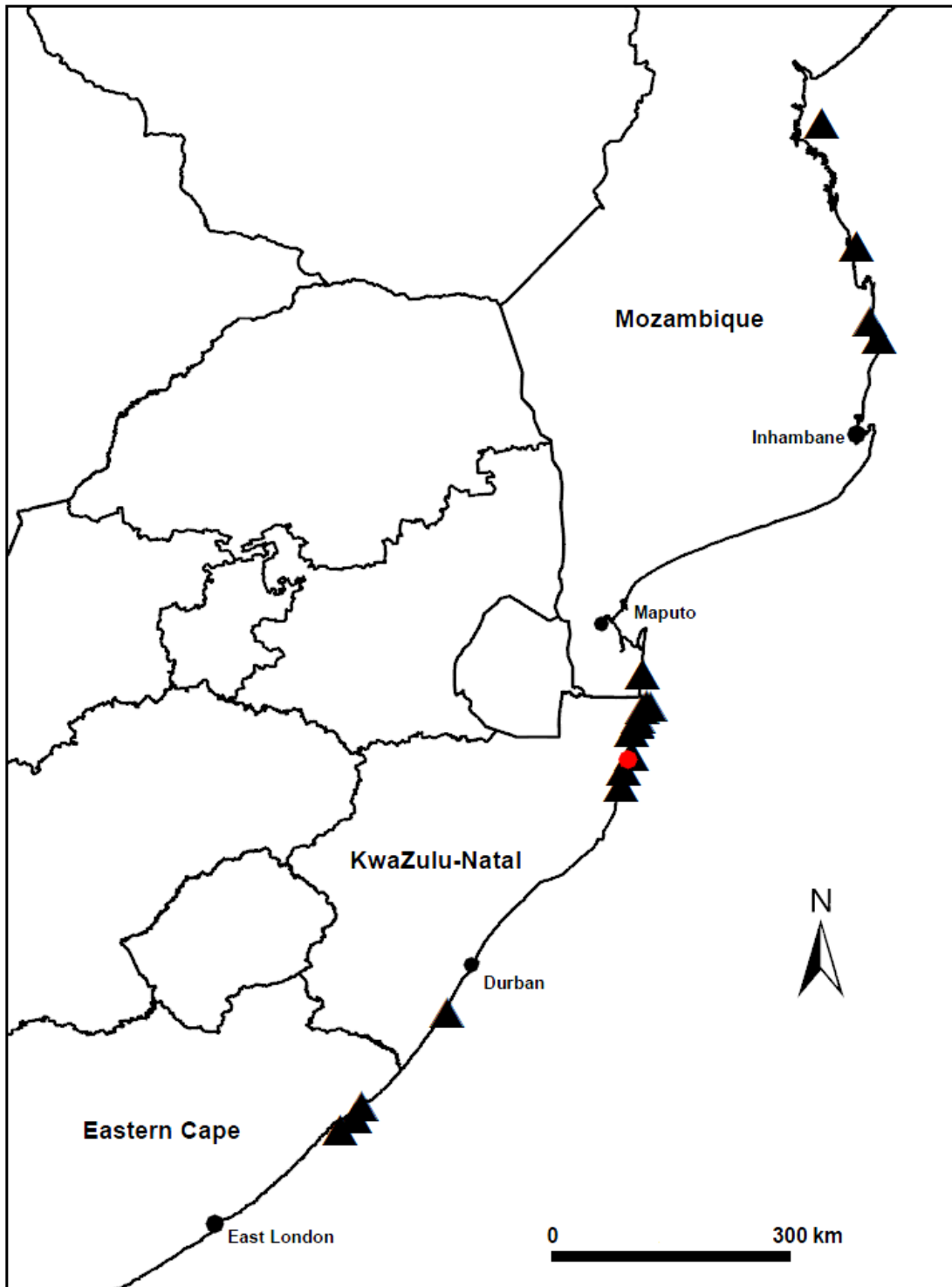


Figure 2.15. Distribution map of *P. solida*. Each black triangle represents one or more site records. Red dot represents a sequenced sample.

Genus *Tricolia* Risso, 1826

Tricolia Risso, 1826: 122; Woodring 1928: 418-420; Robertson 1958: 260-261; Barnard 1963: 206; Robertson 1985: 39-40; Hickman & McLean 1990: 62-67, figs 29-32. Type species, by subsequent designation, Gray 1847: 144: *Turbo pullus* Linnaeus, 1758. Type loc.: "Mediterranean Sea".

Eudora Gray, 1852, non Péron & Lesueur, 1810. Type species, by monotypy: *Eudora varians* Gray, 1852 [= *Tricolia pullus picta* (da Costa, 1778)].

Chromotis Adams & Adams, 1863: 19-20. Type species, by monotypy: *Phasianella neritina* Dunker, 1846 [= *Tricolia neritina* (Dunker, 1846)].

Tricoliella Monterosato, 1884: 110. Type species, by subsequent designation, Pilsbry 1888: 167: *Phasianella "pulla"* (Linnaeus, 1758).

Steganomphalus Harris & Burrows, 1891: 78-79, 112.

Epheriella Pallary, 1920: 48. Type species, by monotypy: *Epheriella algoidea* Pallary, 1920 [= *Tricolia algoidea* (Pallary, 1920)].

Eutricolia Nordsieck, 1973: 4, 10. Type species, by original designation: *Tricolia speciosa* (Mühlfeldt, 1824).

Tricolietta Nordsieck, 1973: 3, 4, 6, 9, 10. Type species, by original designation: *Tricolia picta* (da Costa, 1778) [subspecies of *T. pullus*].

non *Pellax* Finlay, 1926: 368. Type species, by original designation: *Phasianella huttoni* Pilsbry, 1888 [= *Eatoniellidae* Ponder, 1965].

Discussion of synonyms

All *Tricolia* synonyms listed by Robertson (1985) have been re-assessed for validity in relation to *Tricolia* as interpreted here. Synonyms of *Eulithidium* (i.e., *Eucosmia* and *Usatricolia*) and *Hiloa* (i.e., *Eotricolia*) have been excluded.

Of particular relevance in terms of the present study is the taxon *Chromotis*. The evidence obtained during this work strongly supports the hypothesis that *Chromotis* is synonymous with *Tricolia sensu stricto*. Further details are given under conclusions.

Key to species of *Tricolia* in southern Africa
(Based on shell and geographical distribution characters)

1. Shell with distinct spiral sculpture on body whorl2
 - Shell lacking spiral sculpture or with only weak spiral sculpture, primarily on apical whorls.....4
2. Shell biangulate, with numerous close-set spiral ridges3
 - Shell lacking a distinct angle, with ca 8 strong, widely spaced spiral cords..... ***T. striolata***
3. Shell colour dull grey to greyish pink or whitish with extensive pale pink overtones..... ***T. bicarinata***
 - Shell colour brownish-orange or brick-red, usually interrupted by zigzag greenish axial flames on body whorl..... ***T. insignis***
4. Shell with a spiral row of turquoise spots below suture5
 - Shell without turquoise spots.....6
5. Shell relatively large and globular, whorls evenly rounded, relatively shallow suture, aperture ovate-circular, with distinct spiral sculpture on apical whorls ***T. kochii***
 - Shell long and thin, convex whorls, strongly indented suture, a proportionately smaller and circular aperture, lacking any spiral sculpture..... ***T. africana***
6. Apex with a rows of pink spots on apical whorl..... ***T. formosa***
 - Apex without rows of pink spots on apical whorl.....7
7. Shell with neritiform shape, very large aperture..... ***T. neritina***
 - Shell not as above, shape turbiniform to bulimiform.....8
8. Shell patterned with numerous, fine, close-set, sinuous, opisthocline, orange-red lines.....9
 - Shell not as above.....10
9. Shell thick and with a spiral row of white dots on apical region..... ***T. elongata***
 - Shell translucent, lacking white dots on apical region..... ***T. retrolineata***

10. Shell patterned with numerous tiny red dots on body whorl..... ***T. ios***
 – Shell not as above.....11
11. Species distributed along the East coast from Kosi Bay to the Transkei.....12
 – Species distributed along the west coast, from Hermanus to Kunene River mouth...13
12. Shell globose and lower–spired, widely open umbilicus..... ***T. saxatilis***
 – Shell turbiniform, relatively high spire, umbilicus closed..... ***T. adusta***
13. Shell globose turbiniform, slightly angled with fine spiral threads, aperture size height
 relative to spire..... ***T. kraussi***
 – Shell turbiniform or bulimiform, smooth and lacking any angulation, aperture smaller
 than spire ***T. capensis***

Tricolia adusta Nangammbi & Herbert, 2006

Figs 2.16-2.19

Tricolia adusta Nangammbi & Herbert, 2006: 12, figs 1-16. Type loc.: Aliwal Shoal, Cracker Reef (KwaZulu–Natal, South Africa).

Etymology, *adustus* (Latin) – brown, referring to the predominately brown colouration of the shell.

Diagnosis: Shell small, elevated–turbiniform; whorls rounded, without any angulation, suture not strongly indented; smooth, lacking spiral sculpture and with only microscopic growth–lines; colouration highly variable, but typically buffish, patterned with zigzag brown axial lines and subsutural blotches, evidently never with pink dots on first two whorls or with bluish subsutural spots.

Description (Figs 2.16A-H):

Shell small, elevated–turbiniform; teleoconch of up to 4.5 whorls with weakly indented suture; whorls smoothly rounded, lacking any angulation, periphery slightly below mid–whorl and profile usually more strongly curving below this than above; apex broadly rounded. Sculpture weak, shell mostly smooth and glossy, marked only by exceedingly fine growth–lines. Aperture sub–circular, outer lip thin, colour pattern visible internally; inner lip concave and slightly reflected; umbilicus closed in most specimens, remaining as a narrow chink in others. Colouration extremely variable, typically buff to pale yellowish–brown, variously marked with zigzag lines in shades of darker brown, frequently bolder below suture; umbilical region often bordered by a spiral band of alternating dark and light blotches (Fig. 2.16A); some specimens with large, dark brown to black, trapezoid blotches below suture (Fig. 2.16B); others with broad, alternating axial bands of brown and cream–white on apical surface (Fig. 2.16C); occasionally boldly patterned with close–set, red–brown to dark–brown, zigzag axial lines throughout (Fig. 2.16D); last adult whorl with apical surface sometimes almost uniformly whitish, red or dark–brown (Figs 2.16E–G); rarely almost white throughout (Fig. 2.16H).

Protoconch (Figs 2.17A, B): Typically trochoidean, comprising approx. 1.25 whorls; apical beak present but weak, terminal lip lacking a varix, but markedly angulate at mid–whorl; sculpture for the most part smooth, with traces of curved lines towards periphery, and with raised vermiculate sculpture in apical region.

Operculum (Fig. 2.17C): Calcareous, thick and convex; paucispiral with eccentric nucleus; exterior with microscopic granular sculpture and a distinct peripheral groove underlying labral margin.

Radula (Figs 2.17D-F): Formula $\infty + 5 + 1 + 5 + \infty$; transverse rows broadly M-shaped; rachidian tooth with broad, roundly-trigonal base-plate, lacking a cusp, but strongly overlapped by cusps of innermost laterals; base-plates of laterals overlapping extensively, the inner two with alate projections on outer margin; outermost lateral with trigonal base-plate and with a slightly smaller cusp than that of other laterals; cusp morphology of laterals somewhat variable between specimens; cusp usually with 2-4 larger central denticles and a variable number of small endocones and ectocones; one denticle frequently dominant on third and fourth laterals; innermost marginals (the first three or four) with a single broad spatulate cusp, with one strong ectocone and 1 or 2 smaller endocones; marginals progressively smaller toward edge of radula, the spatulate cusp becoming smaller and less distinct, and the ectocones finer and more numerous.

External anatomy (Fig. 2.18): Typically trochoidean; neck-lobes well developed, both digitate; number of digits appears to be a function of specimen size; left neck-lobe broad and outspread with *ca* 12 digits; right neck-lobe slightly smaller and with fewer digits. Three pairs of papillate epipodial tentacles on each side, the middle one somewhat smaller than the other two; an epipodial sense organ present at base of each tentacle; epipodial fold with light brown to purple-brown pigmentation, darkest between first and second epipodial tentacles. Foot longitudinally divided, sole white. Colour pattern of head-foot variable, resembling that of shell.

Measurements: Largest specimen examined – length 4.4 mm, width 2.5 mm. Length:width ratio 1.5-1.8; aperture:length ratio 0.4-0.5 (N=50).

Habitat: A subtidal species inhabiting off-shore reefs; living specimens from shallow infratidal to 70 m, empty shells from beach-drift to 140 m, exceptionally to 300 m.

Geographical range (Fig. 2.19): Endemic to South Africa, ranging from northern KwaZulu-Natal (Kosi Bay) to Eastern Cape (southern Transkei, Qora River).

Type material (Fig. 2.16): A, *T. adusta*, holotype, NMSA E7143/T2013, length 3.3 mm, width 2.2 mm. SOUTH AFRICA: *KwaZulu–Natal*, Aliwal Shoal (30.283°S:30.833°E), Cracker Reef, dived D. Herbert, 30.iv.1989, approx. 23 m, living.

Paratypes: SOUTH AFRICA: *KwaZulu–Natal*: NMSA, W2477/T2014 (59), same collection data as holotype; D9516/T2015 (9), between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), no. 13 reef, 6-18 m, living, dived D. Herbert *et al.*, 12-20.vii.1987; E1005/T2212 (31), off Durban Bluff, 18-22 m, fine sand, leg. R. Kilburn & R. Fregona, 1983; S8687/T2213 (28), Aliwal Shoal, off Scottburgh (30.283°S:30.833°E), approx. 14 m, underwater pump, dived D. Herbert, 02.vi.1991; V1759/T2214 (12), Stiebel Reef, north east of Phumula (30.617°S:30.583°E), hand-dredged sand, ca 20 m, dived D. Herbert, 21.ii.1993.

Eastern Cape: E255/T2016 (60), off Whale Rock (31.948°S:29.225°E), 20-26 m, sand and gorgonians, dredged R.V. *Meiring Naudé*, 16.vii.1982.

Additional material examined (selected samples, all NMSA, unless indicated otherwise): SOUTH AFRICA: *KwaZulu–Natal*: Leadsman Shoal, Raggie Reef (27.800°S:32.867°E), 8-12 m, a mixed algal and coral reef, 1-2 km, north of Leven Point, dived D. Herbert & NPB, 15.v.1988 (E7028); off St. Lucia Lighthouse, 50 m, ex CSIR Water Research (A6172); Richards Bay (28.817°S:32.133°E), *ex pisce*, vi.1985, J.P. Marais, vii.1985 (D1578); off Durban Bluff, near Bluff caves, 10-15 m, dived D. Herbert, 07.v.1989 (E6544); between Umgababa and Umzimbazi River (30.143°S:30.945°E), 70 m, fine sand, dredged R.V. *Meiring Naudé*, 08.vii.1986 (E6999); Aliwal Shoal, off Umkomaas (30.283°S:30.833°E), 25-28 m, hand-dredged sand, dived D. Herbert, 16.xii.1990 (S9877); same data, (30.266°S:30.823°E), 15.5 m, loose rubble, dived ORI, 07.xii.2004 (W2584, living); off Scottburgh, gravel reef, 26.vii.1987 (E405); Park Rynie, 50 m, coarse sand, 25.xi.1976, ex CSIR Water Research, 1977 (B269); Lander's Reef, off Park Rynie, 34 m, sand, dived D. Herbert, 02.vi.1991 (S6082); "B.J.'s Reef", off Hibberdene (30.583°S:30.6°E), 18-26 m, dived D. Herbert, 15.xi.1992 (V1845); off Phumula, 35 m, living on shell of *Bolma andersoni* (Smith, 1902), dived M. Wallace, viii.1996 (V4004); same data, (30.638°S:30.549°E), 36 m, on low profile reef, dived M. Wallace & V. Fraser, 07.xii.2004 (W2586, living); Glenmore Beach, south of Tongazi River mouth, intertidal rocks, leg. D. Herbert & M. Mander, 11.viii.1991 (S4123).

Eastern Cape: off Mtamvuna River (31.153°S:30.250°E), 140 m, sponge rubble, dredged R.V. *Meiring Naudé*, viii.1981 (C827); off Mzamba, from gut of slinger/stumpnose, leg. J.P.

Marais, vii.1977 (A6650); Mzamba (31.083°S:30.183°E), beach–drift, leg. R. Kilburn & D. Herbert, 12-30.v.1986 (D2982); off Mtentu River (31.253°S:30.083°E), 50 m, shell gravel, dredged R.V. *Meiring Naudé*, 12.viii.1981 (C1689); off Port Grosvenor (31.410°S:29.953°E), 80 m, worn coral nodules, dredged R.V. *Meiring Naudé*, 16.viii.1981 (E179); same data, (29.952°S:31.434°E), 100-115 m, sand, some mud, solitary coral, shells, dredged R.V. *Meiring Naudé*, viii.1981 (C1331); Port Grosvenor (31.398°S:29.937°E), 60 m, sand, broken shell, dredged R.V. *Meiring Naudé*, viii.1981 (S3177); Mbotyi (31.450°S:29.733°E), beach–drift, leg. R. Kilburn & D. Herbert, v-vi.1985 (C8450); off Mbotyi (31.484°S:29.751°E), 50 m, mixed sand, mud, abundant worm tubes, dredged R.V. *Meiring Naudé*, viii.1981 (C1750); off Whale Rock (31.948°S:29.225°E), 20-26 m, sand and gorgonians, dredged R.V. *Meiring Naudé*, 16.vii.1982 (E6970, V4049); off Mncwasa Point (32.067°S:29.095°E), 25-30 m, fine sand, gorgonians, dredged R.V. *Meiring Naudé*, 19.vii.1982 (E341); off Qora River (32.560°S:28.813°E), 300 m, coarse sand, some broken shell, dredged R.V. *Meiring Naudé*, 11.vii.1984 (S3166).

Comparison: Specimens of *T. adusta* were previously identified under the name *T. africana*. More thorough investigation, however, has revealed consistent differences in shell morphology. In comparison with *T. adusta*, *T. africana* is more elongate and has a higher spire, a proportionately smaller and more circular aperture, more convex whorls and frequently has light blue spots below the suture. In addition, the two species differ in terms of their habitat preferences: *T. africana* is an intertidal species, living on and under rocks in mid–shore pools, whereas *T. adusta* occurs amongst algal turf on subtidal reefs at depths of up to 70 m. In terms of shell shape *T. adusta* resembles *T. formosa*, but lacks the pink spots on the apical whorls, characteristic of that species. All other species of *Tricolia* occurring in southern African differ markedly from *T. adusta* in terms of shell shape and/or sculpture.

Additional notes: Characters of the radula and external anatomy suggest that *T. adusta* and *T. formosa* are related and differ somewhat from most of the other endemic South African species, which resemble the type species, *T. pullus*, in these features. The inner marginal teeth of the radula of *T. adusta* and *T. formosa* have one strong undivided ectocone, whereas in *T. pullus* and the other endemic southern African species, the ectocone of the inner marginal teeth is bifid or notched, and interlocks with two notches at the base of the cusp of the adjacent outer tooth. In terms of the external anatomy, *T. adusta* and *T. formosa* have one sense organ at the base of each epipodial tentacle, whereas *T. pullus* and the other endemic southern African species have two sense organs at the base of the anterior epipodial tentacle on the right.

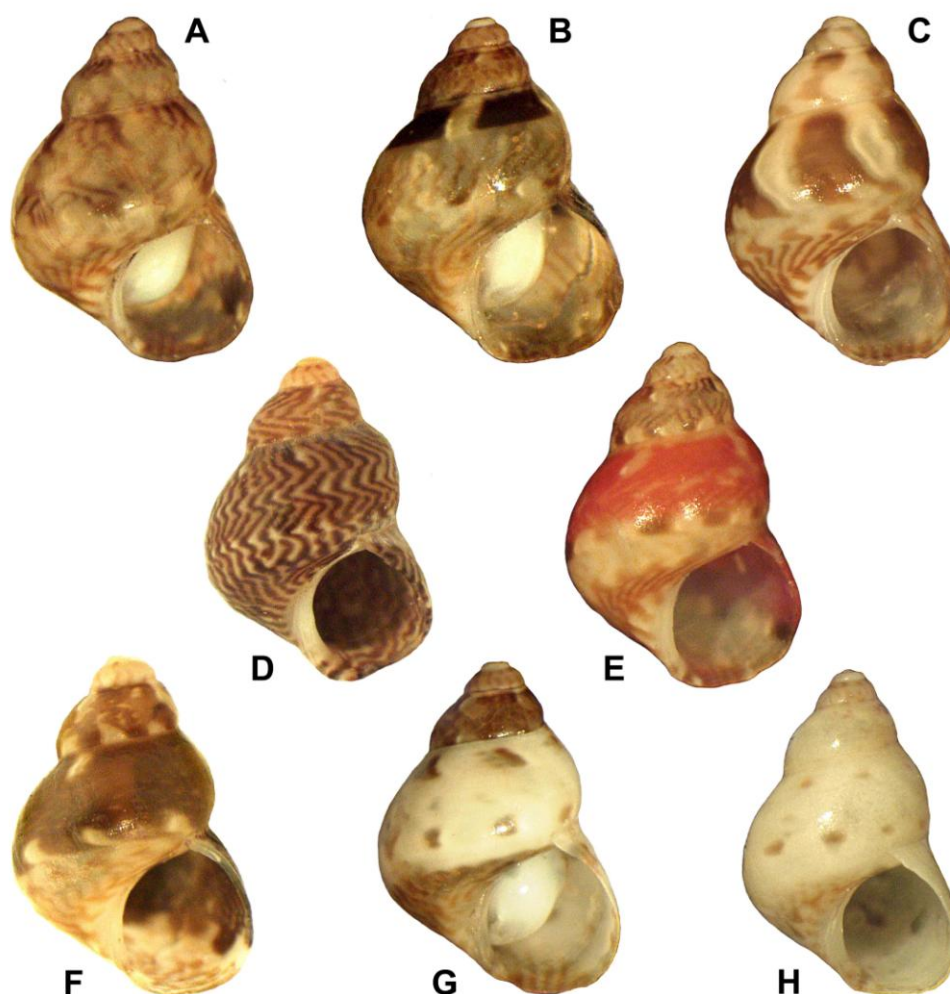


Figure 2.16. Variation in shell colour and pattern of *T. adusta*: (A) holotype, length 3.3 mm, width 2.2 mm, NMSA E7143/T2013, Aliwal Shoal, Cracker Reef, KwaZulu-Natal; (B–H) paratypes: (B) length 2.9 mm, width 1.9 mm, NMSA E1005/T2212, off Durban Bluff, KwaZulu-Natal; (C) length 3.9 mm, width 2.4 mm, NMSA E255/T2016, off Whale Rock, Eastern Cape; (D) length 3.3 mm, width 2.0 mm, NMSA E255/T2016, off Whale Rock, Eastern Cape; (E) length 3.8 mm, width 2.4 mm, NMSA V1759/T2214, Stiebel Reef, KwaZulu-Natal; (F) length 3.3 mm, width 2.2 mm, NMSA E255/T2016, off Whale Rock, Eastern Cape; (G) length 3.1 mm, width 2.1 mm, NMSA E1005/T2212, off Durban Bluff, KwaZulu-Natal; (H) length 3.5 mm, width 2.2 mm, NMSA S8687/T2213, Aliwal Shoal, off Scottburgh, KwaZulu-Natal.

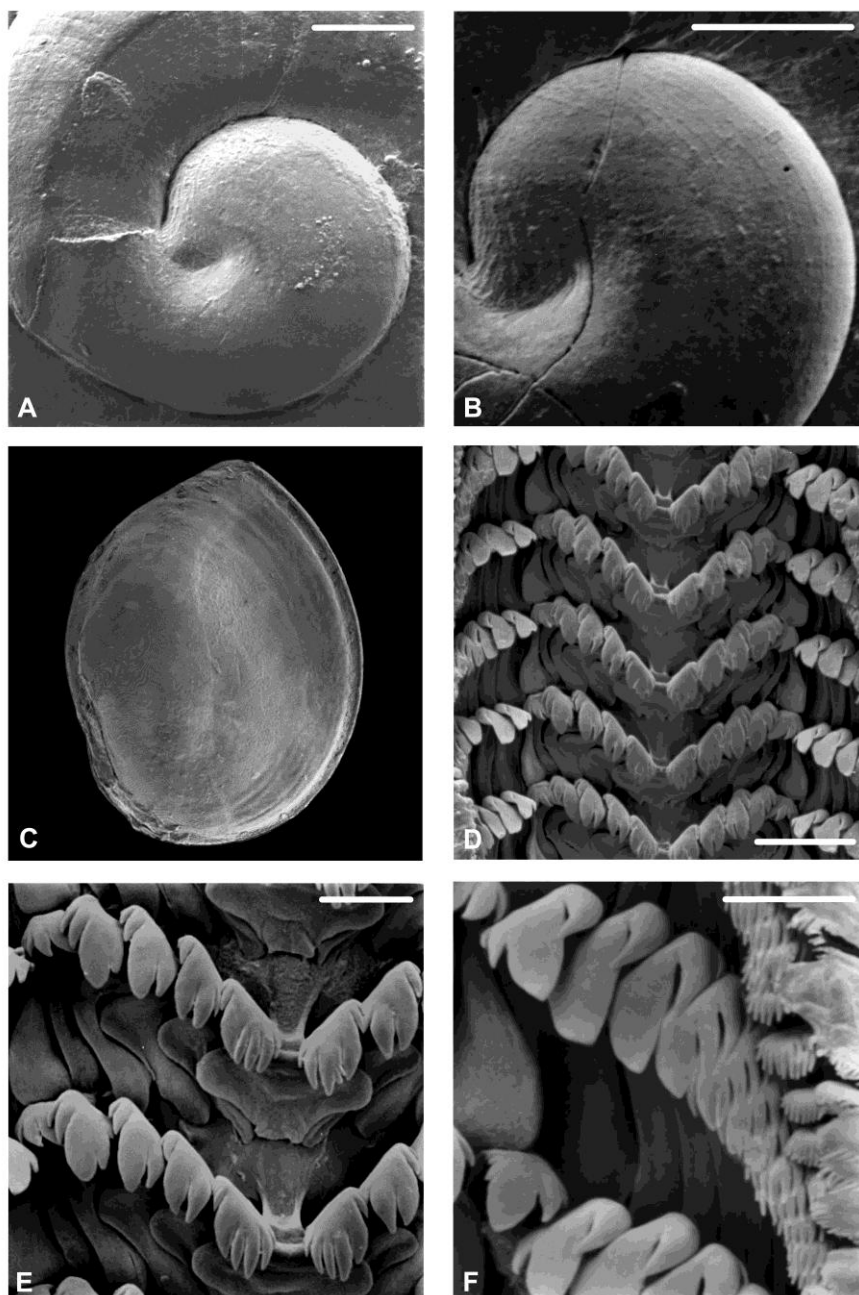


Figure 2.17. Scanning electron microscope of protoconch, operculum and radula of *T. adusta*: (A, B) two views of protoconch, showing traces of curved lines towards periphery and raised vermiculated sculpture in apical region, NMSA W2477, bars = 50 μm ; (C) external surface of operculum, showing microscopic granular sculpture and distinct peripheral groove underlying labral margin, NMSA W2586, maximum diameter 0.9 mm; (D) central portion of radula, NMSA W2586, bar = 25 μm ; (E) rachidian and lateral teeth, NMSA W2586, bar = 10 μm ; (F) inner marginal teeth, NMSA W2586, bar = 10 μm .

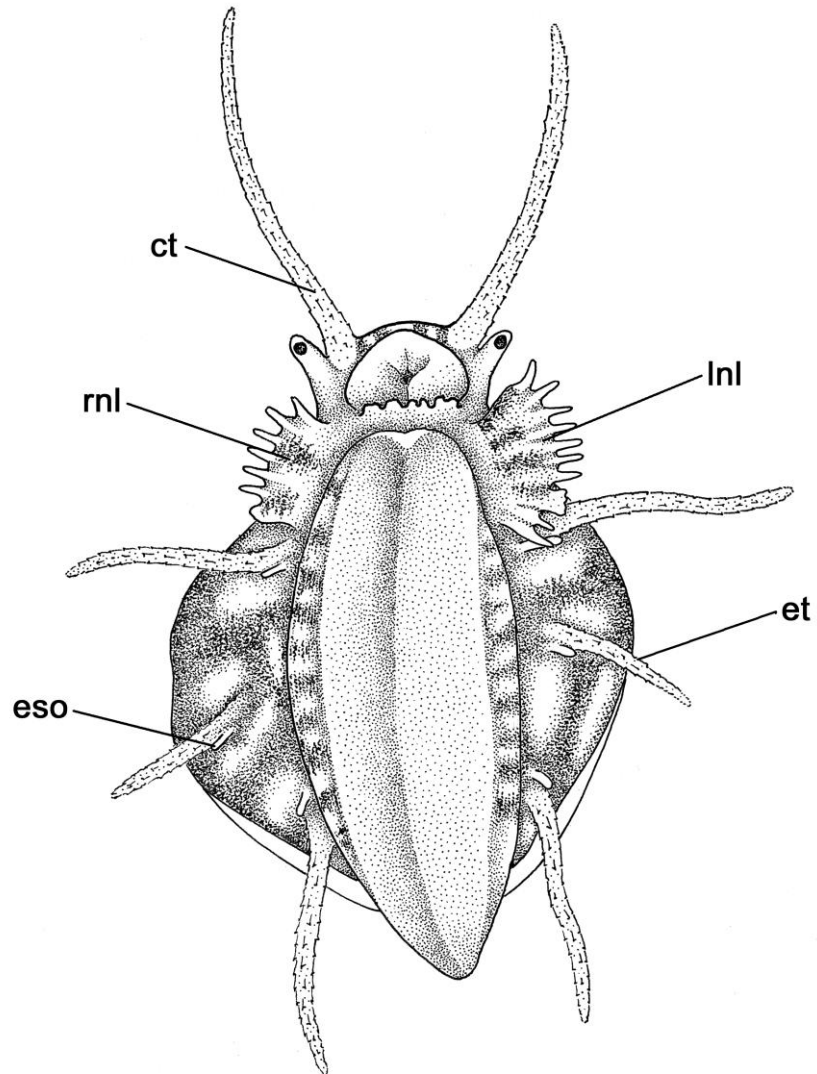


Figure 2.18. External anatomy of *T. adusta*: ct – cephalic tentacles; eso – epipodial sense organ; et – epipodial tentacle; lnl – left neck-lobe; rnl – right neck-lobe.

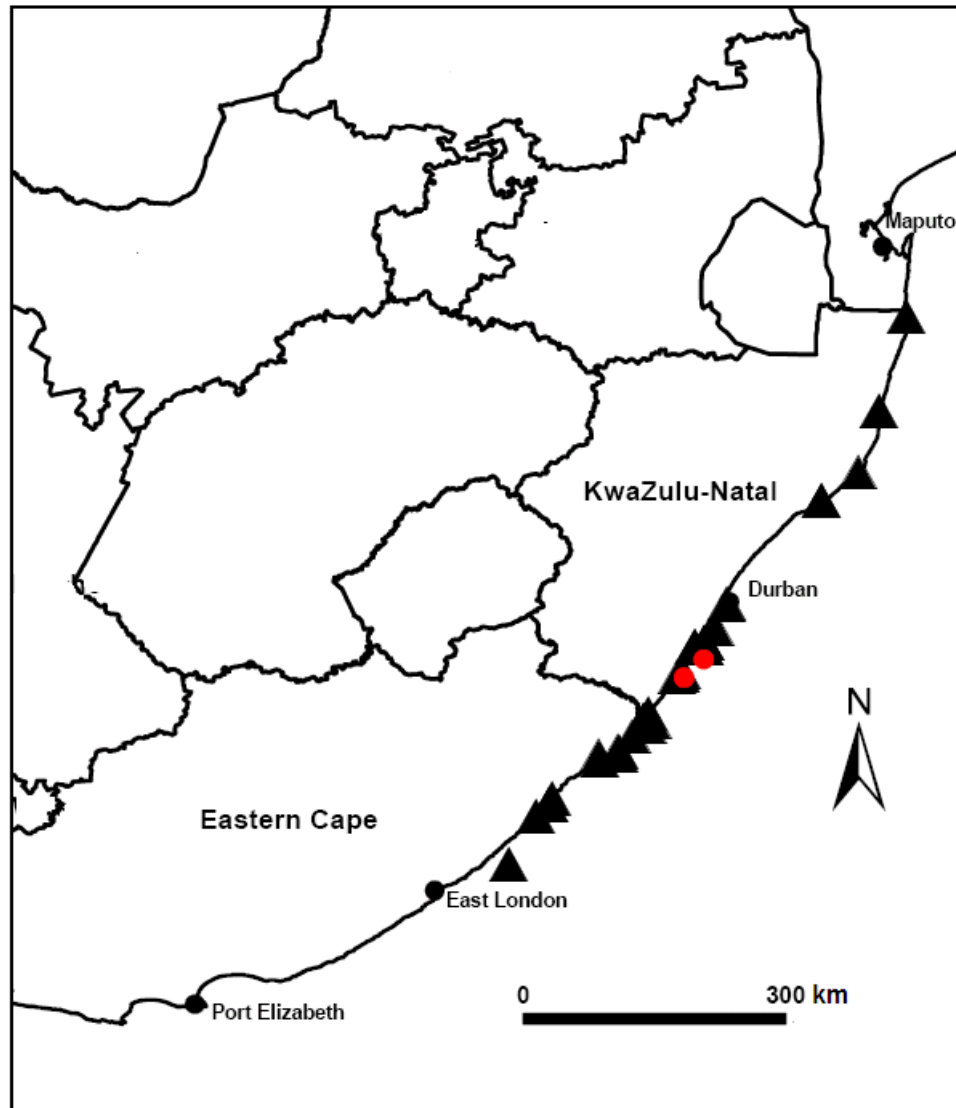


Figure 2.19. Distribution map of *T. adusta*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia africana (Bartsch, 1915)

Figs 2.20-2.23

Phasianella africana Bartsch, 1915: 145, pl. 10, fig. 2; Turton 1932: 174. Type loc.: Port Alfred (Eastern Cape, South Africa).

Phasianella farquhari Turton, 1932: 174, pl. 41, fig. 1234. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella rufanensis Turton, 1932: 174, pl. 41, fig. 1232. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella rufanensis adjacens Turton, 1932: 174, pl. 41, fig. 1233. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Tricolia africana; Barnard 1963: 207-208; Nangammbi & Herbert 2006: 17.

Tricolia farquhari; Barnard 1963: 208-209.

Tricolia rufanensis adjacens; Barnard 1963: 207.

Etymology, *africana* – from Africa.

Diagnosis: Shell elongate–turbiniform; convex whorls; strongly indented suture; a proportionately smaller and circular aperture; smooth, lacking spiral sculpture; colouration highly variable, ground colour light brown to dull orange or yellowish, superimposed by numerous irregular blotches and smudges of various shades of brown and black, which are preceded by white patch, a spiral row of widely spaced, light blue spots are frequently present below suture; ill–defined white blotches occur around umbilicus ridge.

Description (Figs 2.20A-D, 2.21A-I):

Shell elongate–turbiniform with relatively high spire; teleoconch of up to 4.5 whorls with strongly indented suture; whorls convex, without any angulation; apex broadly rounded. Sculpture weak, shell mostly smooth and glossy, lacking any spiral sculpture, but marked only by fine growth–lines. Aperture small and circular, base rather short and rounded; showing exterior markings within; outer lip thin; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; parietal wall covered with a thin callus; umbilicus closed in most specimens, but occasionally remaining as a narrow chink in others. Shell colouration extremely variable, ground colour light brown to dull orange. Superimposed on the ground colouration are numerous irregular blotches and smudges of various shades of brown and black, which are preceded by a white patch. A spiral row of widely spaced, light blue spots is frequently present below suture (Figs 2.21A-C). Ill–defined white blotches occur

around the umbilicus ridge (Figs 2.21A, H); some specimens with large, dark–brown to black, trapezoid blotches below suture (Figs 2.21D, E); others with numerous small, smudged white or black dots on the body whorl (Fig. 2.21G); or with broad, alternating axial bands of pale brown and white on apical surface (Fig. 2.21H); occasionally specimens completely black or pale yellow–orange throughout (Fig. 2.21I).

Protoconch (Fig. 2.22A): Typically vetigastropod, comprising approx. 1.2 whorls; apical beak present but weak, terminal lip lacking a varix; sculpture for the most part smooth.

Operculum (Fig. 2.22B): Similar to *T. adusta*.

Radula (Figs 2.22C–F): Similar to *T. pullus* (Gofas 1982), but with elliptical base–plate.

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985), but with a pair of greenish blotches on snout between and just in front of cephalic tentacles.

Measurements: Largest specimen examined – length 6.9 mm, width 3.1 mm. Length:width ratio 1.6–2.3 (N=50).

Habitat: *T. africana* occurs commonly in the rocky intertidal zone; living on and under rocks in mid–shore pools, empty shells in beach–drift.

Geographical range (Fig. 2.23): Endemic to South Africa, ranging from the Eastern Cape (southern Transkei, Qora River mouth) to the southern Cape (Struis Bay).

Type material (Fig. 2.20): A, *Phasianella africana*, holotype, USNM 186870, length 3.5 mm, diameter 2.7 mm (A is copy of figure from Bartsch 1915); B, *Phasianella farquhari*, holotype, OUM M002780, length 3.7 mm, width 2.3 mm; C, *Phasianella rufanensis*, holotype, OUM M002778, length 5.1 mm, width 3.0 mm; D, *Phasianella rufanensis adjacens*, holotype, OUM M002779, length 6.1 mm, width 3.2 mm. The holotype of *P. africana* from Port Alfred is figured herein (Fig. 2.20A), but the actual specimen was not seen.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Eastern Cape*: Qora River mouth (32.450°S:28.683°E), intertidal zone, leg. D. Herbert, 12–15.ii.1986 (D2048, living); Kei River, East of mouth (32.667°S:28.383°E), leg. R. Kilburn *et al.*, x.1982 (C3560); Kei River mouth (32.683°S:28.383°E), leg. R. Kilburn (A1903). Kwelera, East

London (32.900°S:28.080°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 08.vii.2005 (W3193, living); Gonubie, East London (32.933°S:28.017°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 08.vii.2005 (W3392, living); Fuller's Bay, East London (33.067°S:27.900°E), leg. E. Roscoe, 21.xi.1980 (EM 8883); Hickman's River mouth (33.067°S:27.833°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 07.vii.2005 (W3387, living); Kidd's Beach (33.150°S:27.683°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 09.vii.2005 (W3194, living); Fish River mouth (33.483°S:27.133°E), rocky intertidal zone, under rocks, leg. T. Nangammbi *et al.*, 21.vi.2005 (W1030, living); Rufanes, Port Alfred (33.579°S:26.946°E), rocky intertidal zone, under rocks, leg. T. Nangammbi *et al.*, 29.viii.2003 (W1034, living); Kowie lagoon, Port Alfred (33.650°S:26.900°E), leg. R. Kilburn (8474); Summerstrand, Port Elizabeth (33.983°S:25.650°E), leg. R. Kilburn, 02.i.1972 (W3824, living); Cape Recife, Port Elizabeth (34.027°S:25.655°E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 21.vi.2005 (W3191, living).

Southern Cape: Jeffrey's Bay (34.050°S:24.917°E), leg. R. Kilburn, 1960 (A1668); Coney Glen, Knysna (34.082°S:23.063°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 04.xi.2006 (W4750, living); Buffel's Bay, Goukamma Nature Reserve (34.083°S:22.958°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 04.xi.2006 (W4753, living); Wilderness National Park (34.031°S:22.765°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 04.xi.2006 (W4754, living); Great Brak River mouth (34.033°S:22.217°E), leg. R. Kilburn (A2294); Reebok Reef, between Great and Little Brak River (34.079°S:22.171°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 05.xi.2006 (W4755, living); Die Bakke, Mossel Bay (34.171°S:22.127°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 05.xi.2006 (W4758, living); Mossel Bay Point (34.183°S:22.133°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 05.xi.2006 (W4759, living); Still Bay Point (34.386°S:21.426°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 06.xi.2006 (W4763, living); Struis Bay, site 2 (34.809°S:20.057°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 07.xi.2006 (W4772, living).

Comparison: *T. africana* is considerably different from other southern African *Tricolia* species in having a more elongate shell, convex whorls, a strongly indented suture, and a proportionately smaller and more circular aperture in relation to shell length. This species most closely resembles *T. kochii* in having light blue spots below the suture. Turton's (1932) descriptions of *P. farquhari*, *P. rufanensis* and *P. rufanensis adjacens* were based on shell characteristics similar to those of *T. africana*, and would appear to be colour forms of the

latter. Specimens of *T. adusta* were lumped in with those of *T. africana* until Nangammbi & Herbert (2006) recognized that they were consistently different from *T. africana* and therefore described them as new species.

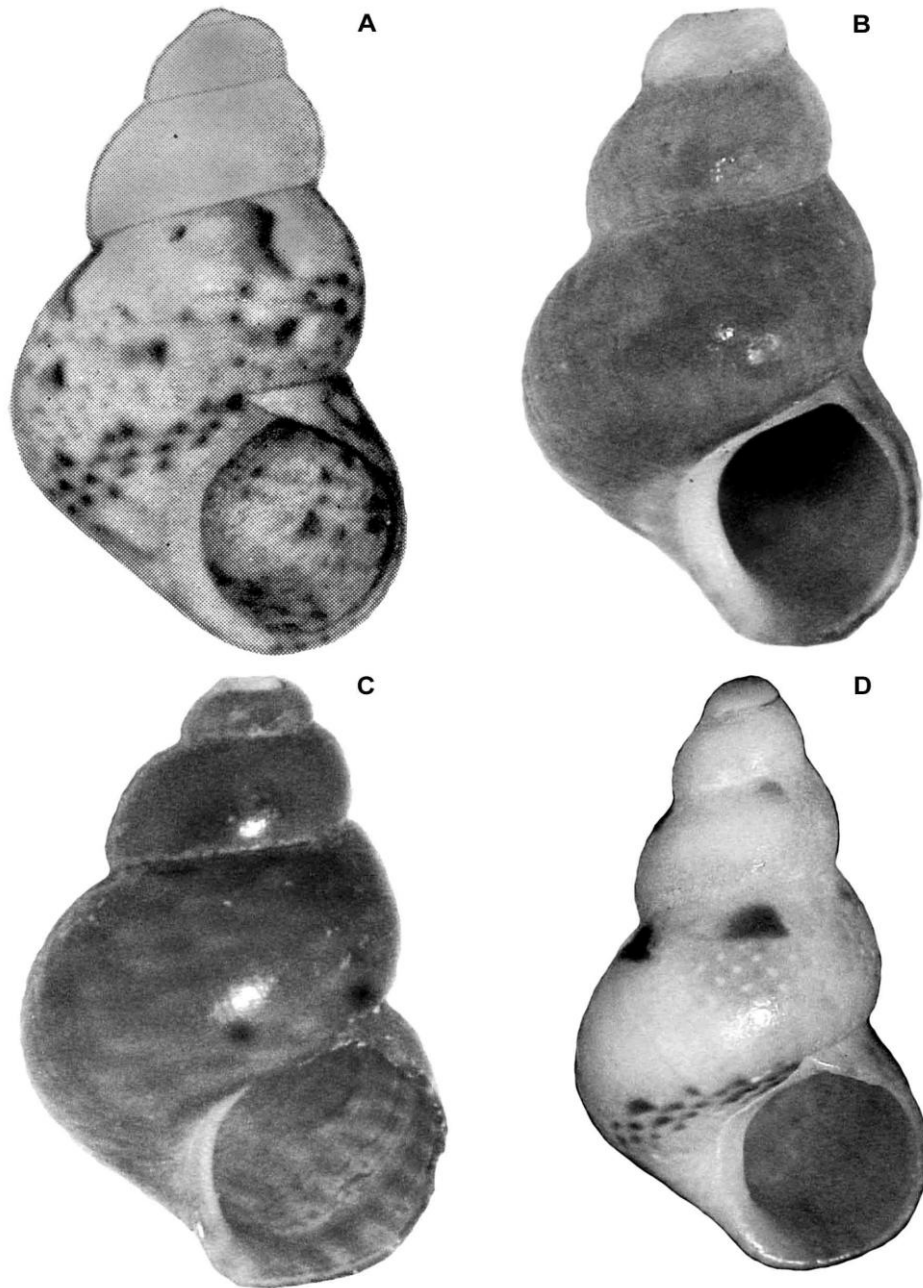


Figure 2.20. Type specimens of *T. africana*: (A) *P. africana*, holotype, USNM 186870, length 3.5 mm, diameter 2.7 mm (A is a copy of figure from Bartsch 1915); (B) *P. farquhari*, holotype, OUM M002780, length 3.7 mm, width 2.3 mm; (C) *P. rufanensis*, holotype, OUM M002778, length 5.1 mm, width 3.0 mm; (D) *P. rufanensis adjacens*, holotype, OUM M002779, length 6.1 mm, width 3.2 mm.



Figure 2.21. Variation in shell colouration of *T. africana*: (A) length 5.3 mm, width 2.9 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (B) length 5.8 mm, width 3.4 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (C) length 6.4 mm, width 3.3 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (D) length 4.5 mm, width 2.5 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (E) length 4.8 mm, width 2.7 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (F) length 5.6 mm, width 2.9 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (G) length 6.0 mm, width 3.3 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (H) length 5.4 mm, width 3.1 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape; (I) length 4.8 mm, width 2.7 mm, NMSA W4750. Coney Glen, Knysna, Southern Cape.

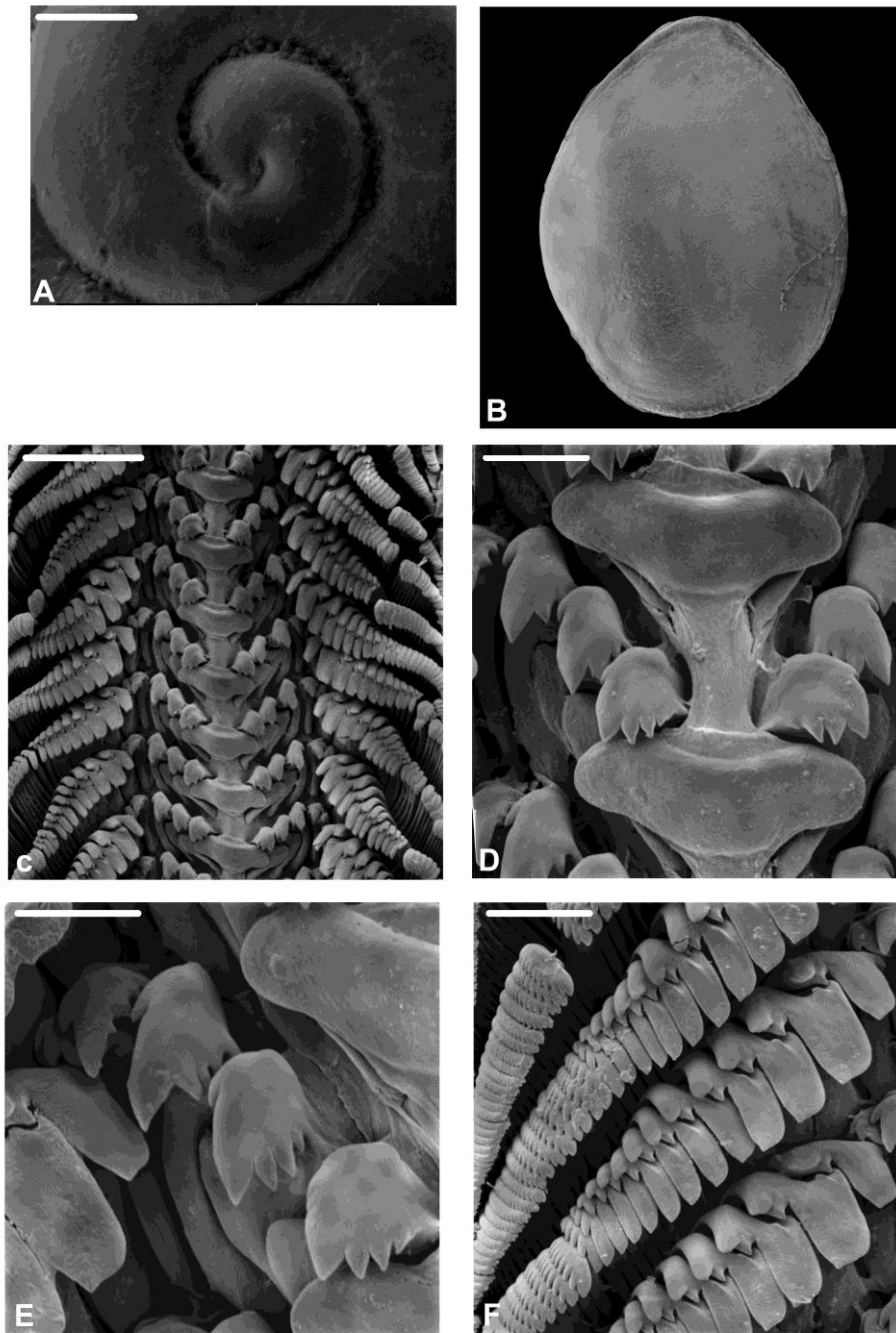


Figure 2.22. Scanning electron microscope of protoconch, operculum and radula of *T. africana*: (A) external surface of protoconch, showing a smooth surface and slightly convex terminal lip, NMSA W4755, bar = 100 μm ; (B) external surface of operculum, showing smooth surface, NMSA W3193, maximum diameter 1.6 mm, (C) central portion of radula, NMSA W1043, bar = 180 μm ; (D) rachidian and inner lateral teeth, NMSA W1034; bar = 40 μm ; (E) lateral teeth, NMSA W1034, bar = 50 μm ; (F) marginal teeth, NMSA W1034, bar = 50 μm .

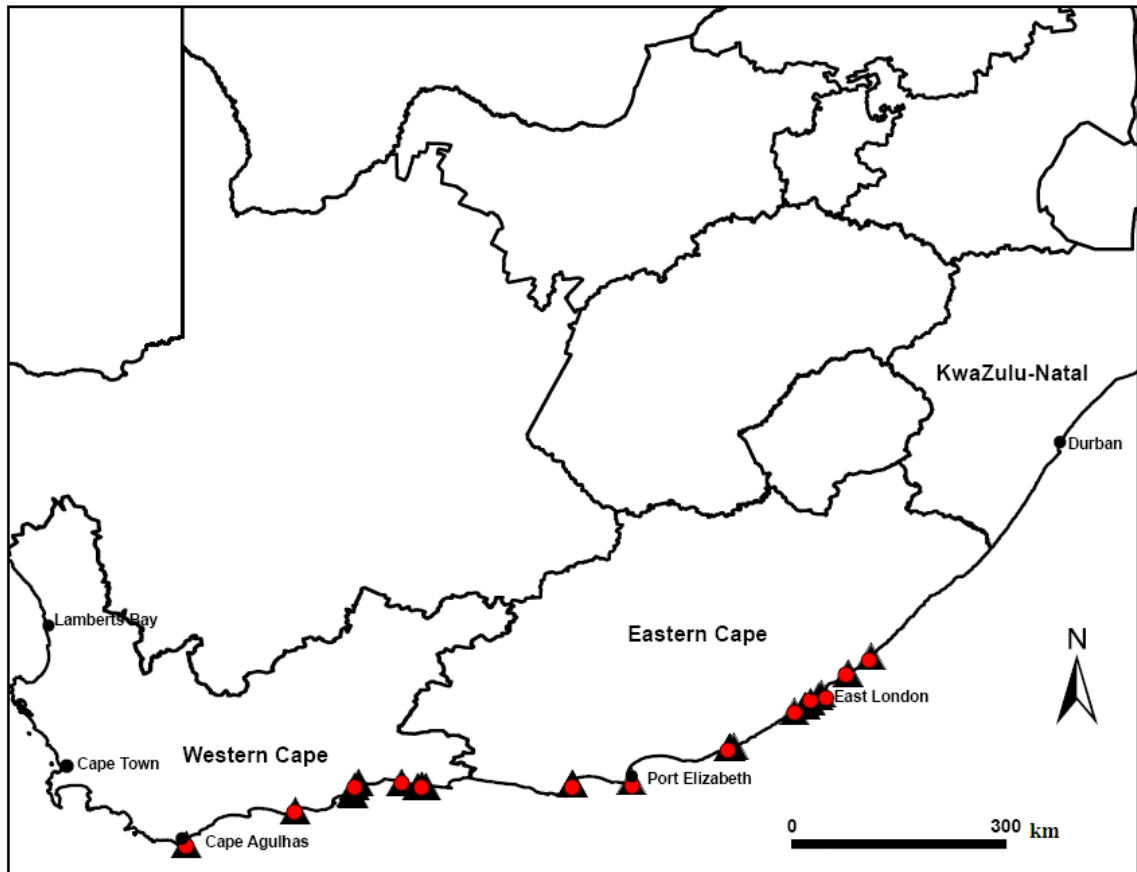


Figure 2.23. Distribution map of *T. africana*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia capensis (Dunker, 1846)

Figs 2.24-2.27

Phasianella capensis Dunker, 1846: 110; Krauss 1848: 104, pl. 6, fig. 5; Philippi 1853: 22, pl. 4, figs 17-20; Paetel 1869: 58; Troschel 1878: 202, pl. 18, fig. 12; Sowerby 1887: 152, pl. 476, figs 34-36; Pilsbry 1888: 170, pl. 39, figs 86-88 (in part); Sowerby 1892: 41 (in part); Smith 1911: 313-314; Bartsch 1915: 145; Turton 1932: 173, pl. 40, fig. 1229; Barnard 1951: 116, pl. 15, fig. 10; Herbert & Warén 1999: 224. Type loc.: “*Prom. Bon. Spei*” [“Cape of Good Hope”, South Africa].

non Phasianella capensis; Turton 1932: 173, pl. 40 [= *T. formosa* (Turton, 1932)]

Tricolia capensis; Barnard 1963: 207-208; Day 1969: 158 (in part); Penrith & Kensley 1970: 248, 250, 252, 263 (in part); Kensley 1973: 52, fig. 143; Kensley 1977: 190, fig. 1; Branch & Branch 1981: pl. 114, fig. f; Kilburn & Rippey 1982: 42-43, pl. 9, figs 7a, b (in part); Robertson 1985: 21; Hodgson & Foster 1992: 89-97; Branch *et al.* 1994: 148, figs 69.6a, b (in part); Hodgson 1995: 169.

non Tricolia capensis; Herbert 1991: 309; Steyn & Lussi 1998: 28, fig. 93 [= *Tricolia kochii* (Philippi *in* Krauss, 1848)].

Etymology, *capensis* – from the Cape.

Diagnosis: Shell variation in shape, elevated–turbiniform to bulimiform, whorls evenly rounded, without any angulation; sculpture weak, shell usually with very fine spiral lines; colouration highly variable, ground colour cream white to light brown patterned with various shades of black or white markings.

Description (Figs 2.24, 2.25A-F):

Shell variation in shape, elevated–turbiniform to bulimiform, with up to 4.75 teleoconch whorls; whorls evenly rounded, without any angulation, suture relatively shallow. Sculpture weak, shell usually with very fine spiral lines. Aperture sub–circular, outer lip thick, colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, remaining as a narrow chink in others. Shell colouration highly variable, ground colour cream–white or light brown mottled with various shades of black or whitish flecks; others with numerous, smudged white or black dots on body whorl (Figs 2.25B, C, D); some specimens with large, black trapezoid blotches below suture (Fig. 2.25D); others with broad, alternating zigzag axial bands of black on apical surface and body

whorl (Fig. 2.25E); others with broad, alternating black axial bands on body whorl (Fig. 2.25F); ill-defined white blotches occur around umbilicus ridge (Figs 2.25A, D).

Protoconch (Fig. 2.26A): Typically vetigastropod, comprising approx. 1.25 whorls; apical beak present but weak, terminal lip lacking a varix, but uniformly convex at mid-whorl; all available museum specimens even juveniles, are badly eroded or damaged.

Operculum (Fig. 2.26B): Similar to *T. adusta*, but with traces of curved lines on labral margin.

Radula (Figs 2.26C-F): Similar to *T. pullus* (Gofas 1982), but rachidian tooth with broad, trapezoid base-plate.

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985), but with a pair of greenish patches on snout between and just in front of cephalic tentacles, mostly in specimens with brownish variegated shells (False Bay), not present in all specimens.

Measurements: Largest specimen examined – length 8.9 mm, width 5.2 mm. Length:width ratio 1.6-1.8 (N=20).

Habitat: *T. capensis* occurs commonly in the rocky intertidal zone, living among seaweeds such as *Ulva* and *Codium fragile capense* (= green algae), *Gigartina radula*, *G. stiriata* and *Ceramium* (= red algae), and *Bifurcariopsis capensis* (= brown algae) at low spring tide level, empty shells in beach-drift.

Geographical range (Fig. 2.27): Endemic to southern Africa, ranging from South Western Cape (Sandbaai near Hermanus) up to Namibian border (Kunene River mouth).

Type material: *Phasianella capensis*, 30 syntypes (one figured herein, Fig. 2.24), ZMHB 108.794, length 4.9 mm, width 3.2 mm.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *South Western Cape*: Sandbaai near Hermanus, Schulphoek (34.428°S:19.204°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 07.ii.2004 (W1532, living); Hawston near harbour (34.401°S:19.122°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 07.ii.2004 (W1533, living); Betty's Bay, Stony Point Marine Nature Reserve (34.371°S:18.893°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 07.ii.2004 (W1535, living).

False Bay: Gordon's Bay (34.150°S:18.850°E), leg. R.M. Lightfoot, x.1901 (SAM 9652); Strandfontein (34.083°S:18.550°E), leg. C.M. Connolly, viii.1962 (A3976); same locality, leg. R. Kilburn (A2194); Muizenberg (34.117°S:18.467°E), leg. C.M. Connolly, i.1974 (A1840; A1845; A1848); St. James (34.118°S:18.442°E), on *Ulva* in low spring tide pool, leg. R. Kilburn, 14.i.1974 (A2132); same locality, leg. C.M. Connolly, iii.1984 (EM W000123, living); same locality, UCT Ecological survey, Stn. CP165, 01.ix.1932 (SAM A55117, living); Kalk Bay (34.133°S:18.450°E), leg. R.M. Lightfoot, 1897 (SAM 4834); Fish Hoek (34.139°S:18.430°E) (SAM A31695); Dalebrook (34.124°S:18.452°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 05.ii.2004 (W1516, living); Glencairn (34.163°S:18.432°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 06-09.ii.2005 (W2559; W2574, living); Simon's Town (34.183°S:18.433°E), dredged C.M. Connolly, 1974 (A1827).

Atlantic Cape: Camel Rocks, Scarborough (34.199°S:18.372°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 06-07.ii.2005 (W2563; W2566, living); Kommetjie (34.140°S:18.320°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 07.ii.2005 (W2569, living); Camp's Bay (33.956°S:18.375°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 08.ii.2005 (W2572, living); Sea Point (33.917°S:18.367°E), leg. C.M. Connolly, i.1974 (A1828); Sea Point, south end of beach (33.917°S:18.385°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 06.ii.2004 (W1524, living); Sea Point, near tidal pool (33.914°S:18.385°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 06.ii.2004 (W1526, living); same locality, leg. D. Herbert & T. Nangammbi, 10.ii.2005 (W2577, living); Rocklands Beach (33.907°S:18.394°E), leg. D. Klerk, 07.ii.1974 (A1336); Three Anchor Bay (33.905°S:18.397°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 08.ii.2004 (W1540, living); Mouille Point (33.899°S:18.405°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 06.ii.2004 (W1529, living); Granger Bay (33.371°S:18.408°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 08.ii.2004 (W1537, living); Bloubergstrand (33.800°S:18.450°E), leg. S. Muller, 18.xi.1983 (EM W000124, living); Melkbosstrand (33.731°S:18.436°E) (SAM A39033); Yzerfontein, near harbour (33.347°S:18.152°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 12.ii.2004 (W1545, living); Langebaan Lagoon, Saldanha Bay (33.094°S:18.001°E), leg. C.M. Connolly (8484); Marcus Island, Saldanha Bay (33.043°S:17.972°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 10.ii.2004 (W1542, living); Port Nolloth (29.250°S:16.867°E), leg. R. Bieler, ix.1980 (B3442).

NAMIBIA: off Orange River mouth (SAM A29846); Lüderitz (26.648°S:15.159°E), leg. R. Bieler, ix.1980 (B3439); Lüderitzbucht (26.633°S:15.167°E) (SAM A31254); between Walvis Bay and Swakopmund (22.800°S:14.500°E), leg. C.T. Stewart, Stn. 2214 Dca, 24.iv.1974 (A1265); 5 km South of Swakopmund, in shallow water, W. Massier, 10.xii.1988 (E5783); Swakopmund (22.667°S:14.567°E), leg. C. Berrisford, ix.1964 (SAM A29903, living); Swakop River mouth (22.683°S:14.533°E), sand, D.P. Eichbaum, i.1977 (E7623, living); Toscanini (20.850°S:13.417°E), leg. C.G. Coetzee, 10.xi.1968 (SAM 31218, living); Torra Bay (20.467°S:13.017°E), leg. C.G. Coetzee, 05.xi.1968 (A31216, living); 42 miles North of Uniab River mouth (19.733°S:12.900°E), leg. C.G. Coetzee, 08.xi.1968 (SAM A31215, living); Möwe Bay (19.383°S:12.700°E), leg. B. Kensley *et al.*, 30.vi.1960 (SAM A31331); Rocky Point (18.983°S:12.483°E) (SAM A31332).

Literature Records: Kunene River mouth (Kensley 1977).

Comparison: This species lacks unique diagnostic characteristics that clearly separate it from other southern African *Tricolia* species. However, it is clearly identifiable by a combination of characters it lacks, which are present in other species. For example, spiral row of turquoise spots below suture present in *T. africana* and *T. kochii*; spiral row of pink or white spots on apical region present in *T. formosa* and *T. elongata* respectively; distinct spiral sculpture on body whorl present in *T. striolata*, *T. bicarinata* and *T. insignis*; neritiform shape and very large aperture of *T. neritina*; numerous tiny red dots on body whorl of *T. ios*; globose or turbiniform shell shape of *T. saxatilis*, *T. adusta* and *T. kraussi*. In terms of shell shape, there is a great variation between individual specimens of *T. capensis*. Some specimens are elongate–turbiniform, whereas others are bulimiform. Specimens with the turbiniform shape resemble *T. formosa*, but lack the pink spots on the apical whorls, which are characteristic of the latter.

There has also been a great confusion in the literature (i.e., Kilburn & Rippey 1982, Herbert 1991, Branch *et al.* 1994, Steyn & Lussi 1998) and the Natal Museum Mollusca collection between specimens of *T. capensis* and *T. kochii*. Specimens of *T. kochii* were previously identified under the name *T. capensis*. However, the two nominal taxa are easily separated by morphological characters of the shell size, sculpture and colouration. *Tricolia kochii* is relatively large and more globular with distinct spiral lines on the first whorl and light blue spots below the suture, whereas *T. capensis* is smaller and lacks the spiral lines and blue spots. In addition, shell colouration is highly variable in specimens of both species, but in *T. kochii* they are usually reddish–brown or greenish–yellow when still alive, and are extremely

common along the KwaZulu–Natal, Eastern Cape and the South Western Cape (up to Cape Agulhas) coastline. Shells of *T. capensis* are a grayish–black patterned with various shades of black or white markings and are common along the Western Cape and Namibia coastline (up to the Kunene River mouth). From the Natal Museum records, the distribution of *T. kochii* ends at Cape Agulhas and that of *T. capensis* begins at Hermanus (some 85 km further west). However, a single specimen of *T. kochii* from Hermanus (Caledon district) is present in the South African Museum (SAM 11398). Nonetheless, during my several field excursions along the South Western Cape, I never found *T. kochii* west of Cape Agulhas and I suspect that the record of *T. kochii* from Hermanus is a stray individual or probably mislocalized.

Additional notes: Literature records of *T. capensis* from East London (Penrith & Kensley 1970: 248, 250, 252, 263, as *Tricolia capensis*); Port Elizabeth (Sowerby 1892); Mauritius, Indian Ocean (Pilsbry 1888: 170, as *Phasianella capensis*, Viader 1937: 54, as *Phasianella capensis*, Penrith & Kensley 1970: 248, 250, 252, 263, as *Tricolia capensis*); La Réunion, Indian Ocean (Deshayes 1863: 76, as *Phasianella capensis*) and Bay of Hakodate, southern Hokkaido, Japan (Schrenck 1867: 366, 903, as *Phasianella capensis*) are erroneous. These locality records were previously rejected by Robertson (1985), who suggested that the records were probably based on mislocalized specimens, and I support his views in rejecting these records. The only *Tricolia* species occurring around Hokkaido is *T. tristis*. It is also possible that Sowerby (1892) might have confused *T. capensis* with *T. kochii*.



Figure 2.24. Syntype of *T. capensis*: *P. capensis*, ZMHB 108.794, length 4.9 mm, width 3.2 mm.

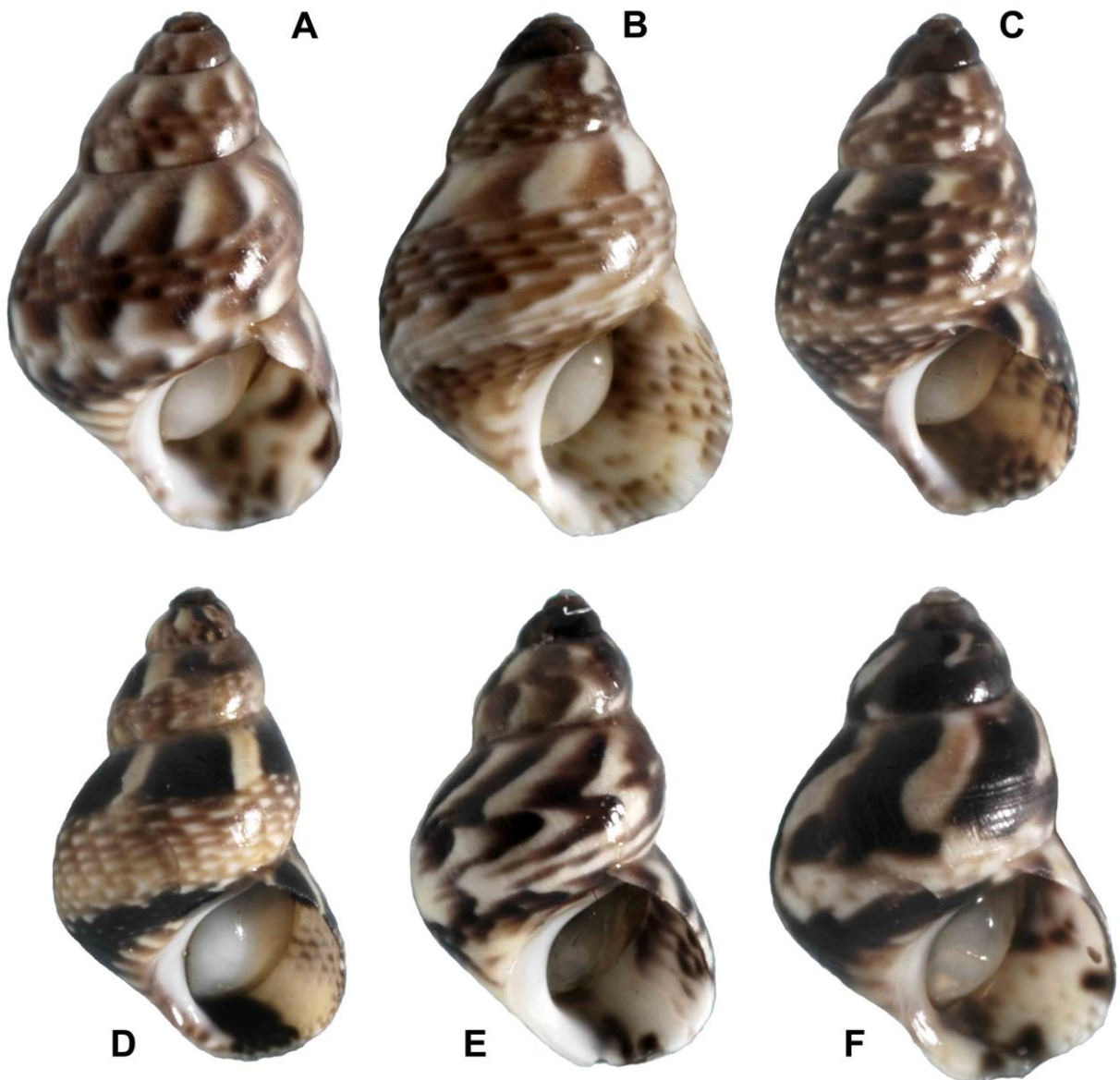


Figure 2.25. Variation in shell shape and colouration of *T. capensis*: (A) length 6.6 mm, width 3.9 mm, NMSA W1524. Sea Point, Atlantic Cape; (B) length 5.9 mm, width 3.8 mm, NMSA W1524. Sea Point, Atlantic Cape; (C) length 7.1 mm, width 4.3 mm, NMSA W1524. Sea Point, Atlantic Cape; (D) length 7.3 mm, width 4.3 mm, NMSA W1524. Sea Point, Atlantic Cape; (E) length 7.1 mm, width 4.4 mm, NMSA W1524. Sea Point, Atlantic Cape; (F) length 5.7 mm, width 3.3 mm, NMSA W1524. Sea Point, Atlantic Cape.

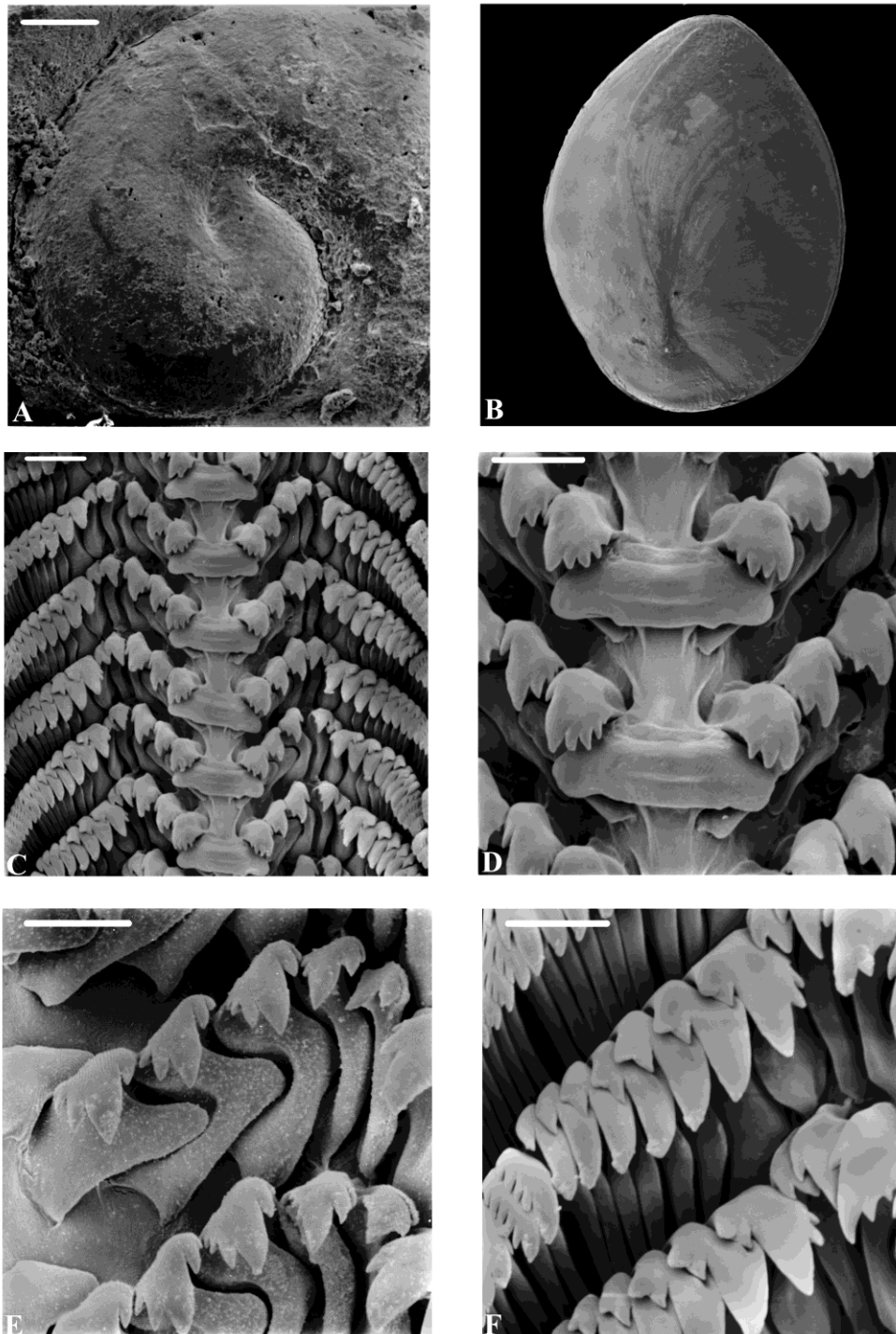


Figure 2.26. Scanning electron microscope of protoconch, operculum and radula of *T. capensis*: (A) external surface of protoconch, showing a convex terminal lip, NMSA W2563, bar = 80 μm ; (B) external surface of operculum, showing traces of curved lines on the labral margin, NMSA W2563, maximum diameter 2.4 mm; (C) central portion of radula, NMSA W1524, bar = 120 μm ; (D) rachidian and inner lateral teeth, NMSA W1524, bar = 25 μm ; (E) lateral teeth, NMSA W2563, bar = 30 μm ; (F) marginal teeth, NMSA W1524, bar = 30 μm .

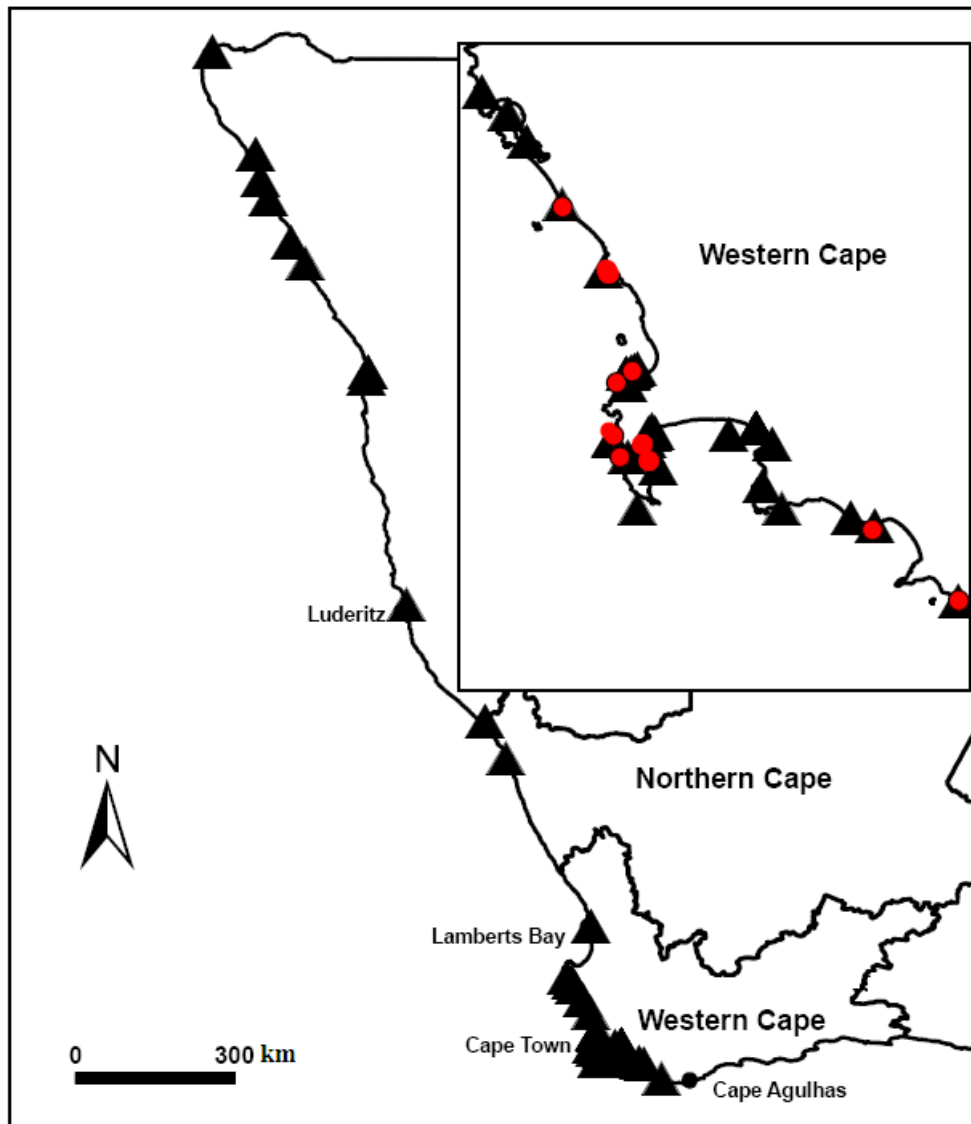


Figure 2.27. Distribution map of *T. capensis*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia bicarinata complex*Tricolia bicarinata* (Dunker, 1846)

Figs 2.28-2.31

Phasianella bicarinata Dunker, 1846: 110; Krauss 1848: 105; Philippi 1853: 17-18, pl. 4, fig. 10; Pilsbry 1888: 176, pl. 39a, fig. 10; Sowerby 1892: 41; Smith 1911: 313; Barnard 1951: 116, pl. 15, fig. 12; Robertson 1958: 280. Type loc.: “*Prom. Bon. Spei*” [“Cape of Good Hope”, South Africa].

non Phasianella bicarinata; Bartsch 1915: 145; Turton 1932: 174 [= *Tricolia insignis* Turton, 1932].

Phasianella tropidophora Tomlin, 1931: 420, pl. 33, fig. 1 (in part). Type loc.: Cape Peninsula (Connolly) and East London (McClelland) (herein restricted to Cape Peninsula).

Tricolia bicarinata; Barnard 1963 (in part): 208-210; Kensley 1973: 52 (in part), fig. 142; Kilburn & Rippey 1982: 47; Trew 1984: 83.

Tricolia tropidophora; Barnard 1963: 209-210 (in part); (*non* Tomlin, 1931 = *T. bicarinata* Dunker, 1846).

Tricolia tropidophora; Kensley 1973: 52, fig. 146 (in part); Kilburn & Rippey 1982: 47; Trew 1984: 84.

Etymology, *bi* (two) *carina* (Latin) – bearing two keels – referring to the two keels on the body whorl.

Diagnosis: Shell turbiniform; biangulate, a distinct angle at shoulder and another below periphery; flattened peripheral region, whorls somewhat convex; suture level with lower angle and relatively shallow; surface with numerous, close-set spiral ridges; colouration relatively constant, ground colour dull grey to greyish pink or whitish with extensive pale pink overtones.

Description (Figs 2.28A-B, 2.29):

Shell turbiniform with relatively high spire, teleoconch of up to 4.27 whorls with moderately indented suture; suture level with lower angle; whorls somewhat convex; a distinct angle at shoulder and another below periphery; with flattened peripheral region, well rounded and less flattened apex. Shell surface with numerous, close-set spiral ridges. Aperture sub-ovate, outer lip thick; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, but remaining as a narrow chink

in others. Shell colouration relatively constant, ground colour dull grey to greyish pink or whitish with extensive pale pink overtones (Fig. 2.28B).

Protoconch (Fig. 2.30A): Typically vetigastropod, comprising approx. 1.1 whorls; apical beak present but weak, terminal lip lacking a varix, but markedly convex at mid-whorl; shell apex badly worn in all available material, but showing traces of spiral lines in apical region and around periphery.

Operculum (Fig. 2.30B): Similar to *T. adusta*, but with curved lines on the labral margin.

Radula (Figs 2.30C-F): Similar to *T. pullus* (Gofas 1982), but rachidian tooth with broad, oval shape base-plate.

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985), but colour pattern of head-foot pale white, does not reflect the pinkish-mauve colour of the shell, black pigmentation around inner lips of mouth; a pair of dark blotches on snout between and just in front cephalic tentacles.

Measurements: Largest un-damaged specimen examined – length 4.6 mm, width 2.9 mm.

Habitat: *T. bicarinata* occurs in the rocky intertidal zone; living on and under rocks at low spring tide level, empty shells beach-drift. This species is not common in the intertidal zone.

Geographical range (Fig. 2.31): Endemic to southern Africa, ranging from the Atlantic Cape of South Africa (Kommetjie) to Namibia (Lüderitz).

Type material: *Phasianella bicarinata*, holotype (Fig. 2.28A), ZMHB 108.796, length 4.1 mm, width 2.8 mm (specimen badly worn, but with traces of spiral ridges on body whorl). *Phasianella tropidophora*, figured specimen, length 3.5 mm, diameter 2.0 mm (Fig. 2.29 is copy of figure from Tomlin 1931). *Phasianella tropidophora*, figured syntypes, East London McClelland, NHMW 1955.158.00969; same locality, NHMW 1955.158.00970; Shelly Beach, NHMW 1955.158, 12881, 12884. *Phasianella tropidophora*, several syntypes, Cape Peninsula, NHMW 1955.158.12882; Lamberts Bay, NHMW 1955.158.12885; Port Nolloth, NHMW 1955.158.12883.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Atlantic Cape*: Kommetjie lighthouse (34.133°S:18.317°E), 04.v.1962, ex C.M. Connolly, i.1974 (A3094, A3895, A1822); Kommetjie (34.133°S:18.317°E), rocky intertidal zone, under rock, leg. D. Herbert & T. Nangammbi, 07.ii.2005 (W2571, living); Sea Point, near tidal pool (33.914°S:18.385°E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 06-08.ii.2004 (W1528, living); same locality, leg. D. Herbert & T. Nangammbi, 10.ii.2005 (W2578, living); same locality, leg. S.C. Fenwick, ex C.M. Connolly, i.1974 (A1842); same locality, leg. C.M. Connolly, vii-ix.1977 (B341); Green point (33.900°S:18.383°E), leg. R. Kilburn (A2180, 8522); Paternoster (32.817°S:17.883°E), intertidal rocks and stones, leg. D. Herbert, xi.1988 (V4050).

NAMIBIA: Diaz Point, Lüderitz (26.648°S:15.159°E), low tide rock pools, iii.1989, leg. W. Massier (E6033).

Comparison: This species resembles *T. insignis* in having a biangulate shell shape and numerous close-set spiral ridges on the body whorl. However, it differs from *T. insignis* in terms of shell colour: *T. bicarinata* is dull grey to greyish pink or whitish with extensive pale pink overtones, whereas *T. insignis* is brownish-orange to brick-red, with the colour usually interrupted by zigzag greenish axial flames on the body whorl. *Tricolia kraussi* resembles *T. insignis* in terms of colour pattern, but differs from it by having fine spiral threads and lacks a distinct angle.

The three species have a parapatric geographical distribution pattern: *T. bicarinata* is a cool-temperate west coast province species endemic to southern Africa and ranging from the Atlantic Cape (Kommetjie) to Namibia (Lüderitz), living on or under rocks in mid-tidal pools. This zone is characterized mainly by cold water species. *Tricolia insignis* is a warm-temperate south coast province species endemic to South Africa and ranging from the Eastern Cape (northern Transkei, Mzamba) to the South Western Cape (off Hawston), living on and under rocks in mid-tidal pools. This zone is characterized mainly by cool water species. *Tricolia kraussi* is both ecologically and geographically intermediate; a warm-temperate South Western Cape species endemic to South Africa and ranging from Gordon's Bay to Buffel's Bay (False Bay) and lives among seaweed, occasionally on or under rocks in low spring tides down to 12 m. This distribution coincides with two of the three marine biogeographical provinces and water temperature is suspected to have the strongest influence on this biogeographical division (Stephenson & Stephenson 1972). The distribution

of each species has shown regional adaptation reflected in their shell sculpture to the different environmental conditions prevalent in each biogeographic province.

In his description of *P. tropidophora*, Tomlin (1931) mentioned a broad, blunt conspicuous keel in the middle of each whorl as a distinguishing characteristic of this species. Dunker's (1846) description of *T. bicarinata* was based on similar shell characteristics, but did not give an illustration. Assessment based on NHMW material collected from East London and Cape Peninsula has revealed that *T. tropidophora* might be a composite of both *T. bicarinata* (Cape Peninsula species) and *T. insignis* (East London species). Kilburn & Rippey (1982) later confirmed that *T. tropidophora* is a correct synonym of *T. bicarinata* based on the pink colour and pattern of the shell. The type locality of *T. tropidophora* is not defined in the original description. However, it is herein restricted to Cape Peninsula.

Additional notes: Records of *T. bicarinata* from Port Alfred (Bartsch 1915) and Kosi Bay, Zululand (Barnard 1963, Kensley 1973) and *T. tropidophora* from Knysna and East London (Tomlin 1931, Barnard 1963, Kensley 1973) are erroneous. I have personally examined Barnard's Zululand material at the Iziko Museum of Cape Town and discovered that the specimens are not *Tricolia bicarinata*. In fact they are not even species of *Tricolia*.

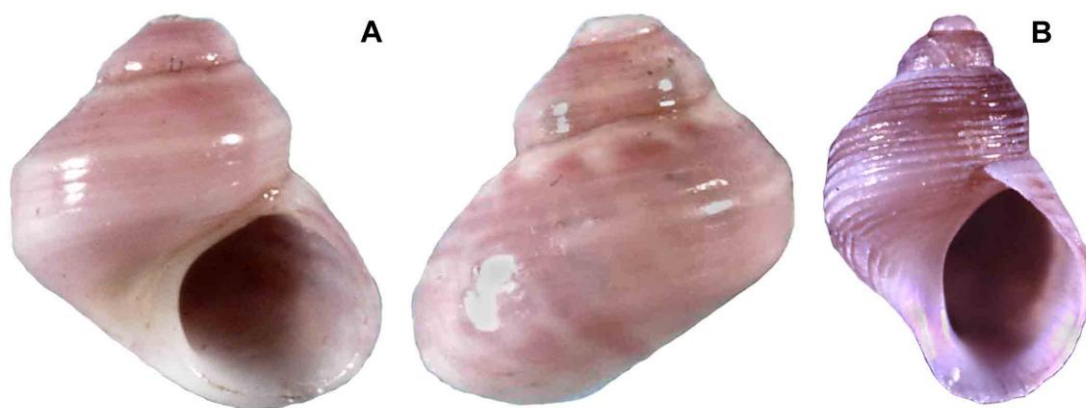


Figure 2.28. (A) Holotype of *T. bicarinata*, ZMHB 108.796, length 4.1 mm, width 2.8 mm (specimen badly worn, but with traces of spiral ridges on body whorl). (B) Shell colouration and pattern of *T. bicarinata*, length 4.6 mm, width 2.9 mm, NMSA W1528. Sea Point, Atlantic Cape.

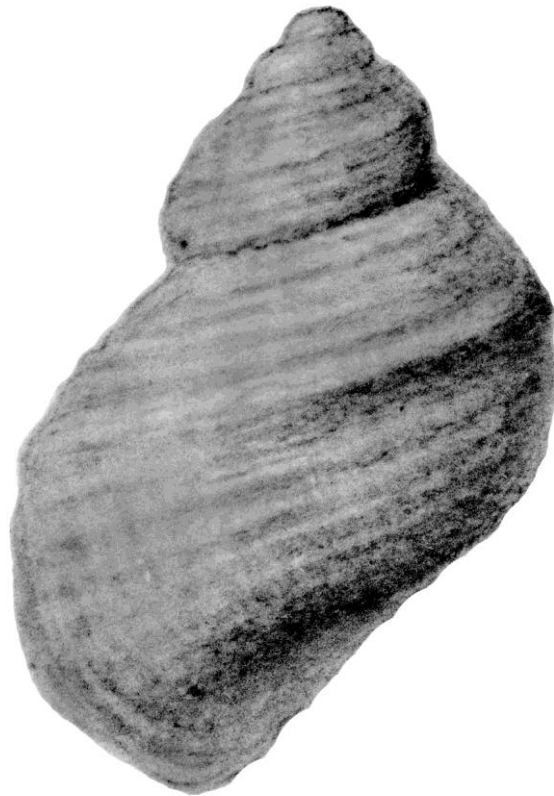


Figure 2.29. Figured specimen of *P. tropidophora*, length 3.5 mm, diameter 2.0 mm (Copy of figure from Tomlin 1931).

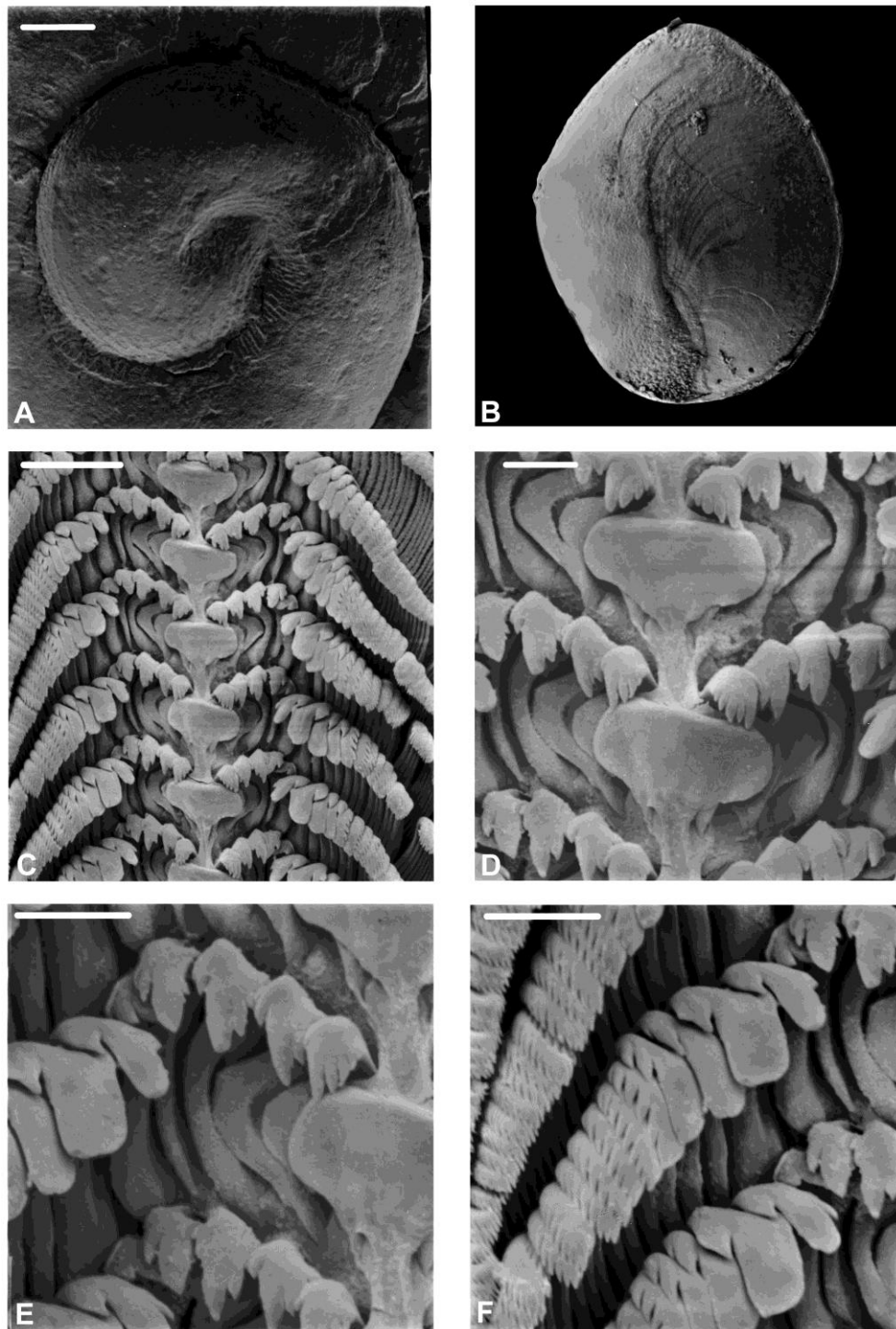


Figure 2.30. Scanning electron microscope of protoconch, operculum and radula of *T. bicarinata*: (A) external surface of protoconch, showing traces of spiral lines and a convex terminal lip, NMSA B341, bar = 140 μm ; (B) external surface of operculum, showing curved lines on the labral margin, NMSA W2578, maximum diameter 1.4 mm; (C) central portion of radula, NMSA W2578, bar = 40 μm ; (D) rachidian and innermost lateral teeth, NMSA W2578, bar = 10 μm ; (E) laterals and inner marginal teeth, NMSA W2578, bar = 10 μm ; (F) marginal teeth, NMSA W2578, bar = 20 μm .

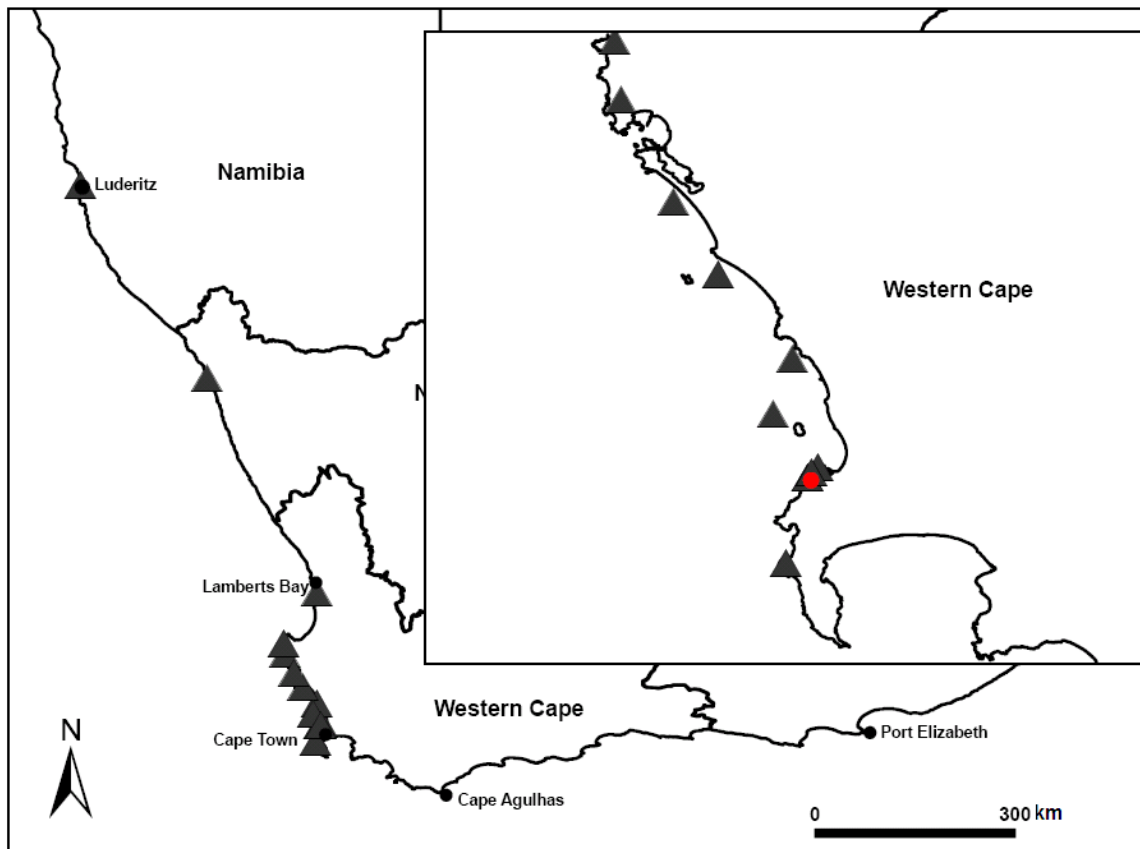


Figure 2.31. Distribution map of *T. bicarinata*. Each black triangle represents one or more site records. Red dot represents a sequenced sample.

Tricolia insignis (Turton, 1932)

Figs 2.32-2.35

Phasianella bicarinata (non Dunker, 1846); Bartsch 1915: 145; Turton 1932: 174.

Phasianella insignis Turton, 1932: 175, pl. 41, fig. 1239. Type loc.: Port Alfred (Eastern Cape, South Africa).

Tricolia insignis; Barnard 1963: 208-209; Kilburn & Rippey 1982: 47.

Etymology, *insignis* (Latin) – remarkable or notable.

Diagnosis: Shell turbiniform, biangulate, one below periphery and another one below suture; flattened peripheral region; surface with numerous, close-set spiral ridges; colouration relatively constant, ground colour reddish-brown, superimposed with vivid wavy pattern of brick-red or brownish-orange with green axial flames on body whorl.

Description (Figs 2.32, 2.33):

Shell turbiniform with relatively high spire; teleoconch of up to 3.1 whorls with relatively shallow suture; whorls convex, with two distinct angles, one below periphery and another one below suture; peripheral region flattened, apex flattened and well rounded. Shell with numerous, close-set spiral ridges. Aperture ovate-circular, outer lip thin; colour pattern visible internally, inner lip concave and slightly reflected over umbilical region; umbilicus closed in most examined specimens, remaining as a narrow chink in others. Shell colouration relatively constant, ground colour brownish-orange, superimposed with vivid wavy pattern of brick-red, and usually interrupted by zigzag greenish axial flames randomly distributed on body whorl (Fig. 2.33).

Protoconch (Fig. 2.34A): Typically vetigastropod, comprising approx. 1.2 whorls; apical beak present but weak, terminal lip lacking a varix, but uniformly convex at mid-whorl; sculpture for the most parts smooth, with traces of curved lines towards apical region.

Operculum (Fig. 2.34B): Similar to *T. adusta*.

Radula (Figs 2.34C-F): Similar to *T. pullus* (Gofas 1982).

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985), but with a pair of dark-brown blotches on snout between and just in front of cephalic tentacles.

Measurements: Largest specimen examined – length 6.1 mm, width 3.6 mm. Length:width ratio 1.3-1.7 (N=50).

Habitat: *T. insignis* occurs commonly in the rocky intertidal zone, living on and under rocks in mid-shore pools; living specimens from shallow infratidal to 30 m, empty shells from beach-drift to 30 m. Not common in the shallow subtidal reefs.

Geographical range (Fig. 2.35): Endemic to South Africa, ranging from the Eastern Cape (northern Transkei, Mzamba) to the South Western Cape (off Hawston).

Type material: *Phasianella insignis*, holotype (Fig. 2.32), OUM M002785, length 3.2 mm, width 2.7 mm.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Eastern Cape:* Mzamba (31.100°S:30.183°E), beach-drift, leg. R. Kilburn & D. Herbert, 12-30.v.1986 (D2945); Msikaba Island, north side (31.183°S:29.600°E), leg. R. Kilburn *et al.*, viii.1983 (C5495); Grosvenor Point (31.397°S:29.883°E), rock pools, leg. R. Kilburn & J. McKay, 30.iv.1976 (B914); Mbotyi (31.450°S:29.733°E), beach-drift, leg. R. Kilburn & D. Herbert, v-vi.1985 (C8462); Lwandile/Mdumbi (31.883°S:29.267°E), leg. R. Kilburn & R. Fregona, vii.1981 (C195); off Whale Rock (31.948°S:29.219°E), 20-26 m, sand and gorgonians, dredged NMDP, 16.vii.1982 (V4046, dead); Coffee Bay (31.967°S:29.150°E), leg. R. Kilburn (A2983); Xora (31.950°S:28.667°E), leg. M. Bursey & D.J. Hodgkinson, Field number X6, 02.vi.1989 (90) (EM W1844, living); Dwesa (32.300°S:28.833°E), beach-drift, leg. R. Kilburn, v.1984 (C6062); Sandy Point (32.567°S:28.550°E), leg. R. Kilburn *et al.*, xi.1982 (C3675); Qolora River mouth (32.633°S:28.417°E), leg. R. Kilburn *et al.*, x.1982, (C3433); Kei River mouth (32.683°S:28.383°E), leg. M. Bursey *et al.*, 09.vi.1990 (EM 12316, living); Marshstrand, East London (32.750°S:28.250°E), rocky intertidal zone, under rocks, leg. T. Nangammbi *et al.*, 27.viii.2003 (W1027, living); same locality, leg. D.J. Hodgkinson, 26.vi.1987 (EM W001137, living); Haga-Haga, East London (32.750°S:28.250°E) (EM 7194); Cintsa West, East London (32.850°S:28.117°E), leg. M. Bursey & D.J. Hodgkinson, Field number CE5, 24.vi.1990 (EM W1932; 12502, living); Glengariff, East London (32.883°S:28.083°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 26.viii.2003 (W1019, living); Kwelera, East London (32.900°S:28.080°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 08.vii.2005 (W3385, living); Sunrise-on-Sea, East London (32.917°S:28.083°E), leg. M. Bursey & A. Gubb, Field number SR-2, 24.iv.1990 (EM W1863, living); Gonubie, East London (32.933°S:28.017°E), rocky intertidal

zone, under rocks, leg. T. Nangammbi & M. Bursey, 08.vii.2005 (W3386, living); Eastern Beach, East London (33.017°S:27.917°E), leg. S.C. Fenwick, 21.vii.1967 (EM 4171, living); West Bank, East London (33.033°S:27.900°E), leg. S. Muller, 28.ii.1983 (EM W000126, living); Fuller's Bay, East London (33.067°S:27.900°E), leg. E. Roscoe, 21.xi.1980 (EM 8891); Hickman's River mouth (33.067°S:27.833°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 07.vii.2005 (W3384, living); Kidd's Beach (33.150°S:27.683°E), rocky intertidal zone, under rocks, leg. T. Nangammbi & M. Bursey, 09.vii.2005 (W3195, living); Bira (33.383°S:27.317°E), leg. M. Bursey, 19.ix.1990 (EM W2032, living); Fish River mouth (33.483°S:27.133°E), rocky intertidal zone, under rocks, leg. T. Nangammbi *et al.*, 28.viii.2003 (W1029, living); Port Alfred (33.600°S:26.900°E), H. Becker coll., ex Transvaal Museum, 1978 (B4736); The Kowie, Port Alfred (33.650°S:26.900°E, NHMW 1955.158.12880); Kelly's Beach (32°45.297'S:27°08.005'E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 30.viii.2003 (W1040); Marine drive, site 2, Port Elizabeth (34.035°S:25.645°E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 22.vi.2005 (W3382, living); Noordhoek, Port Elizabeth (34.044°S:25.636°E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 23.vi.2005 (W3192, living); Beacon Rock, Port Elizabeth (33.967°S:25.600°E), undersides of rocks, leg. R. Kilburn (8485); Periwinkle lane, Port Elizabeth (34.043°S:25.553°E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 24.vi.2005 (W3383, living); Marine drive, site 1, Port Elizabeth (34.046°S:25.523°E), rocky intertidal zone, under rocks, leg. T. Nangammbi, 22.vi.2005 (W3381, living); off Cape Recife, Algoa Bay (34.007°S:25.709°E), 25 m, debris from bryozoan colony, dived B. Hayes, xii.1992 (V157, dead).

Southern Cape: Jeffrey's Bay (34.050°S:24.917°E), leg. R. Kilburn, 1960 (A1663); Storms River mouth (34.017°S:23.900°E), beach–drift, leg. M. Quickelberge, 06.i.1977, ex M. Quickelberge coll'n, 1985 (D2044); Mossel Bay Point (34.183°S:22.133°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 05.xi.2006 (W4761, living); Still Bay Point (34.386°S:21.426°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 06.xi.2006 (W4764, living); Still Bay (34.383°S:21.450°E) (NHMW 1955.158.12879).

South Western Cape: Cape Agulhas (34.824°S:20.017°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 07.xi.2006 (W4766, living); Agulhas National Park (34.831°S:20.007°E), rocky intertidal zone, under rocks, leg. T. & J. Nangammbi, 07.xi.2006 (W4765, living); Hermanus on *Haliotis midae* (34.417°S:19.233°E), 10-30 m, leg. F. Graeve, ex J.P. Marais coll'n, v.1990 (V3543, living); off Hawston near Hermanus (34.400°S:19.067°E), in subtidal kelp forest, 2-5 m, dived D. Herbert, xi.1988 (E6692, living).

Comparison: *T. insignis* resembles *T. bicarinata* and *T. kraussi* more closely than it does any other southern African *Tricolia* species (see taxonomic comparison under *T. bicarinata*). Barnard (1963) considered *T. insignis* to be a synonym of *T. tropidophora*, the name he used for what we now call *T. bicarinata*.

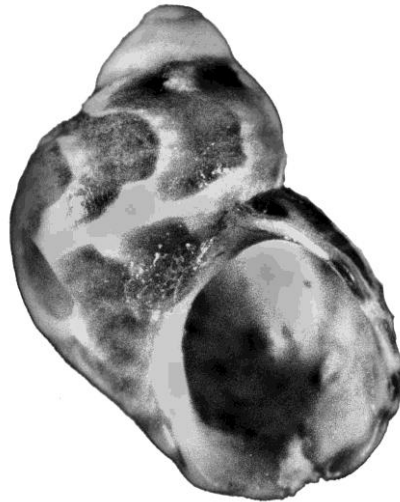


Figure 2.32. Holotype of *P. insignis*, OUM M002785, length 3.2 mm, width 2.7 mm.



Figure 2.33. Shell shape and colour pattern of *T. insignis*: length 3.5 mm, width 2.6 mm, NMSA W3192. Noordhoek, Port Elizabeth, Eastern Cape.

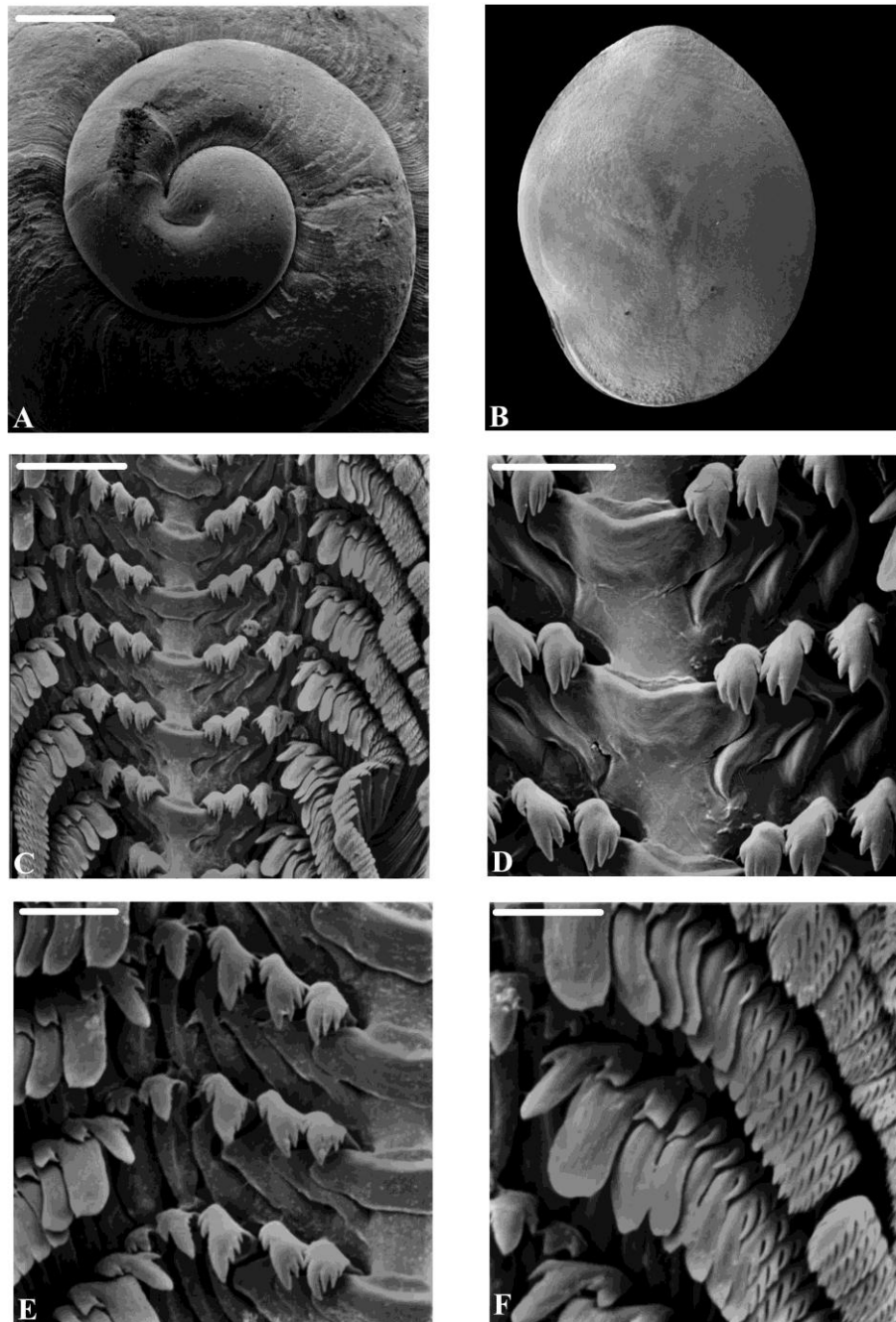


Figure 2.34. Scanning electron microscope of protoconch, operculum and radula of *T. insignis*: (A) external surface of protoconch, showing traces of curved lines towards apical region and a uniformly convex terminal lip, NMSA W3192, bar = 125 μm ; (B) external surface of operculum, showing a smooth surface, NMSA W1040, maximum diameter 1.5 mm; (C) central portion of radula, NMSA W3382, bar = 60 μm ; (D) rachidian and inner lateral teeth, NMSA W1019, bar = 20 μm ; (E) lateral and inner marginal teeth, NMSA W3382, bar = 30 μm ; (F) marginal teeth, NMSA W3382, bar = 25 μm .

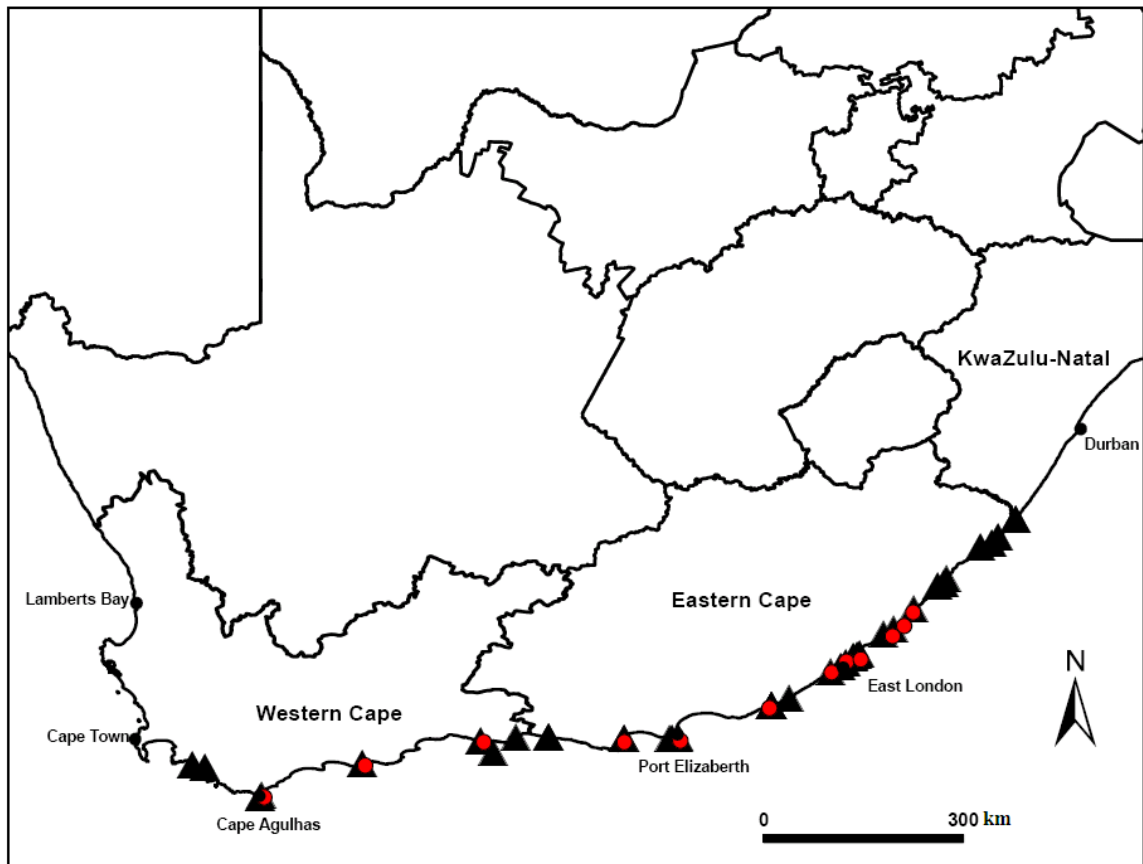


Figure 2.35. Distribution map of *T. insignis*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample

Tricolia kraussi (Smith, 1911)

Figs 2.36-2.39

Phasianella kraussi Smith, 1911: 313-314, 2 un-numbered figures; Type loc.: False Bay (Western Cape, South Africa).

non Phasianella kraussi; Turton 1932: 172 [=? *Tricolia kochii* (Philippi in Krauss, 1848)].

Tricolia kraussi; Barnard 1963: 207; Trew 1984: 83.

Etymology, *kraussi* – Named in honour of Dr Ferdinand Krauss, the well-known author of “*Die Südafrikanischen Mollusken*”.

Diagnosis: Shell turbiniform; body whorls slightly angulated, and relatively large in proportion to the rest of shell; shell with fine spiral threads; colouration relatively constant, predominately reddish-brown with cream white undulating lines, white markings most conspicuous below suture and on body whorl.

Description (Figs 2.36, 2.37):

Shell turbiniform with low spire; teleoconch of up to 3.5 whorls; body whorls slightly angulated, and relatively large in proportion to the rest of shell; suture relatively shallow; depressed, flattened pale and pellucid apex. Shell surface with fine spiral threads. Aperture sub-ovate, outer lip thin; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, but remaining as a narrow chink in others. Shell with relatively constant colour pattern, ground colour reddish-brown to dark-brown or green, with cream white undulating lines; patterned with white markings below suture and on the body whorl, frequently bordered on the anterior margins by dark-brown colour (Fig. 2.37); in some specimens, the white markings are in the form of spots; other specimens with dark purple-brown tint.

Protoconch (Fig. 2.38A): Typically vetigastropod, comprising approx. 1.25 whorls; apical beak present but weak, terminal lip lacking a varix, but with convex terminal lip, sculpture for the most part worn out, but with traces of curved lines towards periphery and in apical region.

Operculum (Fig. 2.38B): Similar to *T. adusta*, but external surface with microscopic granular sculpture.

Radula (Figs 2.38C-F): Similar to *T. pullus* (Gofas 1982), but rachidian tooth with broad, elliptical base–plate; central denticle frequently dominant on the first, second, third and fourth laterals; innermost marginals (the first four) with a single broad spatulate cusp.

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985), but with a pair of black blotches on snout between and just in front cephalic tentacles.

Measurements: Largest un–damaged specimen examined – length 3.7 mm, width 2.7 mm.

Habitat: *T. kraussi* occurs in the rocky intertidal zone, living among seaweed such as *Ulva* and *Codium fragile capense* (= green algae), *Gigartina radula*, *G. stiriata* and *Ceramium* (= red algae), and *Bifurcariopsis capensis* (= brown algae), occasionally on and under rocks at low spring tide level to a depth of 12 m. Not common in the subtidal level.

Geographical range (Fig. 2.39): Endemic to South Africa, ranging from Gordon’s Bay to Buffel’s Bay (False Bay). The presence of three specimens of *T. kraussi* that were dredged from a depth of 90 m on the Agulhas Bank (southern Cape, near the mouth of the Gourits River) seems unusual. This locality is not considered part of the normal distribution range of this species since *T. kraussi* has thus far been found only in False Bay. These specimens were collected dead and small specimens are easily transported in a variety of ways into different depths of the ocean beyond their normal range. However, these records also suggest the possibility that it might occur in sheltered bays east of False Bay. This hypothesis requires further investigation.

Type material: One of two syntypes of *Tricolia kraussi*, BMNH 1911.4.26.1-2 (Fig. 2.36), length 5.5 mm, diameter 4.15 mm.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Southern Cape*: South of Gourits River mouth (34.733°S:21.883°E), fine silty sand, 90 m, dredged NMDP on R.S. *Africana*, Stn. A16564D, 25.ix.1994 (V591).

False Bay: Gordon’s Bay (34.150°S:18.850°E), beach–drift, leg. C.M. Connolly, 1980 (B6877; B6883); Fish Hoek (34.133°S:18.433°E), leg. C.M. Connolly (A2203; V325); Sunny Cove (34.144°S:18.437°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 05.ii.2004 (W1519, living); Glencairn (34.163°S:18.432°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 09.ii.2005 (W2576, living); same locality,

leg. C.M. Connolly, i.1974 (A1847); Simon's Town (34.183°S:18.433°E), dredged C.M. Connolly, i.1974 (A1823, V333); Miller's Point (34.233°S:18.467°E), leg. C.M. Connolly, i.974 (A3385); off Castle Rocks (34.239°S:18.477°E), in subtidal kelp forest, rich soft-coral life, 5-12 m, dived D. Herbert, xi.1988 (E6367; E6365); Bordtjies Reef (34.313°S:18.463°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 11.ii.2004 (W1544; W1727, living); Buffel's Bay (34.317°S:18.467°E), leg. C.M. Connolly, i.1974 (A3066); same locality, leg. R. Kilburn (A2179).

Comparison: In terms of shell shape, *T. kraussi*'s last body whorl is larger in proportion to the rest of the shell, and distinguishes it from other southern African *Tricolia* species. It most closely resembles *T. insignis* and *T. bicarinata* (see taxonomic comparison under *T. bicarinata*).

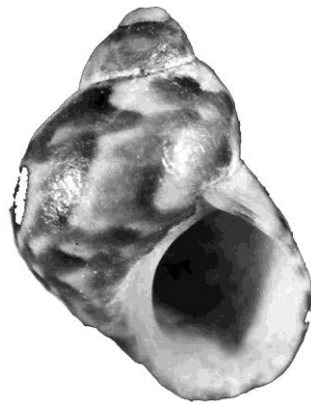


Figure 2.36. One of two syntypes of *T. kraussi*, BMNH 1911.4.26.1-2, length 5.5 mm, diameter 4.15 mm.



Figure 2.37. Shell colouration of *T. kraussi*: length 3.7 mm, width 2.7 mm, NMSA W1544. Bordtjies Reef, False Bay, Western Cape.

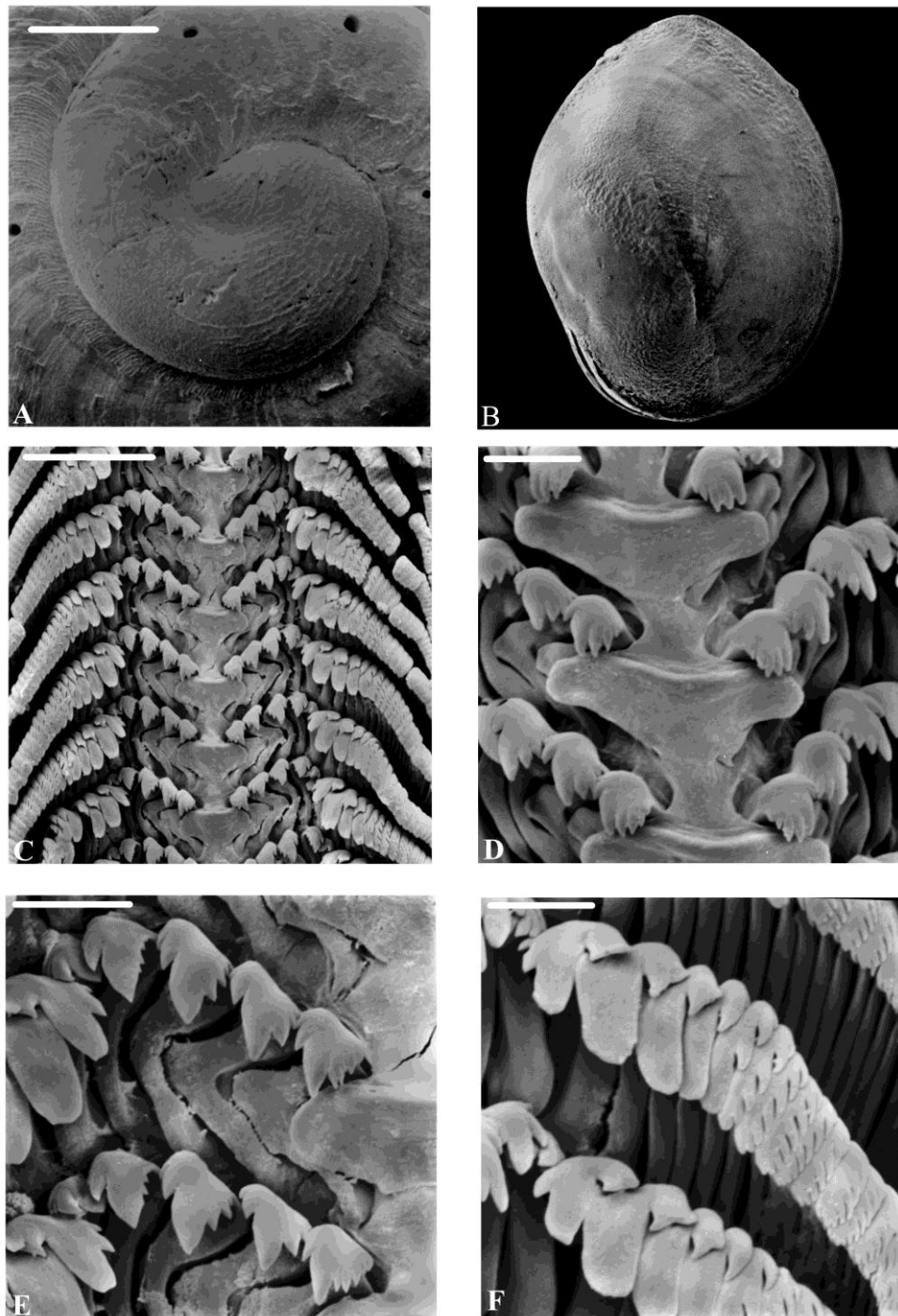


Figure 2.38. Scanning electron microscope of protoconch, operculum and radula of *T. kraussi*: (A) external surface of protoconch, showing traces of curved lines towards periphery and in apical region, and a convex terminal lip, NMSA W1544, bar = 120 μm ; (B) external surface of operculum, showing microscopic granular sculpture and a narrow peripheral groove underlying labral margin, NMSA W1544, maximum diameter 1.4 mm; (C) central portion of radula, NMSA W1544, bar = 90 μm ; (D) rachidian and inner lateral teeth, NMSA W2576, bar = 20 μm ; (E) lateral and inner marginal teeth, NMSA W1544, bar = 20 μm ; (F) inner and outer marginal teeth, NMSA W1544, bar = 20 μm .

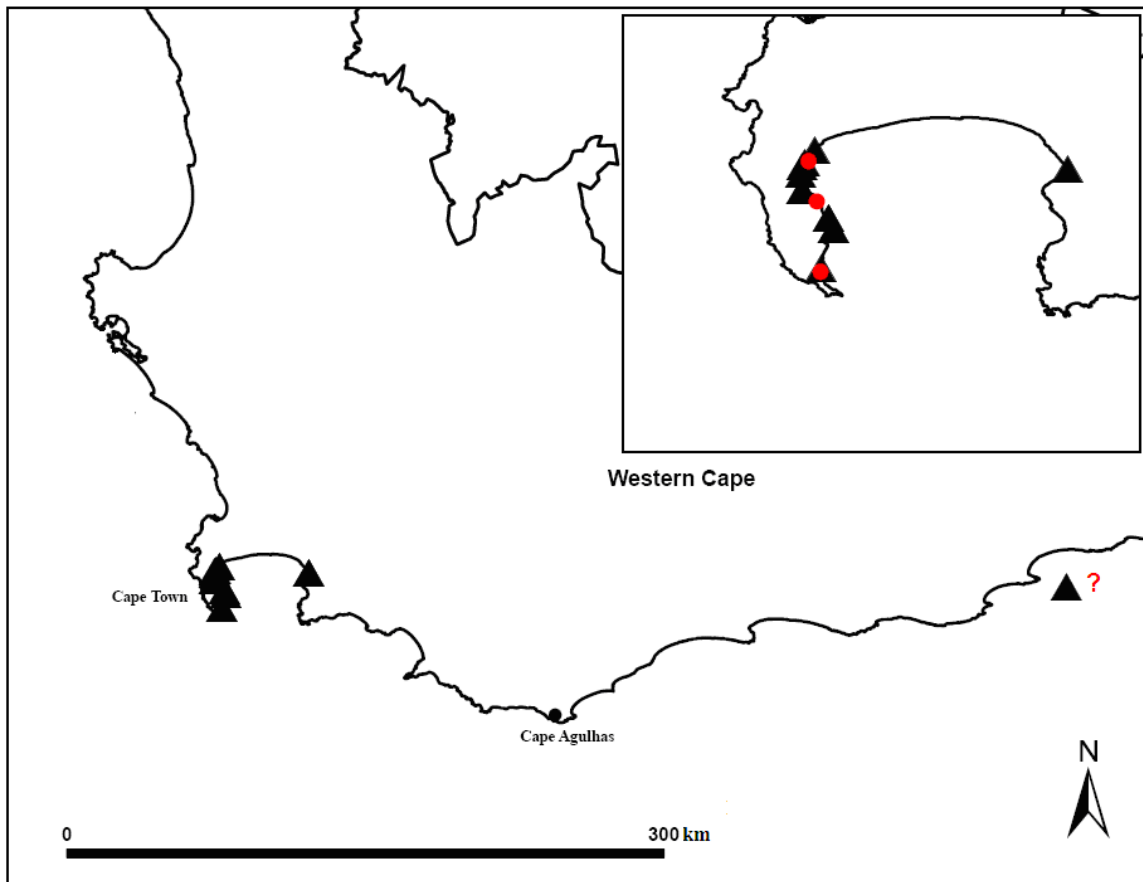


Figure 2.39. Distribution map of *T. kraussi*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia elongata (Krauss, 1848)

Figs 2.40-2.44

Phasianella elongata Krauss, 1848: 104-105, pl. 6, fig. 3; Philippi 1853: 22-23, pl. 4, figs 21-23; Sowerby 1887: 151, pl. 476, fig. 11; Pilsbry 1888: 168, pl. 39a, figs 23-25; Sowerby 1892: 41; Smith 1911: 313; Bartsch 1915: 145; Turton 1932: 172, fig. 1223; Herbert & Warén 1999: 222. Type loc.: “*In litore Capensi*” [“Along the Cape coast”, South Africa].

Phasianella alfredensis Turton, 1932: 173, pl. 40, fig. 1227. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Tricolia elongata; Barnard 1963: 207-209; Kensley 1973: 52; Robertson 1985: 21.

Etymology, *elongata* (Latin) – prolonged – refers to elongate shell shape.

Diagnosis: Shell relatively large, bulimiform; body whorl relatively large in proportion to the rest of the shell; smooth, lacking spiral sculpture; colouration highly variable, ground colour reddish–brown patterned with numerous, fine, close–set, sinuous, opisthocline, orange–red lines, fresh specimens with a row of spiral white dots on apical whorls.

Description (Figs 2.40A-C, 2.41A-H, 2.42):

Shell relatively large, bulimiform, with relatively high spire; teleoconch of up to 3.5 to 4 whorls; whorls lacking a distinct keel or angulation; body whorl evenly rounded and relatively large in proportion to the rest of the shell; suture relatively shallow. Shell surface smooth and glossy, lacking any spiral sculpture, marked only by microscopic fine growth–lines. Aperture ovate–circular, outer lip thick; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, but occasionally remaining as a narrow chink in others. Shell colouration highly variable, commonly reddish–brown patterned with numerous, fine, close–set, sinuous, opisthocline, orange–red lines (Figs 2.41C, D), and often with bold white, red or dark–brown blotches on adapical surface (Figs 2.41A, B, H); or with dark–brown to black axial zigzag lines on adapical surface (Fig. 2.41G); in some specimens the opisthocline lines anastomose, creating a darker reddish network with pale orange spots (Fig. 2.41F); others uniformly brown throughout (Fig. 2.41E); fresh specimens with a row of white, subsutural spots on second teleoconch whorls (Fig. 2.42).

Protoconch (Fig. 2.43A): Typically vetigastropod, comprising approx. 1.5 whorls; apical beak present but weak, terminal lip lacking a varix, but uniformly convex at mid-whorl; sculpture for the most part smooth.

Operculum (Fig. 2.43B): Similar to *T. adusta*.

Radula (Figs 2.43C-F): Similar to *T. pullus* (Gofas 1982), but rachidian tooth with broad, elliptical base-plate.

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985).

Measurements: Largest specimen examined – length 13.4 mm, width 6.9 mm. Length:width ratio 1.7-2.1 (N=50).

Habitat: *T. elongata* occurs commonly in the rocky intertidal zone, living among seaweed such as *Ulva* and *Codium fragile capense* (= green algae), *Gigartina radula*, *G. stiriata* and *Ceramium* (= red algae), and *Bifurcariopsis capensis* (= brown algae) at low spring tide level; living specimens from shallow infratidal to 17 m, empty shells from beach-drift to 75 m.

Geographical range (Fig. 2.44): Endemic to South Africa, ranging from the Eastern Cape (East London) to the Western Cape (Fish Hoek), with undefined records from “Pondoland”.

Type material (Fig. 2.40): A & B, *Phasianella elongata*, holotype, length 6.3 lin, width 3.6 lin (*vide* Krauss) [length 13.7 mm, width 7.9 mm], Stuttgart Museum (A & B are copies of figure from Krauss 1848); C, *Phasianella alfredensis*, holotype (+2 paratypes), OUM M002773, length 8.3 mm, width 4.6 mm.

Material examined (all NMSA, unless otherwise indicated): SOUTH AFRICA: *Eastern Cape*: “Pondoland coast” (V337); same locality, leg. A. Filmer, ex H. Becker coll’n, ex Transvaal Museum (V329); East London (33.000°S:27.900°E), ex B.J. Young coll’n, viii.1979 (V338); Kidd’s Beach (33.150°S:27.683°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi & M. Burse, 09.vii.2005 (W3205, living); Fish River mouth (33.483°S:27.133°E) (W5759, living); Three Sisters, Port Alfred (33.559°S:27.027°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi *et al.*, 31.viii.2003 (W1036, living); same locality, ex Albany Museum, 1980 (D4779); Port Alfred (33.600°S:26.900°E), leg. E.K. Jordan, ex Transvaal Museum, 1978 (V332, living); Algoa Bay (34.833°S:25.833°E), ca 17 m, loose rubble, dived M. Els, 25.vi.2005 (W3196, living).

Southern Cape: Jeffrey's Bay (34.050°S:24.917°E), leg. R. Kilburn (V320); Storms River mouth (34.017°S:23.900°E), beach–drift, leg. M. Quickelberge (V336); Reebok Reef, between Great and Little Brak River (34.079°S:22.171°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 05.xi.2006 (W4774, living); Mossel Bay (34.183°S:22.133°E), ex Albany Museum, 1980 (V321); Struis Bay, site 2 (34.809°S:20.057°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 07.xi.2006 (W4773, living); Struis Bay, site 1 (34.814°S:20.030°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 07.xi.2006 (W4771, living).

South Western Cape: Cape Agulhas (34.824°S:20.017°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 07.xi.2006 (W4769, living).

False Bay: off Macassar Beach (34.120°S:18.715°E), leg. C.M. Connolly, 1974 (V326); Strandfontein (34.083°S:18.550°E), leg. C.M. Connolly (EM 10709, living); Fish Hoek (34.133°S:18.433°E), leg. C.M. Connolly, 1974 (V322).

Comparison: Krauss's original type material of *Phasianella elongata* housed in Stuttgart Museum, Germany, was evidently lost during World War II (Herbert & Warén 1999).

When Turton (1932) described *T. alfredensis*, he mentioned dark reddish–brown streaks that slant down to the left as characteristic of this taxon, the same characteristic which Krauss used in his description of *T. elongata*. Judging by Krauss's description and illustration, this species has a thick shell, with a bulimiform shape, a relatively large body whorl in proportion to the rest of the shell and a distinctive colour pattern of sinuous opisthocline lines similar to those of *T. elongata*. There is no evidence to suggest that this is anything more than a colour form of the variable *T. elongata* (Fig. 2.40C).

Pilsbry (1888) treated this species as a variety of *T. pullus*, with which I disagree since the body whorl of *T. elongata* is relatively large in proportion to the rest of the shell and is patterned with numerous, close–set, sinuous, opisthocline, orange–red lines, characteristics lacking in *T. pullus*. Furthermore, *T. elongata* differs from *T. pullus* in having a spiral row of white, subsutural spots on second teleoconch whorl. However, this is only visible in fresh specimens of this species. Detailed taxonomic comparison of this species is discussed under *T. retrolineata*. In addition, *T. elongata* is endemic to South Africa while *T. pullus* is endemic to Eastern Atlantic/Mediterranean.

Additional notes: Literature records of *T. elongata* from Bay of Hakodate, southern Hokkaido, Japan (Schrenck 1867: 366-367, 903, as *Phasianella elongata*); various localities around Madagascar [Dautzenberg 1929: 528, as *Phasianella (Tricolia) elongata*] and Great Fish Bay, Angola (Thiele 1925: 57) are erroneous and are probably based on mislocalized specimens. Schrenck (1867) and Dautzenberg (1929) locality records were also dismissed by Robertson (1985) who suggested that the Schrenck material could have been *T. tristis* (see under *T. capensis*) and that of Dautzenberg could probably be small *P. solida* and I agree with his decision in rejecting these records.

Krauss (1848: 105) recorded the Mediterranean *Tricolia tenuis* (Philippi, 1844); from the Cape coast as did Turton (1932: 173), who recorded it from Port Alfred. Sowerby (1887: pl. 476, fig. 30; 1892: 41) treated *T. tenuis* (Philippi) as a variety of *T. pullus*. However, *T. tenuis* (Philippi) is a homonym of *T. tenuis* (Michaud, 1829), also a Mediterranean species which likewise does not occur in South Africa. It is possible, however, that Krauss and Turton material represent either *T. elongata* or *T. kochii* from South Africa as previously suggested by Barnard (1963: 208) and Kensley (1973: 52), but from Krauss and Turton's description (neither provided a figure), it is difficult to be certain which species it represents because of the combination of colour varieties found in both species.

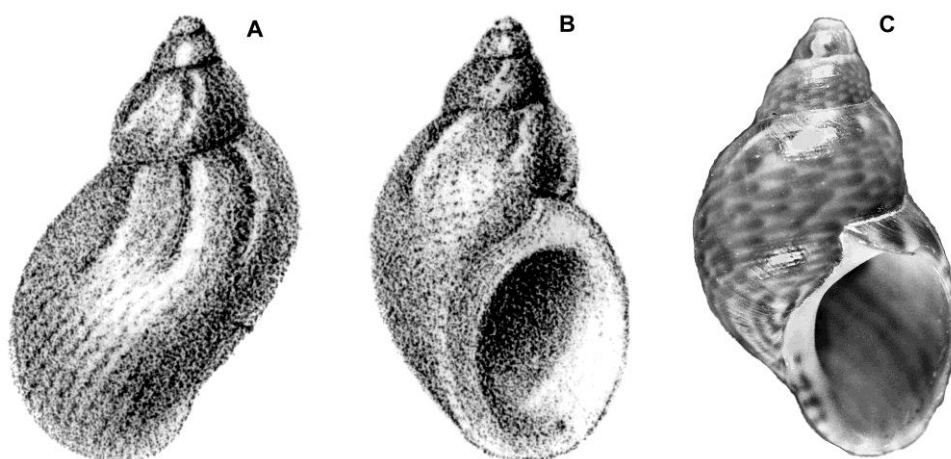


Figure 2.40. Type specimens of *T. elongata*: (A, B) *P. elongata*, holotype, length 6.3 lin, width 3.6 lin (*vide* Krauss) [length 13.7 mm, width 7.9 mm], Stuttgart Museum (A & B are copies of figure from Krauss 1848); (C) *P. alfredensis*, holotype, OUM M002773, length 8.3 mm, width 4.6 mm.

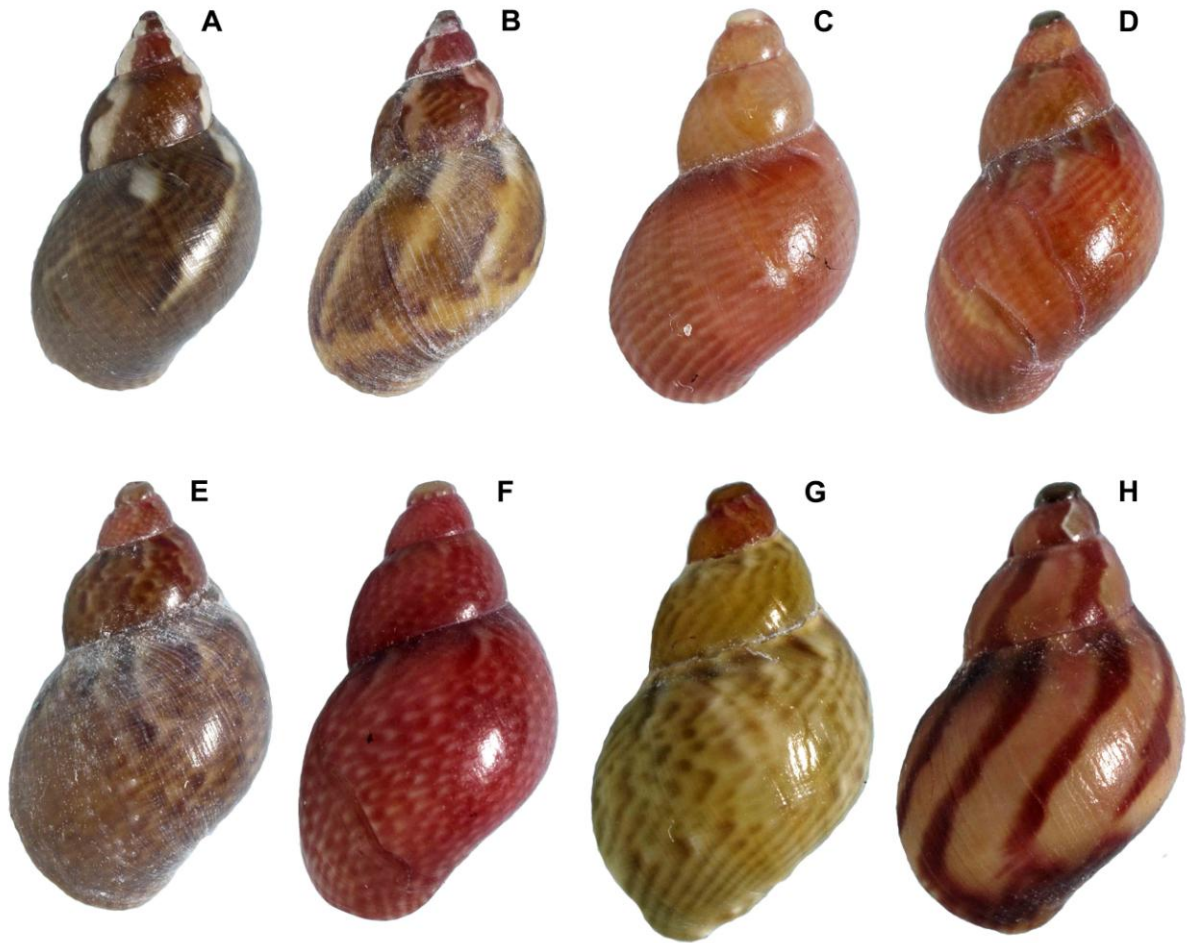


Figure 2.41. Variation in shell colouration of *T. elongata*: (A) length 12.7 mm, width 6.9 mm, NMSA W4769, Cape Agulhas, South Western Cape; (B) length 12.4 mm, width 6.2 mm, NMSA D4779, Three Sisters, Port Alfred, Eastern Cape; (C) length 9.4 mm, width 5.7 mm, NMSA V332, Port Alfred, Eastern Cape; (D) length 9.2 mm, width 5.5 mm, NMSA V332, Port Alfred, Eastern Cape; (E) length 9.3 mm, width 5.7 mm, NMSA V332, Port Alfred, Eastern Cape; (F) length 7.2 mm, width 4.3 mm, NMSA D4779, Three Sisters, Port Alfred, Eastern Cape; (G) length 7.4 mm, width 4.3 mm, NMSA V332, Port Alfred, Eastern Cape; (H) length 7.4 mm, width 4.5 mm, NMSA D4779, Port Alfred, Eastern Cape.

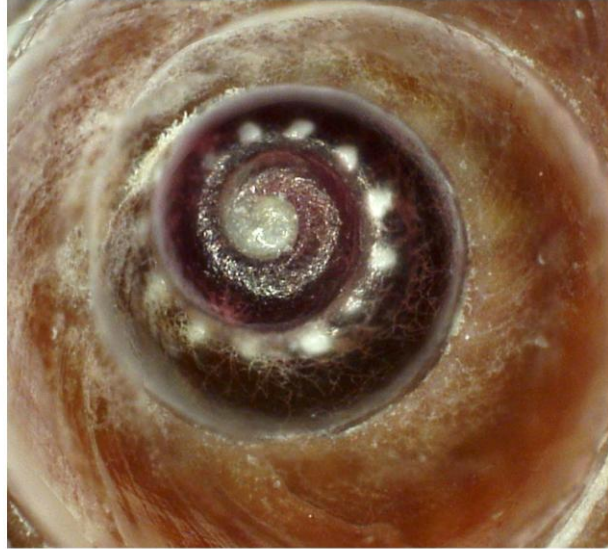


Figure 2.42. Apex of *T. elongata* showing white, subsutural spots on second teleoconch whorl, NMSA W4769, Cape Agulhas, South Western Cape.

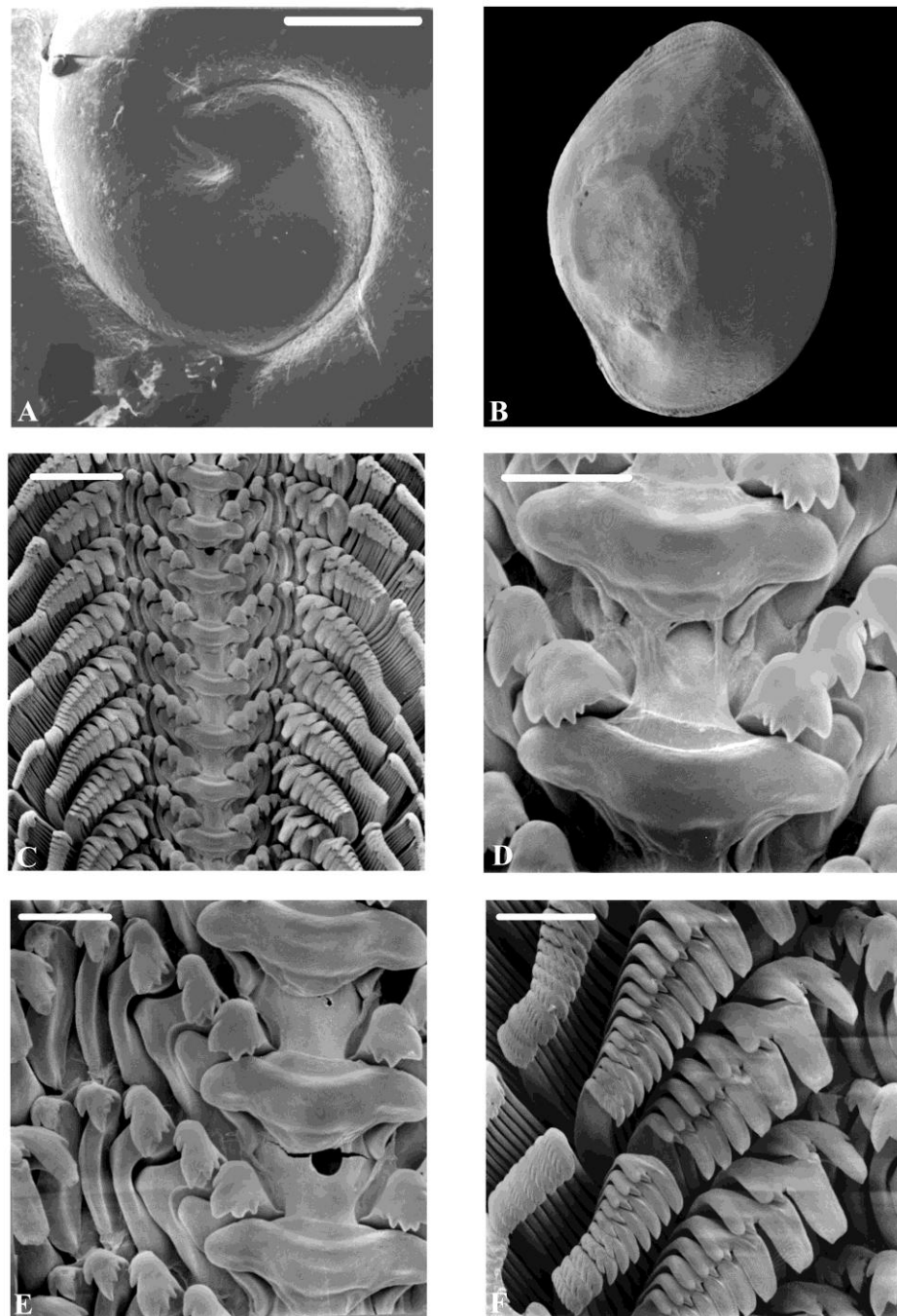


Figure 2.43. Scanning electron microscope of protoconch, operculum and radula of *T. elongata*: (A) external surface of protoconch, showing a smooth surface and a convex terminal lip, NMSA D4778, bar = 75 μm ; (B) external surface of operculum, showing a smooth surface, NMSA W3196, maximum diameter 2.7 mm; (C) central portion of radula, NMSA V322, bar = 210 μm ; (D) rachidian and inner lateral teeth, NMSA V322, bar = 40 μm ; (E) rachidian and lateral teeth, NMSA V322, bar = 40 μm ; (F) marginal teeth, NMSA V322, bar = 70 μm .

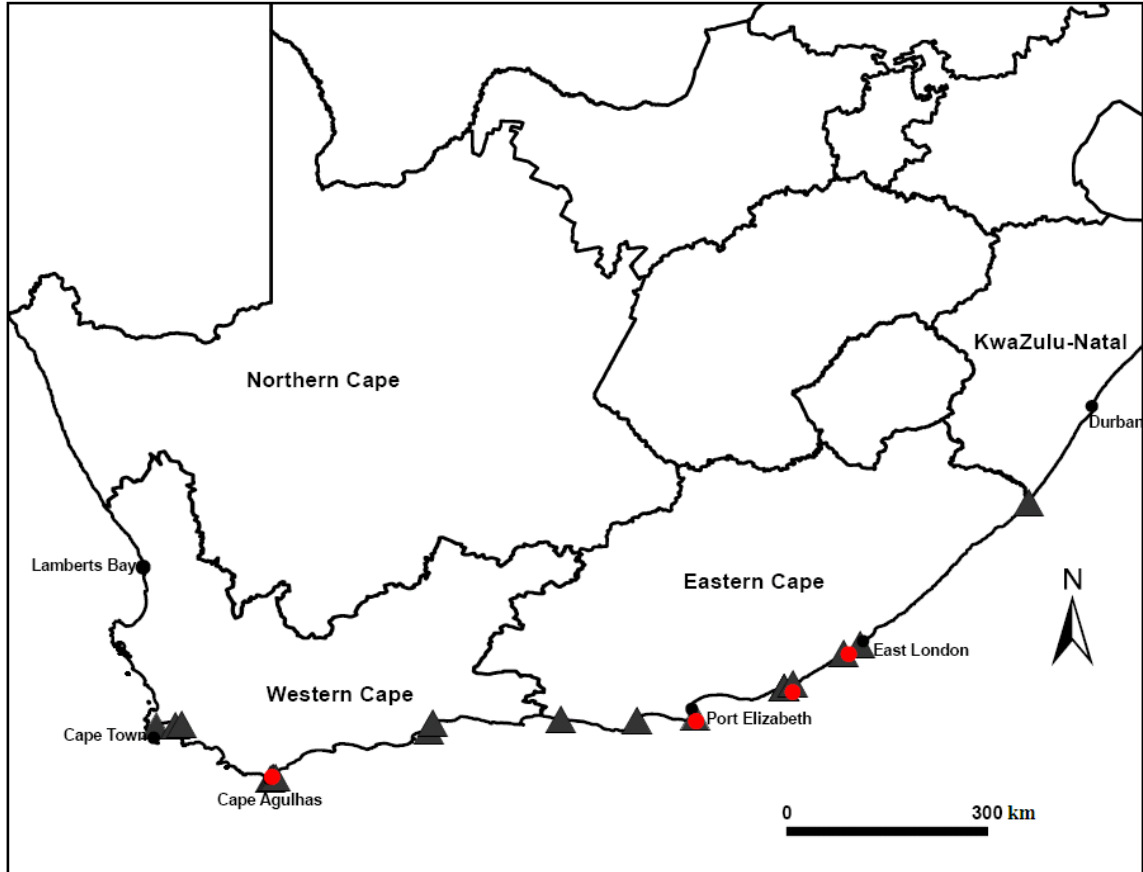


Figure 2.44. Distribution map of *T. elongata*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia formosa (Turton, 1932)

Figs 2.45-2.48

Phasianella formosa Turton, 1932: 173, pl. 41, fig. 1230. Type loc.: Port Alfred (Eastern Cape, South Africa).

Phasianella pallida Turton, 1932: 173-174, pl. 41, fig. 1231. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella capensis (non Dunker, 1846); Turton 1932: 173, pl. 40.

Tricolia formosa; Herbert 1991: 309; Nangammbi & Herbert 2006: 17-22.

Etymology, *formosa* (Latin) – beautiful.

Diagnosis: Shell turbiniform; whorls smoothly rounded, without any angulation; smooth, lacking spiral sculpture; colouration highly variable, predominately with pale brown flecks on a white background, with numerous pink dots on first two whorls; and commonly with large orange to dark-brown or black trapezoid blotches below suture; and or with rectangular or zigzag dark-brown dots or lines at or just below periphery.

Description (Figs 2.45A-B, 2.46A-O):

Shell turbiniform with relatively moderate spire; teleoconch of up to 3.2 whorls with relatively shallow suture; whorls smoothly rounded, without any angulation; base slightly more strongly convex. Sculpture weak, shell usually smooth and glossy, lacking any spiral sculpture, marked only by microscopic fine growth-lines. Aperture ovate-circular, outer lip thin, colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most examined specimens, but remaining as a narrow chink in others. Shell colouration extremely variable, all fresh specimens with spiral rows of numerous deep pink dots on first two whorls (Figs 2.46A, B); ground colour white with predominately pale brown flecks variously patterned with orange, brownish or black markings, frequently in form of broken zigzag lines or closely spaced dots, markings below suture frequently stronger and blotch-like (Figs 2.46B-D); other specimens with two alternating white lines, one below the trapezoid blotches and another one at or just below periphery (Figs 2.46E, F); some specimens with spiral rows of alternating whitish and dark-brown markings below suture and or just above or below periphery (Figs 2.46K, L); others with large dark-brown to black, trapezoid blotches below suture (Figs 2.46G, H); some specimens completely white below suture (Fig. 2.46I); other specimens with zigzag line of brown on the body whorl (Fig. 2.46O);

others with dots of brown below the suture and on body whorl (Figs 2.46M, N); more uniformly brownish in colour.

Protoconch (Fig. 2.47A): Typically vetigastropod, comprising approx.1.5 whorls; apical beak present but weak, terminal lip lacking a varix, but markedly angulate at mid-whorl, sculpture for the most part smooth, but with traces of curved lines towards apical region.

Operculum (Fig. 2.47B): Similar to *T. adusta*.

Radula (Figs 2.47C-F): Similar to *T. adusta*, but rachidian tooth with broad, roundly-trigonal base-plate; one denticle frequently dominant on third, fourth and fifth laterals; a distinct gap between the fifth and innermost marginal teeth.

External anatomy (Fig. 2.7B): Similar to *T. adusta*, but with a pair of dark reddish-brown blotches on snout between and just in front of cephalic tentacles (not present in all specimens).

Measurements: Largest specimen examined – length 7.7 mm, width 4.3 mm. Length:width ratio 1.5-1.8 (N=50).

Habitat: A subtidal species inhabiting off-shore reefs; living specimens from shallow infratidal to 32 m, empty shells from beach-drift to 30 m.

Geographic range (Fig. 2.48): Endemic to South Africa, ranging from the Eastern Cape (central Transkei, off Whale Rock) to the Western Cape (off Miller's Point).

Type material (Fig. 2.45): A, *Phasianella formosa*, holotype, OUM M002776, length 4.1 mm, width 2.5 mm; B, *Phasianella pallida*, holotype, OUM M002777, length 5.4 mm, width 3.2 mm.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Eastern Cape*: off Whale Rock (31.948°S:29.225°E), 20-26 m, sand and gorgonians, dredged NMDP, Stn. M1, 16.vii.1982 (V4047); Marshstrand, East London (32.750°S:28.250°E), leg. M. Burse, 16.x.1989 (EM 13963); off East London (33.032°S:27.937°E), 30 m, fine clean sand, dredged R.V. *Meiring Naudé*, 16.vii.1984 (B7956); Fuller's Bay, East London (33.057°S:27.865°E), leg. E. Roscoe, 21.xi.1980 (EM ex 8883); Kidd's Beach (33.150°S:27.683°E), *ex pisce*, leg.

S. Barnett (EM 10843, living); off Port Alfred (33.700°S:26.933°E), ex gut *Congiopodus torvus*, dredged D. Herbert on R.S. *Africana*, Stn. A19009, 03.v.1997 (V5147, living); Fish Tanks, Port Alfred (33.604°S:26.924°E), ca 17 m, broken reef with rocks and shell sand, Keryn diving school, 02.vii.2005 (W3197, living); Port Alfred (33.600°S:26.900°E), leg. E.K. Jordan, ex Transvaal Museum, 1978 (B4751, B4752, living); same locality, leg. J. Hutt, ex Albany Museum, 1980 (S6104, D4782, living).

Southern Cape: Jeffrey's Bay (34.050°S:24.917°E), ex Albany Museum, 1980 (B9998).

South Western Cape: East of Martha Point (34.488°S:20.548°E), 24 m, stones, marine growths, dredged NMDP, 07.iv.1991 (S9927, living); Agulhas Bank, off Struis Bay (34.753°S:20.162°E), 31 m, sponges stones, dredged NMDP, Stn. CC17, 08.iv.1991 (S7736, living); same locality (34.752°S:20.158°E), 32 m, sponges stones, dredged NMDP, Stn. CC16, 08.iv.1991 (S7686, living); Cape Agulhas (34.833°S:20.000°E), leg. C.M. Connolly, 1974 (V331); Hermanus on *Haliotis midae* (34.417°S:19.233°E), 10-30 m, leg. F. Graeve, ex J.P. Marais coll'n, v.1990 (V3542, living); off Hawston near Hermanus (34.400°S:19.067°E), rocky subtidal reef, ca 23 m, dived D. Herbert, xi.1988 (E6393, living).

False Bay: Gordon's Bay (34.150°S:18.850°E), beach–drift (B6872); off Macassar Beach (34.120°S:18.727°E), 25 m, rocks, broken lace corals, dredged R.V. *Sardinops* and NMDP, Stn. CD16, 10.iv.1991 (S3676, living); same locality (34.120°S:18.715°E), 30 m, coarse sand rocks, dredged NMDP, Stn. CD17, 10.v.1991 (S9228, living); same locality (34.088°S:18.706°E), ca 15 m, rocky subtidal reefs, dived UCT Zoology Department, 10.ii.2005 (W2581, living); Simon's Town (34.188°S:18.433°E), dredged C.M. Connolly, i.1974 (A1831); off Miller's Point (34.163°S:18.432°E), ca 20 m, rocky subtidal reefs, dived UCT Zoology Department, 10.ii.2005 (W2579, living).

Comparison: *T. formosa* is unique among other southern African *Tricolia* species in having spiral rows of pink dots on the apical whorl. However, this species most closely resembles *T. adusta* and *T. capensis* in terms of its turbiniform shell shape. Some specimens of this taxon resemble those of *T. adusta*, *T. africana* and *T. capensis* by having large, dark brown–to–black, trapezoid blotches below the suture, or broad, alternating axial bands of brown and cream–white on the apical surface. In addition, *T. formosa* resembles *T. adusta*, *T. ios* and *T. saxatilis* in terms of its habitat preferences. All are commonly subtidal species inhabiting off–shore reefs.

In his description of *P. pallida*, Turton (1932) identified no genuinely distinctive characteristics for this taxon, stating only that the colour pattern was characteristic. It possesses the same spiral rows of pink dots on the apical whorls and its colour pattern falls well within the range of variation shown by *T. formosa*. These two nominal taxa are without doubt synonyms. Since these two names were published on the same date by the same author and in the same work, following the principle of first reviser (ICZN 1999, Article 24.2), I select *P. formosa* as the name for this taxon. This name was chosen because it appears first in Turton's publication (c.f. ICZN 1999, recommendation 24A). There are no issues of nomenclatural stability and appropriateness which would favour the use of *P. pallida*. In terms of morphology of the innermost marginal teeth of the radula, *T. formosa* more closely resembles *T. adusta* and *T. saxatilis* than any other southern African *Tricolia* species. The innermost marginal teeth of the radula of *T. formosa*, *T. adusta* and *T. saxatilis* have one strong undivided ectocone, whereas in *T. pullus* and the other southern African species, the ectocone is bifid or notched, and interlocks with two notches at the base of the cusp of the adjacent tooth. Furthermore, the external anatomy of *T. formosa* and *T. adusta* has one sense organ at the base of each epipodial tentacle, whereas *T. pullus* and the other southern African species have two sense organs at the base of the anterior epipodial tentacle on the right (Figs 2.7A, D).

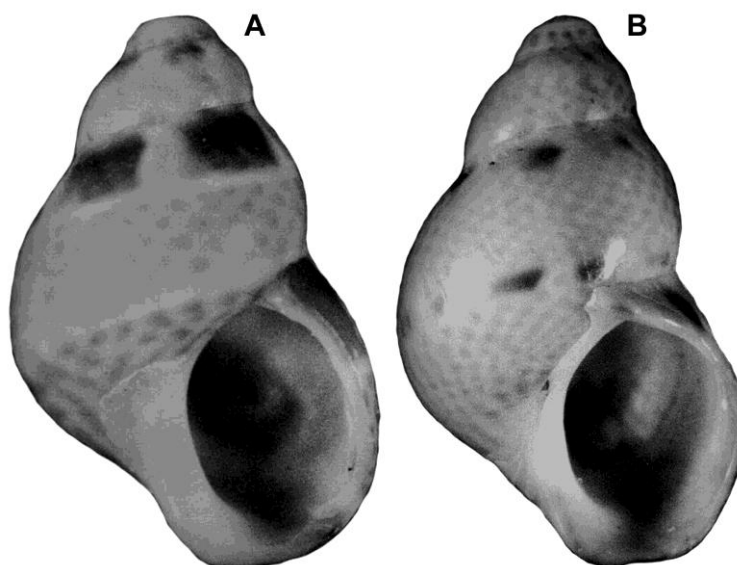


Figure 2.45. Type specimens of *T. formosa*: (A) *P. formosa*, holotype, OUM M002776, length 4.1 mm, width 2.5 mm; (B) *P. pallida*, holotype, OUM M002777, length 5.4 mm, width 3.2 mm.

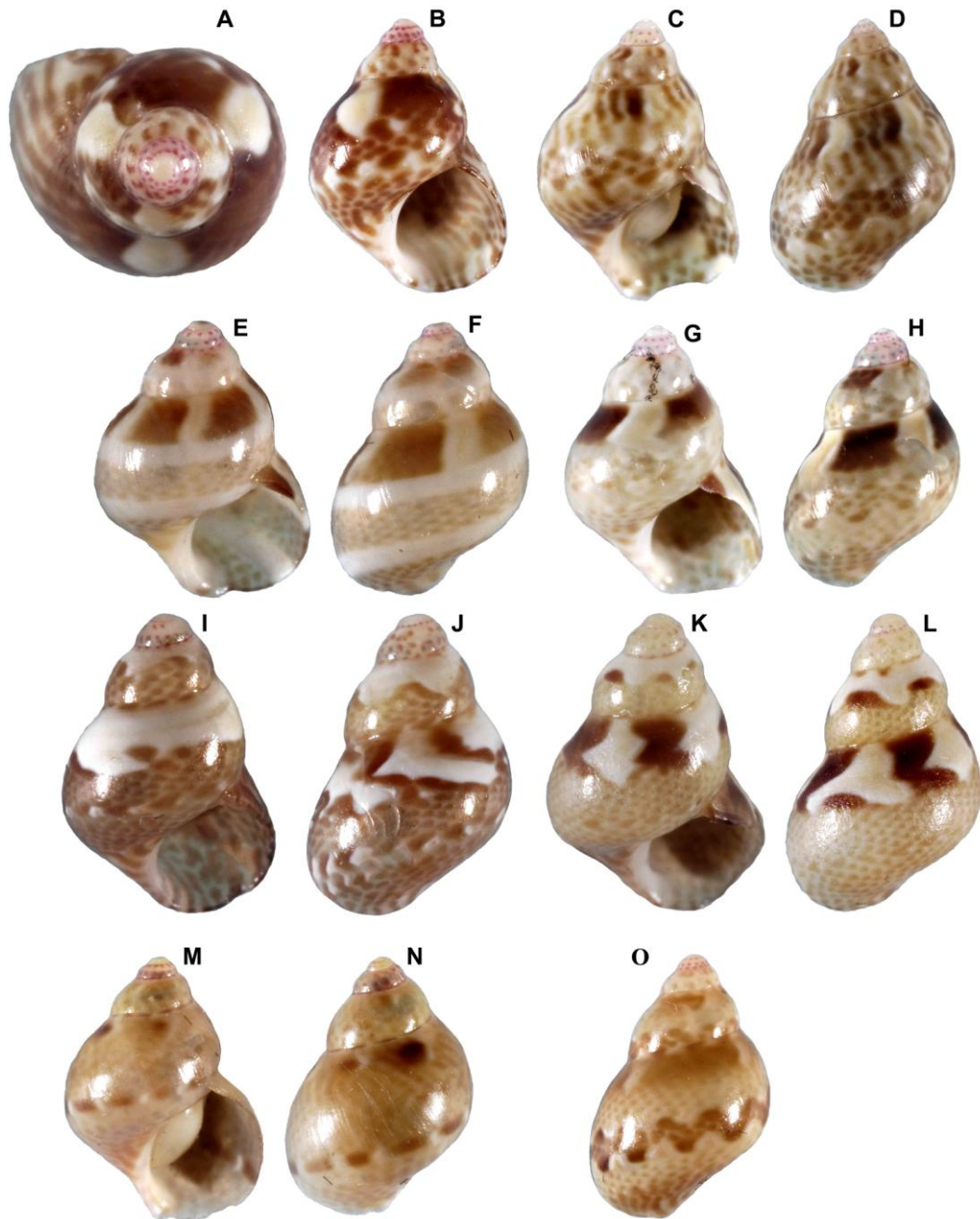


Figure 2.46. Variation in shell colouration of *T. formosa*: (A, B) length 4.7 mm, width 3.2 mm, NMSA S9927. East of Martha Point, South Western Cape; (C, D) length 5.1 mm, width 3.3 mm, NMSA S9927. East of Martha Point, South Western Cape; (E, F) length 4.1 mm, width 2.9 mm, NMSA S9927. East of Martha Point, South Western Cape; (G, H) length 4.5 mm, width 2.9 mm, NMSA S9927. East of Martha Point, South Western Cape; (I, J) length 5.2 mm, width 3.4 mm, NMSA S9927. East of Martha Point, South Western Cape; (K, L) length 5.6 mm, width 3.3 mm, NMSA S9927. East of Martha Point, South Western Cape; (M, N) length 4.0 mm, width 2.8 mm, NMSA S9927. East of Martha Point, South Western Cape; (O) length 5.2 mm, width 3.3 mm, NMSA S9927. East of Martha Point, South Western Cape.

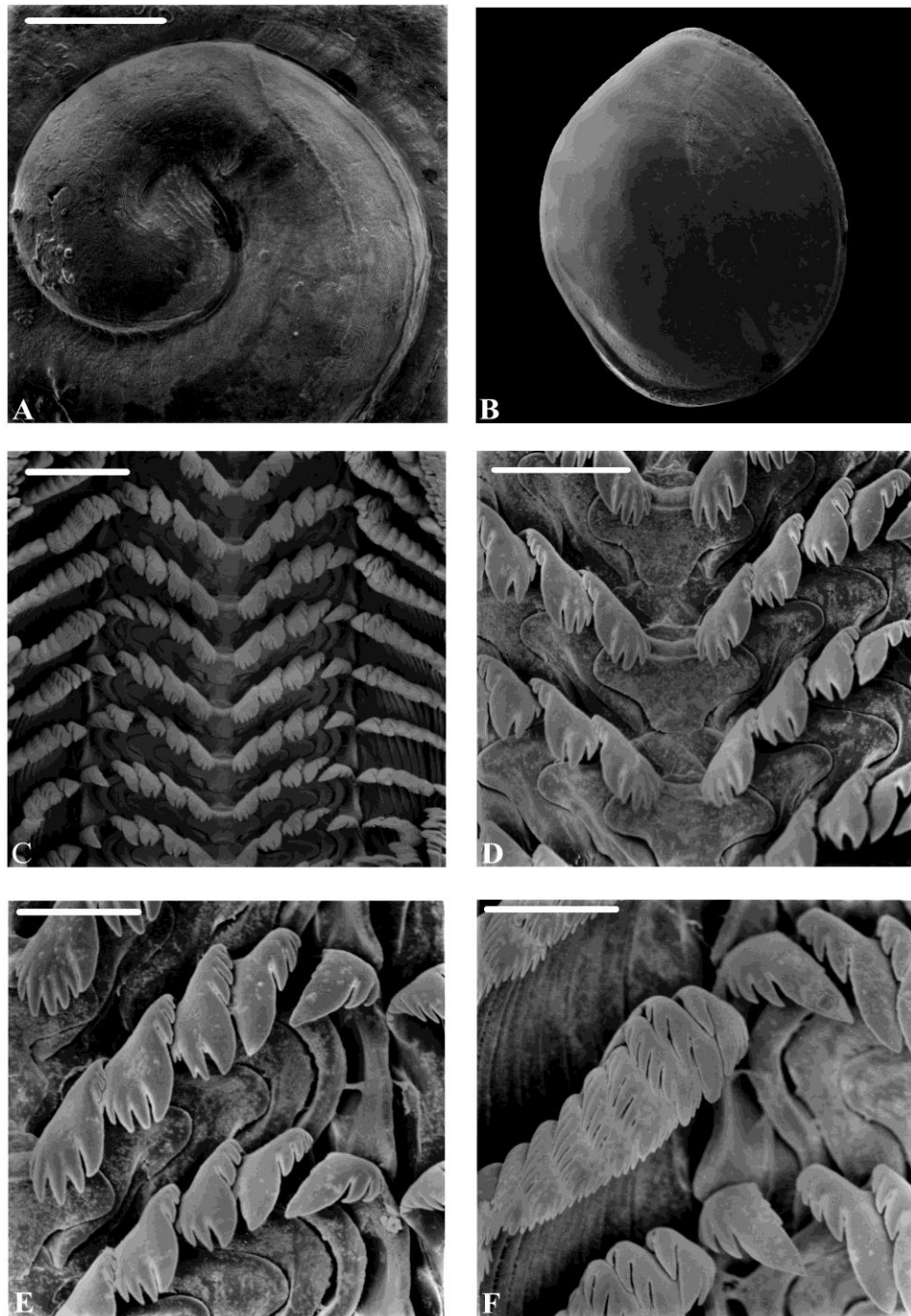


Figure 2.47. Scanning electron microscope of protoconch, operculum and radula of *T. formosa*: (A) external surface of protoconch, showing traces of curved lines towards apical region and distinct angle at mid-whorl, NMSA S9927, bar = 60 μm ; (B) external surface of operculum showing a smooth surface and a narrow peripheral groove underlying labral margin, NMSA W2581, maximum diameter 2.2 mm; (C) central portion of radula, NMSA W2581, bar = 80 μm ; (D) rachidian and inner lateral teeth, NMSA W2581, bar = 15 μm ; (E) lateral teeth, NMSA W2581, bar = 25 μm ; (F) marginal teeth, NMSA W2581, bar = 20 μm .

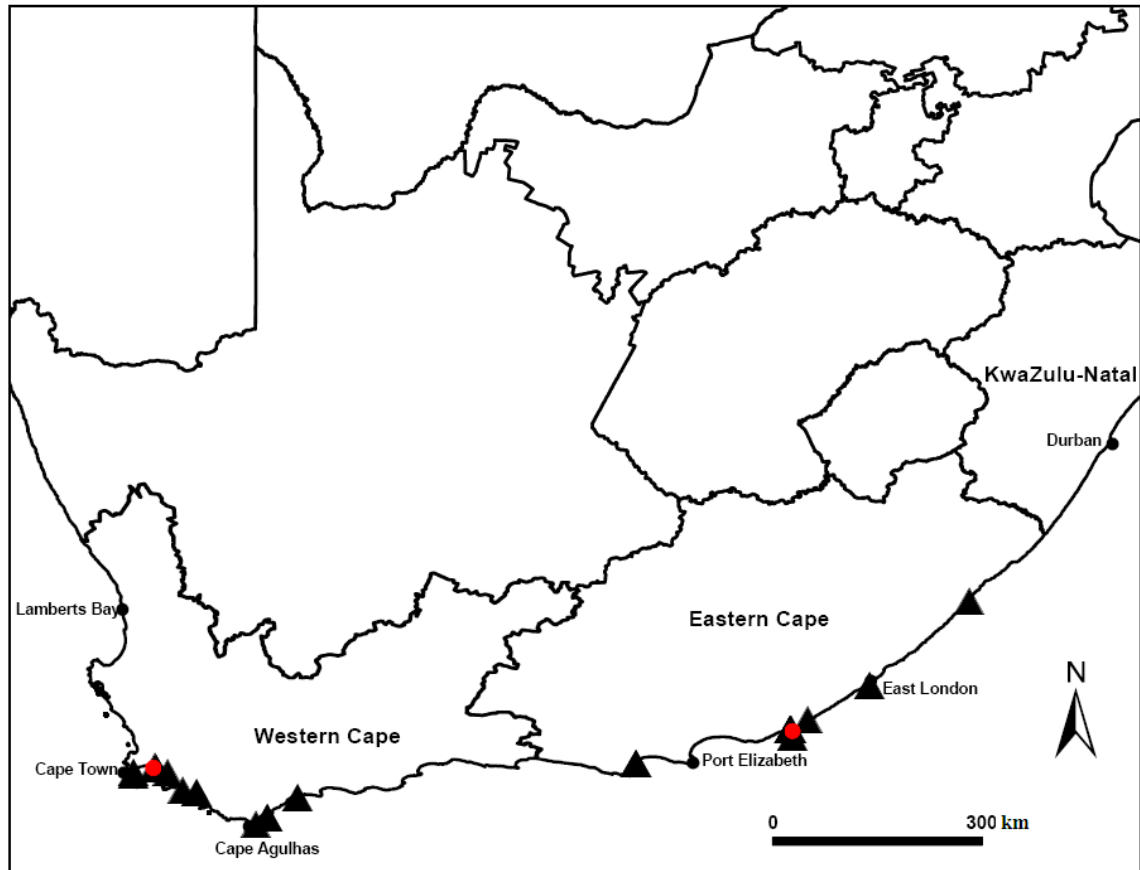


Figure 2.48. Distribution map of *T. formosa*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia ios Robertson, 1985

Figs 2.49-2.51

Tricolia ios Robertson, 1985: 50-53, pls 29-35; Herbert 1991: 308-309, fig. 7; Moolenbeek & Dekker 1993: 147, figs 15-18; Bosch *et al.* 1995: 99; Dekker & Orlin 2000: 18. Type loc.: 19 km North East of Mogadishu, Republic of Somalia.

Etymology, *ios* (Greek) – refers to the numerous red dots on the shell which forms a conspicuous part of the colour pattern.

Diagnosis: Shell turbiniform, surface with incised spiral sculpture, and coarse axial growth-lines; shell surface covered with numerous tiny red dots on white background forming a conspicuous part of colour pattern; translucent columella.

Description (Fig. 2.49):

Shell turbiniform with relatively moderate spire; teleoconch of up to 3.2 whorls with relatively shallow suture; whorls smoothly rounded, without any angulation; base slightly more strongly convex. Sculpture weak, shell usually smooth and glossy, lacking any spiral sculpture, marked only by microscopic fine growth-lines. Aperture ovate-circular, outer lip thin, colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most examined specimens, but remaining as a narrow chink in others. Shell with relatively constant colour pattern, ground colour reddish-white; patterned with numerous red dots on the body whorl forming a conspicuous part of the colour pattern (Fig. 2.49); early whorl with dark black colour.

Protoconch (Fig. 2.50A): Typically vetigastropod, comprising approx. 1.5 whorls; apical beak present but weak, terminal lip lacking a varix, but markedly straight at mid-whorl, sculpture for the most part smooth, but with traces of curved lines towards apical region.

Operculum (Fig. 2.50B): Similar to *T. adusta*.

Radula (Figs 2.50C-F): Similar to *T. adusta*, but rachidian tooth with broad, roundly-trigonal base-plate; one denticle frequently dominant on third and fourth laterals.

External anatomy (Fig. 2.7B): Similar to *T. adusta*, but with a pair of dark reddish–brown blotches on snout between and just in front of cephalic tentacles (not present in all specimens).

Measurements: Largest specimen examined – length 3.2 mm, width 1.9 mm. Length:width ratio 1.3-1.9 (N=30).

Geographical range (Fig. 2.51): Tropical Indo–West Pacific species with its distribution extending into the tropical waters of N.E. South Africa. It has been recorded from East Africa ranging from Somalia to South Africa. The Natal Museum collection includes material from Kenya, southern Mozambique (off Malongane) to central KwaZulu–Natal (Aliwal Shoal, off Scottburgh). For additional geographical distribution records see Robertson (1985); Herbert (1991) and Moolenbeek & Dekker (1993).

Type material: *Tricolia ios*, holotype, 19 km North East of Mogadishu, Somalia Republic ANSP 295535 (Robertson 1985).

Material examined (all NMSA, unless indicated otherwise): MOZAMBIQUE: off Malongane, coral reef, ca 5 km north of Ponta do Ouro, hand–dredged sand, 15-20 m, dived D. Herbert, v.1994 (V1462); Ponta do Ouro (26.85°S:32.917°E), subtidal coral reef, hand–dredged sand, ca 20 m, dived D. Herbert, 14.iv.1997 (L5923).

SOUTH AFRICA: *KwaZulu–Natal*: between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), reef off marker 13 north, northern portion, 4-10 m, dived D. Herbert *et al.*, 07.v.1990 (E3091, S2415); same locality, near pinnacles, 5-11 m, hand–dredged sand, dived D. Herbert, 13.v.1990 (S9172); same locality, algal portion, 5-9 m, underwater pump, dived D. Herbert & K. Bloem, 03.v.1990 (S2864, living); same locality, ca 8 m, underwater pump, dived D. Herbert & K. Bloem, 06.v.1990 (S2681); Kosi Bay (26.900°S:32.867°E), main reef 1-4 km south of estuary mouth, 10-16 m, dived D. Herbert *et al.*, 04-06.v.1990 (S1974); South East of Rocktail Bay (27.202°S:32.813°E), 60 m, coarse sand, dredged NMDP, Stn. ZD9, 08.vi.1990 (V890); off Lala Nek (27.227°S:32.822°E), 75 m, coarse sand, sandstone, dredged R.V. *Sardinops* and NMDP, 08.vi.1990 (S3487); same locality, 74 m, shell, sand, dredged R.V. *Sardinops* and NMDP, Stn. ZDD3, 08.vi.1990 (S3485); Two–Mile Reef, Sodwana Bay (27.517°S:32.691°E), 10-15 m, hand–dredged sand, dived D. Herbert (S4286); off Leven Point (27.917°S:32.583°E), 50-60 m, in mud (S3346); Mission Rocks, St. Lucia beach–drift (28.267°S:32.500°E), leg. J.P. Marais, v.1991 (S3691); St. Lucia Lighthouse

(28.500°S:32.417°E), 100 m, mud and peddles, ex CSIR Water Research, Stn. F3 (A5711); Aliwal Shoal, off Scottburgh (30.283°S:30.833°E), ca 14 m, underwater pump, dived D. Herbert, 02.vi.1991 (S3773).

Extralimital material examined: KENYA: lagoon inshore of coral reef, sand from base of coral outcrop, ca 4 m, dived D. Herbert, 20.xii.1999 (K8008).

Comparison: A detailed description of this species is provided by Robertson (1985). Robertson (1974) suggested that *T. ios* most closely resembles *T. indica* in terms of its shape, size and sculpture, but they differ from each other in terms of the coarseness of their sculpture, colour pattern, in the presence or absence of an umbilical chink, thickness of the shell, and size of the first whorl. He also discussed differences in the radula of the two species: the radula of *T. indica* is much smaller than that of *T. ios* and has smaller teeth, fewer marginals, and the innermost pair of laterals is broadly ovate with a cusp, and only has three pairs of lateral teeth. The radula of *T. ios* is large, with many marginal teeth, and the rachidian tooth is broadly ovate without a cusp and has five pairs of lateral teeth. The two species also differ in terms of habitat preferences: *T. ios* lives among algae while *T. indica* lives on a siliceous sand bottom where there are no macroscopic plants and where the water is opaque with suspended detritus (Robertson 1974).

In southern Africa, this species also resembles *H. variabilis* in having small, numerous red dots on the body whorl forming a conspicuous part of the colour pattern. However, the dots in *H. variabilis* are arranged in spiral rows.



Figure 2.49. Shell colouration of *T. ios*: length 3.5 mm, width 2.4, NMSA K8008. Kenya.

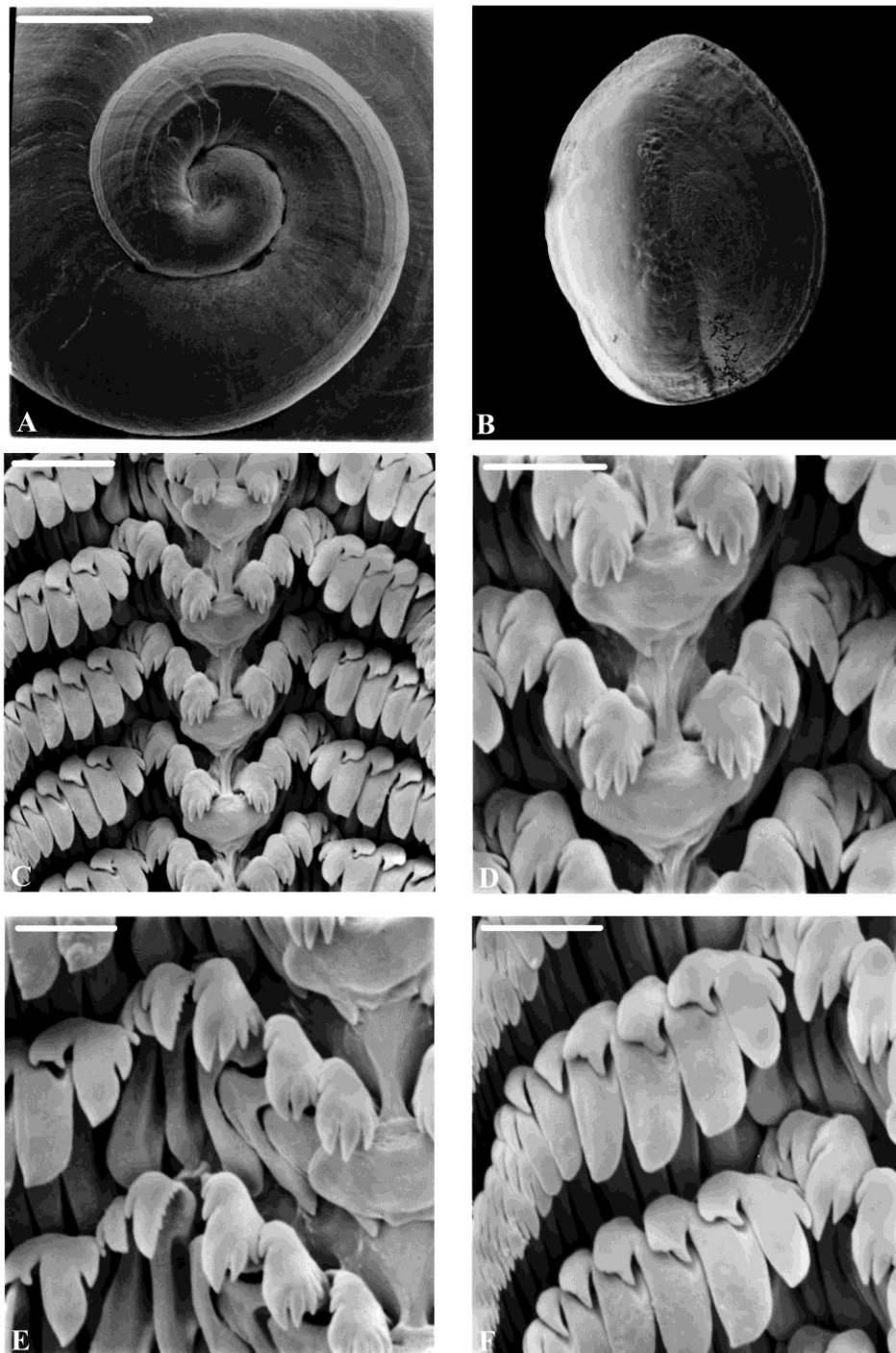


Figure 2.50. Scanning electron microscope of protoconch, operculum and radula of *T. ios*: (A) external surface of protoconch, showing traces of spiral lines and a straight angle at mid-whorl, NMSA S9172, bar = 60 μm ; (B) external surface of operculum, showing a smooth surface and a distinct peripheral groove underlying labral margin, NMSA W5572, maximum diameter 0.9 mm; (C) central portion of radula, NMSA W5573, bar = 50 μm ; (D) rachidian and innermost lateral teeth, NMSA W5572, bar = 10 μm ; (E) lateral teeth, NMSA W5572, bar = 20 μm ; (F) marginal teeth, NMSA W5572, bar = 15 μm .

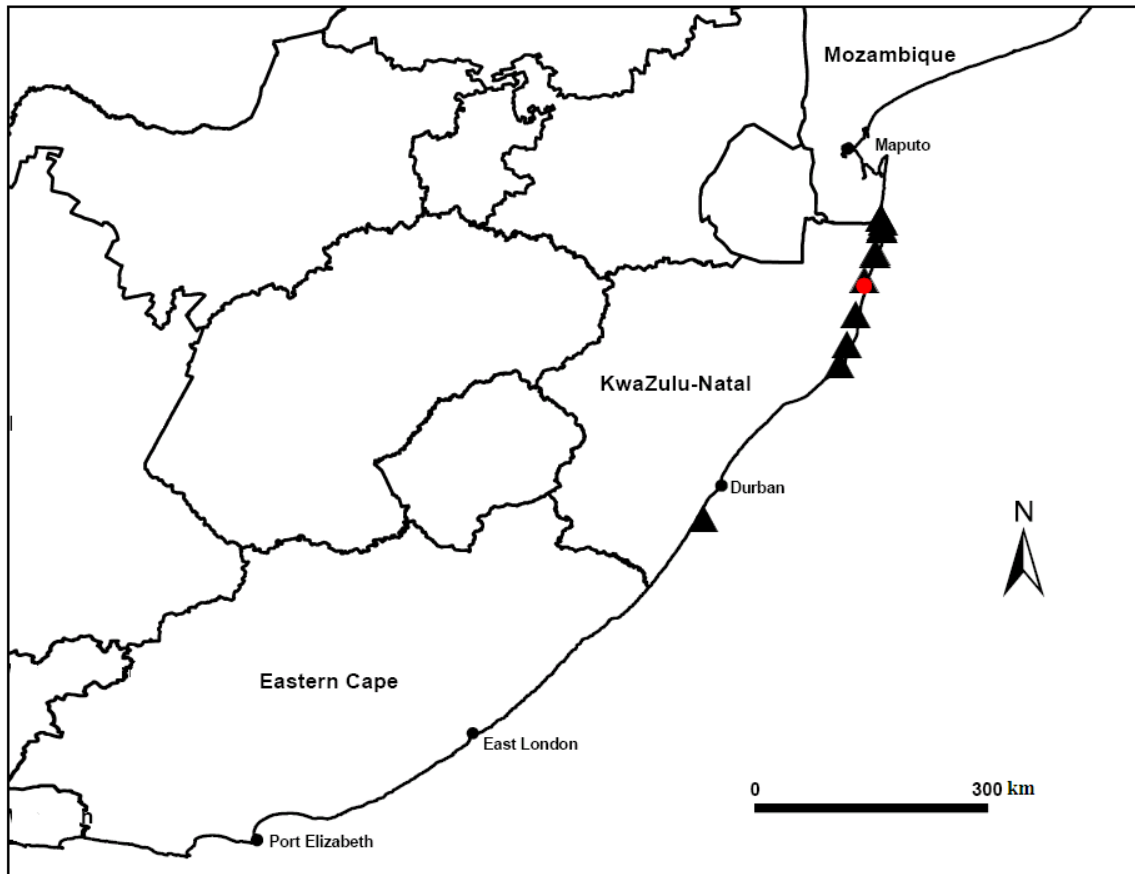


Figure 2.51. Distribution map of *T. ios*. Each black triangle represents one or more site records. Red dot represents a sequenced sample.

Tricolia kochii (Philippi in Krauss, 1848)

Figs 2.52-2.55

Phasianella kochii Philippi in Krauss, 1848: 104, pl. 6, fig. 4; Philippi 1853: 26, pl. 5, figs 9-11; Reeve 1862: pl. 5, sp. 13a, b (in part); Paetel 1869: 58; Troschel 1878: 202, pl. 18, fig. 11; Sowerby 1887: 151, pl. 476, figs 15, 16; Pilsbry 1888: 170, pl. 37, figs 37, 38 (in part); Sowerby 1892: 41 (in part); Smith 1911: 313; Bartsch 1915: 144-145; Turton 1932: 172, pl. 40, fig. 1218; Cox 1939: 42; Barnard 1962: 190; Eisenberg 1981: 44; pl. 26, sp. 15; Herbert & Warén 1999: 224. Type loc.: “*In litore Capensi*” [“Along the Cape coast”, South Africa].

Phasianella carinata Turton, 1932: 172-173, pl. 40, fig. 1226. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella fuscomaculata Turton, 1932: 173, pl. 40, fig. 1228. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella kochii maculata Turton, 1932: 172, pl. 40, fig. 1220. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella kochii nigra Turton, 1932: 172, fig. 1221. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Phasianella kochii viridis Turton, 1932: 172, fig. 1219. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Tricolia carinata; Barnard 1963: 207.

Tricolia fuscomaculata; Barnard 1963: 209.

Tricolia kochii; Barnard 1963: 207-209; Kensley 1973: 52, fig. 144 (in part); Branch & Branch 1981: pl. 114, fig. e; Richards 1981: 38, pl. 11, sp. 84 (in part); Robertson 1985: 23.

Tricolia kochii nigra; Barnard 1963: 208.

Tricolia kochii viridis; Barnard 1963: 208.

Tricolia capensis (non Dunker, 1846); Kilburn & Rippey 1982: 42-43, pl. 9, figs 7a, b; Herbert 1991: 309; Branch *et al.* 1994: 148, figs 69.6a, b; Steyn & Lussi 1998: 28, fig. 93 [= *Tricolia kochii* (Philippi in Krauss, 1848)].

Etymology, *kochii* – Named in honour of Carl Jakob Wilhelm Ludwig Koch (1827-1882). Born in Heidelberg, Germany, and was a Zoologist.

Diagnosis: Shell relatively large, turbiniform; whorls evenly rounded, lacking any angulation; last adult whorl smooth, lacking spiral sculpture; early shell whorl with distinct spiral sculpture; colouration highly variable, commonly reddish-brown or greenish-yellow,

patterned with alternating axial white lines or bands on apical surface, most specimens with subsutural turquoise spots.

Description (Figs 2.52A-F, 2.53A-K):

Shell relatively large, turbiniform, with fairly high spire; teleoconch of up to 3.4 whorls with relatively shallow suture; whorls evenly rounded, lacking any angulation. Sculpture weak, last adult whorl mostly smooth and glossy, lacking any spiral sculpture, marked only by exceedingly fine growth-lines; early shell whorl with fine spiral sculpture. Aperture ovate-circular, outer lip thick; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, remaining as a narrow chink in others. Shell colouration extremely variable; live taken specimens with spiral row of turquoise spots below suture; usually reddish-brown or greenish-yellow often with broad alternating axial bands of cream-white on apical surface or below periphery (Figs 2.53B, H, J); some specimens with cream-white band below periphery or near the base (Fig. 2.53G); some specimens patterned with numerous, fine, close-set, sinuous, opisthoclinal, reddish-brown lines on the body whorl (Figs 2.53A, D, E); others with numerous fine dots of white and black (Figs 2.53I, K); some specimens almost white, green or red throughout (Figs 2.53C, F); columella margin bordered with red and white blotches.

Protoconch (Fig. 2.54A): Typically vetigastropod, comprising approx. 1.25 whorls; apical beak present but weak, terminal lip lacking a varix, but markedly angulate at mid-whorl; sculpture for the most part smooth, with traces of curved lines towards periphery.

Operculum (Fig. 2.54B): Similar to *T. adusta*.

Radula (Figs 2.54C-F): Similar to *T. pullus* (Gofas 1982).

External anatomy (Fig. 2.7A): Similar to *T. pullus* (Robertson 1985), but with a pair of dark green spots on snout between and just in front of cephalic tentacles.

Measurements: Largest specimen examined – length 16.8 mm, width 6.1 mm. Length:width ratio 1.4-1.9 (N=50).

Habitat: *T. kochii* occurs commonly in the rocky intertidal zone, living among seaweed such as *Ulva* and *Codium fragile capense* (= green algae), *Gigartina radula*, *G. stiriata* and

Ceramium (= red algae), and *Bifurcariopsis capensis* (= brown algae) at low spring tide level, occasionally on and under rocks, empty shells from beach–drift to 250 m.

Geographical range (Fig. 2.55): Endemic to southern Africa, ranging from central Mozambique (Baía dos Cocos, Jangamo district), perhaps up to Inhambane (Barnard 1962) to the South Western Cape (Cape Agulhas).

Type material (Figs 2.52A-F): A, *Phasianella kochii*, syntype, BMNH 1923.7.13.19, diameter 1.2 mm (A is a copy of figure taken by D. Herbert); B, *Phasianella carinata*, holotype, OUM M002772, length 8.2 mm, width 5.1 mm; C, *Phasianella fuscomaculata*, holotype, OUM M002774, length 8.2 mm, width 5.2 mm; D, *Phasianella kochii maculata*, five syntypes, OUM M002766, length 5.6 mm, width 3.8 mm; E, *Phasianella kochii nigra*, five syntypes, OUM M002767, length 5.9 mm (specimen broken to measure width size); F, *Phasianella kochii viridis*, five syntypes, OUM M002765, length 6.0 mm, width 4.3 mm.

Material examined (all NMSA, unless indicated otherwise): MOZAMBIQUE: Baía dos Cocos, Jangamo district, leg. A. Jenner, vi.1974 (G2385); Inhaca Island (26.028°S:32.904°E), *Cymodocea* sand flats, leg. P. Reavell, ix.1972 (L6715); Cabo de Santa Maria, Delagoa Bay (26.087°S:32.960°E), leg. R. & E. Kilburn, vii.1970 (6343); off Malongane, coral reef, ca 5 km north of Ponta do Ouro, hand–dredged sand, 15–20 m, dived D. Herbert, v.1994 (V1524); Ponta do Ouro (26.850°S:32.917°E), subtidal coral reef, hand–dredged sand, ca 20 m, dived D. Herbert, 14.iv.1997 (L5937).

SOUTH AFRICA: *KwaZulu–Natal*: between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), reef off marker 13 north, near pinnacles, 10–12 m, hand–dredged sand, dived D. Herbert, 12.v.1990 (S2411); same locality, algal portion, 5–9 m, underwater pump, dived D. Herbert & K. Bloem, 03.v.1990 (S2847, S2821); same locality, ca 8 m, underwater pump, dived D. Herbert & K. Bloem, 06.v.1990 (S2746); Kosi Bay (26.900°S:32.867°E), marker 13 north, intertidal rocks and beach–drift, leg. D. Herbert *et al.*, v.1990 (S1276); off Lala Nek (27.225°S:32.825°E), 74 m, shells, sand, dredged NMDP, Stn. ZDD3, 08.vi.1990 (S7407); same locality (27.917°S:32.647°E), 250 m, coarse sand, dredged NMDP, Stn. ZL5 (S9363); Sodwana Bay (27.533°S:32.683°E), 20 m, ex CSIR Water Research, 1976 (A4457); same locality, 6–18 m, dived D. Herbert *et al.*, 12–20.vii.1987 (D9518); off Jesser Point (27.627°S:32.682°E), 65–70 m, fine sand, dredged R.V. *Meiring Naudé*, 09.vi.1987 (D8623); Leadsman Shoal, Raggie Reef (27.800°S:32.617°E), 8–12 m, mixed algal and coral reef, 1–2 km north of Leven Point, dived D. Herbert & NPB, 15.v.1988 (E6838); Leven Point

(27.917°S:32.583°E), sorted from stranded coralline algal debris washing ashore in bay immediately north of point (E2786); same locality, beach–drift, leg. R. Kilburn & D. Herbert, 24-30.iv.1987 (D5543); off Leven Point (27.925°S:32.608°E), 50-60 m, mud, dredged R.V. *Meiring Naudé*, 09.vi.1988 (E5866); off Cape Vidal (28.135°S:32.583°E), 30 m, medium sand, dredged R.V. *Meiring Naudé* (E3525); Six–Mile Reef, near Cape Vidal (28.128°S:32.550°E), ORI, 1972 (A1901); Mission Rocks (28.267°S:32.500°E), ca 9 m, north of St. Lucia, leg. R. Kilburn, 15.xi.1971 (9269); Mission Rocks/Perrier Rocks (28.267°S:32.500°E), littoral, leg. R. Kilburn & D. Herbert, 24-30.iv.1987 (D5601); Mapelane (28.400°S:32.433°E), algal washings, intertidal, leg. D. Herbert & R. Kilburn, v.1982 (S3369); Umvoti River mouth (29.600°S:31.617°E), leg. R. Kilburn, 18.xi.1971 (A1622); off Sheffield Beach (29.495°S:31.262°E), 25 m, fine sand, dredged NMDP, Stn. ZU5, 19.vi.1985 (E9396, E9365); Umhlali (29.500°S:31.233°E), leg. C.W. Alexander (A4519); Shaka's Rock tidal pool (29.517°S:31.233°E), rocky intertidal zone, leg. T. Nangammbi *et al.*, 14.x.2004 (W2311, living); Ballito Bay (29.533°S:31.217°E), corallines, leg. R. Kilburn (A2182); same locality (29.533°S:31.217°E), among corallines, leg. R. Kilburn (EM 5657, living); Tongaat (29.567°S:31.183°E), H.C. Burnup coll'n (A4520); South of Tongaat Beach (29.567°S:31.175°E), 5 km, 8-15 m, dived D. Herbert (D5021); Tongaat River mouth (SAM 11249); Umdloti (29.683°S:31.113°E), rocky intertidal zone, on multiple algae, leg. D. Herbert *et al.*, 25.ii.2005 (W3217, living); Durban (29.883°S:31.017°E), collected from reclamation dump sand, dredged off Durban Bluff, 18-20 m, leg. R. Kilburn & D. Herbert, 25-26.viii.1984 (B8949); Brighton Beach (29.933°S:31.017°E), corallines, H.C. Burnup coll'n (B5718); Umkomaas (30.200°S:30.800°E), H.C. Burnup coll'n (A896, B3207); Claustal lighthouse (30.250°S:30.800°E), leg. F. Graeve, iv.1981, ex J.P. Marais coll'n (V3527); 30 miles North of Aliwal Shoal, off Scottburgh (30.283°S:30.833°E), 10-20 m, hand–dredged sand, dived D. Herbert, 30.vi.1991 (S7954); same locality, ca 14 m, underwater pump, dived D. Herbert, 02.vi.1991 (S8668); Umzinto (30.317°S:30.667°E), H.C. Burnup coll'n (1148); Rocky Bay (EM 7186); Park Rynie (30.317°S:30.733°E), rocky intertidal zone, amongst low shore coralline algae, leg. D. Herbert *et al.*, 20.v.2003 (W832, living); Sezela (30.417°S:30.683°E), leg. W. Falcon, W. Falcon coll. (A4517); Mtwalume (30.483°S:30.633°E), rocky intertidal zone, leg. T. Nangammbi *et al.*, 15.ix.2004 (W2310, living); off Hibberdene (30.583°S:30.633°E), 100 m, dredged ex CSIR Water Research, 20.iii.1975 (A5906); Stiebel Reef, north east of Phumula (30.617°S:30.583°E), hand–dredged sand, ca 20 m, dived D. Herbert, 21.ii.1993 (V1761); Umtentweni (30.717°S:30.467°E), leg. H.W. Bell–Marley, 1980, ex Albany Museum (B9996); Port Shepstone (30.750°S:30.450°E), Falcon coll'n (A898); Mbango, south of Port Shepstone (30.750°S:30.433°E), intertidal rocks, leg. D. Herbert & M.

Mander, 10.viii.1991 (S4095); Glenmore Beach, south of Tongazi River mouth (31.017°S:30.250°E), intertidal rocks, leg. D. Herbert & M. Mander, 02.viii.1991 (S4116).

Eastern Cape: "Pondoland coast", leg. C.M. Connolly, i.1994 (A1826); same locality, leg. A. Filmer, H. Becker coll., ex Transvaal Museum, 1978 (B4734, B4747); same locality, leg. G.C. Shortridge (SAM 11398); Mzamba "Pondoland", 1952 (EM 7181); Mzamba (31.100°S:30.183°E), beach–drift, leg. R. Kilburn & D. Herbert, 12-30.v.1986 (D2980); Mkambati, Mgwetyana River mouth (31.283°S:29.933°E), leg. R. Kilburn *et al.*, viii.1983 (C5651); Msikaba Island (31.183°S:29.600°E), north side, leg. R. Kilburn & H. Young, viii.1983 (C5528); Mbotyi (31.450°S:29.733°E), beach–drift (C8272); off Mbotyi (31.553°S:29.865°E), 250 m, coarse sand, stones, dredged R.V. *Meiring Naudé* (E7000); Port St. Johns (31.617°S:29.550°E), G.C. Shortridge (SAM 11398); Mpande (31.758°S:29.371°E), on green algae in low shore pools, scarce, leg. D. Herbert & L. Davis, 21.iv.2005 (W3218, living); Hluleka, Shelly Beach (31.817°S:29.300°E), leg. R. Kilburn, 27.vii.1981 (C1498); Presley's Bay, Umtata River (31.879°S:29.263°E) (EM 7189); Lwandile/Mdumbi (31.883°S:29.267°E), leg. R. Kilburn & R. Fregona, vii.1981 (C162); off Whale Rock (31.948°S:29.225°E), 20-26 m, sand and gorgonians, dredged NMDP, Stn. M1, 16.vii.19823 (V4041); off Mncwasa Point (32.067°S:29.095°E), 25-30 m, fine sand and gorgonians, dredged NMDP, 19.vii.1982 (V4045); same locality (32.085°S:29.085°E), 40-45 m, coarse sand (mainly pink barnacle fragments), dredged R.V. *Meiring Naudé*, 19.vii.1982 (C2379); Xora (31.95°S:28.667°E), leg. M. Bursey, 01-08.vi.1989 (EM 11868); Nkanya (32.183°S:29.967°E), leg. V.V. Wood, 1839-1960 (EM 7187); Nthlonyane (32.204°S:28.948°E), leg. R. Kilburn (8521, A2621); Dwesa (32.279°S:28.884°E), beach–drift, leg. R. Kilburn, v.1984 (C6040); Ngabara (32.233°S:28.717°E), beach–drift, leg. R. Kilburn, v.1984 (C6180); Qora (32.433°S:28.683°E), leg. M. Bursey, Stn. KI3b, 19.iii.1991 (EM W2172, living); Qora River mouth (32.450°S:28.683°E), intertidal zone, leg. D. Herbert, 12-15.ii.1986 (D2363); off Qora River (32.462°S:28.673°E), 14-18 m, fine sand, dredged R.V. *Meiring Naudé* (C3922); Cebe (32.550°S:28.567°E), on *Caulerpa*, leg. C. Watters, 02.vi.1972 (9870); Sandy Point (32.567°S:28.553°E), leg. R. Kilburn *et al.*, xi.1982 (C3745); Qolora River mouth (32.633°S:28.417°E), leg. R. Kilburn *et al.*, x.1982 (C3367); Kei River, East of mouth (32.683°S:28.383°E), leg. R. Kilburn *et al.*, x.1982 (C3527, C3465); Kei River mouth (32.684°S:28.384°E), coll. H. Jeffrey (EM 7183); same locality, near whispering waves, leg. M. Bursey, 10.ix.1988 (EM 11779); Marshstrand, East London (32.750°S:28.250°E), leg. M. Bursey, 14.vi.1988 (EM 11703); Haga–Haga, East London (32.750°S:28.250°E) (EM 7188); Cefane, north of East London (31.700°S:28.233°E), leg. M. Bursey, 29.vi.1989 (EM 12100); Cintsa, East London (32.834°S:28.117°E), on coralline, 12.iv.2002 (EM 13317); Cintsa West,

East London (32.850°S:28.117°E), leg. M. Bursey, 01.vii.1989 (EM 12150); Glengariff, East London (32.883°S:28.083°E), rocky intertidal zone, on green and brown algae, leg. T. Nangammbi & M. Bursey, 26.viii.2003 (W1021, living); Kwelera, East London (32.900°S:28.080°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi & M. Bursey, 08.vii.2005 (W3378, living); Gonubie, East London (32.933°S:28.017°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi & M. Bursey, 08.vii.2005 (W3379, living); East London (33.033°S:27.917°E), UCT Ecological survey, Stn. L65 (SAM A36717, living); Shelly Beach, East London (33.050°S:27.883°E), leg. E. Roscoe, 21.xi.1980 (EM 8887); Fuller's Bay, East London (33.067°S:27.900°E), leg. E. Roscoe, 21.xi.1980 (EM 8885); Cove Rock (33.100°S:27.833°E), leg. D.H. Kennelly, 1962 (EM 7182); Hickman's River mouth (33.067°S:27.833°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi & M. Bursey, 07.vii.2005 (W3377, living); Kidd's Beach (33.150°S:27.683°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi & M. Bursey, 09.vii.2005 (W3380, living); Bira, Ciskei (33.383°S:27.317°E), leg. M. Bursey, 16.vi.1988 (EM 11733); Fish River mouth (33.483°S:27.133°E), leg. J.P. Marais, iv.1978 (W5759); Three Sisters, Port Alfred (33.559°S:27.027°E, numerous specimens in NMSA), rocky intertidal zone, on green and brown algae, leg. T. Nangammbi *et al.*, 31.viii.2003 (W1035, living); Cannon Rocks (33.750°S:26.550°E), leg. F. Graeve, ex J.P. Marais coll'n (W5758); Port Elizabeth (33.967°S:25.583°E), Falcon coll'n (A6348); Cape Recife (34.027°S:25.655°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 21.vi.2005 (W3376, living); Schoenmakerskop (34.061°S:18.338°E), leg. M. Christensen, 20.ii.1977 (SAM A33680, living); Noordhoek, Port Elizabeth (34.044°S:25.636°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 23.vi.2005 (W3390, living); Marine drive, site 1, Port Elizabeth (34.046°S:25.523°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 22.vi.2005 (W3391, living); Sea Reserve, Port Elizabeth, leg. S. Barnett, 26.xii.1975 (EM 9117); Kini Bay (34.016°S:25.383°E), leg. F. Graeve, ex J.P. Marais coll'n (V3544).

Southern Cape: Jeffrey's Bay (34.050°S:24.917°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 19.vi.2005 (W3389, living); same locality, 20.vi.2005 (W3219, living); Storms River mouth (34.017°S:23.900°E), beach–drift, leg. M. Quickelberge, 06.i.1977, ex M. Quickelberge coll'n, 1985 (D2024); Coney Glen, Knysna (34.082°S:23.063°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 04.xi.2006 (W4752, living); Reebok Reef, between Great and Little Brak River (34.079°S:22.171°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 05.xi.2006 (W4756, living); Die Bakke, Mossel Bay (34.171°S:22.127°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 05.xi.2006 (W4757, living); Mossel Bay (34.133°S:22.157°E), ex Albany Museum, 1980 (B9997); Still

Bay Point (34.386°S:21.426°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 06.xi.2006 (W4762, living); Struis Bay, site 1 (34.814°S:20.030°E), rocky intertidal zone, on algae, leg. T. & J. Nangammbi, 07.xi.2006 (W4770, living).

South Western Cape: Cape Agulhas (34.824°S:20.017°E), rocky intertidal zone, on multiple algae, leg. T. & J. Nangammbi, 07.xi.2006 (W4768, living); Hermanus (Caledon district) (34.417°S:19.233°E), leg. R.M. Lightfoot, 1902 (SAM 11398).

Literature Records: Mozambique, Inhambane (Cox 1939 *in* Barnard 1962); Chidenguele, Mozambique (Cox 1939, reference from Moura 1969); Kleinemonde and Port Natal (Bartsch 1915); Delagoa Bay (Kilburn & Rippey 1982).

Comparison: *T. kochii* resembles *T. africana* in having turquoise spots below the suture. Some specimens of this species resemble those of *T. elongata* and *T. retrolineata* in having sinuous opisthocline lines. It differs from other southern African *Tricolia* species by being relatively large and globular, and by having a distinct spiral sculpture on the apical whorls. The spiral lines are lacking on the shell surface of the last adult whorl. Living material of this species is extremely variable in colouration and Turton's (1932) descriptions of the colour patterns of *P. carinata*, *P. fuscomaculata*, *P. kochii nigra*, *P. k. maculata* and *P. k. viridis* all fall within the colour range of *T. kochii*. Turton mentioned no distinctive characteristics of the above listed species, which are evidently nothing more than colour forms of the highly variable *T. kochii*. The authorship of this species was discussed by Herbert & Warén (1999).

Additional notes: Literature records of *T. kochii* from La Réunion, Indian Ocean (Deshayes 1863: 76, as *Phasianella kockii*); Port Jackson (Sydney), New South Wales, Australia (Angas 1867: 213, as *Eutropia (Tricolia) kochii*); Mauritius, Indian Ocean (Liénard 1877: 48, as *Phasianella rockii*, Viader 1937: 54, as *Phasianella kochi*); Mauritius, Port Jackson and Australia (Pilsbry 1888: 170, as *Phasianella kochi*); Table Bay and Simon's Bay (Sowerby 1892); South Australia (Adcock 1893: 8, as *Phasianella (Tricolia) kochii*, Verco 1908: 5, as *Phasianella kochii*, Cotton & Godfrey 1938: 202, as *Tricolia tomlini* and *T. gabiniana*); False Bay (Kensley 1973, Richards 1981); Namibia (Kilburn & Rippey 1982) and along the Atlantic Cape coastline (Branch *et al.* 1994) are erroneous. Robertson (1985) discussed all the wrongly recorded specimens of this species from four or five different localities in the Indo–West Pacific.

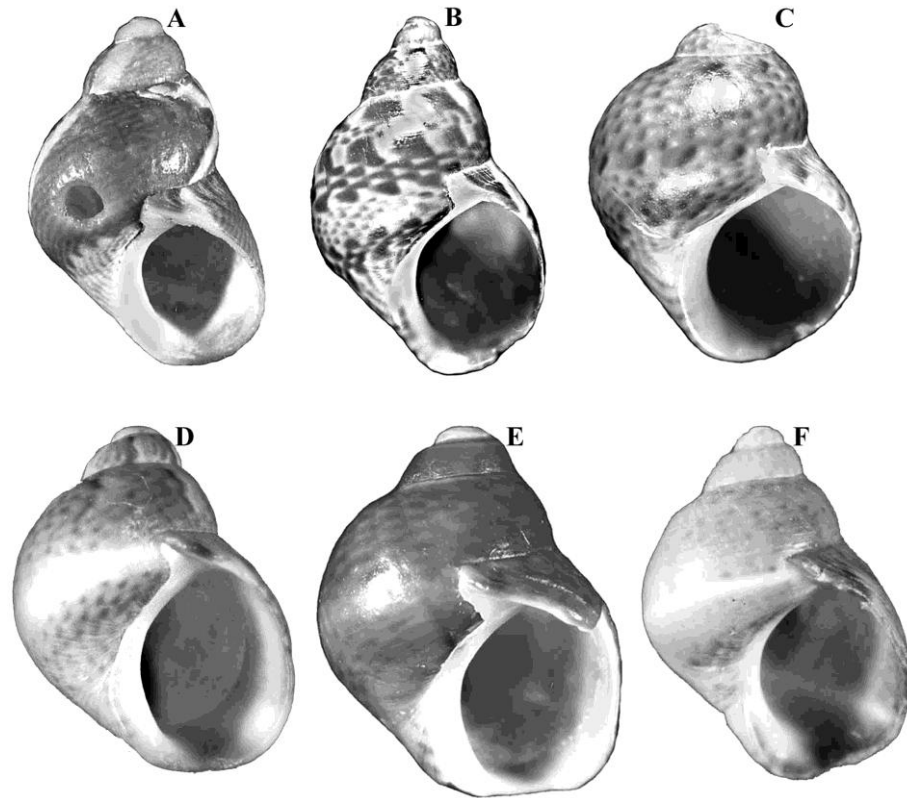


Figure 2.52. Type specimens of *T. kochii*: (A) *P. kochii*, syntype, BMNH 1923.7.13.19, diameter 1.2 mm (A is a copy of figure taken by D. Herbert); (B) *P. carinata*, holotype, OUM M002772, length 8.2 mm, width 5.1 mm; (C) *P. fuscomaculata*, holotype, OUM M002774, length 8.2 mm, width 5.2 mm; (D) *P. kochii maculata*, syntype, OUM M002766, length 5.6 mm, width 3.8 mm; (E) *P. kochii nigra*, syntype, OUM M002767, length 5.9 mm; (F) *P. kochii viridis* Turton, 1932, syntype, OUM M002765, length 6.0 mm, width 4.3 mm.

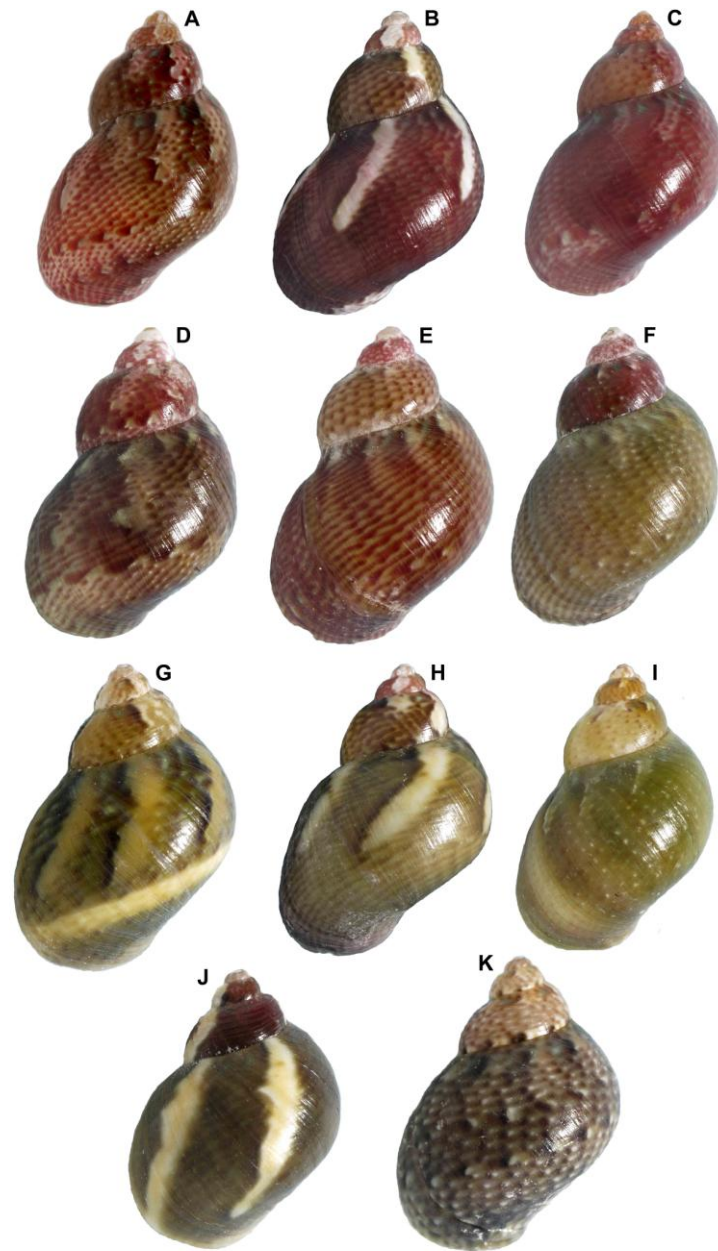


Figure 2.53. Variation in shell colour and pattern of *T. kochii*: (A) length 11.2 mm, width 6.8 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (B) length 12.9 mm, width 6.2 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (C) length 12.5 mm, width 6.4 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (D) length 10.1 mm, width 6.9 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (E) length 11.6 mm, width 6.3 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (F) length 10.3 mm, width 6.9 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (G) length 5.7 mm, width 4.3 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (H) length 10.4 mm, width 5.3 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (I) length 10.5 mm, width 5.3 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (J) length 10.5 mm, width 7.1 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape; (K) length 6.8 mm, width 4.5 mm, NMSA W3219. Jeffrey's Bay, Eastern Cape.

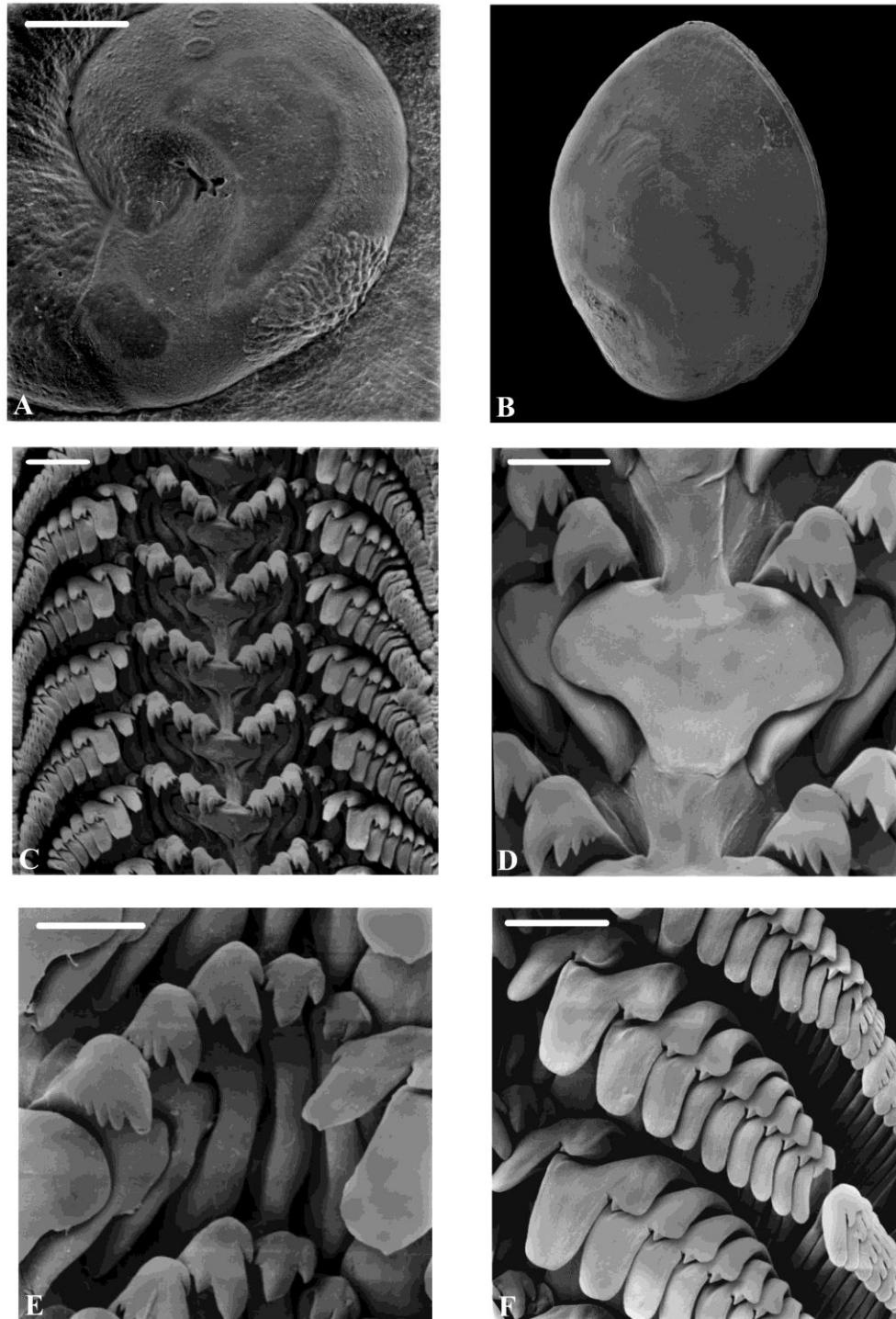


Figure 2.54. Scanning electron microscope of protoconch, operculum and radula of *T. kochii*: (A) external surface of protoconch, showing a smooth surface and a distinct terminal lip at mid-whorl, NMSA W832, bar = 60 μ m; (B) external surface of operculum, showing a smooth surface and a narrow peripheral groove underlying labral margin, NMSA W3219, maximum diameter 1.6 mm; (C) central portion of radula, NMSA W1030, bar = 100 μ m; (D) rachidian and inner lateral teeth, NMSA W1035, bar = 30 μ m; (E) lateral teeth, NMSA W1035, bar = 40 μ m; (F) inner marginal teeth, NMSA W1035, bar = 70 μ m.

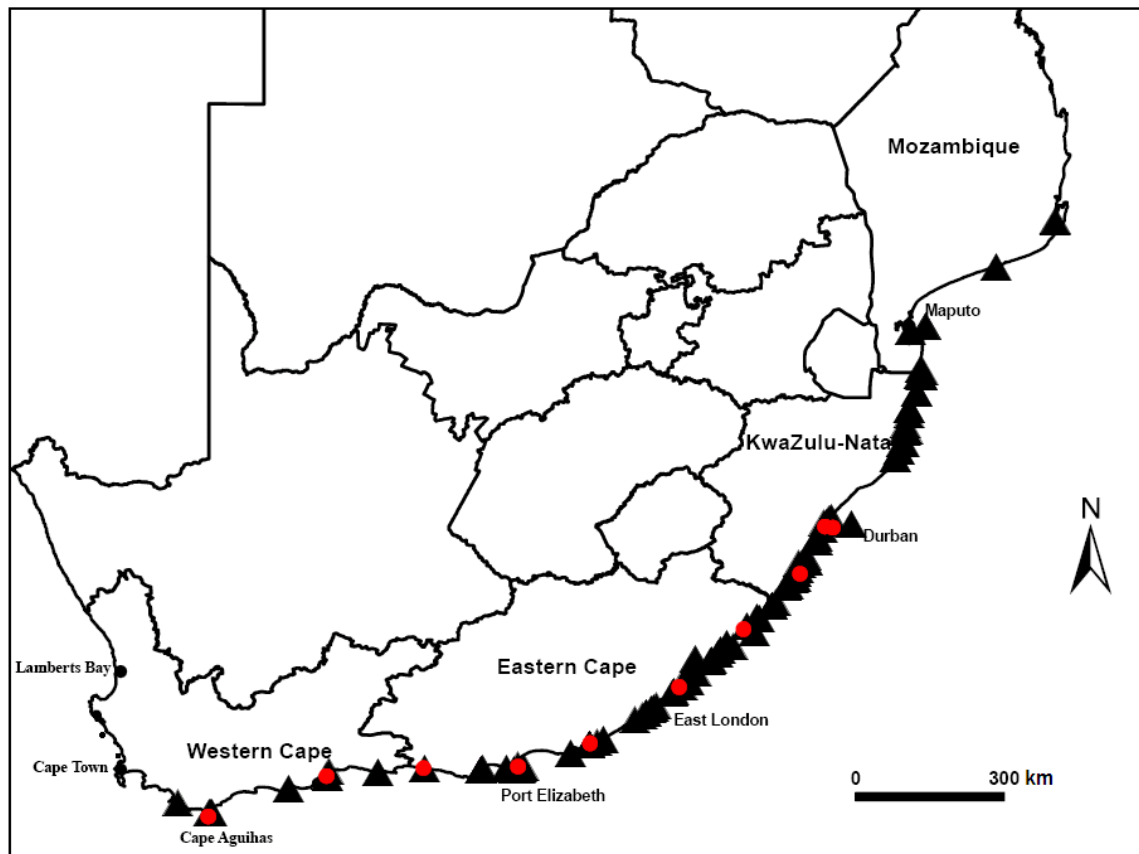


Figure 2.55. Distribution map of *T. kochii*. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia neritina (Dunker, 1846)

Figs 2.56-2.60

Phasianella neritina Dunker, 1846: 110; Krauss 1848: 105, pl. 6, fig. 6; Philippi 1853: 24-25, pl. 5, fig. 6; Vélain 1877: 117; Sowerby 1887: 151, pl. 476, fig. 10; Pilsbry 1888: 176-177, pl. 40, figs 10, 11; Sowerby 1892: 41; Smith 1911: 313; Bartsch 1915: 146; Barnard 1951: 116, pl. 15, fig. 11. Type loc.: “*Prom. Bon. Spei*” [“Cape of Good Hope”, South Africa].

Gena lineata Adams, 1850: 39; Sowerby 1855: pl. 173, figs 26, 27; Pilsbry 1890: 45, pl. 55, figs 17, 18; Smith 1911: 313; Viader 1937: 54. Type loc.: Unknown.

Tricolia neritina; Wenz 1938: 361-362, fig. 856; Barnard 1963: 208-211, fig. 3b; Day 1969: 158; Kensley 1972: 177; Kensley 1973: 52, fig. 145; Kensley 1977: 191; Branch & Branch 1981: pl. 114, fig. 9; Kilburn & Rippey 1982: 47, pl. 9, fig. 8; Trew 1984: 84; Robertson 1985: 24, 40-41; Branch *et al.* 1994: 148, fig. 69.7.

Etymology, *neritina* – diminutive of *nerita* (Latin) – refers to the shape of the shell which is similar to the snails of the genus *Nerita*.

Diagnosis: Shell with neritiform shape, very low spire; whorls strongly convex; apex depressed; patulate aperture; smooth, lacking spiral sculpture; colouration highly variable, ground colour whitish to pale yellowish–brown, boldly marked with fine close–set oblique reddish to dark–maroon black lines, commonly with blotches below suture and below periphery.

Description (Figs 2.56, 2.57, 2.58A-Q):

Shell with neritiform shape, very low spire; teleoconch of up to 2.75 whorls, suture relatively shallow; whorls strongly convex, lacking any angulation, very depressed and almost flattened apex. Sculpture weak, shell usually smooth and glossy, lacking any spiral sculpture, marked only by exceedingly fine growth–lines. Aperture large, obliquely ovate; outer lip thin; colour pattern visible internally; inner lip concave; umbilicus closed in most examined specimens, but remaining a narrow chink in others. Shell colouration variable; ground colour whitish to pale yellowish–brown, boldly marked with fine close–set oblique reddish to dark–maroon black lines, commonly with blotches below suture and below periphery, occasionally specimens lacking spiral colour pattern (Figs 2.58N, O, P).

Protoconch (Fig. 2.59A): Typically vetigastropod, comprising approx. 1.1 whorls; apical beak present but weak, terminal lip lacking a varix, but uniformly convex at mid-whorl, sculpture for the most part worn, but with traces of curved lines towards periphery.

Operculum (Fig. 2.59B): Similar to *T. adusta*, but the external surface with traces of curved lines.

Radula (Figs 2.59C-F): Similar to *T. pullus* (Gofas 1982), but rachidian tooth with broad, oblong oval base-plate.

External anatomy: Similar to *T. pullus* (Fig. 2.7D, Robertson 1985), but colour pattern of head-foot variable, yellowish specimens much paler than red specimens, but still reflective of shell colouration; and a pair of black blotches on snout between and just in front cephalic tentacles.

Measurements: Largest specimen examined – length 5.0 mm, width 3.4 mm. Length:width ratio 1.2-2.0 (N=50).

Habitat: *T. neritina* occurs commonly in the rocky intertidal zone, living among seaweeds such as *Ulva* and *Codium fragile capense* (= green algae), *Gigartina radula*, *G. stiriata* and *Ceramium* (= red algae), and *Bifurcariopsis capensis* (= brown algae), occasionally under rocks at low spring tide level. Not common in the shallow subtidal level.

Geographical range (Fig. 2.60): *T. neritina* is endemic to southern Africa ranging from the Eastern Cape (Port Alfred) to Angola.

Type material: *Phasianella neritina*, six syntypes (Fig. 2.56), ZMHB 108.795, length 3.8 mm, width 2.9 mm. *Gena lineata*, lectotype, BMNH 1963308 (⁴R Robertson 2008, personal communication, Fig. 2.57 taken from Sowerby 1855).

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Eastern Cape*: Port Alfred (33.600°S:26.900°E), H. Becker coll., ex Transvaal Museum (B4746); Algoa Bay (34.007°S:25.709°E), leg. F. Graeve, 06.1976, ex J.P. Marais coll'n (V3525); Marine drive, site 1, Port Elizabeth (34.046°S:25.523°E), rocky intertidal zone, on multiple algae, leg. T.

⁴ Dr R Robertson, Department of Malacology, Academy of Natural Sciences, Philadelphia, 1900 Benjamin Franklin Parkway, PA 19103, USA

Nangammbi, 22.vi.2005 (W3372, living); Periwinkle lane, Port Elizabeth (34.043°S:25.553°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 24.vi.2005 (W3220, living).

Southern Cape: Jeffrey's Bay (34.050°S:24.917°E), leg. R. Kilburn, 1960 (5404, A1679); Storms River mouth (34.017°S:23.900°E), beach–drift, leg. M. Quickelberge, 06.i.1977, ex M. Quickelberge coll'n, 1985 (D2026); Mossel Bay (34.133°S:22.167°E), ex Albany Museum (B9994); Mossel Bay Point (34.183°S:22.158°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. & J. Nangammbi, 07.xi.2006 (W4760, living); same locality, beach–drift, A. Jenner, 27.xii.1977 (B225); Still Bay (34.383°S:21.450°E) (SAM A31690).

South Western Cape: Cape Agulhas (34.824°S:20.017°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. & J. Nangammbi, 07.xi.2006 (W4767, living); Danger Point (34.633°S:19.300°E), UCT Ecological survey, Stn. DP1, 12.xii.1939 (SAM A55223, living); Hermanus (34.417°S:19.233°E), UCT Ecological survey, Stn. HM7, 30.vi.1939 (SAM A54916); Sandbaai near Hermanus, Schulphoek (34.428°S:19.204°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 07.ii.2004 (W1531, living); off Hawston near Hermanus (34.400°S:19.067°E), in subtidal kelp forest, 2-4 m, dived D. Herbert, xi.1988 (E6699); Hawston area near Harbor (34.401°S:19.122°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 07.ii.2004 (W1534, living); Betty's Bay, Stony Point Marine Nature Reserve (34.371°S:18.893°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 07.ii.2004 (W1536, living).

False Bay: Gordon's Bay (34.150°S:18.850°E), beach–drift, leg. C.M. Connolly, 1980 (B6884); Strandfontein (34.083°S:18.550°E), leg. C.M. Connolly, i.1974 (A1835); St. James (34.118°S:18.442°E), UCT Ecological survey, Stn. CP67, 04.iv.1938 (SAM A55116, living); Kalk Bay (34.133°S:18.450°E), leg. R.M. Lightfoot, 1896 (SAM 4770); Fish Hoek, Sunny Cove (34.144°S:18.437°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 05.ii.2004 (W1518, living); Glencairn (34.163°S:18.432°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 09.ii.2005 (W2575, living); Simon's Town (34.183°S:18.433°E), dredged C.M. Connolly, i.1974 (A1839); Windmill Beach (34.200°S:18.467°E), UCT Ecological survey, 4-5 m, dived below high tide level, Stn. FAL112.V, 27.i.1953 (SAM A54751; A36719); Miller's Point (34.233°S:18.467°E), leg. R. Kilburn, vii.1969 (7042); Bordtjies Reef (34.313°S:18.463°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 11.ii.2004 (W1543, living).

Atlantic Cape: Camel Rocks, Scarborough (34.199°S:18.372°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 07.ii.2005 (W2564, living); Kommetjie (34.142°S:18.320°E), leg. M. Burseley & D.J. Hodgkinson, 05.xii.1990 (EM W2099, living); Oudekraal (33.985°S:18.356°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 08.ii.2005 (W2568, living); Camp's Bay (33.956°S:18.375°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 08.ii.2005 (W2570, living); Sea Point, south end of beach (33.917°S:18.385°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 06.ii.2004 (W1525, living); Sea Point, near tidal pool (33.914°S:18.385°E), rocky intertidal zone, on multiple algae, leg. D. Herbert & T. Nangammbi, 10.ii.2005 (W2560, living); Granger Bay (33.371°S:18.408°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 08.ii.2004 (W1538, living); Table Bay (33.883°S:18.450°E), leg. K.H. Barnard, 1913 (SAM A5234, living); Robben Island (33.818°S:18.379°E), rocky intertidal zone, on multiple algae, leg. T. Nangammbi, 12.ii.2005 (W2580, living); Marcus Island, Saldanha Bay (33.043°S:17.972°E), rocky intertidal zone, on multiple algae and under rocks, leg. T. Nangammbi, 10.ii.2004 (W1541, living); Paternoster (32.817°S:17.883°E), intertidal rocks and stones, leg. D. Herbert, xi.1988 (V4051).

NAMIBIA: off mouth of Orange River, leg. K. Emmerson (SAM A29841, living); Lüderitzbucht (26.633°S:15.167°E), leg. B. Kensley *et al.*, 16-18.ii.1969 (SAM A31265); Griffith Bay, Lüderitzbucht (26.633°S:15.167°E), leg. M.L. Penrith & B. Kensley (SAM A30541).

Literature records: Hondeklip Bay (UCT), False Bay and Still Bay (SAM, Barnard 1963); Angola (Kensley 1972); South West Africa (Kensley 1973, 1977); Langebaanweg (fossil) (Kensley 1977); Cape of Good Hope and Cape Town (Bartsch 1915); Namibia (Kilburn & Rippey 1982).

Comparison: *T. neritina* differs from other southern African *Tricolia* species in having a neritiform shell shape, very low spire, large aperture and oblique lineation forming a conspicuous part of its colour pattern. Its shell shape is similar to species belonging to the Neritidae. On account of these peculiarities, this species was described under another supraspecific name *Chromotis*, which was later treated as a synonym of *Tricolia* by Keen & Robertson (1960) and Robertson (1985). In the molecular analysis (chapter 4), *T. neritina* is nested within the southern African clade B. Since there is no anatomical or molecular data suggesting that it is distinct from other southern African *Tricolia* species, henceforth *Chromotis* should be considered a synonym of *Tricolia sensu stricto*.

This species closely resembles *Tricolia munieri* (Vélain, 1877) from St. Paul and Amsterdam Islands (southern Indian Ocean) in terms of its neritiform shell shape, very low spire, large aperture and oblique lineation, which forms a conspicuous part of its colour pattern (Robertson 1985). However, Robertson (1985) mentioned that *T. neritina* shells are larger in terms of size than those of *T. munieri* (maximum length 5.0 mm in *T. neritina* versus 3.0 mm in *T. munieri*). The radula of the two species are also similar with five pairs of lateral teeth, broadly ovate rachidian tooth without a cusp and numerous marginal teeth, which are characteristics of a typical *Tricolia*. The operculum of both species is white, calcareous, thick, externally convex, and paucispiral with an eccentric nucleus, which is also characteristic of a typical *Tricolia*. Even though *T. neritina* closely resembles *T. munieri* in terms of the above mentioned morphological characteristics, differences in the shell size could be due to microhabitat influences or differences in water temperature or environmental conditions between South Africa, Amsterdam and St. Paul Islands. However, the relationship between the two species needs further investigation.

Vélain (1877) also mentioned that the South Africa marine mollusc fauna is closely related to that of St. Paul and Amsterdam Islands, and recorded other southern African species occurring in these Islands i.e., *Fissurella* species. His argument was also supported by the fact that ocean currents flow from west to east in the southern Indian Ocean (Meincke 1980).

Following Smith (1911) and Viader (1937), *Gena lineata* is herein treated as a synonym of *T. neritina*.

Additional notes: Literature records of *T. neritina* from East London (Kensley 1973, 1977, Von Martens 1880) require confirmation. The records of this species from Mauritius (Von Martens 1880: 293, as *Phasianella (Chromotis) neritina*, Viader 1937: 54, as *Phasianella neritina*) are erroneous and could be a misidentification.



Figure 2.56. Images of one syntype of *P. neritina*, ZMHB 108.795, length 3.8 mm, width 2.9 mm.



Figure 2.57. Original figure of *G. lineata* (Copy of figure taken from Sowerby 1855).

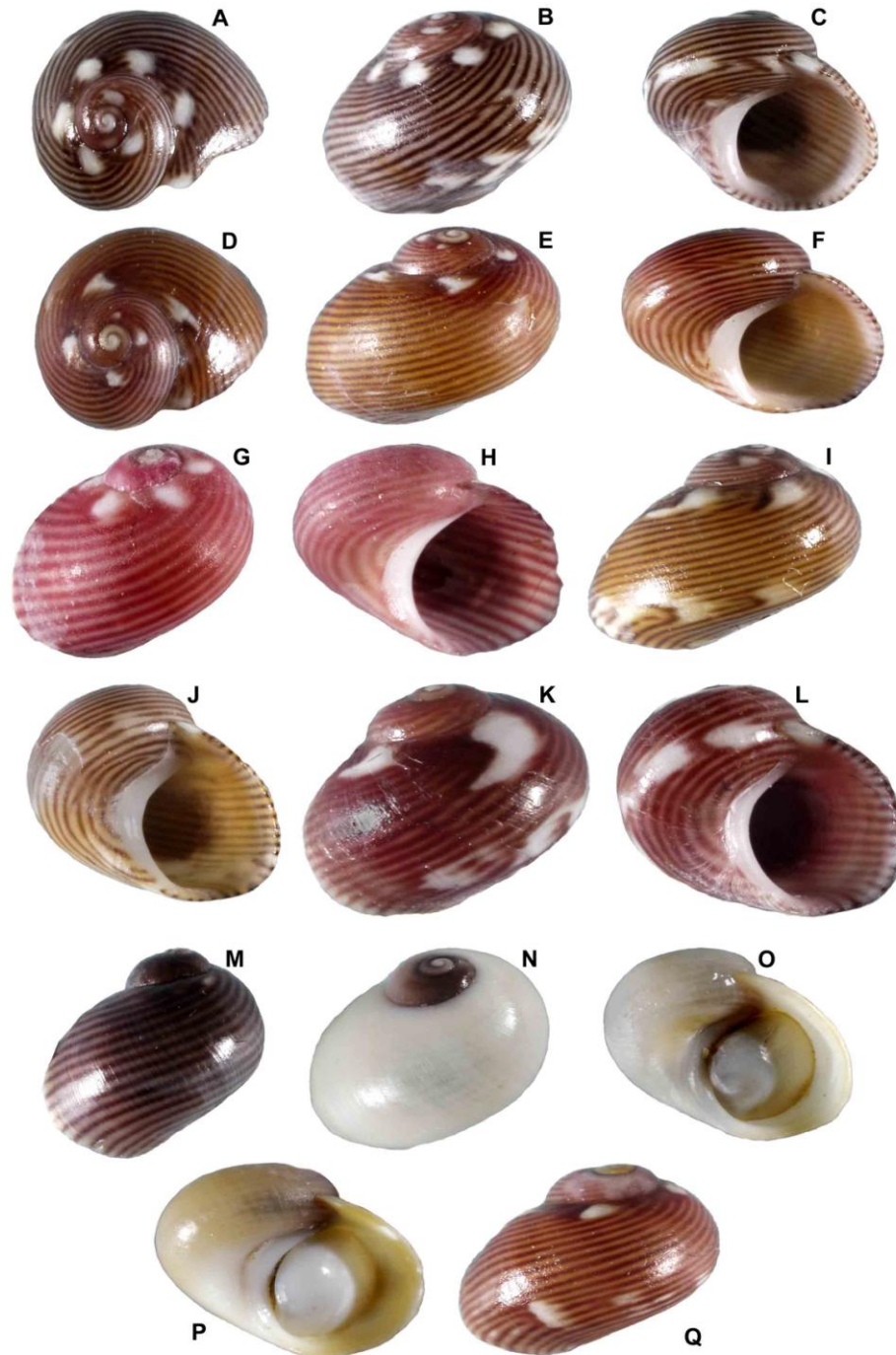


Figure 2.58. Variation in shell colouration of *T. neritina*: (A, B, C) length 3.9 mm, width 3.2 mm, NMSA W1525. Sea Point, Atlantic Cape; (D) length 3.8 mm, width 2.9 mm, NMSA W1525. Sea Point, Atlantic Cape; (E, F) length 3.9 mm, width 3.1 mm, NMSA W1525. Sea Point, Atlantic Cape; (G, H) length 3.8 mm, width 2.7 mm, NMSA B4746. Sea Point, Atlantic Cape; (I, J) length 4.0 mm, width 3.1 mm, NMSA W1525. Sea Point, Atlantic Cape; (K, L) length 3.5 mm, width 2.9 mm, NMSA W1525. Sea Point, Atlantic Cape; (M) length 4.0 mm, width 3.3 mm, NMSA W1525. Sea Point, Atlantic Cape; (N, O) length 3.9 mm, width 2.8 mm, NMSA W1525. Sea Point, Atlantic Cape; (P) length 3.5 mm, width 3.1 mm, NMSA W1525. Sea Point, Atlantic Cape; (Q) length 3.7 mm, width 2.8 mm, NMSA W1525. Sea Point, Atlantic Cape.

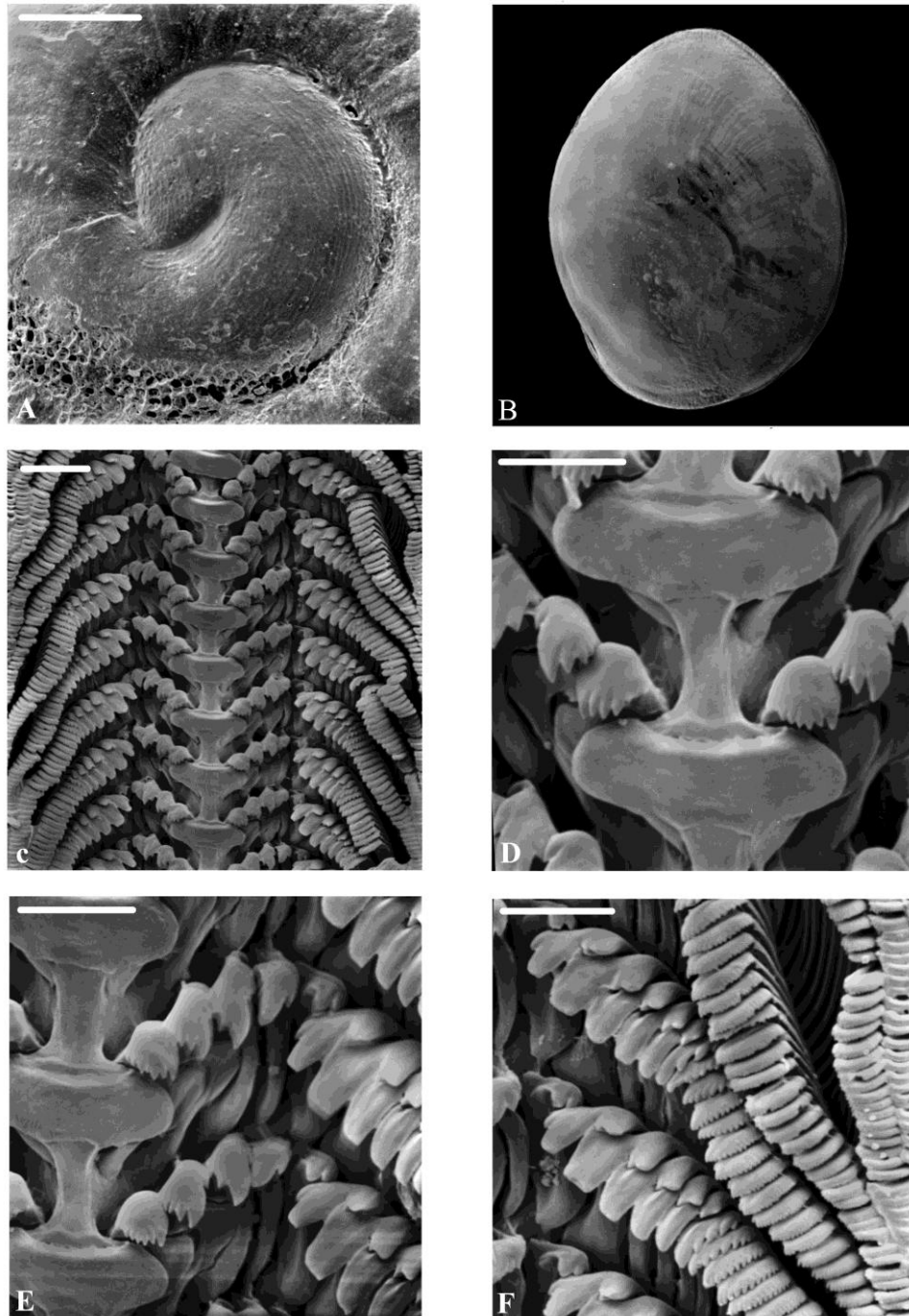


Figure 2.59. Scanning electron microscope of protoconch, operculum and radula of *T. neritina*: (A) external surface of protoconch, showing traces of curved lines towards periphery and uniformly convex at mid-whorl, NMSA B9994, bar = 100 μm ; (B) external surface of operculum showing traces of curved lines and a narrow peripheral groove underlying labral margin, NMSA W1541, maximum diameter 1.9 mm; (C) central portion of radula, NMSA W1530, bar = 120 μm ; (D) rachidian and innermost lateral teeth, NMSA W1530, bar = 20 μm ; (E) rachidian, lateral and inner marginal teeth, NMSA W1530, bar = 40 μm ; (F) marginal teeth, NMSA W1530, bar = 30 μm .

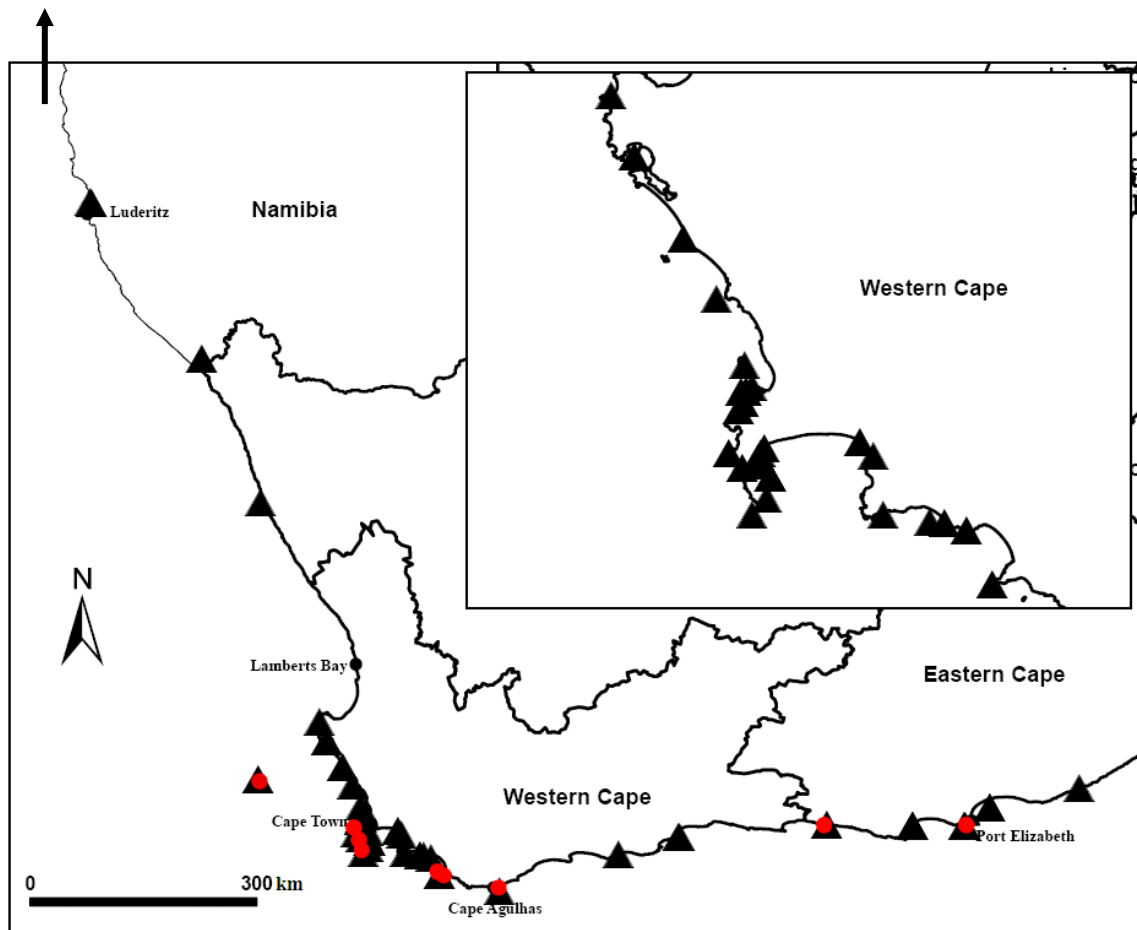


Figure 2.60. Distribution map of *T. neritina*. The distribution of this species extends north into Angola. Each black triangle represents one or more site records. Each red dot represents a sequenced sample.

Tricolia retrolineata Nangammbi & Herbert, 2008

Figs 2.61-2.64

Tricolia retrolineata Nangammbi & Herbert, 2008: 14, figs 1-12, 15b-17. Type loc.: Ponta do Ouro (Mozambique).

Etymology, From Latin *retro* (backward) and *lineata* (lined), referring to the opisthocline lines which usually form a conspicuous element of the colour pattern.

Diagnosis: Shell small, bulimiform; whorls lacking a distinct keel or angulation, but noticeably more strongly rounded below periphery; body whorl relatively large in proportion to the rest of shell; suture relatively shallow; surface smooth and somewhat glossy; fresh specimens translucent with variable colouration, but typically yellowish brown patterned with numerous, fine, close-set, sinuous, orange-red, opisthocline lines, and with bold, white, red or dark brown blotches or zigzag axial lines on adapical surface of each whorl; apical whorls lacking white subsutural spots.

Description (Figs 2.61A-L, 2.62B):

Shell small, bulimiform, with up to 3.5 teleoconch whorls; body whorl relatively large in proportion to the rest of shell (ca 80 % of total length); whorls lacking a distinct keel or angulation, but noticeably more strongly rounded below periphery; suture relatively shallow. Shell usually smooth and glossy, lacking spiral sculpture, marked only by fine growth-lines. Aperture ovate-circular, outer lip thin; colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, but occasionally remaining as a narrow chink. Shell translucent with variable colouration; ground colour yellowish, typically patterned with numerous, fine, close-set, sinuous, orange-red, opisthocline lines, and commonly with bold white and red or dark brown blotches on adapical surface (Figs 2.61A, B, G, H), or with alternating darker orange-red and paler zigzag axial lines (Figs 2.61C-F); in some specimens the opisthocline lines anastomose, creating a darker reddish network with yellowish-orange spots (Figs 2.61I, J); umbilical region often bordered by a broad white band traversed by the red opisthocline lines which by this stage appear almost axial; apical whorls lacking white subsutural spots (Fig. 2.62B).

Protoconch: Unknown (shell apex worn in all the material available, no specimens suitable for scanning electron microscope).

Operculum (Fig. 2.63): Calcareous, thick and convex; paucispiral with eccentric nucleus; exterior somewhat eroded in the single operculum available, but clearly showing a narrow peripheral groove underlying labral margin.

Radula and external anatomy: Unknown.

Measurements: Largest specimen – length 7.4 mm, width 4.1 mm. Length:width ratio 1.2-1.3 (N=10).

Habitat: On the available evidence, *T. retrolineata* is a subtidal species inhabiting off-shore reefs; the bulk of material has been collected from swash accumulations of dead shells in coral reef gulleys, suggesting that the animals were living on the reefs themselves. The single live-collected specimen was found on a coral-dominated reef between 7 and 11 m. Empty shells have also been collected on more algae-dominated reefs and this may be the principal habitat at southern localities where coral-dominated reefs are absent.

Comparison: The smooth, glossy shell with bright, variegated colour pattern, as well as the convex, paucispiral, calcareous operculum and lack of interior nacre clearly place this species in the Phasianelloidea. The bulimiform shape of the shell, combined with its small size and lack of capillary lines in the colour pattern are typical of *Tricolia sensu lato* (Robertson 1985, Hickman & McLean 1990).

Specimens of this new taxon were previously identified under the name *Tricolia alfredensis*, primarily on account of their bulimiform shape and distinctive colour pattern of sinuous opisthocline lines. However, *T. alfredensis* is now considered to represent nothing more than a colour form of the variable *T. elongata*. Although *T. retrolineata* resembles *T. elongata* more than it does any other southern African *Tricolia* species, it differs from this in attaining a smaller size (maximum length 7.4 mm versus 13.7 mm in *T. elongata*) and in having a thin, translucent shell. This species is represented by a sample size of more than 100 specimens in the Natal Museum collection, and the probability of adult shells being represented in this sample would be high. *Tricolia elongata* (Fig. 2.62A) also differs from *T. retrolineata* in having a spiral row of white, subsutural spots on second teleoconch whorl. However, this is only visible in fresh specimens of this species.

Furthermore, the two species differ in their habitat preferences: *T. retrolineata* is a subtidal species, whereas *T. elongata* occurs commonly in the rocky intertidal zone, living among

seaweed at low spring tide level. Unfortunately, prior to this species being identified as an undescribed taxon, the body of the single live-collected specimen was used for DNA extraction in relation to phylogenetic studies of the southern African *Tricolia* radiation. However, the DNA was not successfully extracted, possibly due to relaxation of the specimen in $MgCl_2$ prior to preservation. Comparative data on the radula and external anatomy are therefore not available.

Holotype (Figs 2.61A, B): MOZAMBIQUE: Ponta do Ouro (26.850°S:32.917°E), subtidal reef, hand-dredged sand, ca 20 m, 14.iv.1997, dived D. Herbert (NMSA L5938/T2238). Length 6.4 mm, width 3.5 mm.

Paratypes: MOZAMBIQUE: 25 specimens, same collection data as holotype (NMSA L7357/T3339); 15 specimens, Malongane (24.798°S:32.890°E), coral reef north, hand-dredged sand, 10-20 m, 16.iv.1997, dived D. Herbert (NMSA L6904/T2240).

SOUTH AFRICA: *KwaZulu-Natal*: 2 specimens (one alive), Leadsman Shoal (27.800°S:32.867°E), main portion of coral reef, 7-11 m, 14.v.1988, dived D. Herbert & NPB (NMSA E2476/T2241, Figs 2.60K, L, 2.62); one specimen, between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), algal portion, 5-9 m, underwater pump, 03.v.1990, dived D. Herbert & K. Bloem (NMSA S2851/T2242).

Eastern Cape: 26 specimens, Mzamba (31.100°S:30.183°E), x.1979, leg. J.P. Marais (NMSA W1935/T2243).

Material examined (all NMSA, unless indicated otherwise): MOZAMBIQUE: off Malongane, coral reef ca 5 km, north of Ponta do Ouro, hand-dredged sand, 15-20 m, v.1994, dived D. Herbert (V1501).

SOUTH AFRICA: *KwaZulu-Natal*: between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), reef off marker 13 north, near pinnacles, 10-12 m, hand-dredged sand, 12.v.1990, dived D. Herbert (S2427); same locality, ca 8 m, underwater pump, 06.v.1990, dived D. Herbert & K. Bloem (S2737); off Lala Nek (27.227°S:32.822°E), 75 m, coarse sand, sandstone, coral, dredged NMDP, Stn. ZDD4, 08.vi.1990 (S9014); "B.J.'s Reef", off Hibberdene (30.583°S:30.600°E), 18-26 m, 15.xi.1992, dived D. Herbert (V1833).

Eastern Cape: Mzamba (31.100°S:30.183°E), beach–drift, 12-30.v.1986, leg. R. Kilburn & D. Herbert (D2933).

Distribution and Biogeography (Fig. 2.64): *T. retrolineata* is a subtropical species endemic to south–east Africa, ranging from just north of the South Africa–Mozambique border (Malongane) south to the extreme north–east of Eastern Cape, South Africa (Mzamba).

The southern distribution limit of *T. retrolineata* lies approximately 300 km to the north of the known range of *T. elongata*. However, a gap of similar extent occurs within the range of *T. retrolineata*, namely between Leadsman Shoal and Hibberdene. The significance of these gaps differs. The interval within the range of *T. retrolineata* occurs in the Natal Bight and is probably caused by lack of suitable habitat in this area. A number of large, sediment–laden rivers enter the sea here (Umfolosi, Thukela, Umgeni, Umkomaas) and rocky subtidal habitats are scarce in this region, re–appearing again in number only off the KwaZulu–Natal south coast, to the south of Scottburgh. Many subtropical reef species and tropical stragglers exhibit a similar hiatus in distribution records in this region and the shore at Mzamba is well known as a site where shells of unusual tropical taxa regularly wash ashore i.e., *Tonna pernix* (Linnaeus, 1758), *Agabus agabus* Jousseaume, 1894, *Strombus gibberulus* Linnaeus, 1758, *Conus obscurus* Sowerby, 1833, *Talparia talpa* (Linnaeus, 1758), and *Latirus turritus* (Gmelin, 1791). It is thus quite possible that shells of a species such as *T. retrolineata*, which is known from reefs off the KwaZulu–Natal south coast (as recorded at Hibberdene), could also wash ashore at Mzamba. The gap in its distribution in the Natal Bight is thus typical rather than exceptional for such warm–water taxa. Furthermore, the Natal Bight is also known to be impacted by the upwelling of cold, nutrient–rich water (Meyer *et al.* 2002), which may well be of significance to tropical/subtropical species accustomed to warmer water with lower nutrient content.

The similar sized gap between the southern population of *T. retrolineata* and the northern limit of *T. elongata* is of a very different nature. The southern African coastline is divided into three marine biogeographical provinces namely a subtropical east coast province, a warm–temperate south coast province and a cold–temperate west coast province (Stephenson & Stephenson 1972, Brown & Jarman 1978, Day & Grindley 1981, Emanuel *et al.* 1992, Bustamante 1994, Turpie *et al.* 2000, Harrison 2003). The boundaries between these provinces are defined by changes in species composition and water temperatures. The precise position of the interchange between the subtropical and the warm–temperate provinces on the east coast of South Africa appears to vary with the taxon under

consideration and has been cited as Port St. Johns (Stephenson & Stephenson 1972), Port Edward (Brown & Jarman 1978, Turpie *et al.* 2000), Great Kei River (Day & Grindley 1981), East London (Emanuel *et al.* 1992), and Mdumbi estuary (Harrison 2003). For the pheasant shells (Phasianelloidea) of southern African this boundary lies between the Mbashe River and East London (Fig. 2.71). Thus the region separating the distributions of *T. retrolineata* and *T. elongata* has in many cases been identified as a region of major faunal turnover and biogeographic significance. In this context, *T. retrolineata* is a subtropical east coast species, whereas *T. elongata* is a warm–temperate south coast taxon.



Figure 2.61. Variation in shell colour and pattern of *T. retrolineata*: (A, B) holotype, length 6.5 mm, width 3.5 mm, NMSA L5938/T2238, Ponta do Ouro, Mozambique; (C–L) paratypes: (C, D) length 5.8 mm, width 3.3 mm, NMSA S2851/T2242, between Bhanga Nek and Kosi Bay, KwaZulu–Natal; (E, F) length 7.1 mm, width 3.8 mm, NMSA L7357/T3339, Ponta do Ouro, Mozambique; (G, H) length 6.0 mm, width 3.4 mm, NMSA L6904/T2240, Malongane, Mozambique; (I, J) length 6.5 mm, width 3.4 mm, NMSA W1935/T2243, Mzamba, Eastern Cape; (K, L) length 7.4 mm, width 4.1 mm, NMSA E2476/T2241, Leadsman Shoal, KwaZulu–Natal.

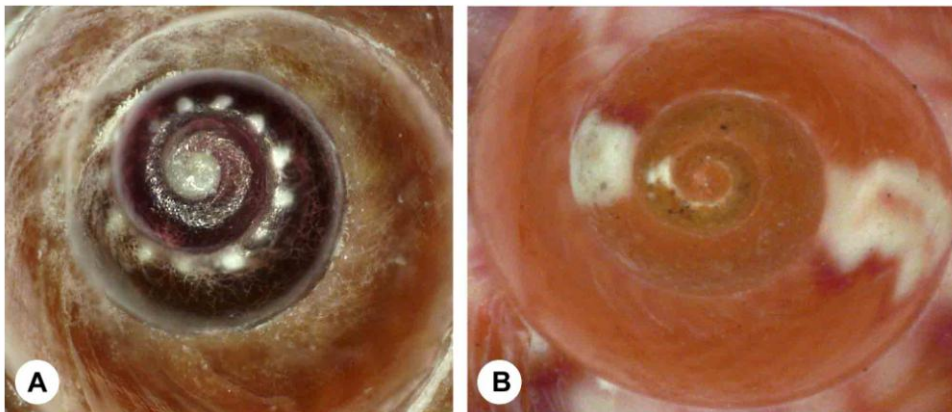


Figure 2.62. Apices of *T. elongata* and *T. retrolineata*: (A) *T. elongata* showing white, subsutural spots on second teleoconch whorl, NMSA W4769, Cape Agulhas, South Western Cape; (B) *T. retrolineata* lacking spots on apical region, NMSA L5938/T2238, Ponta do Ouro, Mozambique.



Figure 2.63. Scanning electron microscope of the external surface of operculum of *T. retrolineata*, showing distinct peripheral groove underlying labral margin, paratype, maximum diameter 2.9 mm, NMSA E2476/T2241.

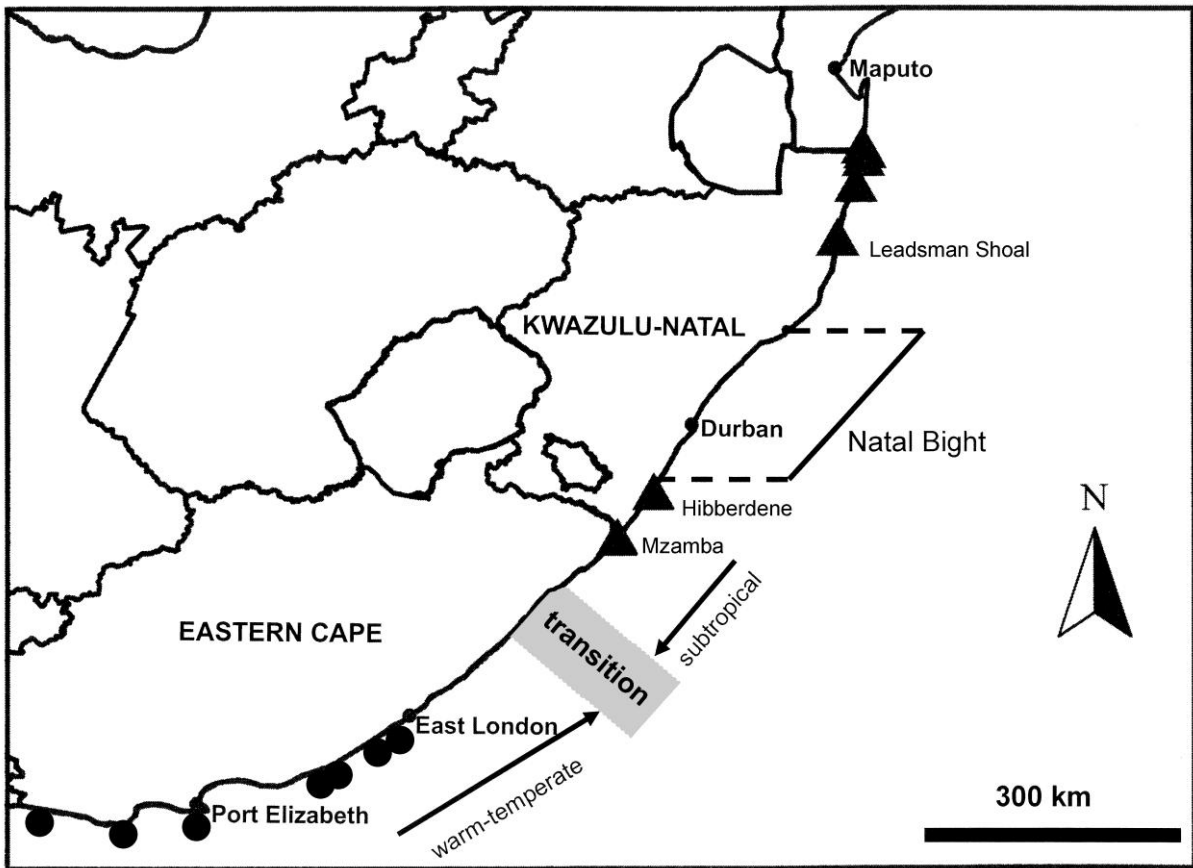


Figure 2.64. Distribution map of *T. retrolineata* (▲) and *T. elongata* (●).

Tricolia saxatilis Nangammbi & Herbert, 2006

Figs 2.65-2.67

Tricolia saxatilis Nangammbi & Herbert, 2006: 17, figs 17-28. Type loc.: off Whale Rock (Eastern Cape, South Africa).

Etymology, *saxatilis* (Latin) – found among rocks.

Diagnosis: Shell small and thin, turbiniform with low–spire and globose outline; whorls well rounded, suture strongly indented; sculpture of fine raised spiral threads; umbilicus open, colouration variable, usually axially patterned in shades of red or brown on a whitish or pinkish ground; operculum granulate, with a deep pit at nucleus.

Description (Figs 2.65A-D):

Shell small and thin, turbiniform with globose outline and relatively low, rounded spire; teleoconch of up to 2.25 whorls with strongly indented suture. Sculpture of fine raised spiral threads. Aperture sub–circular; umbilicus open, with a distinct channel behind inner lip leading to umbilicus. Shell somewhat translucent, colouration variable; ground colour frequently pinkish–white to dark pink or maroon, rarely tinged with amber; frequently with alternating reddish and white spots below the suture and at periphery of last adult whorl (Figs 2.65A, B), or with reddish axial stripes on a white ground (Fig. 2.65C); body whorl occasionally almost uniformly white and apical whorls dark red–brown (Fig. 2.65D); base frequently with a broad, reddish spiral band, separated from umbilicus by a similar whitish band.

Protoconch (Figs 2.66A, B): Typically trochoidean, comprising approx. 1.25 whorls; apical beak present but very weak, terminal lip lacking a varix and with no mid–whorl angulation; sculptured with very fine spiral lines.

Operculum (Fig. 2.66C): Calcareous, thick and convex; paucispiral with eccentric nucleus; external surface with deep pit at nucleus and relatively coarse, irregularly granulate sculpture, and with a narrow, but distinct peripheral groove underlying labral margin.

Radula (Figs 2.66D-F): Similar to *T. adusta*, but denticles on cusps of innermost laterals more or less equal in size.

External anatomy (Fig. 2.7C): Typically trochoidean, but differs from most *Tricolia* species in the form of the neck-lobes – left neck-lobe broad with ca 5 digits, right neck-lobe broad and smooth; middle epipodial tentacle much smaller than the other two, with no sense organ evident at its base.

Measurements: Holotype (Fig. 2.65A), length 2.0 mm, width 1.7 mm (= largest specimen); l/w 1.0-1.4, a/l = 0.5-0.6 (N = 50).

Habitat: A subtidal species inhabiting off-shore reefs; living specimens 8-36 m, empty shells to 50 m.

Geographical range (Fig. 2.67): Endemic to South Africa, ranging from northern KwaZulu-Natal (Zululand) to Eastern Cape (Port Alfred).

Holotype: SOUTH AFRICA: *Eastern Cape*: NMSA, V4048/T2129, off Whale Rock (31.948°S:29.225°E), 20–26 m, sand and gorgonians, dredged NMDP, 16.vii.1982.

Paratypes (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Eastern Cape*: W4299/T2215 (3), same data as holotype. *KwaZulu-Natal*: E7144/T2128 (11), Aliwal Shoal, Cracker Reef (30.283°S:30.833°E), approx. 23 m, living, dived D. Herbert, 30.iv.1989; W2584/T2127 (33), Aliwal Shoal (30.266°S:30.823°E), approx. 15.5 m, loose rubble, living, dived ORI, 07.xii.2004; W2582/T2125 (8), Aliwal Shoal (30.260°S:30.827°E), ca 8 m, loose rubble, living, dived ORI, 09.xii.2004; S6773/T2124 (52), Aliwal Shoal (30.283°S:30.833°E), 10-20 m, sand, dived D. Herbert, 30.vi.1991; S8662/T2119 (61), Aliwal Shoal (30.283°S:30.833°E), approx. 14 m, underwater pump, dived D. Herbert, 02.vi.1991; S8215/T2120 (52), Aliwal Shoal (30.283°S:30.833°E), 10 m, sand and reef debris, hand-dredged, D. Herbert, 04.iv.1992; W2717/T2126 (1), off Phumula (30.638°S:30.549°E), approx. 36 m, low profile reef, living, dived M. Wallace & V. Fraser, 07.xii.2004.

Additional material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *KwaZulu-Natal*: off Hully Point (27.337°S:32.770°E), 40 m, very fine muddy sand, algae, dredged R.V. *Meiring Naudé*, 05.vi.1987 (E1458); off Park Rynie, 50 m, coarse sand, ex CSIR Water Research (B5666); Aliwal Shoal (30.283°S:30.833°E), ca 16 m, hand-dredged sand, dived D. Herbert, 26.v.1990 (S5992); same data, 9-15 m, dived D. Herbert & R.

Emanuel, 27.xi.1988 (E6197, E6273); Aliwal Shoal (30.283°S:30.833°E), approx. 20 m, hand-dredged sand, dived D. Herbert, 25.x.1992 (S7920); Aliwal Shoal (30.283°S:30.833°E), 25-27 m, sand and reef debris, hand-dredged D. Herbert, 04.iv.1992 (S7158); Aliwal Shoal, off Umkomaas (30.283°S:30.833°E), 25-28 m, hand-dredged sand, dived D. Herbert, 16.xii.1990 (S9881).

Eastern Cape: off Mbotyi (31.487°S:29.757°E), 50 m, sand, dredged R.V. *Meiring Naudé*, viii.1981 (E185); off Port Alfred (33.700°S:26.933°E), 65 m, ex gut *Congiopodus torvus*, leg. D. Herbert on R.V. *Africana*, 3.v.1997 (V5161).

Comparison: In comparison with all other species of *Tricolia* occurring in southern Africa, *T. saxatilis* is smaller, lower-spired, has more convex whorls, and a more distinct umbilicus. In its globose shape and small size, *T. saxatilis* resembles *T. deschampsi*, *T. entomocheila*, *T. nordsiecki*, *T. punctura*, and *T. tingitana*, from the Mediterranean. It differs notably from these, however, in its coarsely granular, pitted operculum.

Additional notes: In *T. saxatilis*, the inner marginal radula teeth are of the same form as in *T. adusta* and *T. formosa*, but its shell shape, operculum sculpture and external anatomy differ markedly from those of the latter species. The coarsely granular external surface of the operculum in *T. saxatilis*, and its deep pit, are distinctive. A similar pit has been reported from juvenile *Tricolia* species (Robertson 1958), suggesting that this might be a paedomorphic character, and is concordant with the small size of the species. The form of the neck-lobes of *T. saxatilis* resembles that of the Mediterranean *T. tingitana*, in that the left neck-lobe of both species has relatively few digits and the right-lobe is broad with a non-digitate margin (Gofas 1986, 1993). Additionally, in *T. tingitana* the terminal lip of the protoconch, like that of *T. saxatilis*, lacks a distinct angulation. The possibility thus exists that *T. saxatilis* may be more closely related to *T. tingitana* and perhaps other small Mediterranean *Tricolia* species than it is to the larger, conchologically more typical species. However, some of these shared features may perhaps result from convergence related to size reduction and further comparative study will be required to clarify this. None of the small Mediterranean species appears to possess the coarsely granular operculum with a nuclear pit seen in *T. saxatilis*.

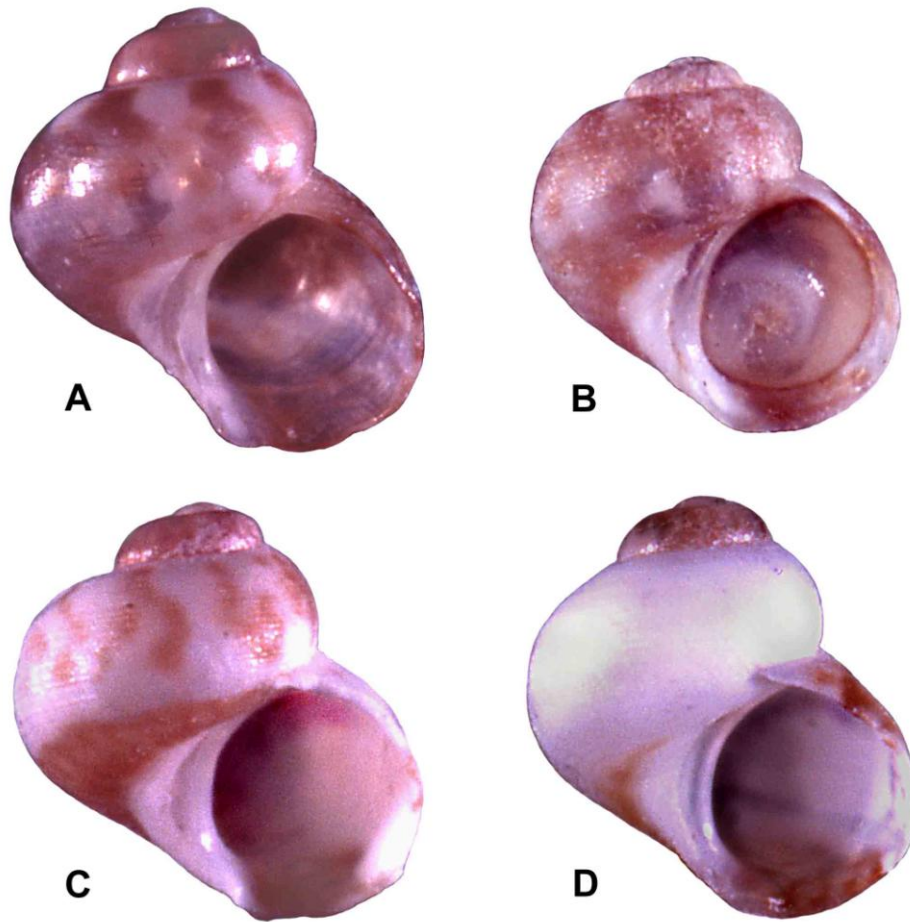


Figure 2.65. Variation in shell colour and pattern of *T. saxatilis*: (A) holotype, length 2.0 mm, width 1.7 mm, NMSA V4048/T2129, off Whale Rock, Eastern Cape; (B–D) paratypes: (B) length 1.4 mm, width 1.2 mm, NMSA E7144/T2128, Aliwal Shoal, Cracker Reef, KwaZulu–Natal; (C) length 1.8 mm, width 1.5 mm, NMSA S6773/T2124, Aliwal Shoal, KwaZulu–Natal; (D) length 1.6 mm, width 1.3 mm, NMSA E7144/T2128, Aliwal Shoal, Cracker Reef, KwaZulu–Natal.

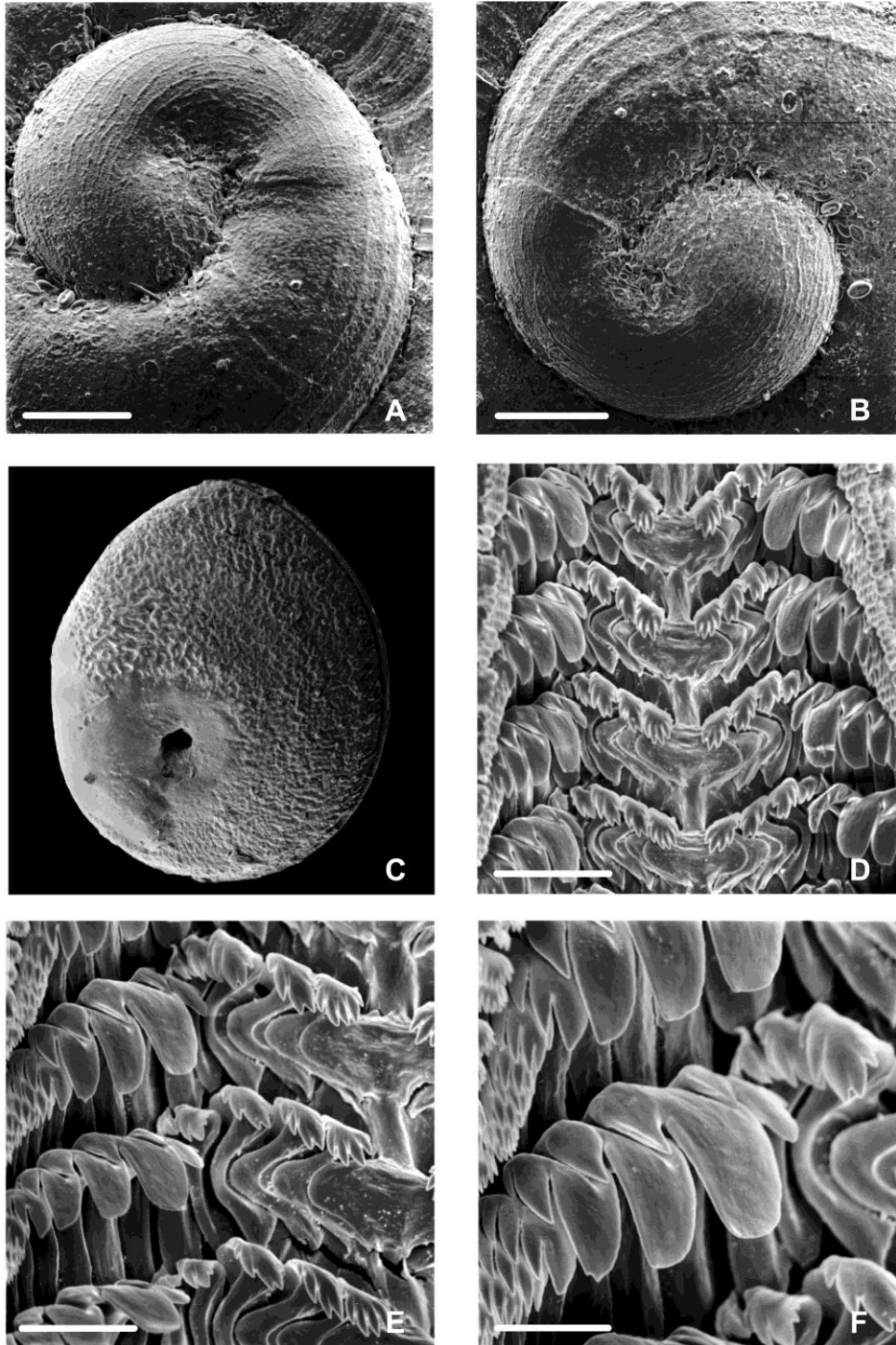


Figure 2.66. Scanning Electron Microscope of protoconch, operculum and radula of *T. saxatilis*: (A, B) two views of protoconch, showing fine irregular spiral sculpture, NMSA W2585, bar = 60 μm ; (C) external surface of operculum, showing irregularly granulate sculpture and deep pit at nucleus, NMSA W2585, maximum diameter 0.6 mm; (D) central portion of radula, NMSA W2585, bar = 50 μm ; (E) lateral and inner marginal teeth, NMSA W2585, bar = 15 μm ; (F) inner marginal teeth, NMSA W2585, bar = 10 μm .

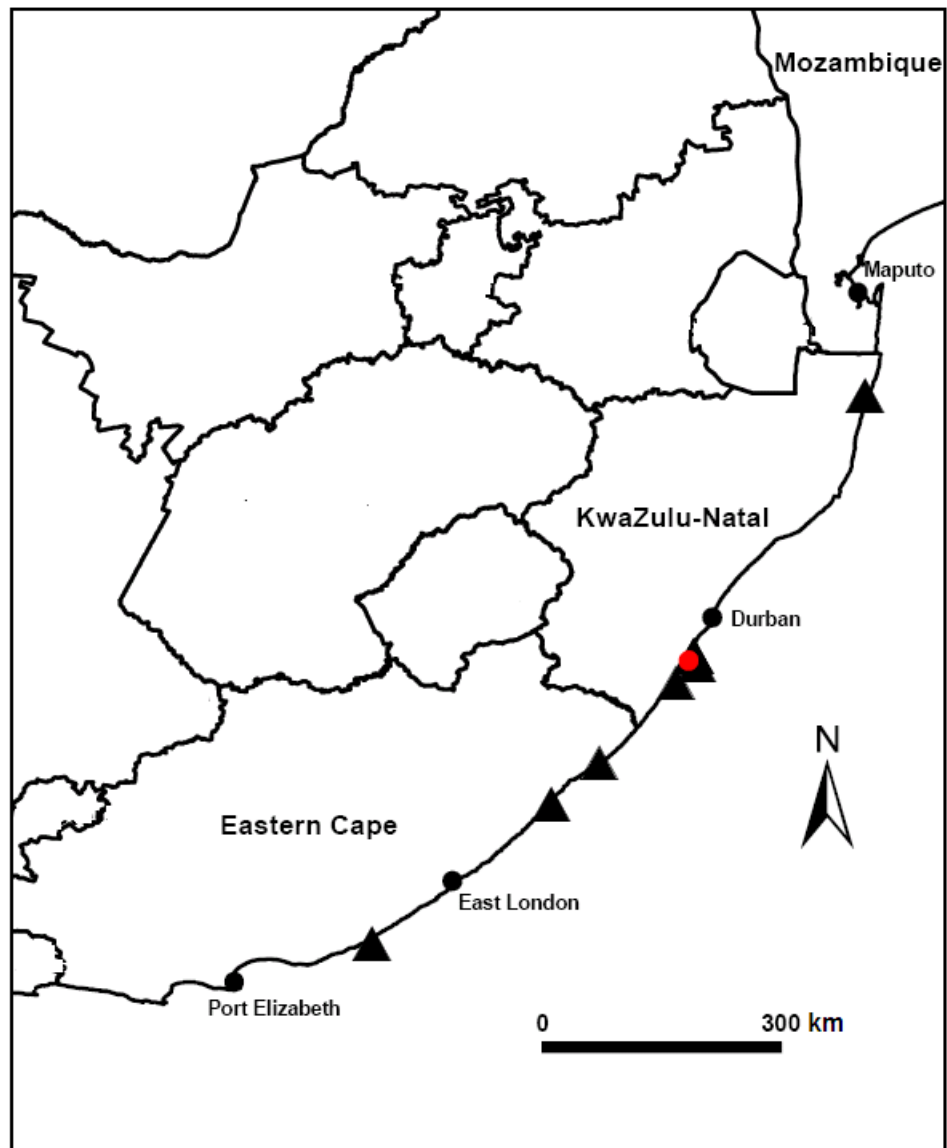


Figure 2.67. Distribution map of *T. saxatilis*. Each black triangle represents one or more site records. Red dot represents a sequenced sample.

Tricolia striolata (Turton, 1932)

Figs 2.68-2.70

Phasianella striolata Turton, 1932: 174, pl. 41, fig. 1237. Type loc.: Port Alfred (Eastern Cape, South Africa).

Phasianella piperata Turton, 1932: 175, pl. 41, fig. 1238. Type loc.: Port Alfred (Eastern Cape, South Africa). **Syn. nov.**

Tricolia piperata; Barnard 1963: 208.

Tricolia striolata; Barnard 1963: 208.

Etymology, *striolata* – diminutive of *stria* (Latin) – a furrow or channel – referring to the grooves between the strong spiral cords.

Diagnosis: Shell globose or roundly turbiniform; whorls evenly rounded, without a distinct angle; shell with widely spaced spiral cords; umbilicus open; colouration relatively constant; ground colour white to pale pink, apical surface reddish–brown, and with brownish–red streaks on body whorl, occasionally with green spots below suture.

Description (Figs 2.68A-B, 2.69):

Shell globose or roundly turbiniform with relatively low spire; teleoconch of up to 3.2 whorls; suture relatively shallow. Sculpture relatively coarse, thick, widely spaced spiral cords on body whorl. Aperture ovate–circular; outer lip thick; colour pattern visible internally; inner lip concave; umbilicus widely open, but narrow. Shell with relatively constant colour pattern; ground colour white to pale pink; apical surface reddish–brown, and with brownish–red streaks on body whorl, occasionally with green spots below the suture (Fig. 2.69).

Protoconch, operculum, radula and external anatomy: Unknown.

Measurements: Largest specimen examined – length 5.2 mm, width 4.1 mm. Length:width ratio 1.2-2.3 (N=50).

Habitat: *T. striolata* is a presumably a shallow subtidal species inhabiting off–shore reefs. Living specimens were not found intertidally or in deep waters. However, shallow subtidal reefs have yet to be well sampled in the Eastern Cape so it is presumed that these may be the source of shells washing onto shorelines.

Geographical range (Fig. 2.70): Endemic to South Africa, and restricted to the Eastern Cape (from East London to Port Alfred).

Type material (Figs 2.68A-B): A, *Phasianella piperata*, holotype, OUM M002784, length 4.3 mm, width 3.4 mm; B, *Phasianella striolata*, holotype (+1 paratype), OUM M002783, length 4.3 mm, width 3.1 mm.

Material examined (all NMSA, unless indicated otherwise): SOUTH AFRICA: *Eastern Cape*: Kwelera, East London (32.900°S:28.080°E), leg. C.M. Connolly, i.1974 (A1752); Gonubie, East London (32.933°S:28.017°E), leg. E. Roscoe, 28.xii.1980 (EM 8957); same locality, leg. R. Kilburn (8518); Fuller's Bay, East London (33.067°S:27.900°E), coll. S. Muller (EM 10731); same locality, leg. P.V. Palmer (EM 10730); Hickman's River mouth (33.067°S:27.833°E), coll. R. Kilburn (5402); Port Alfred (33.600°S:26.900°E), J. Hutt coll'n, ex Albany Museum, 1980 (E2195, D4788).

Comparison: This species differs from other local *Tricolia* species in having strong spiral cords on the body whorls and a globose or roundly turbiniform shell shape. *Tricolia striolata* most closely resembles *T. insignis* and *T. bicarinata*, but the spiral cords are much fewer and more widely spaced and the shell lacks the biangulate shape. When Turton (1932) described *P. piperata*, he identified no genuinely distinctive characteristics of this species, stating only that the colour pattern was diagnostic. *Phasianella piperata* possess the same spiral cords on the body whorl and its colour pattern falls well within the range of *T. striolata*; thus the two nominal taxa are without doubt synonyms. Since these two names were published on the same date by the same author and in the same work, following the principle of first reviser (ICZN 1999, Article 24.2), I select *P. striolata* as a valid name for this taxon. This name was chosen because it appeared first in Turton's publication (c.f. ICZN 1999, recommendation 24A). There are no issues of nomenclatural stability and appropriateness which would favour *P. piperata*.

Despite efforts of collecting in the intertidal rocky shores and subtidal reefs in the Eastern Cape, living material of *T. striolata* was not found resulting in an absence of morphological and molecular data.

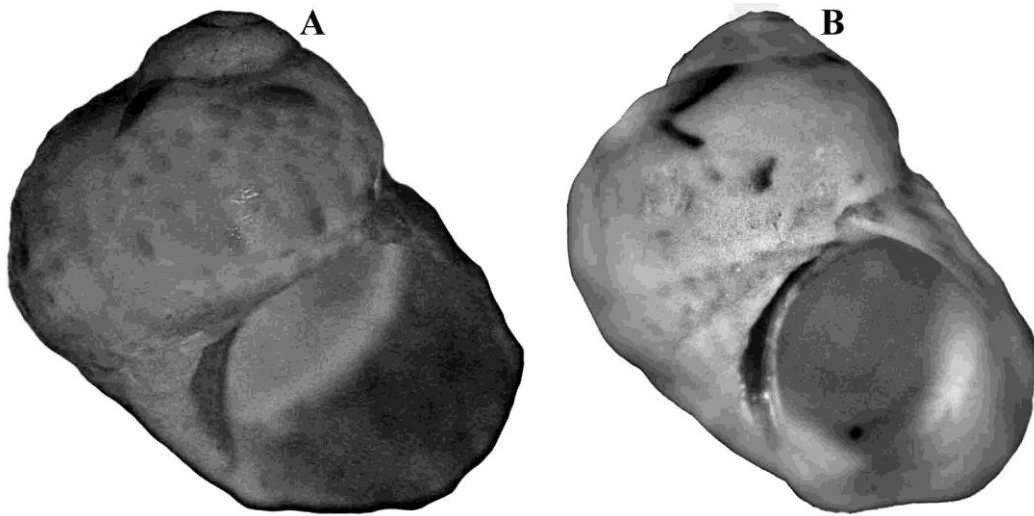


Figure 2.68. Type specimens of *T. striolata*: (A) *P. piperata*, holotype, OUM M002784, length 4.3 mm, width 3.4 mm; (B) *P. striolata*, holotype, OUM M002783, length 4.3 mm, width 3.1 mm.



Figure 2.69. Shell colouration of *T. striolata*: length 3.7 mm, width 2.8 mm, NMSA 8518. Gonubie, East London, Eastern Cape.

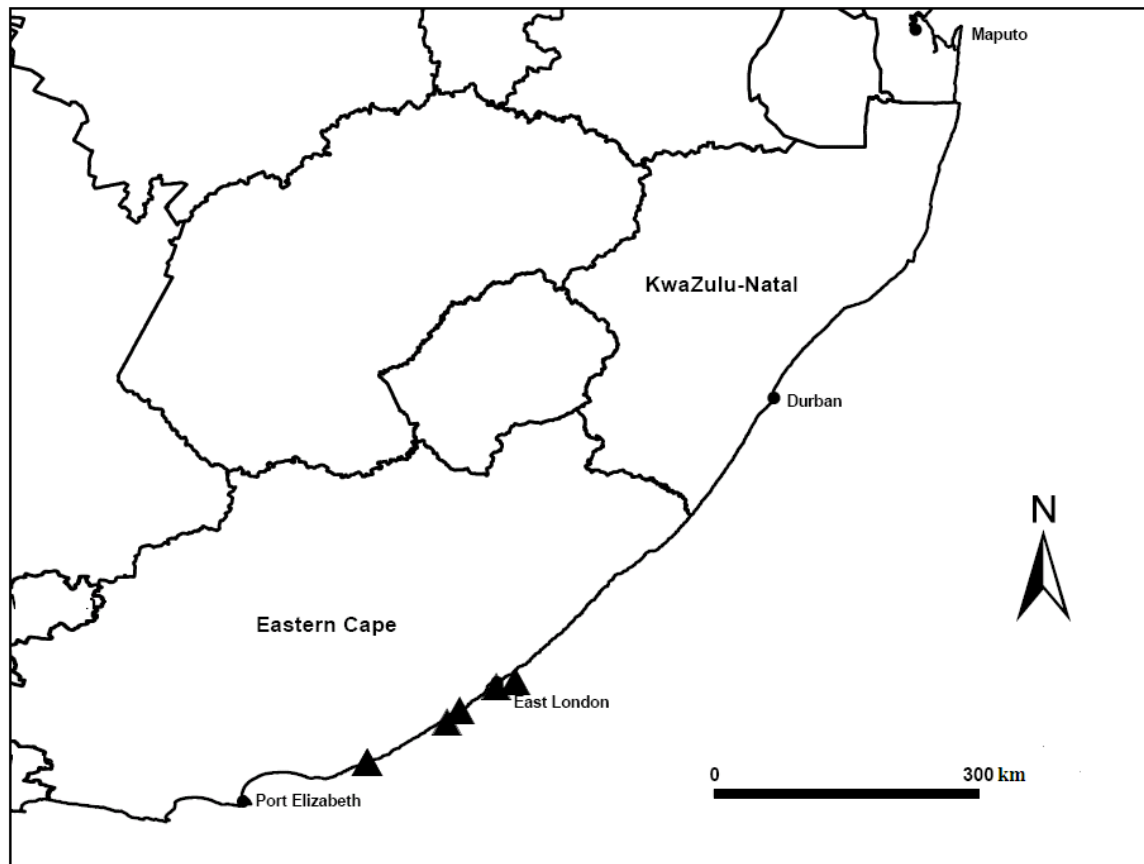


Figure 2.70. Distribution map of *T. striolata*. Each black triangle represents one or more site records.

2.5. DISCUSSION

The southern African region includes three phasianellid genera namely *Hiloo*, *Phasianella* and *Tricolia*. *Hiloo* and *Phasianella* are both represented by a single species, *H. variabilis* and *P. solida* respectively, whereas *Tricolia* is represented by 14 morphologically distinct species. The southern African fauna has a greater diversity of *Tricolia* species than any other part of the world, the more so considering the much smaller geographical area involved (Fig. 2.72). The following species are endemic to southern Africa: *T. adusta*, *T. africana*, *T. bicarinata*, *T. capensis*, *T. elongata*, *T. formosa*, *T. insignis*, *T. kochii*, *T. kraussi*, *T. neritina*, *T. retrolineata*, *T. saxatilis* and *T. striolata*.

In the molecular analysis chapter (3) of this study, the COI and 16S phylogenies recovered *T. bicarinata*, *T. insignis* and *T. kraussi* as a single, but mixed group, clade 4 (BS=98 and 77%). These may in fact be one ecologically variable species. However, this study defers synonymising the three species until the issue has been studied further. As a result, the number of the endemic southern African *Tricolia* species still stands at 13. The number of tropical Indo–West Pacific pheasant shell species so far recorded in southern Africa is *H. variabilis* and *P. solida*, and one tropical East African species *T. ios*. Originally, the tropical Indo–West Pacific region included three species of *Tricolia* before *Hiloo* was elevated to a genus level.

2.5.1. Morphological characters used at generic level

Different morphological characters have been studied at generic and species level, and the following characters were found to distinguish between genera: apex shape, rachidian tooth and number of lateral teeth of the radula; colour pattern (spiral capillary lines); cephalic lappets and shell muscles.

Morphological features characteristic of *Hiloo* include: protoconch is exserted, apex narrowly rounded; operculum coarsely granulated on the external surface; rachidian tooth of the radula well–developed with prominent cusp, and with three pairs of lateral teeth per transverse row. As opposed to *Tricolia* and *Phasianella* species, *Hiloo* retains an ancestral radula plan in having a cusped rachidian tooth, whereas in *Tricolia* and *Phasianella* species, the cusped rachidian tooth is present only in juveniles. These are evidently autapomorphic characters and provide little information about the relationship.

Morphological characters of *Phasianella* include: colour pattern including spiral capillary lines; radula without a functional rachidian tooth; cephalic lappets present and well-developed; one shell muscle is present.

Morphological characters of *Tricolia* include: protoconch usually low, apex bluntly rounded; rachidian tooth usually broadly ovate and lacking a cusp; if protoconch exerted then rachidian tooth is reduced to a narrow vestige (all southern Australian *Tricolia* species).

The generic affinities of a number of Indo–West Pacific and southern Australian species traditionally referred to *Tricolia* are currently unclear. These exhibit atypical character states and may belong to undescribed genera. The issue of one (*Phasianella*) or two (*Tricolia*) shell muscles is also pertinent to distinguish between genera but needs further study.

2.5.2. Morphological characters used at species level

Selection, description and coding of these characters have been done. Unfortunately, these characters could not be analyzed in a phylogenetic context since many of them are autapomorphies, and therefore not useful to trace phylogenetic relationships.

2.5.2.1. Shell

Within the southern African *Tricolia* species, there is great variation in terms of shell shape. Some species have a turbiniform shape while others are bulimiform. *Tricolia neritina* is diagnosable from other local species in having a neritiform shape, whereas *T. saxatilis* is globose and low–spired and most closely resembles the small Mediterranean *Tricolia* as well as *Gabrielona* species. *Tricolia elongata* and *T. kochii* are the largest species among the southern African *Tricolia* fauna. Two of the southern African *Tricolia* species are distinctly biangulate in shell shape, i.e., *T. bicarinata* and *T. insignis*. All *Phasianella* species have a bulimiform shell shape, while *Hiloa* is turbiniform.

In terms of the shell sculpture, several of the southern African species have a distinct spiral sculpture on their body whorl, i.e., *T. bicarinata*, *T. insignis*, *T. kochii*, *T. kraussi* and *T. striolata*, but the sculpture differs in the level of strength. For example, *T. kraussi* has very fine spiral threads, whereas *T. bicarinata* and *T. insignis* have numerous close–set spiral ridges, and *T. striolata* has strong, widely spaced spiral cords. The remaining species have weak sculpture; shells are usually smooth and glossy, marked only by exceedingly fine

growth-lines. In both *Tricolia* and *Phasianella* species, shell colouration is extremely variable within individuals of the same species.

2.5.2.2. Operculum

The external surface of the operculum of southern African *Tricolia* is uniform in all species and resembles that of the type species (*T. pullus*) with the exception of *T. saxatilis*, which possesses a granulated external surface and a deep pit. The external surface of the operculum of *H. variabilis* and the south Australian *T. tomlini* are coarsely granulated and sub-circular. A morphological character shared between *Hiloa*, *Tricolia* and *Phasianella* species is the convex shape of the external surface of the operculum, whereas that of *Gabrielona* is externally concave.

2.5.2.3. Radula

Thorough investigation on the radula has shown that there is very little radula variation within the southern African *Tricolia* species. All the species have broadly ovate rachidian tooth, lacking a cusp, five pairs of lateral teeth per transverse row and numerous marginal teeth. However, two forms of inner marginal dentition were found within the southern African *Tricolia* species. In one form, the ectocone of the inner marginal teeth is bifid or notched, and interlocks with two notches at the base of the cusp of the adjacent outer tooth and is found in most species. The other form has one strong undivided ectocone, which is only found in *T. adusta*, *T. formosa* and *T. saxatilis*.

2.5.2.4. External anatomy

There is little difference in the anatomy of the southern African *Tricolia* species. Most species have two sense organs at the base of the right anterior epipodial tentacle, whereas *T. adusta* and *T. formosa* have a single epipodial sense organ. *Tricolia saxatilis* differs markedly from other southern African *Tricolia* species in the form of the neck-lobes. The left neck-lobe is broad with relatively few digits and the right neck-lobe is broad with a non-digitate margin. This feature resembles that of the Mediterranean *T. tingitana*.

2.5.3. Distribution and Biogeography

Figure 2.71 highlights that the highest number of pheasant shell species occurs between Cape Agulhas and Cape Town with nine species. The second most diverse region is: East London and Port Elizabeth with seven species. The Cape south coast is regarded as pheasant shell hotspots where seven species occur. The lowest number of species was found on the east coast (between Quirimba and Kosi Bay, three tropical species), and on the west coast (from between Cape Town and Benguela, three cold-temperate species). These results are congruent with three marine biogeographical provinces identified by Stephenson & Stephenson (1972), Brown & Jarman (1978), Day & Grindley (1981), Emanuel *et al.* (1992), Bustamante (1994), Turpie *et al.* (2000), and Harrison (2003). A summary of these provinces is given under *T. retrolineata*. For the pheasant shells of southern Africa, a subtropical east coast province is from southern Mozambique (Inhambane) to Mbashe River (Transkei); a warm-temperate south coast province is from Mbashe River to Cape Agulhas and a cold-temperate west coast province is from Cape Agulhas to Kunene River mouth.

The boundaries between these provinces are defined by changes in species composition and water temperatures, and have been previously identified as Port St. Johns (Stephenson & Stephenson 1972), Port Edward (Brown & Jarman 1978, Turpie *et al.* 2000), Great Kei River (Day & Grindley 1981), East London (Emanuel *et al.* 1992), and Mdumbi estuary (Harrison 2003). In this study, figure 2.71 show increased faunal turnover at the subtropical-warm-temperate boundary, between Mbashe River and East London, and also the warm-temperate-cool-temperate boundary, between Cape Agulhas and Cape Town.

A decrease in the number of southern African pheasant shell species was also observed in the northeast and the west coast regions. Similar results have been found in other marine taxa. For example, Stephenson & Stephenson (1972) found a steady decline in the number of rocky-shore plant and animal species from east to west. Emanuel *et al.* (1992) reported a decrease in species richness of marine intertidal and subtidal invertebrates from the Mozambique coast in the east to the Namibian coast in the west. The marine mollusc fauna of the west coast of South Africa was found to be less diverse than that of the warmer east coast (Kilburn & Rippey 1982).

The course of decline in the diversity of estuarine fish species along the South African coastline from the east to west was reported as a result of the loss of tropical marine species, which is linked to the southward-flowing Agulhas Current through its influence on sea

temperatures and the dispersal of these fishes in a southerly direction (Day & Grindley 1981, Whitfield & Bruton 1989, Whitfield 1998, 1999). Along the west coast, the lower number of species is a result of the cold upwelled water associated with the Benguela upwelling system, which probably acts as a barrier to the distribution of tropical and subtropical taxa from both the west and east coasts and thus accounts for the low species abundance in this region (Whitfield 1983, 1996, 1999).

There is also strong morphological evidence suggesting that the South African *T. neritina* is closely related to *T. munieri* from Amsterdam and St. Paul Islands. Waters & Roy's (2004) study on the biogeography of sea-stars revealed that closely related populations of the sedentary *Parvulastra exigua* (Lamarck, 1816) occurred on far-flung continents and oceanic islands of the Southern Hemisphere. They concluded that this wide geographic distribution could only have arisen through a number of independent rafting events. Simultaneously, Donald *et al.* (2005)'s phylogenetic research on trochid gastropods further indicated that the topshell *Diloma nigerrima* (Gmelin, 1791) recently migrated across the Pacific Ocean, from New Zealand to Chile probably by rafting on fronds of the buoyant bull-kelp, *Durvillaea antarctica*.

Mortensen (1933) suggested that *P. exigua* colonized St. Helena by rafting from South Africa on the holdfasts of detached *Ecklonia*, buoyant seaweed that regularly drifts north to St. Helena via the Benguela Current (Waters 2008). The widespread biogeographic distribution of many species of marine invertebrates with short-lived larval stages or direct development is believed to be the result of rafting, and it has been proposed that rafting may be the only possible means of dispersal over large stretches of oceans for marine organisms possessing a larval stage of less than a month (Donald *et al.* 2005, Jackson 1986).

Even though there is a general lack of direct evidence for rafting dispersal occurring in benthic marine invertebrates, there has been increasing awareness that rafting seems to be the best dispersal mechanism for wide distribution of intertidal marine organisms that do not have long-lived, feeding larvae, i.e., oysters (Ó Foighil *et al.* 1999); bivalves, copepods and isopods (Thiel & Gutow 2004); sponges and ascidians (Jackson 1986); calyptraeid limpets (Collin 2003); and gastropods (Donald *et al.* 2005).

Tricolia species have short-lived planktotrophic larvae (Manly 1976, Hickman 1992), and transoceanic dispersal is highly unlikely since short-lived planktonic larvae cannot survive many months in the open ocean. However, it is possible that *T. neritina* dispersed from South

Africa to St. Paul and Amsterdam Islands by the rafting of adults on macroalgae assisted by the West Drift Wind, which then colonized in these isolated Indian Ocean Islands. This needs further investigation.

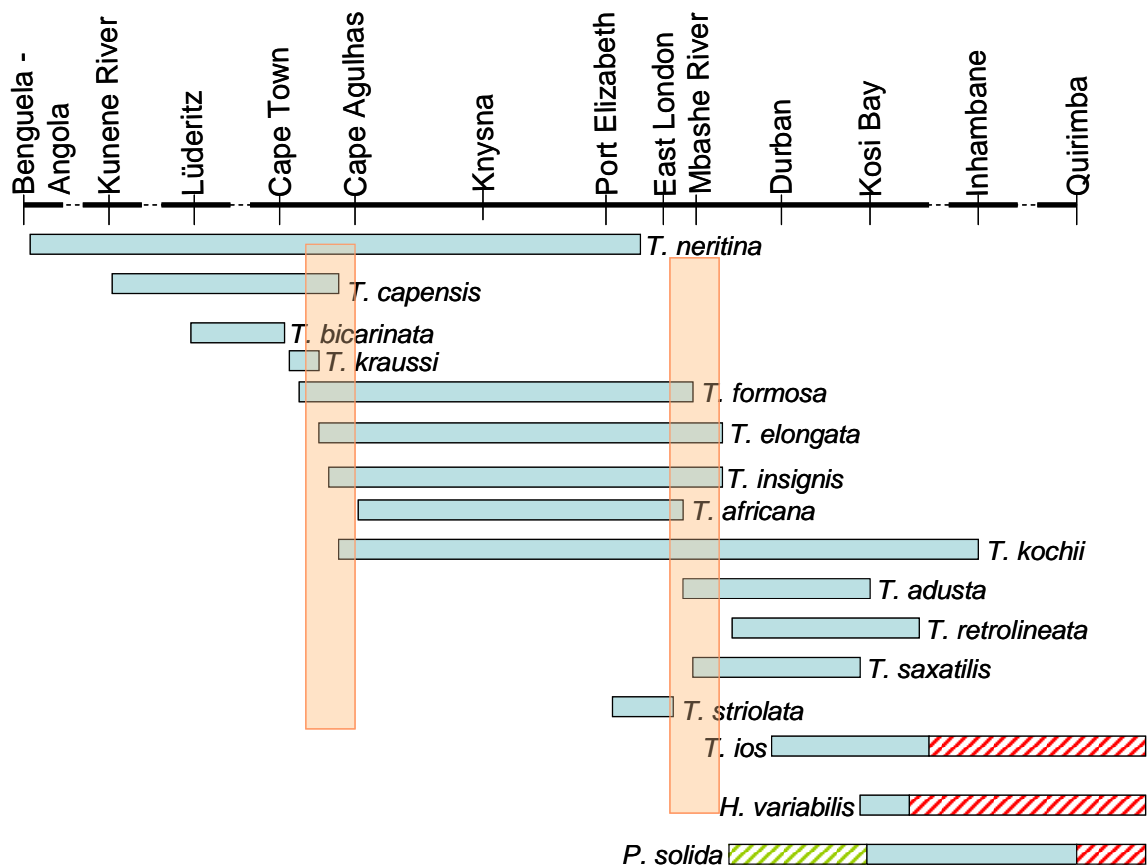


Figure 2.71. Bar chart showing distribution range of pheasant shell species along the southern Africa coastline. Red cross hatched bars show the range of species extending beyond the southern African coastline. Green cross hatched bar show the range of fossil specimens in *P. solida*. The orange horizontal bars show areas with increased faunal turnover.

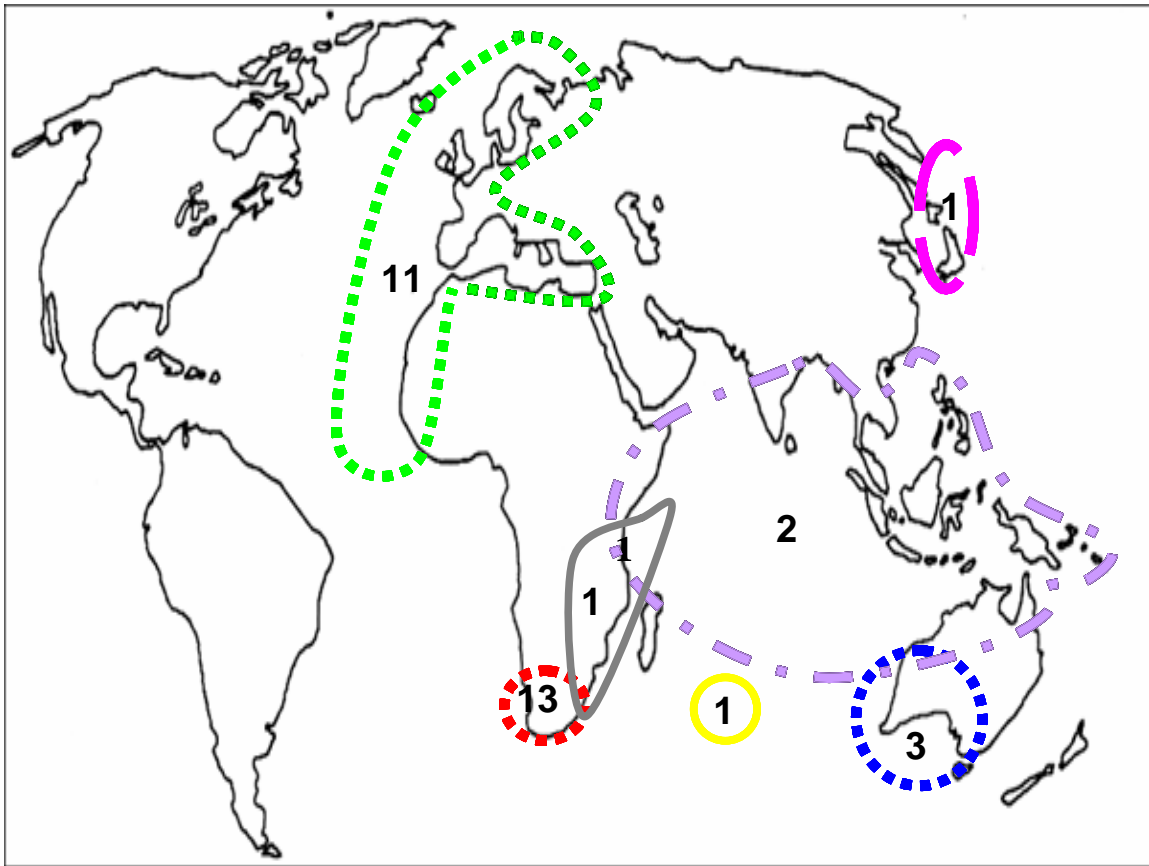


Figure 2.72. World map showing the distribution of *Tricolia* species. The numbers represent species recorded in each region. *Eulithidium*, *Hilola* and *Phasianella* species are excluded from this distribution map.

2.6. REFERENCES

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CHAPTER 3: A MOLECULAR PHYLOGENY OF THE SOUTHERN AFRICAN *TRICOLIA* SPECIES BASED ON MITOCHONDRIAL SEQUENCE DATA

ABSTRACT

This chapter assesses the validity of *Tricolia* species in southern African as recognized in chapter 2 based on the mtDNA COI and 16S rRNA sequence data. Phylogenies obtained from both COI and 16S recovered seven distinct clades within the southern African *Tricolia* species. *Tricolia adusta*, *T. elongata*, *T. formosa*, *T. kochii*, *T. saxatilis* and *T. neritina* were recovered as distinct species. In all analyses, *T. africana* and *T. capensis* are genetically indistinguishable. However, morphological characters of the shell are clearly diagnosable. A possible explanation why the two species are clustered within a single clade could be due to incomplete sorting of ancestral polymorphism after recent speciation or recent speciation with rapid morphological and ecological divergence co-incident with geographical separation. Similarly, there is little genetic differentiation between *T. bicarinata*, *T. insignis* and *T. kraussi*. This is also supported by morphological data as the three species are conchologically similar with intergrading shell characters and might even be one species exhibiting ecogeographic variation in shell form. Monophyly of the southern African *Tricolia* species is not supported as well as the relationship between these and the European *Tricolia pullus*.

3.1. INTRODUCTION

The Tricoliinae is presently considered to include two genera, *Tricolia* and *Eulithidium* (Hickman & McLean 1990). *Tricolia* has been divided into two subgenera: *Tricolia* comprising approximately 31 species and *Hilola* containing a single species. The taxonomy of these subgenera is poorly understood. *Hilola* is confined to the Indo–West Pacific and includes only *Hilola variabilis*. The subgenus *Tricolia* is widely distributed in the Atlantic, Indian and Pacific Oceans with species that are found in: southern Africa (13), East Africa (1), Eastern Atlantic/Mediterranean (11), southern Australia (3), the Indo–West Pacific (2) and northern Japan (1) – see chapter 1 for further information pertaining to the global distribution of this genus. The number of taxonomically valid species within *Tricolia* is still a matter of conjecture. Previous taxonomic revisions of the genus mainly focused on the Indo–West Pacific and the Eastern Atlantic regions (Robertson 1985, Gofas 1982, 1986, 1993). To date, a detailed taxonomic revision including the southern African *Tricolia* species has not been undertaken, yet species referred to this genus are well represented in southern Africa. The

first thorough taxonomic revision on the southern African *Tricolia* species based on morphological characters of the shell, operculum, protoconch, radula and external anatomy is presented in chapter 2. However, the validity of the described nominal southern African *Tricolia* species has not as yet been tested using molecular sequence data. Given that conflicting topologies are often generated between morphological and molecular analysis, the compilation of a comprehensively sampled molecular phylogeny of the southern African taxa is an important goal of this thesis. In this chapter, I present molecular phylogenies based on partial sequences of the mitochondrial protein-coding COI gene and the 16S rRNA gene in order to assess the taxonomic validity of *Tricolia* species in southern Africa as recognised in chapter 2. In addition, I seek to determine whether the southern African taxa represent a monophyletic radiation within the region.

3.2. MATERIALS AND METHODS

3.2.1. Taxon sampling

Table 3.1 details the southern African taxa studied and includes collecting localities, DNA extraction numbers, museum accession numbers and details of the molecular markers sequenced. The type species of *Tricolia*, *T. pullus* was used as the outgroup. Vouchers of the South African species sequenced are deposited in the Natal Museum, Pietermaritzburg.

3.2.2. Laboratory protocols

Tissue samples were obtained from 11 of the 13 currently recognized southern African *Tricolia* species (Table 3.1). The two southern African species missing for DNA sequencing were *T. striolata* and *T. retrolineata*. This was because there was no live collected material for the former, and DNA extraction did not succeed with the one preserved specimen of the latter. Genomic DNA was isolated from the foot (large specimens) or the entire body (small specimens) using three equally successful DNA isolation protocols: DNeasy Tissue Kit (Qiagen), SV Total RNA Isolation System (Promega) and an ammonium acetate protocol Nicholls *et al.* (2000).

For the DNeasy Tissue Kit technique, the tissue was placed in a 1.5 ml tube containing 180 μ l ATL buffer and 20 μ l proteinase K. The mixture was then vortexed and incubated on a shaking water bath at 55°C for 3 hours. Following tissue digestion, 200 μ l buffer AL was added to the sample, vortexed for 15 seconds and incubated at 70°C for 10 minutes. After incubation, 200 μ l ethanol (96-100%) was added to the sample and mixed thoroughly by

vortexing. The solution was then transferred into a 2 ml DNeasy spin column collection tube and centrifuged at 8000 rpm for 1 minute. The supernatant DNA was washed with 500 µl of buffer AW1 and spun at 8000 rpm for 1 minute, and washed again with 500 µl buffer AW2 and spun at 13000 rpm for 3 minutes. The DNA was eluted twice in 100 µl ethanol (100%) or elution buffer and stored at -20°C.

For the SV Total RNA Isolation technique, the tissue was added to a 1.5 ml tube containing 175 µl SV RNA Lysis buffer and mixed thoroughly by inversion. Three hundred and fifty microliter of SV RNA dilution buffer was added to the tissue mixture and mixed by inverting the tube 3-4 times, then heated at 70°C for three minutes. The solution was then centrifuged at 13000 rpm for 10 minutes. The mixture was added to 200 µl 95% ethanol and transferred to a spin basket assembly and centrifuged at 13000 rpm for 1 minute. DNA supernatant was washed twice with 600 µl and once with 250 µl SV RNA wash solution. For the 600 µl wash, the supernatant was centrifuged at 13000 rpm for 1 minute, and two minutes for the 250 µl wash. The DNA was eluted with 100 µl Nuclease-Free water and stored at -20°C.

Other samples were extracted using the ammonium acetate protocol described in Nicholls *et al.* (2000). Foot tissue was first digested at 50°C for 4-6 hours with agitation in a buffer solution (20 mM EDTA, 50 mM Tris, 120 mM NaCl and 1% SDS, pH 8.0.) containing 5 µl (10 mg/ml) proteinase K. Following tissue digestion, an equal volume (250 µl) of 4M ammonium acetate solution was added. The samples were vortexed and incubated at room temperature for 15 minutes with agitation, with vortexing every 5 minutes. The samples were cooled for 10 minutes at room temperature, centrifuged at 13000 rpm for 10 minutes in order to pellet the precipitate, and the supernatant was transferred into a clean 1.5 ml tube. Two volumes (1 ml) of 100% ethanol were added, vortexed thoroughly (at least 10 seconds) and spun at 13000 rpm for 8-10 minutes. The supernatant was poured out, 1 ml of 70% ethanol was added to rinse the pellet, and the tubes were vortexed and spun at 13000 rpm for 8-10 minutes. The supernatant was discarded, and the DNA pellet dried for 30 minutes. To dissolve the DNA, 50-100 µl TE buffer was added, and incubated at room temperature for 15-30 minutes to allow complete dissolution. DNA was stored at -20°C.

Amplification of the mitochondrial Cytochrome-c Oxidase subunit I (COI) was achieved using universal primers LCO1490 (forward) and HCO2198 (reverse; Folmer *et al.* 1994). For samples that resisted amplification using these primers, two additional primers were used to amplify the COI gene in stages: the universal LCO1490 primer was used in combination with K699 and the universal HCO2198 primer was used in combination with RON. These primers were originally designed to sequence the COI gene in insects (Simon *et al.* 1994), but proved

to be very successful for the present study. Amplifications of the mitochondrial 16S rRNA gene were achieved with universal forward primer 16Sar and reverse primer 16Sbr (Palumbi *et al.* 1991; Table 3.2).

PCR reactions were carried out in 50 μ l volumes with the following reagents: distilled water (36.8 μ l), 10 X amplification buffer with 15 mM MgCl₂ (5 μ l), dNTP solution with 10 mM concentration of each dNTP (1 μ l), Super Therm Gold Taq (0.2 μ l), 5 μ M solution of each primer (3 μ l) and DNA template (1 μ l). A negative control containing all reagents except the template was run with each set of reactions. Super Therm Gold Taq was used in PCR with the following cycling conditions: 11 minutes at 95°C (initial denaturation), followed by 35 cycles of 1 minute at 94°C (denaturation), 1 minute 30 seconds at gene-specific annealing temperatures (annealing), and 1 minute 30 seconds at 72°C (extension). The cycling was terminated with 5 minutes at 72°C (sequence extension). Annealing temperatures were between 47°C and 50°C for CO1, and 50°C for 16S rRNA. Amplifications were performed on a Perkin Elmer GeneAmp PCR System 9600 (Applied Biosystems). The presence of the PCR products was determined by electrophoresis of 2.5 μ l PCR products on a 1.3% TAE agarose gel stained with ethidium bromide and visualized under UV fluorescence.

Amplified DNA was purified for cycle-sequencing using either the QIAQuick PCR purification kit (Qiagen) or the 1:4 ammonium acetate protocol (Moussalli *et al.* 2005). For the 1:4 ammonium acetate protocol, 2 volumes (45 μ l) of 1:4 ammonium acetate (10 M:100% ethanol) were added to the sample. The sample was then centrifuged at top speed for 10-15 minutes. All supernatant was aspirated. The pellet was then washed with 150 μ l of 70% ethanol and centrifuged for 8 minutes at top speed. All supernatant was aspirated and the pellet was air dried at room temperature for 10-15 minutes. The purified product was resuspended with 10 μ l of 10 mM Tris (pH 8) or sterile water. All PCR products were sequenced in both directions using the BigDye (Perkin-Elmer) procedure, and the original amplification primers.

Cycle-sequencing was performed in reaction volumes of 20 μ l including the following reagents: distilled water (10.2 μ l), 2.5 X cycling-sequencing buffer (6 μ l), BigDye[®] Terminator v3.1 Cycle-sequencing Kit (Applied Biosystems, 2 μ l), primer (0.8 μ l), and DNA template (1 μ l). Cycle-sequencing was performed using a Perkin Elmer GeneAmp PCR System 9600 (Applied Biosystems), and comprised 32 cycles of 96°C for 10 seconds (denaturation), 50°C for 30 seconds (annealing), and 60°C for 4 minutes (extension), terminating with an indefinite 4°C soak phase. Cycle-sequencing products were purified using either Ethanol/EDTA/NaAc

precipitation or Isopropanol precipitation. Nucleotide sequences were determined using an ABI PRISM 3100 Genetic Analyser (Applied Biosystems), or sent to the MACROGEN DNA sequencing facility in South Korea.

Table 3.1. List of samples used to study phylogenetic relationships among the southern Africa *Tricolia* species. The samples listed include collecting locality data, DNA extraction numbers, museum accession numbers and gene fragments sequenced. Localities are in South Africa unless otherwise stated. *Tricolia pullus* (European) was used as the outgroup.

Species	Collecting localities	DNA extraction #	Museum #	Gene fragment sequenced	
				COI	16S
<i>Tricolia adusta</i>	Aliwal Shoal, KwaZulu–Natal	482	W2584	–	•
<i>Tricolia africana</i>	Gonubie, East London, Eastern Cape	100	W3392	•	•
<i>Tricolia africana</i>	Hickman's River mouth, Eastern Cape	101	W3387	•	•
<i>Tricolia africana</i>	Coney Glen, Knysna, Western Cape	102	W4750	•	•
<i>Tricolia africana</i>	Goukamma Nature Reserve, Western Cape	103	W4753	•	•
<i>Tricolia africana</i>	Wilderness National Park, Western Cape	104	W4754	•	•
<i>Tricolia africana</i>	Reebok Reef, Mossel Bay, Western Cape	105	W4755	•	•
<i>Tricolia africana</i>	De Bakke, Mossel Bay, Western Cape	106	W4758	•	•
<i>Tricolia africana</i>	Mossel Bay Point, Western Cape	107	W4759	•	•
<i>Tricolia africana</i>	Still Bay Point, Western Cape	108	W4763	•	•
<i>Tricolia africana</i>	Struis Bay, Western Cape	109	W4772	•	•
<i>Tricolia africana</i>	Rufanes, Port Alfred, Eastern Cape	374	W1034	•	•
<i>Tricolia africana</i>	Fish River mouth, Eastern Cape	466	W1030	•	–
<i>Tricolia africana</i>	Cape Recife, Eastern Cape	503	W3191	•	•
<i>Tricolia africana</i>	Kwelera, East London, Eastern Cape	504	W3193	•	•
<i>Tricolia africana</i>	Kidd's Beach, Eastern Cape	505	W3194	•	•
<i>Tricolia bicarinata</i>	Sea Point, Western Cape	380	W1528	•	•
<i>Tricolia capensis</i>	Hawston, Western Cape	128	W1533	•	–
<i>Tricolia capensis</i>	Sandbaai, Western Cape	129	W1532	•	•
<i>Tricolia capensis</i>	Betty's Bay, Western Cape	130	W1535	•	•
<i>Tricolia capensis</i>	Marcus Island, Western Cape	131	W1542	•	•
<i>Tricolia capensis</i>	Yzerfontein, Western Cape	132	W1545	•	•
<i>Tricolia capensis</i>	Sea Point3, near tidal pool, WC	133	W1525		•
<i>Tricolia capensis</i>	Mouille Point, Western Cape	134	W1529	•	•
<i>Tricolia capensis</i>	Sea Point 2, Western Cape	135	W2577	•	•

Species	Collecting localities	DNA extraction #	Museum #	Gene fragment sequenced	
				COI	16S
<i>Tricolia capensis</i>	Granger Bay, Western Cape	136	W1537	•	•
<i>Tricolia capensis</i>	Three Anchor Bay, Western Cape	137	W1540	•	•
<i>Tricolia capensis</i>	Kommetjie, Western Cape	163	W2569	•	—
<i>Tricolia capensis</i>	Sea Point 1, Western Cape	377	W1524	•	—
<i>Tricolia capensis</i>	Glencairn, False Bay, Western Cape	469	W2559	•	•
<i>Tricolia capensis</i>	Scarborough, Western Cape	470	W2563	•	•
<i>Tricolia capensis</i>	Camp's Bay, Western Cape	472	W2572	•	•
<i>Tricolia capensis</i>	Dalebrook, False Bay, Western Cape	644	W1516	—	•
<i>Tricolia elongata</i>	Cape Agulhas, Western Cape	117_1	W4769	•	•
<i>Tricolia elongata</i>	Cape Agulhas, Western Cape	118_2	W4769	•	•
<i>Tricolia elongata</i>	Cape Agulhas, Western Cape	119_3	W4769	•	•
<i>Tricolia elongata</i>	Cape Agulhas, Western Cape	120_4	W4769	•	•
<i>Tricolia elongata</i>	Struis Bay, site 1, Western Cape	121	W4771	•	•
<i>Tricolia elongata</i>	Struis Bay, site 2, Western Cape	122	W4773	•	•
<i>Tricolia elongata</i>	Reebok Reef, Mossel Bay, Western Cape	164	W4774	—	•
<i>Tricolia elongata</i>	Three Sisters, Port Alfred, Eastern Cape	375	W1036	•	•
<i>Tricolia elongata</i>	Algoa Bay, Eastern Cape	511	W3196	•	•
<i>Tricolia elongata</i>	Kidd's Beach, Eastern Cape	512	W3205	•	•
<i>Tricolia formosa</i>	off Macassar Beach, Western Cape	481	W2581	•	•
<i>Tricolia formosa</i>	Fish Tanks, off Port Alfred, Eastern Cape	509	W3197	•	•
<i>Tricolia insignis</i>	Mossel Bay Point, Western Cape	110	W4761	•	•
<i>Tricolia insignis</i>	Still Bay Point, Western Cape	111	W4764	•	•
<i>Tricolia insignis</i>	Agulhas National Park, Western Cape	112	W4765	•	•
<i>Tricolia insignis</i>	Qolora River Mouth Eastern Cape	138	C3433	•	•
<i>Tricolia insignis</i>	Marine Drive 1, Port Elizabeth, Eastern Cape	139	W3381	•	•
<i>Tricolia insignis</i>	Marine Drive 2, Port Elizabeth, Eastern Cape	140	W3382	•	•
<i>Tricolia insignis</i>	Gonubie, East London, Eastern Africa	141	W3386	•	•
<i>Tricolia insignis</i>	Hickman's River Mouth, Eastern Cape	169	W3384	•	—
<i>Tricolia insignis</i>	Kwelera, East London, Eastern Cape	170	W3385	•	—
<i>Tricolia insignis</i>	Marshstrand, East London, Eastern Cape	279	W1027	•	—

Species	Collecting localities	DNA extraction #	Museum #	Gene fragment sequenced	
				COI	16S
<i>Tricolia insignis</i>	Marshstrand, East London, Eastern Cape	312	W1027	–	•
<i>Tricolia insignis</i>	Glengariff, East London, Eastern Cape	463	W1019	•	–
<i>Tricolia insignis</i>	Kidd's Beach, Eastern Cape	506	W3195	•	•
<i>Tricolia insignis</i>	Noordhoek, Port Elizabeth, Eastern Cape	507	W3192	•	•
<i>Tricolia kochii</i>	Mpande, Eastern Cape	124	W3218	•	•
<i>Tricolia kochii</i>	Cape Recife, Western Cape	125	W3376	•	•
<i>Tricolia kochii</i>	Reebok Reef, Mossel Bay, Western Cape	126	W4756	•	•
<i>Tricolia kochii</i>	Cape Agulhas, Western Cape	127	W4768	•	•
<i>Tricolia kochii</i>	Mtwalume, KwaZulu–Natal	161	W2310	–	•
<i>Tricolia kochii</i>	Glengariff, East London, Eastern Cape	162	W1021	–	•
<i>Tricolia kochii</i>	Three Sisters, Port Alfred, Eastern Cape	277	W1035	•	–
<i>Tricolia kochii</i>	Three Sisters, Port Alfred, Eastern Cape	308	W1035	–	•
<i>Tricolia kochii</i>	Glengariff, East London, Eastern Cape	473	W1021	•	–
<i>Tricolia kochii</i>	Mtwalume, KwaZulu–Natal	474	W2310	•	–
<i>Tricolia kochii</i>	Shaka's Rock, KwaZulu–Natal	475	W2311	•	•
<i>Tricolia kochii</i>	Umdloti, KwaZulu–Natal	476	W3217	•	–
<i>Tricolia kochii</i>	Jeffrey's Bay, Eastern Cape	524	W3219	–	•
<i>Tricolia kochii</i>	Jeffrey's Bay, Eastern Cape	534	W3219	•	–
<i>Tricolia kraussi</i>	Bordtjies Reef, Western Cape	379	W1544	•	–
<i>Tricolia kraussi</i>	Miller's Point, False Bay, Western Cape	464	W1522	•	•
<i>Tricolia kraussi</i>	Glencairn, False Bay, Western Cape	493	W2576	•	–
<i>Tricolia kraussi</i>	Glencairn, False Bay, Western Cape	522	W2576	•	–
<i>Tricolia neritina</i>	Mossel Bay Point, Western Cape	145	W4760	•	•
<i>Tricolia neritina</i>	Hawston, Western Cape	157	W1534	•	–
<i>Tricolia neritina</i>	Betty's Bay, Western Cape	158	W1536	•	•
<i>Tricolia neritina</i>	Bordtjies Reef, Western Cape	159	W1543	•	•
<i>Tricolia neritina</i>	Cape Agulhas, Western Cape	160	W4767	•	•
<i>Tricolia neritina</i>	Sunny Cove, False Bay, Western Cape	376	W1518	•	–
<i>Tricolia neritina</i>	Robben Island, Western Cape	478	W2580	•	•
<i>Tricolia neritina</i>	Camp's Bay, Western Cape	479	W2570	•	•

Species	Collecting localities	DNA extraction #	Museum #	Gene fragment sequenced	
				COI	16S
<i>Tricolia neritina</i>	Scarborough, Western Cape	480	W2564	•	•
<i>Tricolia neritina</i>	Periwinkle Lane, Port Elizabeth, Eastern Cape	517	W3220	–	•
<i>Tricolia neritina</i>	Periwinkle Lane, Port Elizabeth, Eastern Cape	528	W3220	•	–
<i>Tricolia neritina</i>	Sunny Cove, False Bay, Western Cape	645	W1518	–	•
<i>Tricolia saxatilis</i>	Aliwal Shoal, KwaZulu–Natal	648	W2585	•	•
<i>Tricolia pullus</i>	Gower Peninsula, Limeslade, United Kingdom	541	L6883	–	•
<i>Tricolia pullus</i>	Wembury, Plymouth, United Kingdom	–	AM049358	•	–

Table 3.2. Forward (F) and reverse (R) nucleotide sequences of PCR primers used to amplify two molecular markers in the present study.

Gene	Name of primer	Sequence of primer (5' to 3')	References
CO1	LCO1490 (F)	5'– GGTC AACAAATCATAAAGATATTGG –3'	Folmer <i>et al.</i> (1994)
	HCO2198 (R)	5'– TAAACTTCAGGGTGACCAAAAAATA –3'	Folmer <i>et al.</i> (1994)
	K699 (R)	5'– WGGGGGGTAAACTGTTCATCC –3'	Simon <i>et al.</i> (1994)
	RON (F)	5'– GGAGCYCCWGATATAGCTTTCCC –3'	Simon <i>et al.</i> (1994)
16SrRNA	16SAR(F)	5'– CGCCTGTTTATCAAAAACAT –3'	Palumbi <i>et al.</i> (1991)
	16SBR (R)	5'– CCGGTCTGAACTCAGATCACGT –3'	Palumbi <i>et al.</i> (1991)

3.2.3. Sequence alignment

For each taxon, multiple fragments obtained by sequencing with different primers were edited and assembled using the Staden package 2002.0 (Staden *et al.* 2003) and MEGA 3.0 (Kumar *et al.* 2004). All sequences were aligned using the Multiple Sequence Alignment programme MAFFT version 6 (Kato 2009). As expected for a protein-coding gene COI sequences required no insertion of gaps and this was checked prior to any phylogenetic analyses. No stop codons were present either. Due to the stem-loop structure of the 16S rDNA gene, MAFFT optimised the placement of gaps. Gaps were treated as missing data in all analyses. Following sequence alignment and the insertion of gaps (where applicable), sequence lengths were 636 bp for COI (Appendices 3.1) and 634 bp for 16S rRNA (Appendices 3.2) genes, respectively.

3.2.4. Phylogenetic analysis

Phylogenetic analysis included several individuals from different localities to represent each southern African *Tricolia* species when available. For some species, such as *T. bicarinata* and *T. saxatilis*, which are rarely found alive, I was unable to include many individuals.

Maximum likelihood analyses were performed using the fast maximum likelihood algorithm as implemented in the programme RaxML (Randomized accelerated maximum likelihood, Stamatakis *et al.* 2008). The general time-reversible (GTR) model plus a gamma shape parameter (Γ) were implemented to account for rate heterogeneity. Clade support was estimated by computing 100 nonparametric bootstrap pseudoreplicates.

During the preliminary analyses of this study, it was discovered that *T. capensis* and *T. africana*, as well as *T. bicarinata*, *T. insignis* and *T. kraussi* form two species complexes with very low maximum sequence divergence among the respective taxa. According to Posada & Crandall (2001) network approaches are more effective than classical phylogenetic methods for representing intraspecific evolution or among closely related species where it cannot be assumed that the ancestral phenotype went extinct, an explicit assumption of all tree-based phylogenetic methods. As a consequence haplotype networks of the mitochondrial COI and 16S sequences for the two rapidly diverging *Tricolia* clades: clade 1 represented by *T. africana* and *T. capensis*; and clade 2 represented by *T. insignis*, *T. kraussi* and *T. bicarinata* were estimated using the statistical parsimony method (Templeton *et al.* 1992) implemented in the program TCS version 1.13 (Clement *et al.* 2000). The method links haplotypes with the smallest number of differences as defined by a 95% confidence criterion.

3.3. RESULTS

3.3.1. Cytochrome–Oxidase subunit I (COI)

The aligned COI data matrix (Appendices 3.1) contained 80 specimens and 636 characters. Maximum likelihood recovered seven distinct clades within the endemic southern African *Tricolia* species (Fig. 3.1). The COI analysis supports the recognition of *T. elongata* (clade 2, bootstrap support value = 100%) (BS), *T. neritina* (clade 3, BS=98%), *T. kochii* (clade 5, BS=91%), *T. formosa* (clade 6, BS=100%), *T. saxatilis* (clade 7) as independent valid species in agreement with my earlier morphological analyses. However, the COI phylogeny did not support *T. africana* and *T. capensis* as two distinct species, instead they cluster together within a strongly supported, clade 1 (BS=100%). The COI phylogeny recovered *T. bicarinata*, *T. insignis* and *T. kraussi* as a single, but mixed group, clade 4 (BS=77%). The monophyly of the southern African *Tricolia* species relative to *T. pullus* was not supported in the COI dataset (BS < 50%).

3.3.2. 16S rRNA

The aligned 16S rRNA data matrix (Appendices 3.2) contained 72 specimens and 634 characters. As for the COI dataset, the 16S maximum likelihood phylogeny recovered seven distinct clades within the southern African *Tricolia* species (Fig. 3.2). The 16S analysis supports *T. elongata* (clade 2, BS=88%), *T. neritina* (clade 3, BS=99%), *T. kochii* (clade 5, BS=100%), *T. saxatilis* (clade 7), as independent valid species. *Tricolia adusta* (for which COI data was not available) was recovered as sister to *T. formosa*, clade 6 (BS=100%). *Tricolia bicarinata*, *T. insignis* and *T. kraussi* were again recovered as a mixed group, clade 4 (BS=98%), as were *T. africana* and *T. capensis*, clade 1, but with no support (BS=<50%). As in the COI phylogeny, the monophyly of the southern African *Tricolia* species relative to *T. pullus* was not supported (BS < 50%).

3.3.3. Combined COI and 16S datasets

The aligned COI and 16S rRNA data matrix contained 61 specimens and 1270 characters. As for the individual gene datasets above, the combined mtDNA maximum likelihood phylogeny recovered seven distinct clades within the southern African *Tricolia* species assemblage (Fig. 3.3). The combined analysis supports *T. elongata* (clade 2, BS=100%), *T. neritina* (clade 3, BS=100%), *T. kochii* (clade 5, BS=96%), *T. saxatilis* (clade 7), as independent valid species. *Tricolia adusta* was recovered as sister to *T. formosa*, clade 6

(BS=100%). *Tricolia bicarinata*, *T. insignis* and *T. kraussi* were again recovered as a mixed group, clade 4 (BS=94%), as were *T. africana* and *T. capensis*, clade 1 (BS=100%). As in the COI and 16S phylogenies, the monophyly of the southern African *Tricolia* species relative to *T. pullus* was not supported (BS <50%).

3.3.4. Haplotype network

The network analysis of 29 COI sequences from 15 specimens of *T. africana* and 14 specimens of *T. capensis* is presented in Fig. 3.4. Network analysis recovered 15 haplotypes, 12 of which are represented by a single individual, one by two individual, one by nine individual and one by six individual. Network analysis of *T. bicarinata*, *T. insignis* and *T. kraussi* complex recovered 13 haplotypes (Fig. 3.5). Haplotype 169_*T. insignis* is represented by three individuals whereas haplotype 111_*T. insignis* is represented by two individuals. All other haplotypes are represented by a single individual. There was no evidence of *T. capensis* or *T. africana* forming distinct groupings within the network; rather haplotypes from the two taxa were intermixed. Similarly, although significant genetic variation exists within the *T. bicarinata*/*T. insignis*/*T. kraussi* complex, taxa do not form distinct subnetworks.

Haplotype network analysis of *T. africana* complex based on the 16S dataset recovered seven haplotypes (Fig. 3.6) with 100_*T. africana* represented by 20 individuals and 129_*T. capensis* by two individuals. The other haplotypes are represented by a single individual. Network analysis of *T. bicarinata*, *T. insignis* and *T. kraussi* complex based on the 16S dataset recovered four haplotypes (Fig. 3.7) with 110_*T. insignis* represented by seven individual specimens. Haplotypes 112_*T. insignis* and 312_*T. insignis* are both represented by two individuals and 464_*T. kraussi* is represented by a single individual. As for the COI dataset there is no evidence of members of either complex forming distinct groupings within the network, rather lineages seem to be intermixed.

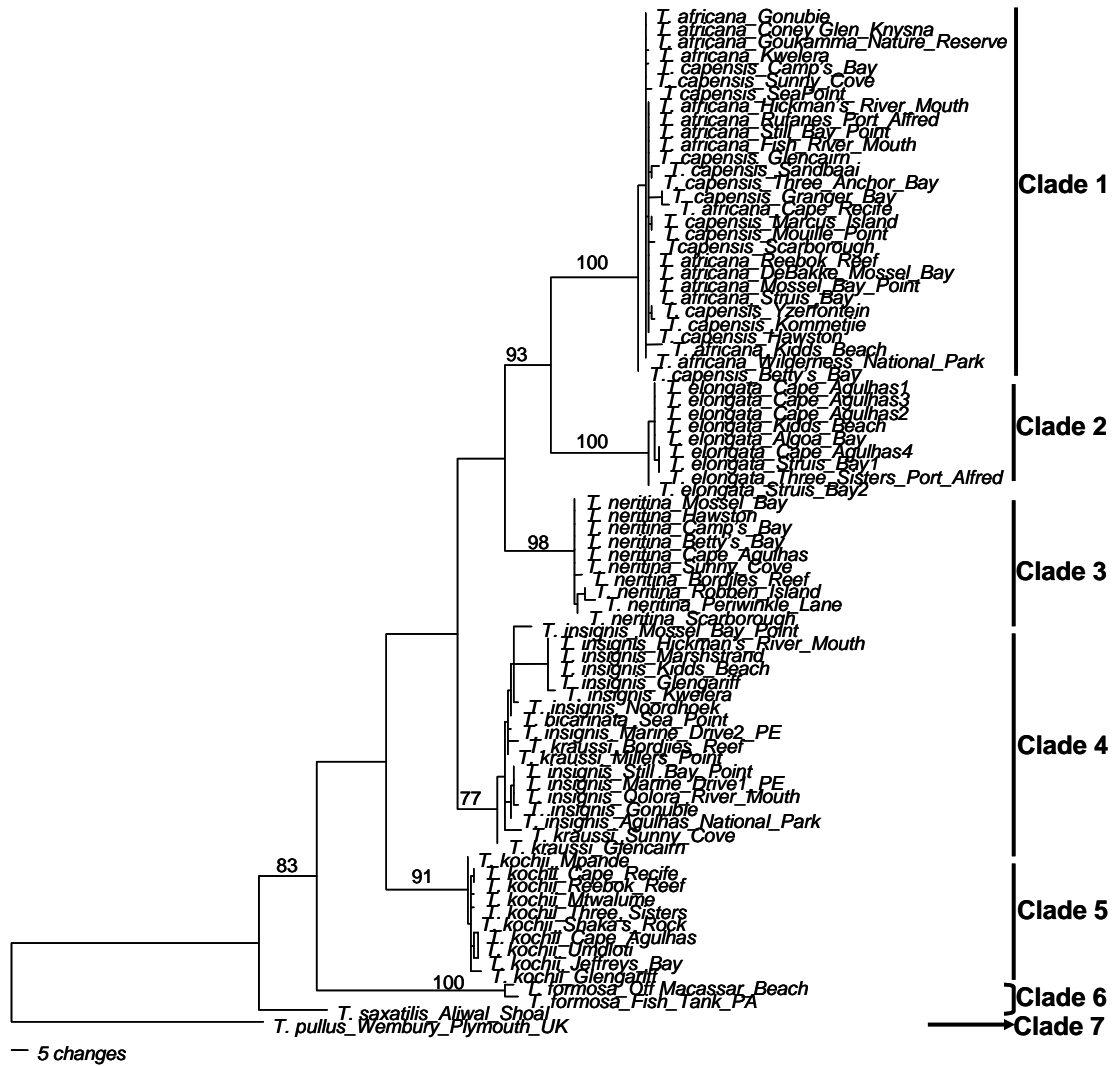


Figure 3.1. Best maximum likelihood tree constructed from mtDNA COI sequence data. Clade 1, *Tricolia africana* and *T. capensis*; Clade 2, *T. elongata*; Clade 3, *T. neritina*; Clade 4, *T. bicarinata*, *T. insignis* and *T. kraussi*; Clade 5, *T. kochii*; Clade 6, *T. formosa*, Clade 7, *T. saxatilis*. Values above nodes are bootstrap values.

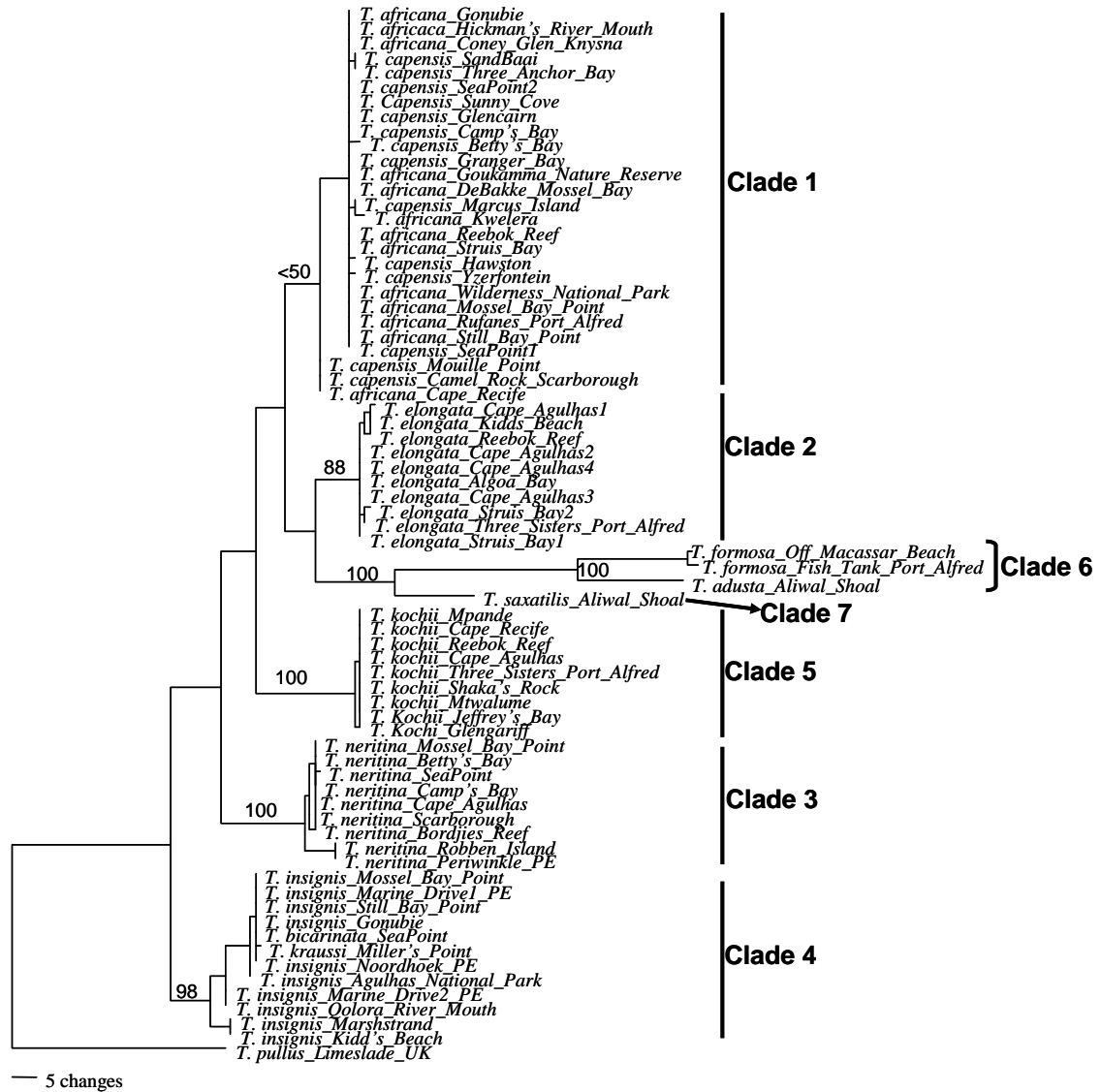


Figure 3.2. Best maximum likelihood tree constructed from mtDNA 16S rRNA sequence data. Clade 1, *Tricolia africana* and *T. capensis*; Clade 2, *T. elongata*; Clade 3, *T. neritina*; Clade 4, *T. bicarinata*, *T. insignis* and *T. kraussi*; Clade 5, *T. kochii*; Clade 6, *T. formosa*; Clade 7, *T. saxatilis*. Values above nodes are bootstrap values.

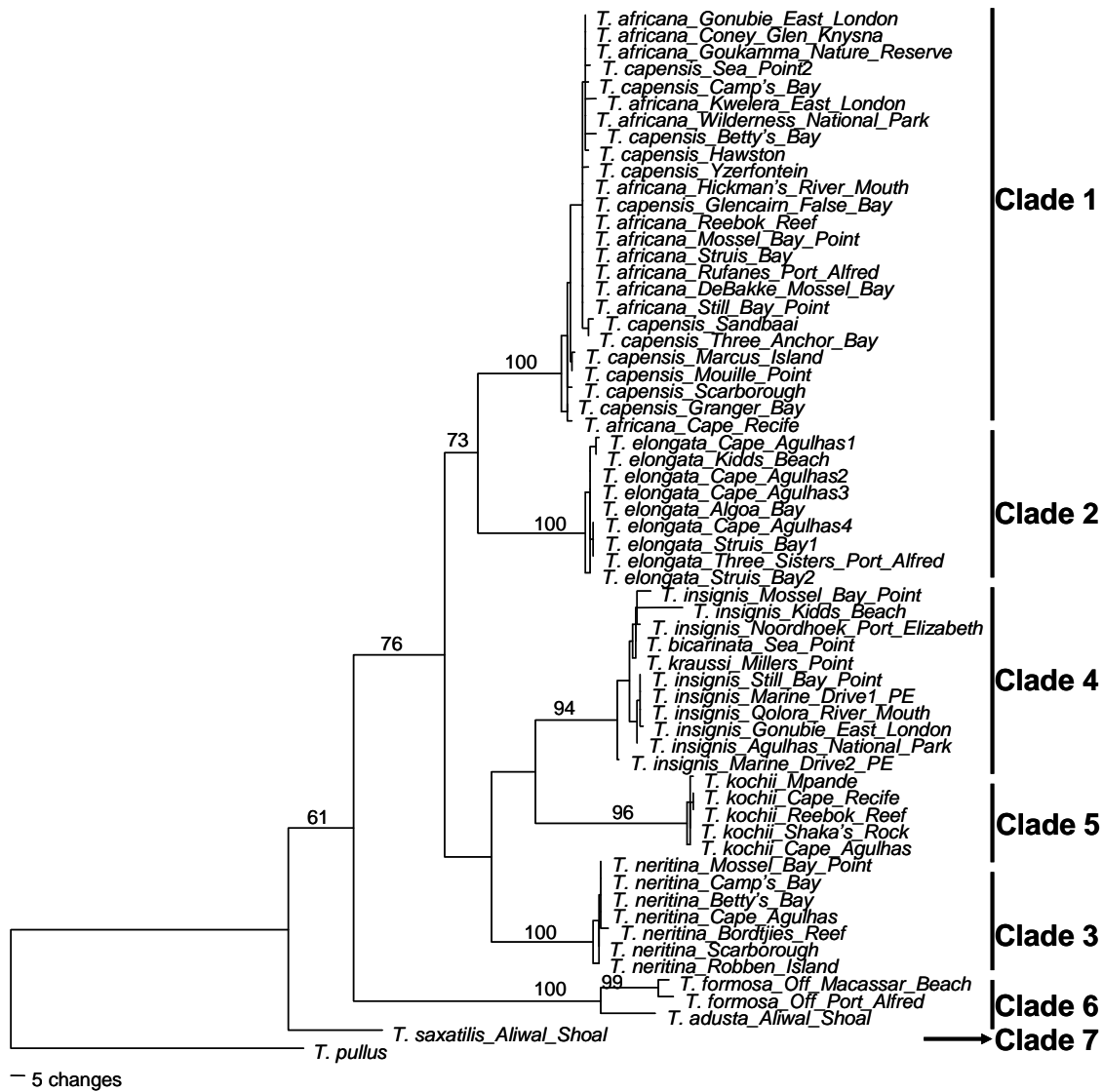


Figure 3.3. Best maximum likelihood tree constructed from the combined COI and 16S rRNA sequence data. Clade 1, *Tricolia africana* and *T. capensis*; Clade 2, *T. elongata*; Clade 3, *T. neritina*; Clade 4, *T. bicarinata*, *T. insignis* and *T. kraussi*; Clade 5, *T. kochii*; Clade 6, *T. formosa*; Clade 7, *T. saxatilis*. Values above nodes are bootstrap values.

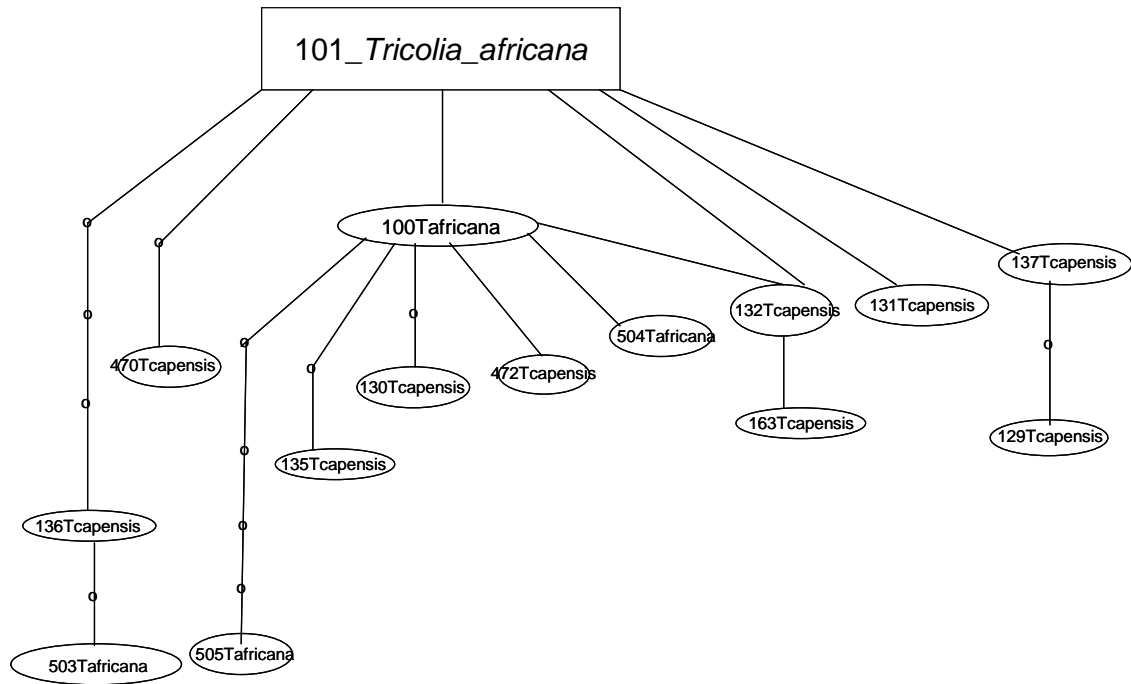


Figure 3.4. TCS haplotype network of *T. africana* and *T. capensis* based on COI sequence data. The square represents the haplotype identified as basal. The extent of the circle indicates the relative number of individuals with that haplotype. Each line represents a single nucleotide substitution and each dot indicates an unsampled or extinct intermediate haplotype.

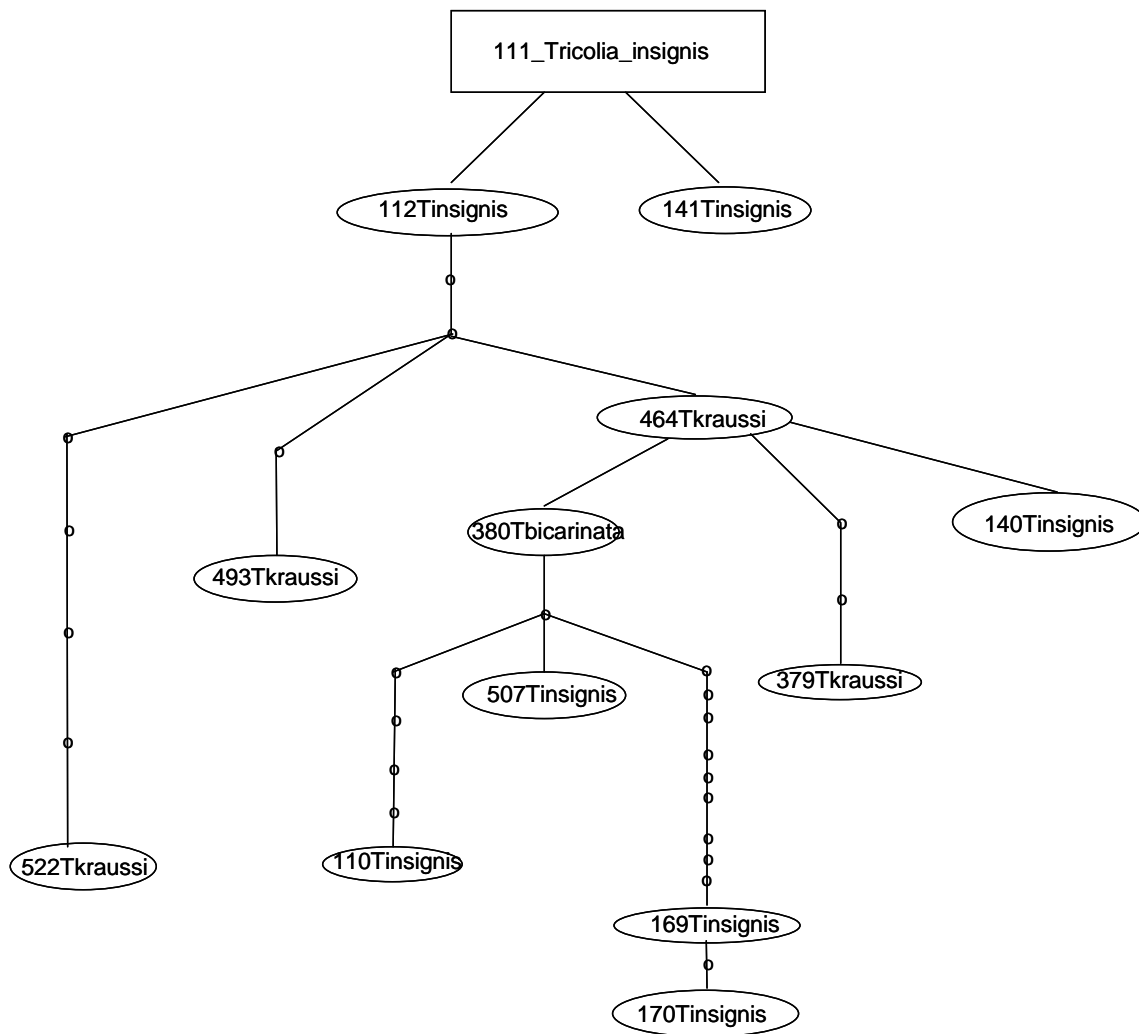


Figure 3.5. TCS haplotype network of *T. bicarinata*, *T. insignis* and *T. kraussi* based on COI sequence data. The square represents the haplotype identified as basal. The extent of the circle indicates the relative number of individuals with that haplotype. Each line represents a single nucleotide substitution and each dot indicates an unsampled or extinct intermediate haplotype.

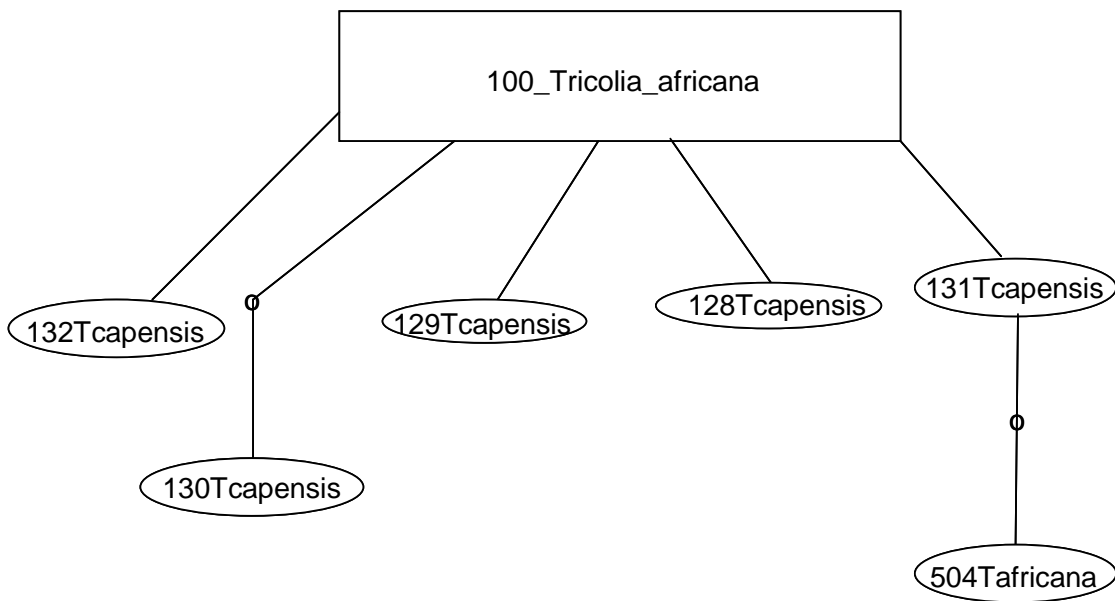


Figure 3.6. TCS haplotype network of *T. africana* and *T. capensis* based on 16S rRNA sequence data. The square represents the haplotype identified as basal. The extent of the circle indicates the relative number of individuals with that haplotype. Each line represents a single nucleotide substitution and each dot indicates an unsampled or extinct intermediate haplotype.

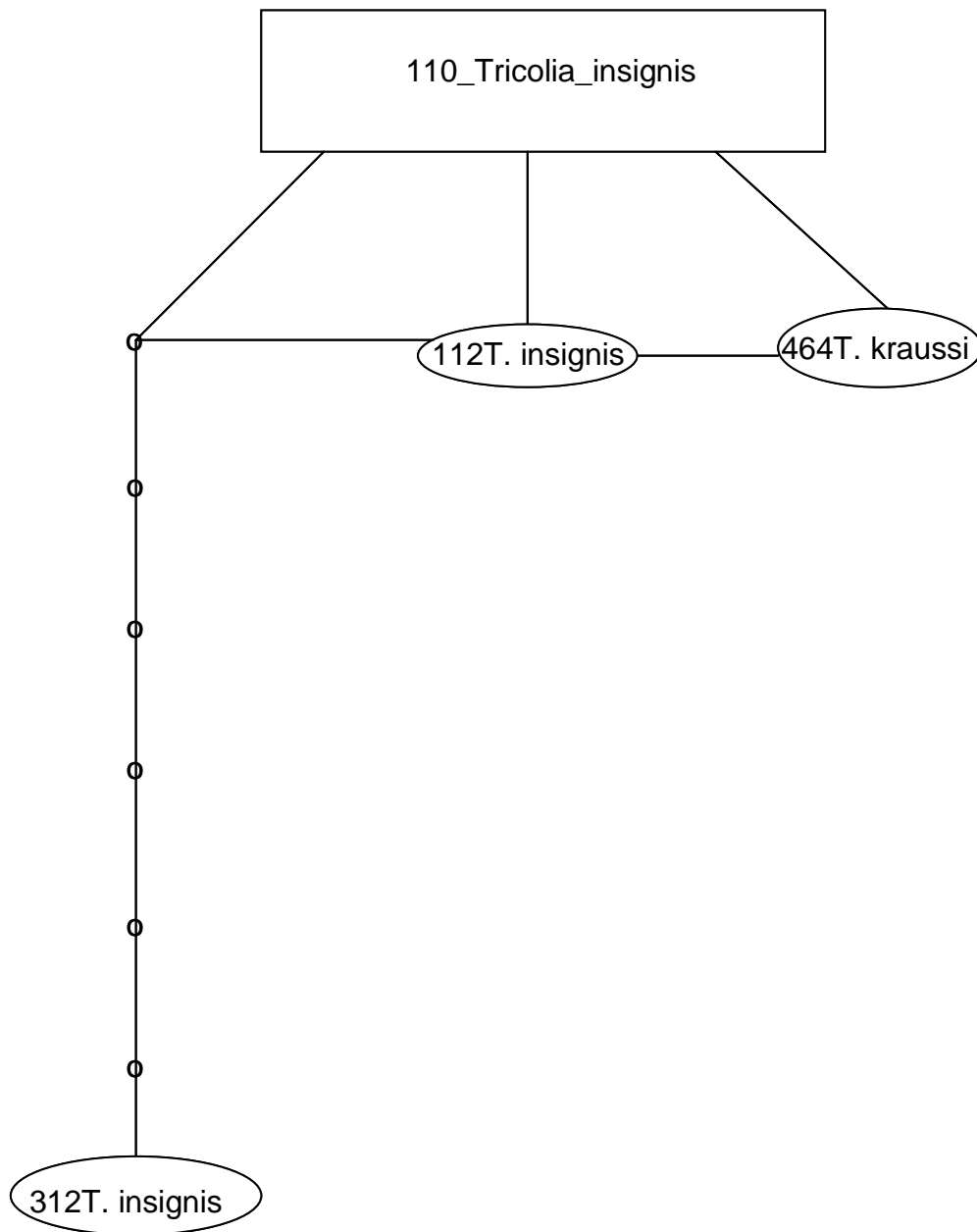


Figure 3.7. TCS haplotype network of *T. bicarinata*, *T. insignis* and *T. kraussi* based on 16S RNA sequence data. The square represents the haplotype identified as basal. The extent of the circle indicates the relative number of individuals with that haplotype. Each line represents a single nucleotide substitution and each dot indicates an unsampled or extinct intermediate haplotype.

3.4. DISCUSSION

3.4.1. Comparison among COI, 16S and the combined datasets

To date, many studies have focused on the mitochondrial genome, mainly at the level of DNA sequences. This is due to its fast rate of evolution relative to nuclear DNA (i.e., Brown *et al.* 1979, Pesole *et al.* 1999, Avise 2000), making mtDNA particularly suited to studies at lower taxonomic levels, for example within genera (i.e., Moritz *et al.* 1987, Moore & DeFilippis 1997, Hewitt 2001, Zink & Barrowclough 2008). Thus, analysis of mtDNA data allows resolution of species in many groups that are otherwise difficult to resolve. Newly formed species in the absence of selection are expected to become distinct in their mtDNA haplotype phylogenies long before they become distinct in nuclear based markers (Zink & Barrowclough 2008) as a consequence of the faster coalescent time of mtDNA. From a practical perspective, mitochondrial DNA is also relatively easy to PCR amplify and sequence due to the availability of universal primers (Palumbi 1996, Quinn 1997).

In this study, the mitochondrial COI phylogeny provided good evidence that species identified on conchological grounds in chapter 2 are in fact real entities. The COI datasets recovered seven distinct clades within the southern African *Tricolia* species. *Tricolia adusta*, *T. elongata*, *T. formosa*, *T. kochii*, *T. saxatilis* and *T. neritina* were recovered as distinct species. However, the COI analysis failed to discriminate between *T. africana* and *T. capensis*, as well as among *T. bicarinata*, *T. insignis* and *T. kraussi* as genetically distinct species. The fact that COI could not discriminate between these species is interesting and draws attention to a taxonomic issue.

The mitochondrial ribosomal RNA markers are argued to be the most conserved markers in the mitochondrial genome, but still evolve much more rapidly than the nuclear ribosomal RNA markers (Hillis & Dixon 1991). Phylogeny based on the mtDNA 16S rRNA marker were congruent with the COI in recovering seven southern African *Tricolia* clades. However, the 16S dataset failed to support the relationship between *T. africana* and *T. capensis*.

There is much disagreement as to whether different datasets should be combined or analyzed separately in phylogenetic inference (Huelsenbeck *et al.* 1996, Nixon & Carpenter 1996, Wiens 1998). My analysis of the combined dataset was congruent with the individual analysis of the COI and 16S datasets in recovering seven distinct clades within the southern African *Tricolia* species, and also failed to discriminate between *T. africana* and *T. capensis*, as well as among *T. bicarinata*, *T. insignis* and *T. kraussi*. However, bootstrap analysis

results between *T. africana* and *T. capensis* was 100% in both the COI and the combined analyses, with no support in the 16S analysis. The COI and the combined datasets further support the relationship between clade 1 (*T. africana* and *T. capensis*) and clade 2 (*T. elongata*) by 73 and 93% respectively. The relationship between clades 1 and 2 to clades 3, 4 and 5 received 76% bootstrap support. The relationship between clades 3, 4, and 5 to clade 6 was supported by 61%. Monophyly of the endemic southern African *Tricolia* radiation was not supported in all three analyses, as well as the relationship between these and the European species *T. pullus*. In order to determine whether the southern African *Tricolia* species are monophyletic or not, further analysis with additional members of the Tricoliinae from South Australia, the Indo–West Pacific, East Africa and Japan is required. In addition to increased taxon sampling, the use of slower evolving nuclear markers (28S and 18S) may help resolve the more basal branches within the radiation with support. These approaches are adopted and discussed in chapter 4 of this thesis.

3.4.2. The validity of the described nominal *Tricolia* species in southern African

In this study, the mitochondrial COI, 16S rRNA and the combined maximum likelihood phylogenies recovered seven distinct clades within the endemic southern African *Tricolia* species. Even though the mitochondrial markers failed to discriminate between *T. capensis* and *T. africana*, as well as among *T. bicarinata*, *T. insignis* and *T. kraussi*, they were able to discriminate *T. adusta*, *T. elongata*, *T. formosa*, *T. kochii* and *T. neritina* as distinct operational taxonomic units (OTUs). The fact that *T. neritina* clustered within the southern African *Tricolia* species further supports *Chromotis* as a junior synonym of *Tricolia sensu stricto*. This is good evidence suggesting that for the most part the morphological discrimination of species in chapter 2 was based on sound diagnostic characters.

In this study, some of the morphologically distinct species identified in chapter 2 clustered as mixed species clades, and the level of sequence divergence within these clades was low. There are two competing hypotheses regarding conflict in genetics and morphological data of these species. These hypotheses are either that these taxa present examples of recent speciation with incomplete lineage sorting or alternatively that the taxa represent a single species with morphological polymorphism (i.e., shell form and colouration) reflecting adaptation to different environmental conditions. Intraspecific phenotypic plasticity is common in many marine invertebrates and, is generally correlated with different environmental conditions (Teske *et al.* 2007). This creates what might in reality be phenotypically diagnosable ecomorphs, rather than evolutionary distinct species. For example, *Gibbula capensis* (Gmelin, 1791) specimens found on the west coast of South

Africa tend to be less boldly marked, and generally more greyish as compared to those found on the south coast (Cape Agulhas) (TC Nangammbi 2006, personal observation).

In chapter 2, *T. capensis* and *T. africana* were regarded as two separate species based on morphological characters of the shell, microhabitat preferences and distribution range. In terms of shell characters, *T. africana* is more elongate and has a higher spire, a proportionately smaller and more circular aperture, more convex whorls and frequently has light blue spots below the suture. In contrast, *T. capensis* is broad and thick with evenly rounded whorls and lacks the subsutural spots. In addition, the two species differ in terms of their habitat preferences: *T. africana* lives on and under rocks in mid-shore pools, whereas *T. capensis* occurs amongst seaweed in low-tide pools. Furthermore, the two species are geographically separated: *T. africana* is a warm-temperate south coast species ranging from the Eastern Cape (Transkei, Qora River mouth) to the southern Cape (Struis Bay near Cape Agulhas), whereas *T. capensis* is essentially a cool-temperate west coast taxon, ranging from the south-western Cape (Hermanus) to Namibia (Kunene River mouth). The ranges of the two species are separated by a distance of ca 85 km in the Western Cape, between Cape Agulhas and Hermanus. This might be a true gap that exists between the two species or might be an artificial gap due to insufficient sampling between Cape Agulhas and Hermanus.

In this chapter, the two species are indistinguishable based on DNA sequence data from the mtDNA COI, 16S markers and the combined datasets. One possible explanation why the two species are clustered within a single clade could be due to incomplete sorting of ancestral polymorphisms after recent speciation. This result was based on mitochondrial markers, which are maternally inherited and haploid (Gyllensten *et al.* 1985, Watanabe *et al.* 1985, Berlin & Ellegren 2001), and due to these factors, have a rapid rate of lineage sorting (four-fold faster than nuclear markers) (Avice 2004). Since the mtDNA failed to discriminate between the species, this suggests that these species are unlikely to be phylogenetically separable with any conventional genetic marker. However, it may be possible to distinguish these species reliably using population genetic differences (particularly in the occurrence of private alleles) using even faster evolving markers such as nuclear microsatellites. Microsatellites (short tandem polynucleotide repeats) are highly variable due to their rapid mutation rate. Although microsatellites have the same coalescent times as other nuclear markers, their higher mutation rate offers greater potential to identify genetic patterns that arose very recently.

However, even if fast evolving markers do not distinguish *T. capensis* and *T. africana* this can still be understood as recent speciation with rapid morphological and ecological divergence co-incident with geographical separation. It is possible that the morphological and ecological differences observed between these forms could be explained by ecotypic variation. Given the geographical separation between them it is also unlikely that the sharing of genes is due to ongoing hybridization. However, based on molecular results, I strongly suggest that the two species should be synonyms, but I choose not to formally synonymise them in this thesis due to the need for formal integration of morphology with molecular data, which is beyond the scope of this chapter.

There is also very little genetic differentiation between *T. bicarinata*, *T. insignis* and *T. kraussi*. The three species represent a single species since they are conchologically similar with intergrading shell characters. For example, *T. bicarinata* and *T. insignis* are biangulate with numerous close-set spiral ridges on the body whorl and *T. kraussi* is slightly angulate with very fine spiral threads. Precisely why *T. kraussi* should differ from the other species in this way is perhaps due to differing environmental effect related to the sheltered False Bay coast.

The three species comprising this unresolved clade have a parapatric geographical distribution: *T. bicarinata* is a cool-temperate west coast species, *T. insignis* is a warm-temperate south coast species, and *T. kraussi* is both ecologically and geographically intermediate, occurring in False Bay, on the eastern side of the Cape Peninsula. This distribution coincides with two of the three marine biogeographical provinces and water temperature is suspected to have the strongest influence on this biogeographical division (Stephenson & Stephenson 1972). The distribution of each species has shown regional adaptation to the different environmental conditions prevalent in each biogeographic province. The molecular data strongly suggest that these three species form a closely related, monophyletic group and might even be one species exhibiting ecogeographic variation in shell form.

The three species hypothesis could be tested by performing translocation experiments between *T. bicarinata* and *T. insignis* under False Bay environmental conditions. Small individuals or juvenile specimens of both species could be reared or placed under False Bay environmental conditions in the laboratory to see what the hybrids or cross-fostered offspring would look like. One possible result is that they may produce red, green or pink offspring with perhaps very fine spiral sculpture on the early whorls and the sculpture might become

smooth towards the last body whorl as in *T. kraussi*. The second alternative to test the three species hypothesis is by performing crossbreeding experiments and see if the three species can actually interbreed with each other. However, the logistics of actually performing the proposed experiments can be difficult. A third alternative would be to sequence more rapidly evolving nuclear markers such as microsatellites to see if any finer scale patterns of spatial structure can be detected. The three taxa (*T. bicarinata*, *T. insignis* and *T. kraussi*) are synonyms and also an example of ecotypic variation that may with time lead to speciation, but as for *T. africana* and *T. capensis*, I choose not to formally synonymise them in this thesis.

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APPENDICES

Appendix 3.1. mtDNA COI sequence alignment using the Multiple Sequence Alignment programme MAFFT version 6.

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103Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
104Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
105Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
106Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
107Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
108Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
109Tafrica TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
110Tinsign TTATACTTGATTTTTGGTATTTGATCAGGGCTTATTGGTACTGCTTTGAGGTTGCTTATT
111Tinsign TTATACTTGATTTTTGGTATTTGATCAGGGCTTATTGGTACTGCTTTGAGGTTGCTTATT
112Tinsign TTATACTTGATTTTTGGTATTTGATCAGGGCTTATTGGTACTGCTTTGAGGTTGCTTATT
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125Tkochii TTATACCTAATTTTTGGAATTTGATCAGGGCTGATTGGTACTGCTTTAAGACTATTAATT
126Tkochii TTATACCTAATTTTTGGAATTTGATCAGGGCTGATTGGTACTGCTTTAAGACTATTAATT
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464Tkrauss TTATACTTGATTTTTGGTATTTGATCAGGGCTTATTGGTACTGCTTTGAGGTTGCTTATT

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 470Tcapens TTATATTTGATTTTTGGTATTTGATCAGGGCTTATCGGTACTGCTTTGAGGCTACTTATT
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 648Tsaxati ACTTTTTTTGACCCGGCAGGGGGAGGGGATCCATTAA
tpAM049358 AGGTTTTTTGACCCGGCAGGAGGGGGAGATCCATTTT

Appendix 3.2. mtDNA 16S rRNA sequence alignment using the Multiple Sequence Alignment programme MAFFT version 6.

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CHAPTER 4: A MOLECULAR PHYLOGENY OF THE PHEASANT SHELL GENERA BASED ON MITOCHONDRIAL AND NUCLEAR SEQUENCE DATA

ABSTRACT

A molecular phylogeny based on sequence data from mitochondrial markers (COI, 16S rRNA), nuclear markers (18S rRNA, 28S rRNA) and the combined dataset (COI, 16S, 18S, and 28S) is presented for the Phasianelloidea, including representative species from its five currently recognised genera *Tricolia*, *Hiloa*, *Eulithidium*, *Phasianella* and *Gabrielona*. A bayesian inference analysis performed on combined nuclear data support the monophyly of the genera *Eulithidium*, *Phasianella* and *Tricolia sensu stricto*. *Tricolia sensu lato* is not monophyletic, as its southern Australian and the Indo–West Pacific species do not cluster with its southern African and Eastern Atlantic representatives. Traditionally, the southern Australian, the Indo–West Pacific species, *Hiloa* and *Eulithidium* were grouped under *Tricolia sensu lato*. However, molecular data suggest that each represent a distinct lineage. This separation is also supported by morphological characters of the shell, operculum, radula and external anatomy. On the basis of these morphological characteristics, *Eulithidium* should be assigned to a subfamily of its own. *Phasianella* is the sister taxon to *Tricolia sensu stricto*, and monophyly of this genus is also supported by morphological characters of the shell, radula, external anatomy and the number of shell muscles. The position of *Hiloa* and *Gabrielona* within the Phasianelloidea is unresolved. Phylogenetic reconstructions using bayesian inference based on the 28S and 18S combined sequence data support monophyly of the Phasianelloidea.

4.1. INTRODUCTION

Phylogenetic analysis in chapter 3 divided the southern African *Tricolia* species into seven major clades and also failed to support the monophyly of the southern African *Tricolia* radiation relative to the East Atlantic species *Tricolia pullus*. In the present chapter, I assess phylogenetic relationships and biogeographical affinities of the southern African members belonging to *Tricolia* based on the same two mitochondrial markers, as well as the nuclear 18S and 28S rRNAs. In so doing, I aim to test whether the southern African species of *Tricolia* are monophyletic by investigating the phylogenetic relationship among the species from this region as well as their affinities with *Tricolia* species from Eastern Atlantic, East Africa, Indo–West Pacific and southern Australia. Secondly, I assess the validity of the available supraspecific names within *Tricolia sensu lato* and establish to which of these the southern African species belong.

Finally, I investigate phylogenetic relationships of *Tricolia sensu lato* with three other genera in the Phasianelloidea, namely *Eulithidium*, *Phasianella* and *Gabrielona*. A molecular phylogenetic study by Williams and Ozawa (2006) on the Turbinidae established that the Phasianelloidea forms a monophyletic assemblage. However, their study did not include representative members from all genera of the Phasianelloidea (*Eulithidium* was not represented), nor did it include members of *Tricolia* from southern Australia and southern Africa.

4.2. MATERIALS AND METHODS

4.2.1. Taxon sampling

Table 4.1 details all the taxa studied and includes collection localities, DNA extraction numbers, museum accession numbers and details of molecular markers sequenced. The following additional *Tricolia* samples were obtained, three species endemic to the tropical Indo–West Pacific region, *T. fordiana*, *T. ios* and *Hiloa variabilis*, two southern Australian species, *T. tomlini* and *T. rosea*, and one Eastern Atlantic species (the type species of the genus) *T. pullus*. *Eulithidium* from the Eastern Pacific and Western Atlantic is represented by *E. perforatum*, *E. affine* and *E. bellum*. Two further genera from the tropical Indo–West Pacific and southern Australia, *Phasianella* and *Gabrielona* are represented by the following taxa: *P. australis*, *P. solida*, *P. variegata*, *Phasianella* species (unidentified) and *G. pisinna*, respectively.

Voucher specimens of additional comparative material of *Tricolia*, *Hiloa*, *Eulithidium*, *Phasianella* and *Gabrielona* were provided on loan and are deposited in the different museums listed in the acknowledgements. Additional sequences of ingroup and outgroup taxa for mitochondrial COI, nuclear 18S rRNA and 28S rRNA were obtained from GenBank, with accession numbers listed in Table 4.2. Ten species from five closely related genera (*Bothropoma*, *Collonista*, *Homalopoma*, *Cinysca* and *Turbo*) were used as outgroup taxa, selected on the basis of the results from Williams and Ozawa (2006) since these taxa are placed as the sister-group to the pheasant shell genera. The total taxon sample for this study consisted of 36 species including the outgroup taxa.

4.2.2. Laboratory protocols

Genomic DNA was isolated with the DNeasy Tissue Kit (Qiagen), SV Total RNA Isolation System (Promega) or by using an ammonium acetate (Nicholls *et al.* 2000) extraction protocol as described in chapter 3. Amplifications and DNA sequencing of the mitochondrial COI and 16S rRNA were performed using the methods described in chapter 3. Amplifications of the nuclear 28S rRNA were performed with forward primer LSU2 and reverse primer LSU4 (Wade & Mordan 2000). The nuclear 18S rRNA amplifications were achieved with forward primer 18S5 (Winnepenninckx *et al.* 1998) and reverse primer 18S1100 (Williams *et al.* 2003). The primer information is presented in Table 4.3. PCR reactions and sequencing were carried out as described in chapter 3. However, annealing temperatures were 50°C for 18S rRNA and 58°C for the 28S rRNA gene.

Table 4.1. List of samples used in this study with collecting localities, DNA extraction numbers, museum accession numbers and molecular markers sequenced.

Species	Collecting localities	DNA extraction #	Museum #	Molecular markers sequenced			
				C01	16S	18S	28S
<i>Tricolia adusta</i>	off Phumula, KwaZulu–Natal	483	W2586	–	–	•	•
<i>Tricolia adusta</i>	Aliwal Shoal, KwaZulu–Natal	482	W2584	–	•	–	–
<i>Tricolia africana</i>	Rufanes, Port Alfred, Eastern Cape	374	W1034	•	•	•	–
<i>Tricolia africana</i>	Rufanes, Port Alfred, Eastern Cape	278	W1034	–	–	–	•
<i>Tricolia bicarinata</i>	Sea Point, Western Cape	380	W1528	•	•	•	•
<i>Tricolia capensis</i>	Scarborough, Western Cape	470	W2563	•	•	•	•
<i>Tricolia elongata</i>	Three Sisters, Port Alfred, Eastern Cape	375	W1036	•	•	•	•
<i>Tricolia formosa</i>	off Macassar Beach, Western Cape	481	W2581	•	•	•	•
<i>Tricolia insignis</i>	Marshstrand, East London, Eastern Cape	279	W1027	•	–	–	–
<i>Tricolia insignis</i>	Marshstrand, East London, Eastern Cape	312	W1027	–	•	•	•
<i>Tricolia ios</i>	¼ Mile Reef, Sodwana Bay, KwaZulu–Natal	604	W5572	•	–	•	•
<i>Tricolia kochii</i>	Three Sisters, Port Alfred, Eastern Cape	277	W1035	•	–	–	•
<i>Tricolia kochii</i>	Three Sisters, Port Alfred, Eastern Cape	308	W1035	–	•	•	–
<i>Tricolia kraussi</i>	Miller's Point, False Bay, Western Cape	464	W1522	•	•	•	•
<i>Tricolia neritina</i>	Sunny Cove, False Bay, Western Cape	376	W1518	•	–	•	•
<i>Tricolia neritina</i>	Sunny Cove, False Bay, Western Cape	645	W1518	–	•	–	–
<i>Tricolia saxatilis</i>	Aliwal Shoal, KwaZulu–Natal	648	W2585	•	•	•	•
<i>Tricolia pullus</i>	Gower Peninsula, Limeslade Bay, United Kingdom	541	L6883	–	•	–	–
<i>Tricolia fordiana</i>	Houtman Abrolhos Island, Western Australia	468	L7356	•	•	•	–
<i>Tricolia rosea</i>	Jurien Bay, Western Australia	635	WAM S29227	•	–	•	–

Species	Collecting localities	DNA extraction #	Museum #	Molecular markers sequenced			
				C01	16S	18S	28S
<i>Tricolia rosea</i>	Jurien Bay, Western Australia	649	WAM S29227	–	–	–	•
<i>Tricolia tomlini</i>	off Cervantes, Western Australia	634	WAM S16030	•	–	•	–
<i>Tricolia tomlini</i>	off Cervantes, Western Australia	633	WAM S16030	–	–	–	•
<i>Hiloa variabilis</i>	Tuamotu Archipelago, Rangiroa, United States	488	356951	–	•	–	–
<i>Gabrielona pisinna</i>	Hamelin Bay, Western Australia	637	WAM S29215	•	–	–	–
<i>Phasianella australis</i>	Cervantes, Western Australia	642	WAM S15954	–	•	–	–
<i>Phasianella solida</i>	2 Mile Reef, Sodwana Bay, KwaZulu–Natal	487	W3388	–	•	–	–
<i>Phasianella variegata</i>	Jurien Bay, North Essex, Western Australia	632	WAM S15989	•	–	–	–
<i>Phasianella</i> species	Jurien Bay, inside Favorite Island, Western Australia	643	WAM S15986	•	–	–	–
<i>Eulithidium perforatum</i>	Punta Chile, Mazatlan, Mexico	543	L7036	•	•	–	•
<i>Eulithidium bellum</i>	Oceanside of Snake Creek, Florida	646	308186	–	–	•	•
<i>Eulithidium affine</i>	Jewfish Basin, Lower Florida, Western Atlantic	638	308190	–	–	–	•
<i>Cinysca dunkeri</i>	Rufanes, Port Alfred, Eastern Cape	286	W1037	•	•	•	–
<i>Turbo cidaris</i>	Marshstrand, East London, Eastern Cape	309	W1023	•	•	•	•
<i>Turbo coronatus</i>	Marshstrand, East London, Eastern Cape	310	W1025	•	•	•	•
<i>Turbo sarmaticus</i>	Glengariff, East London, Eastern Cape	311	W1020	•	•	•	•

Table 4.2. List of samples, localities and accession numbers of mitochondrial COI, nuclear 18S and 28S rRNA sequences downloaded from GenBank.

Species	Collecting localities	GenBank Accession numbers		
		COI	18S	28S
<i>Tricolia pullus</i>	Wembury, Plymouth, United Kingdom	AM049358	AM048661	AM048722
<i>Tricolia (Hiloa) aff. variabilis</i>	Senda, Chiba Prefecture, Japan	AM049359	AM048662	AM048723
<i>Gabrielona pisinna</i>	Aguni Island, Okinawa Prefecture, Japan	–	AM048660	AM048721
<i>Phasianella australis</i>	Esperance Bay, Western Australia	AM049351	AM048657	AM048717
<i>Phasianella solida</i>	Chikura, Chiba Prefecture, Japan	AM049353	AM048658	AM048719
<i>Phasianella ventricosa</i>	Wylie Bay, Esperance, Western Australia	AM049355	AM048659	AM048720
<i>Bothropoma pilula</i>	Aguni Island, Okinawa Prefecture, Japan	AM049344	AM048650	AM048711
<i>Collonista amakusaensis</i>	Minatogawa, Okinawa Prefecture, Japan	AM049345	AM048651	AM048712
<i>Collonista costulosa</i>	Seragaki, Okinawa Prefecture, Japan	AM049346	AM048652	AM048713
<i>Homalopoma nocturnum</i>	Mitsuishi, Kanagawa Prefecture, Japan	AM049348	AM048653	AM048714
<i>Homalopoma rotundata</i>	Fish River Mouth, Eastern Cape	AM049349	AM048654	–
<i>Homalopoma sangarensense</i>	Ohtsuchi Bay, Iwate Prefecture, Japan	AM049350	AM048655	–
<i>Cinysca dunkeri</i>	Rufanes, Port Alfred, Eastern Cape	–	–	AM048724

Table 4.3. Forward (F) and reverse (R) nucleotide sequences of PCR primers used to amplify four molecular markers in the present study.

Gene	Name of primer	Sequence of primer (5' to 3')	References
CO1	LCO1490 (F)	5'– GGTCAACAAATCATAAAGATATTGG–3'	Folmer <i>et al.</i> (1994)
	HCO2198 (R)	5'– TAAACTTCAGGGTGACCAAAAAATA–3'	Folmer <i>et al.</i> (1994)
	K699 (R)	5'– WGGGGGGTAAACTGTTCATCC–3'	Simon <i>et al.</i> (1994)
	RON (F)	5'– GGAGCYCCWGATATAGCTTTCCC–3'	Simon <i>et al.</i> (1994)
16S rRNA	16Sar (F)	5'– CGCCTGTTTATCAAAAACAT–3'	Palumbi <i>et al.</i> (1991)
	16Sbr (R)	5'– CCGGTCTGAACTCAGATCACGT –3'	Palumbi <i>et al.</i> (1991)
18S rRNA	18S–5' (F)	5'– CTGGTTGATYCTGCCAGT–3'	Winnepenninckx <i>et al.</i> (1998)
	18S–1100 (R)	5'– CTTCGAACCTCTGACTTTTCG –3'	Winnepenninckx <i>et al.</i> (1998)
28S rRNA	LSU–2 (F)	5'– GGGTTGTTTGGGAATGCAGC –3'	Wade & Mordan (2000)
	LSU–4 (R)	5'– GGTAGACTCCTTGGTCCGTG –3'	Wade & Mordan (2000)

4.2.3. Sequence alignment and phylogenetic analysis

All sequences were edited, assembled and aligned as in chapter 3. In this study, each gene was analyzed separately and in different combinations. Following sequence alignment, sequence lengths were: 630 base pairs (bp, COI), 707 bp (16S), 558 bp (28S) and 1057 bp (18S), respectively. The combined datasets totaled: mtDNA 1337 bp (COI and 16S), nDNA 1558 bp (28S and 18S), and combined 2895 bp (mtDNA and nDNA, all four genes), respectively. For the combined mitochondrial analyses four different data partitions were used: COI codon position 1, COI codon position 2, COI codon position 3 and 16S. For the total data inference six different data partitions were used: COI codon position 1, COI codon position 2, COI codon position 3, 16S, 18S and 28S.

Sequence analyses were performed using parsimony (MP), maximum likelihood (ML), and bayesian inference (BI) algorithms. Maximum likelihood analyses were performed as described in chapter 3.

Maximum parsimony tree searches, using PAUP*4.0b10 (Swofford 2002), were initiated treating all characters as having equal weight, type “unordered” (with all multi-state characters run as unordered) and with gaps coded as missing data. Heuristic searches were performed by stepwise addition of taxa, with tree-bisection-reconnection (TBR) branch-swapping rearrangement and with 1000 random replicates. To gauge the robustness of the recovered phylogeny, a nonparametric bootstrap analysis (Felsenstein 1985) was performed with 100 replications, each executed as a heuristic search as described above, but with 5 random-addition replicates per bootstrap pseudoreplicate.

The computer programme Mr Bayes 3.0 (Huelsenbeck & Ronquist 2001) was used to conduct a bayesian approach to phylogenetic inference. Four Metropolis coupled MCMC chains (one cold and three heated chains) were run simultaneously to optimize efforts to find peaks in tree-space. To check that equilibrium had been reached, the fluctuating value of the log-likelihood was plotted in Microsoft Excel. The number of cycles to discard (the burn-in period) was estimated empirically from the log-likelihood plots. This search strategy was repeated twice with each run beginning from a random tree. The General-Time-Reversible model of nucleotide substitution with a gamma distribution (estimated using four rate categories) and invariable sites

(GTR + I + G) was used in the bayesian analyses. A Dirichlet distribution was assumed for estimation of the base frequency parameters and an uninformative (flat) prior was used for the topology. Trees were sampled every 500 generations, resulting in a sample of 2001 trees for each one million generation run.

4.3. RESULTS

4.3.1. Cytochrome–Oxidase subunit I (COI)

The aligned COI data matrix (Appendices 4.1) contained 33 taxa and 630 characters of which 268 were parsimony informative and 60 variable sites but uninformative. The search resulted in six equally most parsimonious trees of 1828 steps with a consistency index (CI) of 0.334 and a retention index (RI) of 0.485. Maximum parsimony and maximum likelihood analyses derived from this dataset were largely unresolved along the backbone and at some terminal nodes and are shown in figure 4.1a and 4.1b, respectively. All bootstrap values below 50% are not shown in the trees.

4.3.2. 16S rRNA

The aligned 16S rRNA data matrix (Appendices 4.2) contained 21 taxa and 707 characters of which 254 were parsimony informative and 109 variable but uninformative. The search resulted in two most parsimonious tree of 1041 steps with a CI of 0.566 and a RI of 0.534. Maximum parsimony and maximum likelihood analyses divide the southern African *Tricolia* species into two distinct clades (Figs 4.2a, b). Clade A was comprised of *T. adusta* and *T. formosa*, and clade B comprised all the other southern African *Tricolia* species. Clade A is well supported (BS=100% MP, ML) whereas clade B is weakly support by maximum parsimony (BS=79%), and not support by maximum likelihood analysis. The relationship between the two clades was not supported in either analyses. *Tricolia pullus* (European, the type species of the genus *Tricolia*) and *T. fordiana* (Indo-West Pacific) are sister species in both analyses, but the relationship is weakly supported in the maximum parsimony analysis (BS=55%) and not supported in the maximum likelihood analysis. However, in the maximum likelihood analysis the two species are placed within the two southern African *Tricolia* clades. *Tricolia sensu stricto* (includes southern Africa and European *Tricolia* species) is not monophyletic in both analysis. Both analyses support monophyly of *Phasianella* (BS=100% ML, BS=98% MP). Monophyly of the

Phasianelloidea was also supported in both analyses (BS=99% MP, BS=99% ML). Both analyses grouped *Hilola variabilis* and *E. perforatum* (Eastern Pacific) outside the Tricoliinae, resulting in the subfamily being paraphyletic.

4.3.3. Combined mtDNA (COI + 16S rRNA)

The aligned COI and 16S data matrix combined contained 36 taxa and 1337 characters of which 522 were parsimony informative and 169 variable sites but uninformative. The search resulted in three equally most parsimonious trees of 2898 steps with a CI of 0.415 and a RI of 0.492. Separate analyses (maximum parsimony, maximum likelihood and bayesian Inference) of the combined COI and 16S rRNA datasets were largely unresolved at the backbone and terminal nodes and are shown in figure 4.3a, b and c, respectively.

4.3.4. 18S rRNA

The aligned 18S rRNA data matrix (Appendices 4.3) contained 32 taxa and 1057 characters of which 212 were parsimony informative and 170 were variable but uninformative. The search resulted in 337 equally most parsimonious trees of 874 steps with a CI of 0.669 and a RI of 0.744. Parsimony analysis recovered monophyly of *Tricolia sensu stricto*, but the relationship is not supported (Fig. 4.4a). The genus *Phasianella* is unresolved in the parsimony analysis, but resolved and supported in the likelihood analysis (BS=82%). Again, the southern Australian and the Indo-West Pacific *Tricolia* species, *Hilola* and *Eulithidium* were grouped outside the Tricoliinae, resulting in the subfamily being paraphyletic. Results obtained from maximum likelihood topology were largely unresolved (Fig. 4.4b).

4.3.5. 28S rRNA

The aligned 28S rRNA data matrix (Appendices 4.4) contained 32 taxa and 558 characters of which 185 were parsimony informative and 67 variable but uninformative. The parsimony search resulted in two equally most parsimonious trees of 809 steps with a CI of 0.517 and a RI of 0.659. The results obtained from maximum parsimony and maximum likelihood analyses were not congruent (Figs 4.5a, b). Parsimony recognized the two southern African *Tricolia* clades recovered by the mtDNA, but maximum likelihood did not. Monophyly of *Tricolia sensu stricto* is weakly supported in the parsimony analysis. Monophyly of *Phasianella* is not supported in the parsimony analysis, although supported in the maximum likelihood analysis (BS=76%). Sister relationship of *Eulithidium* to *Gabrielona* was not

supported in the parsimony analysis and its position was uncertain in the maximum likelihood analysis. The southern Australian *Tricolia* species, *Hilola* and *Eulithidium* were grouped outside the Tricoliinae, resulting in the subfamily being paraphyletic. However, monophyly of *Eulithidium* was supported in the maximum likelihood analyses (BS=90%), but weakly supported in the parsimony analysis (BS=60%). Results obtained from maximum likelihood analyses are highly unresolved and are presented in Fig. 4.5b.

4.3.6. Combined nDNA (28S + 18S rRNA)

The aligned 28S and 18S data matrix combined contained 36 taxa and 1558 characters of which 365 were parsimony informative and 227 variable but uninformative. The search resulted in two equally most parsimonious trees of 1573 steps with a CI of 0.596 and a RI of 0.694. Maximum parsimony and bayesian analyses divided the southern African *Tricolia* species into two distinct clades (Figs 4.6a, c), but the relationship between the two clades is not supported in the parsimony analyses, and not statistically significant in the bayesian inference analysis (PP=75%). In the parsimony analysis, *Tricolia pullus* was recovered as the sister taxon to the southern African clade A, but the relationship is not supported. However, bayesian analysis placed *T. pullus* as a sister taxon to both clade A and B (PP=86%). Maximum parsimony and bayesian analyses recovered monophyly of *Tricolia sensu stricto* (BS=94%, PP=86%). The southern Australian and the Indo-West Pacific *Tricolia* species, *Hilola* and *Eulithidium* were grouped outside the Tricoliinae, resulting in the subfamily being paraphyletic. Monophyly of *Eulithidium* was recovered in all analyses (BS=88% ML, PP=98% BI), but not supported in the parsimony analysis. Again, the genus *Phasianella* is unresolved in the parsimony analysis, but resolved and supported in the maximum likelihood (BS=80%) and bayesian analyses (PP=94%). The position of the genus *Gabrielona* and *Tricolia fordiana* is uncertain in all analyses. Monophyly of the Phasianelloidea is strongly supported in the maximum likelihood and bayesian inference analyses (BS=100%, PP=100%), and weakly supported in the parsimony analysis (BS=55%).

4.3.7. All molecular data combined

The combined data matrix (COI, 16S, 28S and 18S) contained 36 taxa and 2895 characters of which 887 were parsimony informative and 396 variable but uninformative. The search resulted in two equally most parsimonious trees of 4544 steps with a CI of 0.470 and a RI of 0.555. Parsimony and bayesian analyses divided

the southern African *Tricolia* species into two distinct clades (Figs 4.7a, c), but the relationship between the two clades is not supported. In the parsimony analysis, *Tricolia pullus* was recovered as the sister taxon to the southern African clade A, but the relationship is not supported. Monophyly of clade B is well supported in the parsimony analysis (BS=94). Monophyly of *Tricolia sensu stricto* was recovered in the parsimony analysis (BS=63%), and unresolved in the bayesian and maximum likelihood analyses. The genus *Phasianella* was not monophyletic in both parsimony and maximum likelihood analyses, but recovered in the bayesian inference analysis, but not statistically significant. The position of the genus *Gabrielona* is uncertain in all analyses. The southern Australian and the Indo-West Pacific *Tricolia* species, *Hilola* and *Eulithidium* were grouped outside the Tricoliinae, resulting in the subfamily being paraphyletic. Monophyly of *Eulithidium* was recovered in all analyses (BS=84% ML, PP=100% BI), but not supported in the parsimony analysis. Monophyly of the Phasianelloidea is strongly supported in the maximum likelihood and bayesian inference analyses (BS=99%, PP=97%), and not supported in the parsimony analysis.

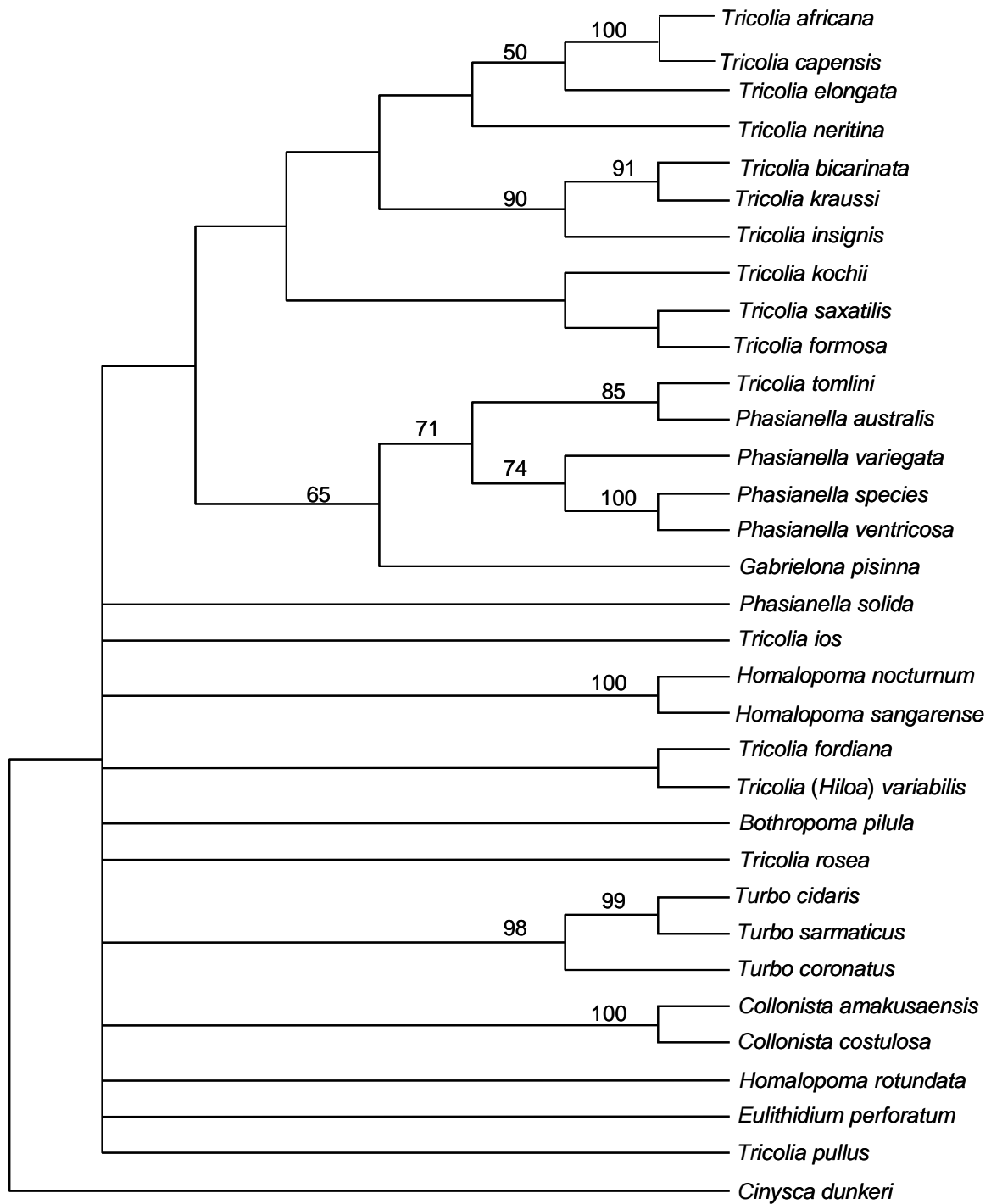


Figure 4.1.a. A strict consensus tree recovered using mtDNA COI sequence data. Numbers above nodes are bootstrap values.

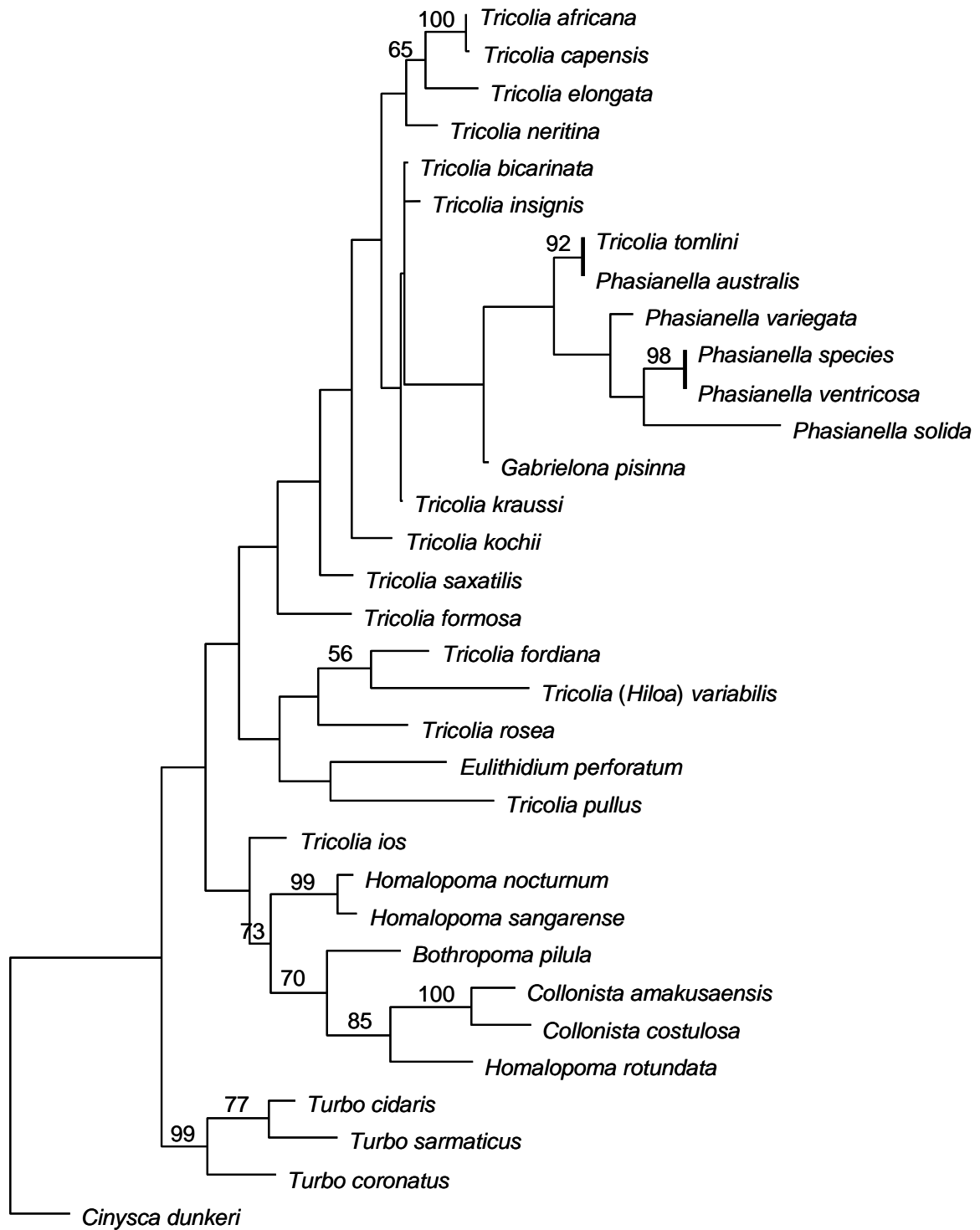


Figure 4.1.b. Best maximum likelihood tree obtained from mtDNA COI sequence data. Numbers above nodes are bootstrap values.

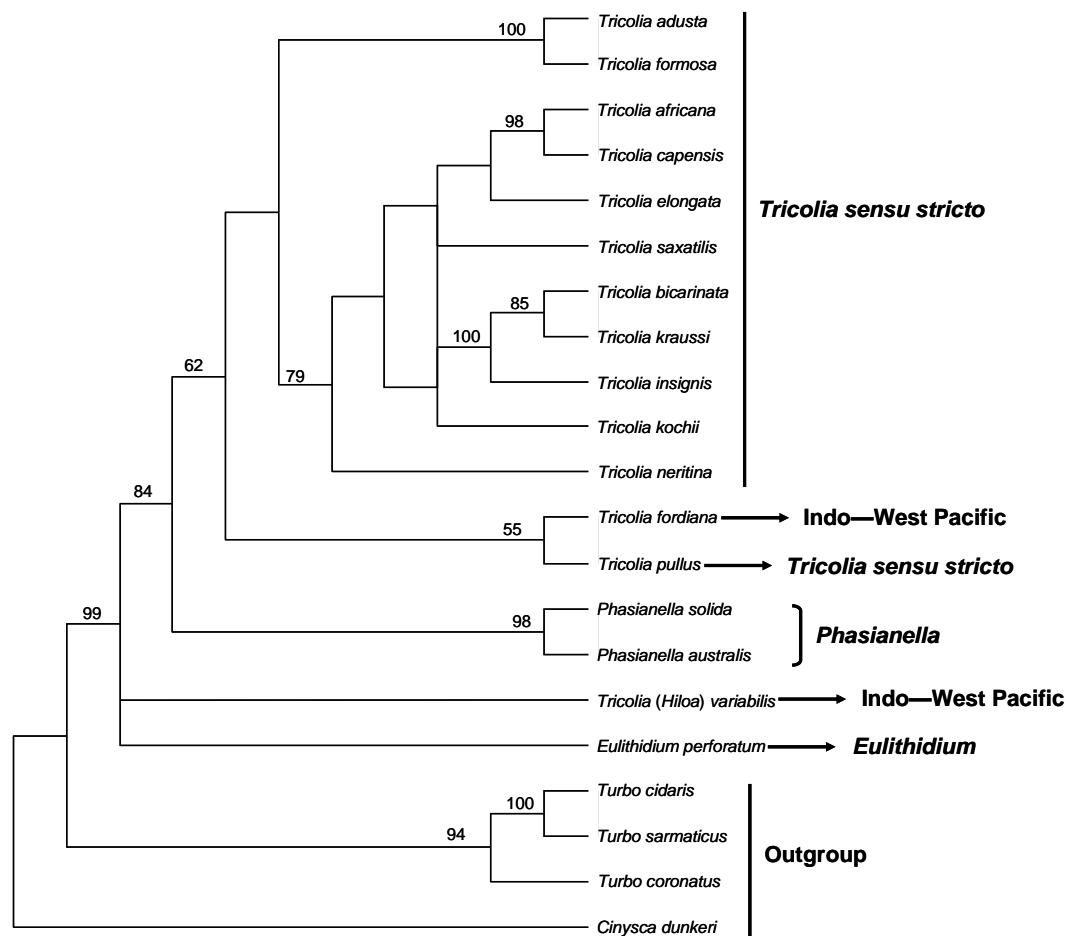


Figure 4.2.a. A strict consensus tree recovered using mtDNA 16S rRNA sequence data. Numbers above nodes are bootstrap values.

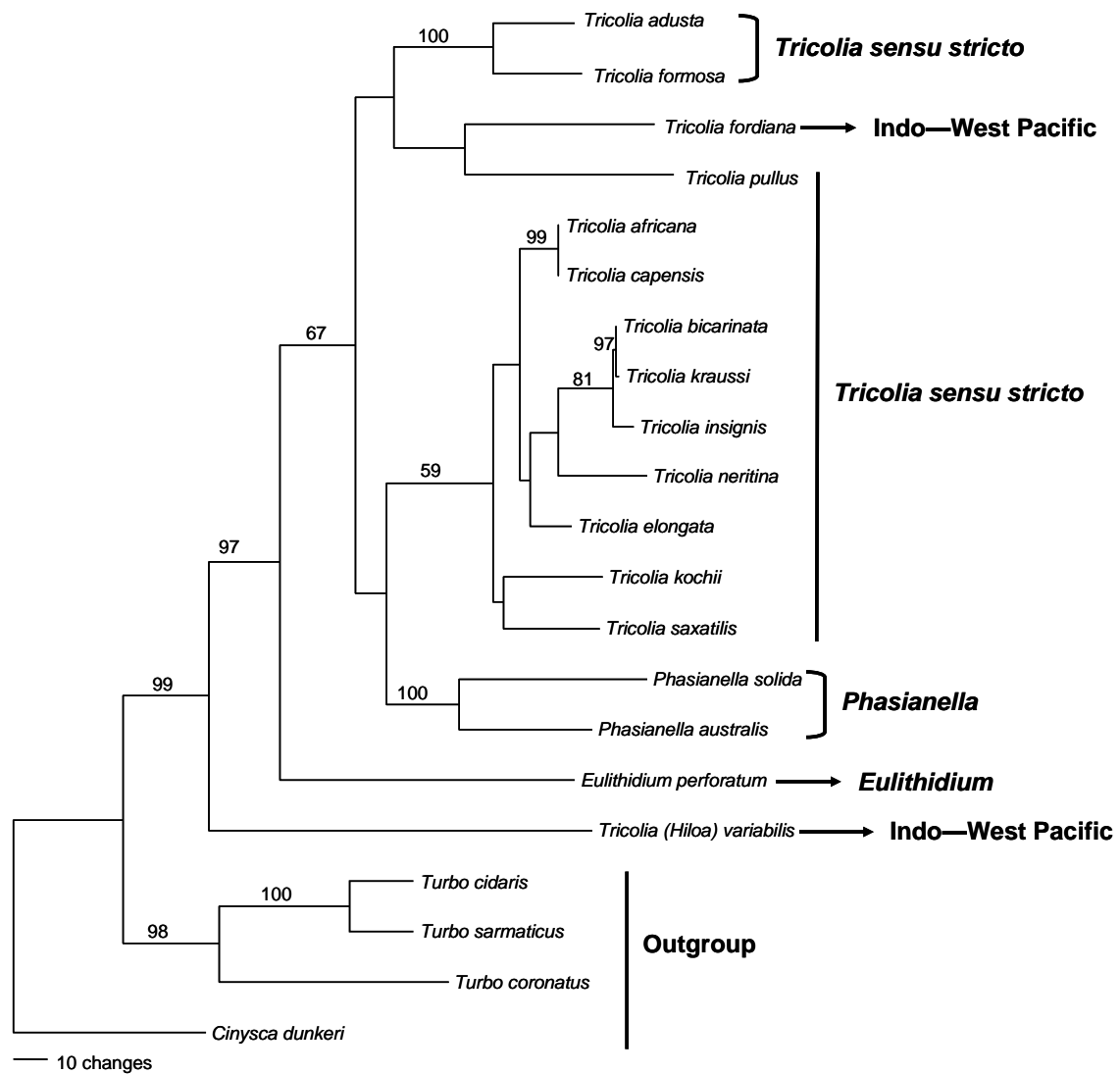


Figure 4.2.b. Best maximum likelihood tree obtained from mtDNA 16S rRNA sequence data. Numbers above nodes are bootstrap values.

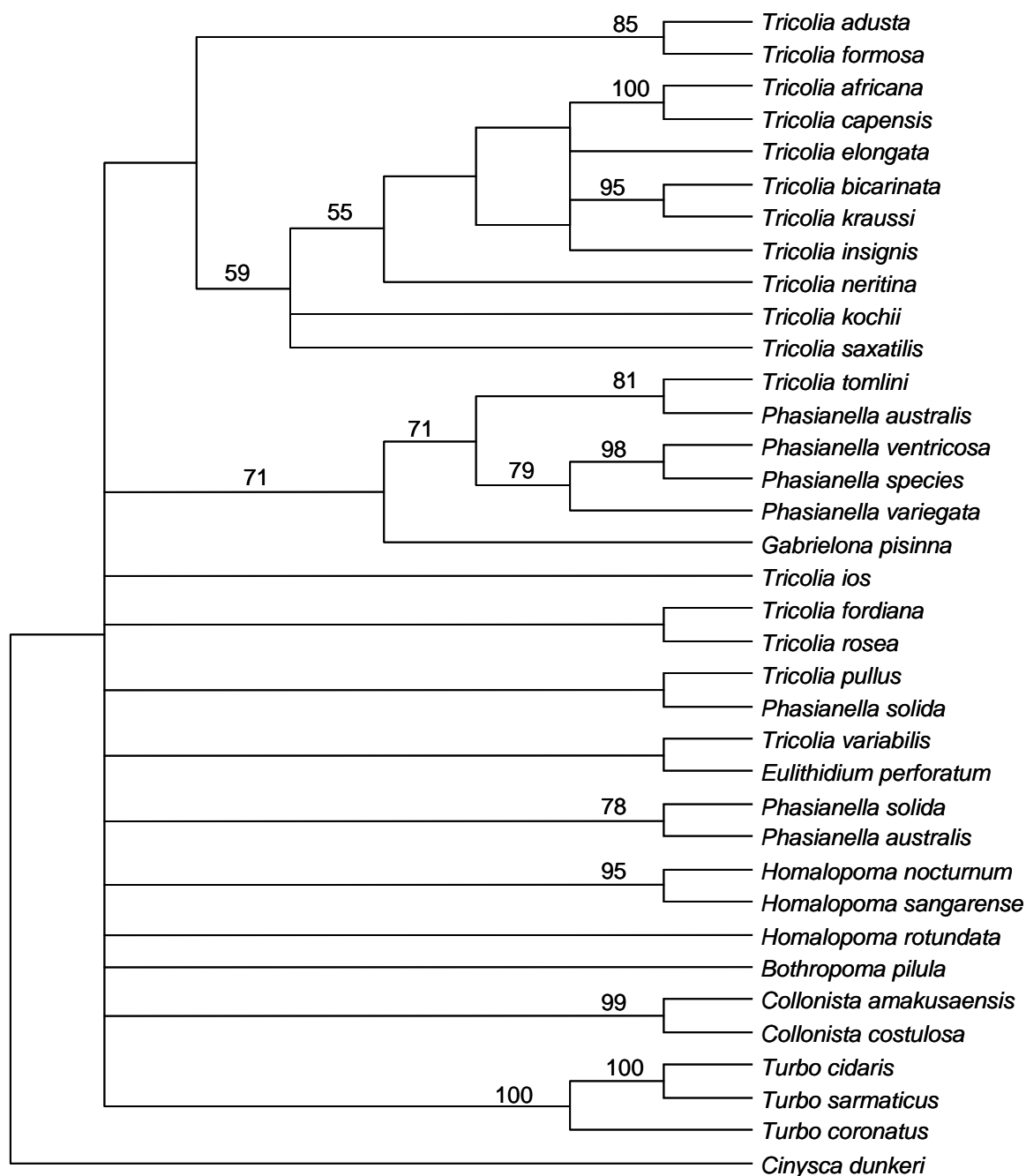


Figure 4.3.a. A strict consensus tree recovered using combined mtDNA COI and 16S rRNA sequence data. Numbers above nodes are bootstrap values.

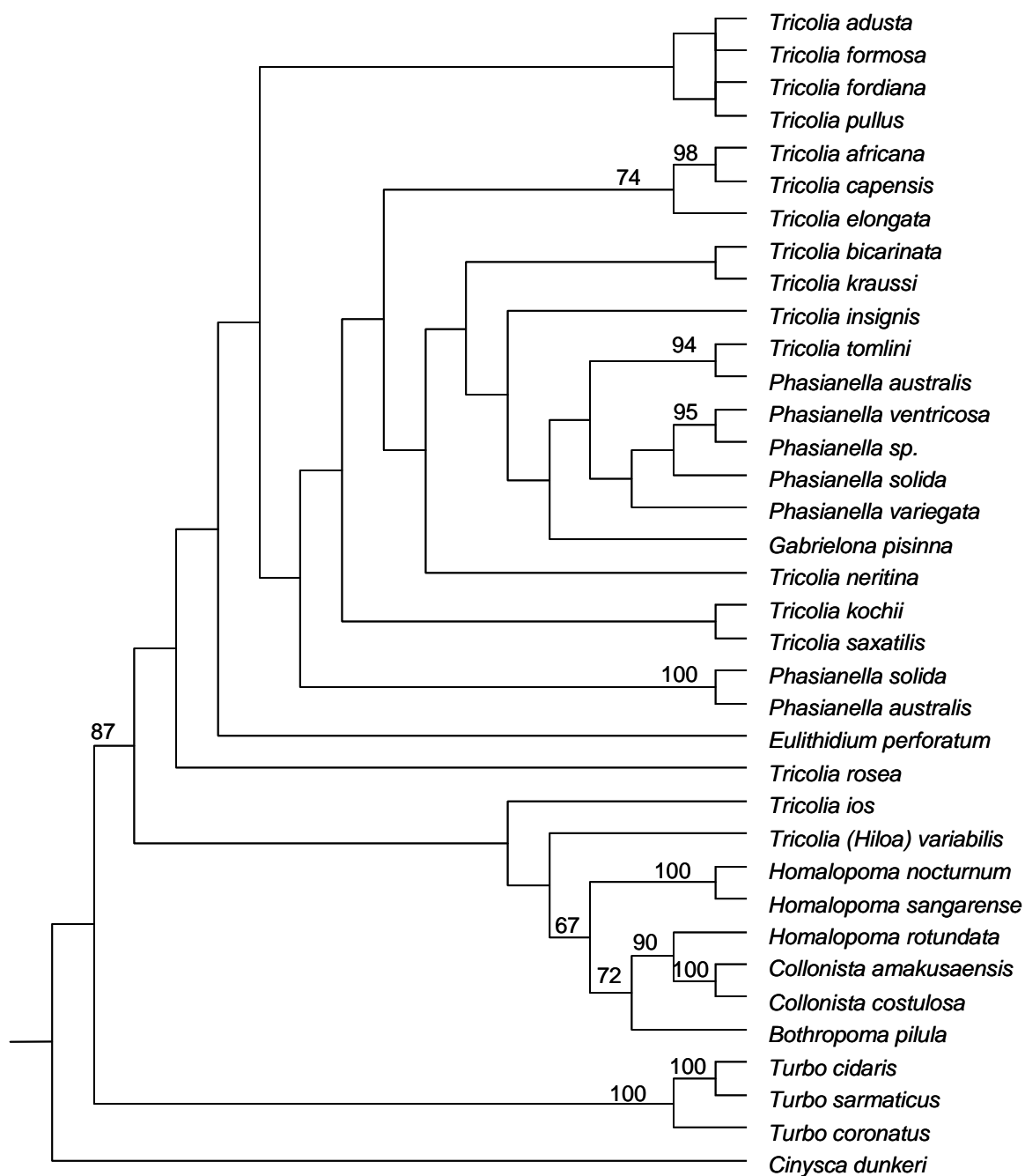


Figure 4.3.b. Best maximum likelihood tree obtained for the combined COI and 16S rRNA sequence data. Numbers above nodes are bootstrap values.

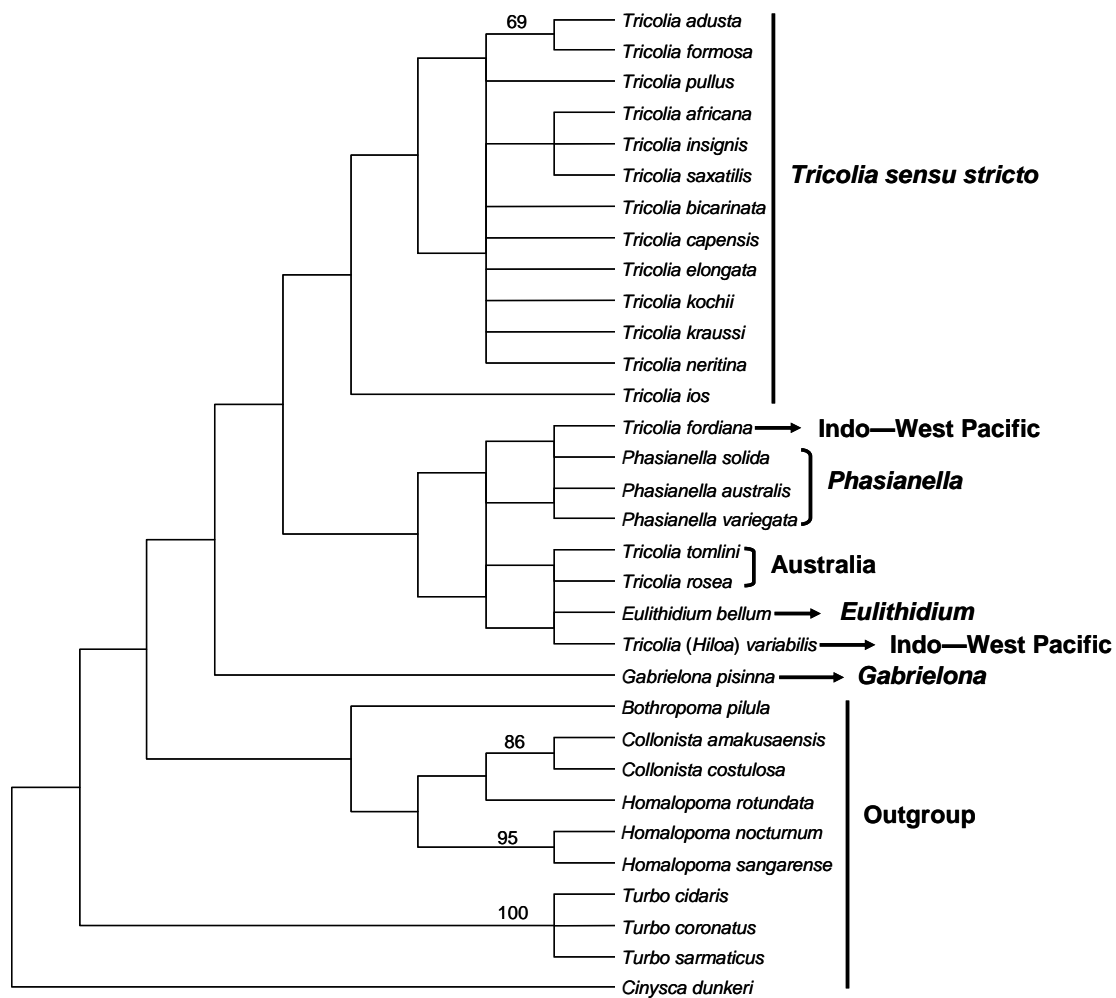


Figure 4.4.a. A strict consensus tree recovered using 18S rRNA sequence data. Numbers above nodes are bootstrap values.

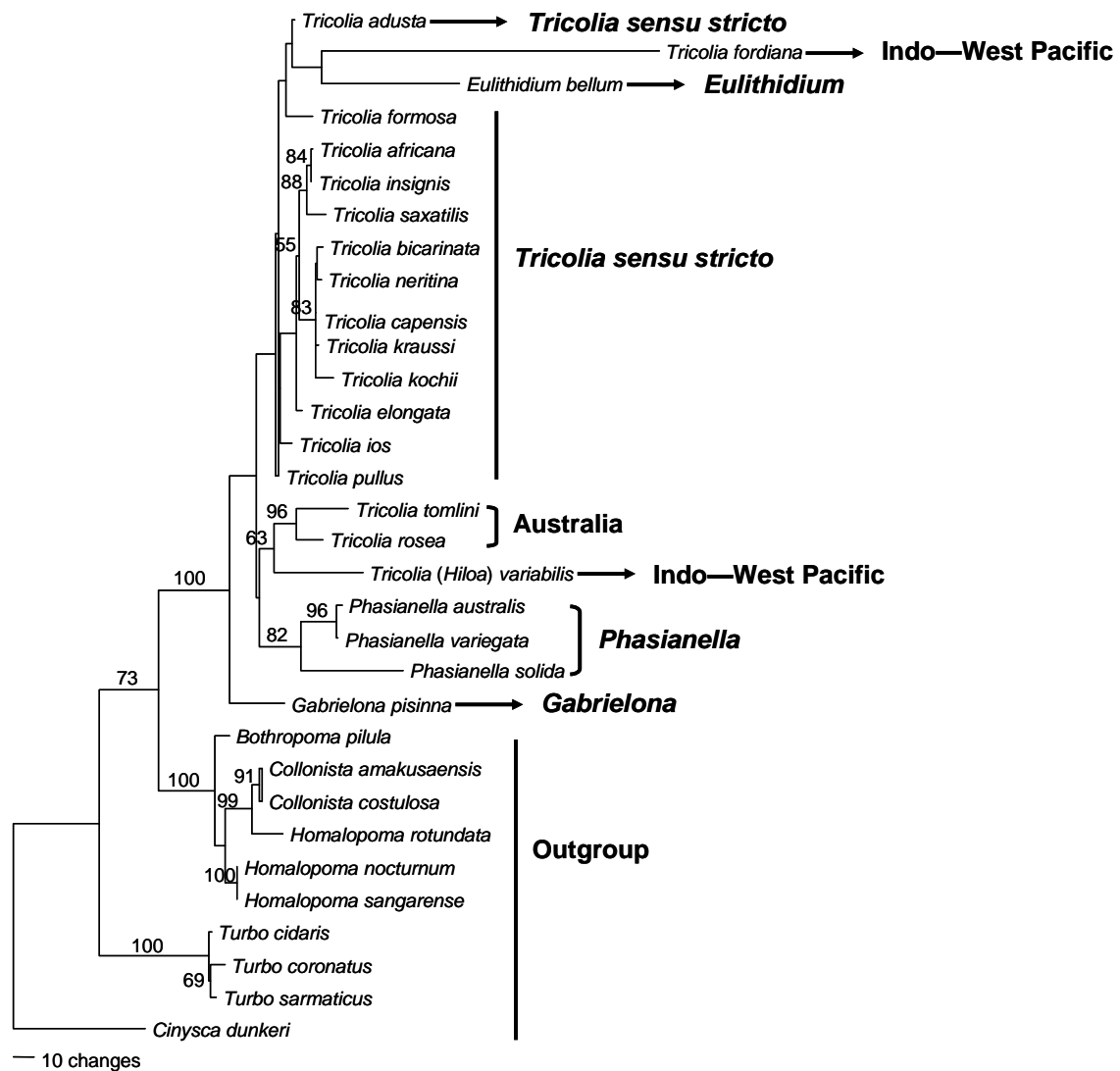


Figure 4.4.b. Best maximum likelihood tree obtained from 18S rRNA sequence data. Numbers above nodes are bootstrap values.

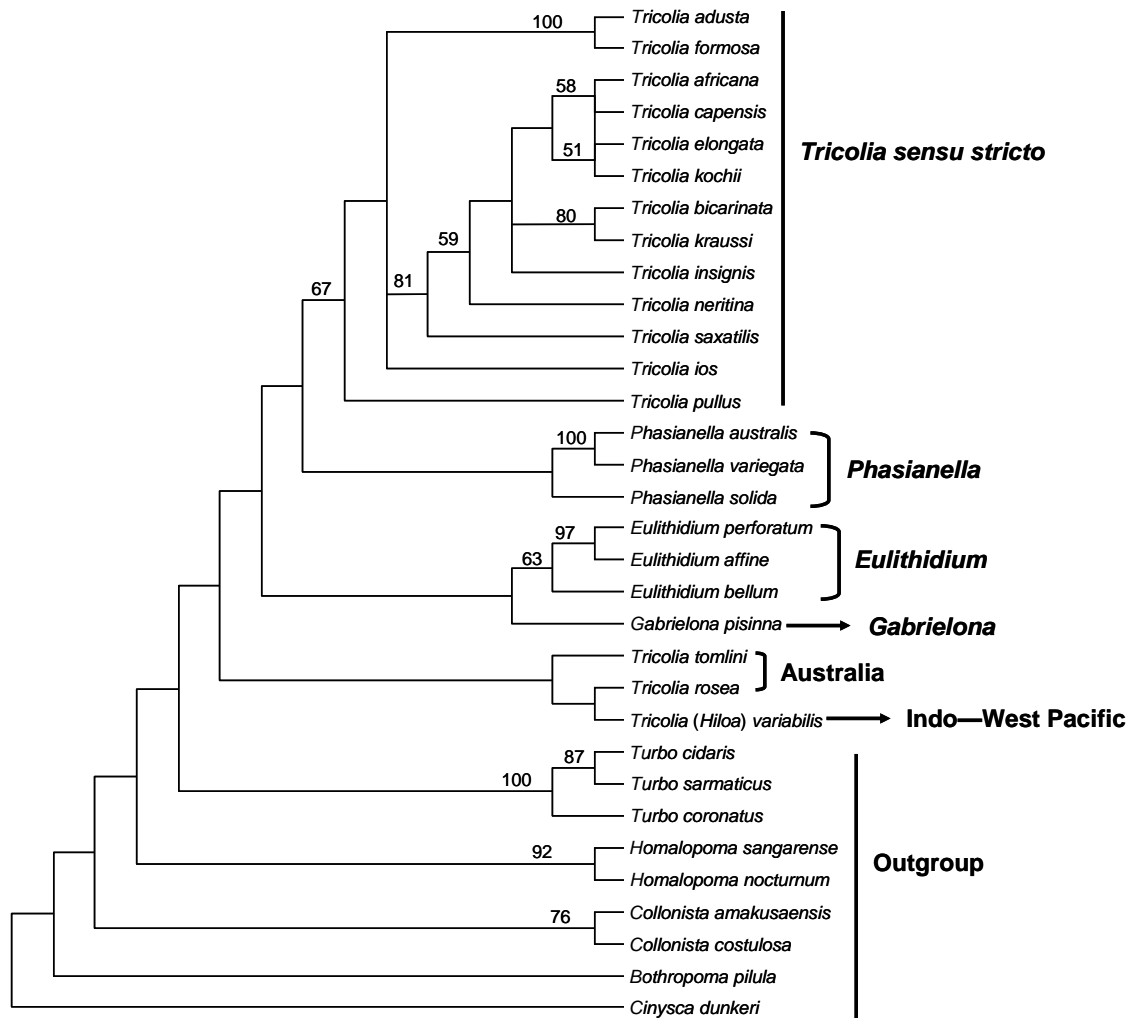


Figure 4.5.a. A strict consensus tree recovered using 28S rRNA sequence data. Numbers above nodes are bootstrap values.

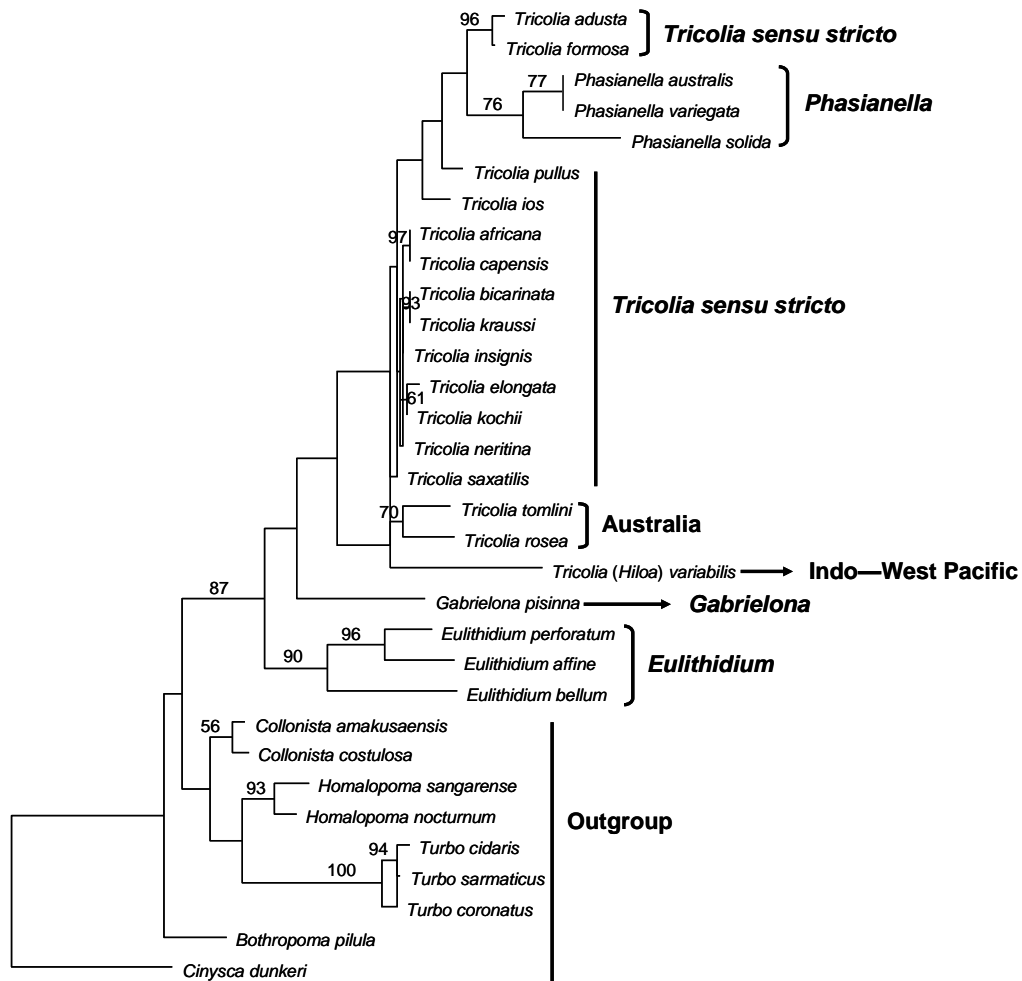


Figure 4.5.b. Best maximum likelihood tree obtained from 28S rRNA sequence data. Numbers above nodes are bootstrap values.

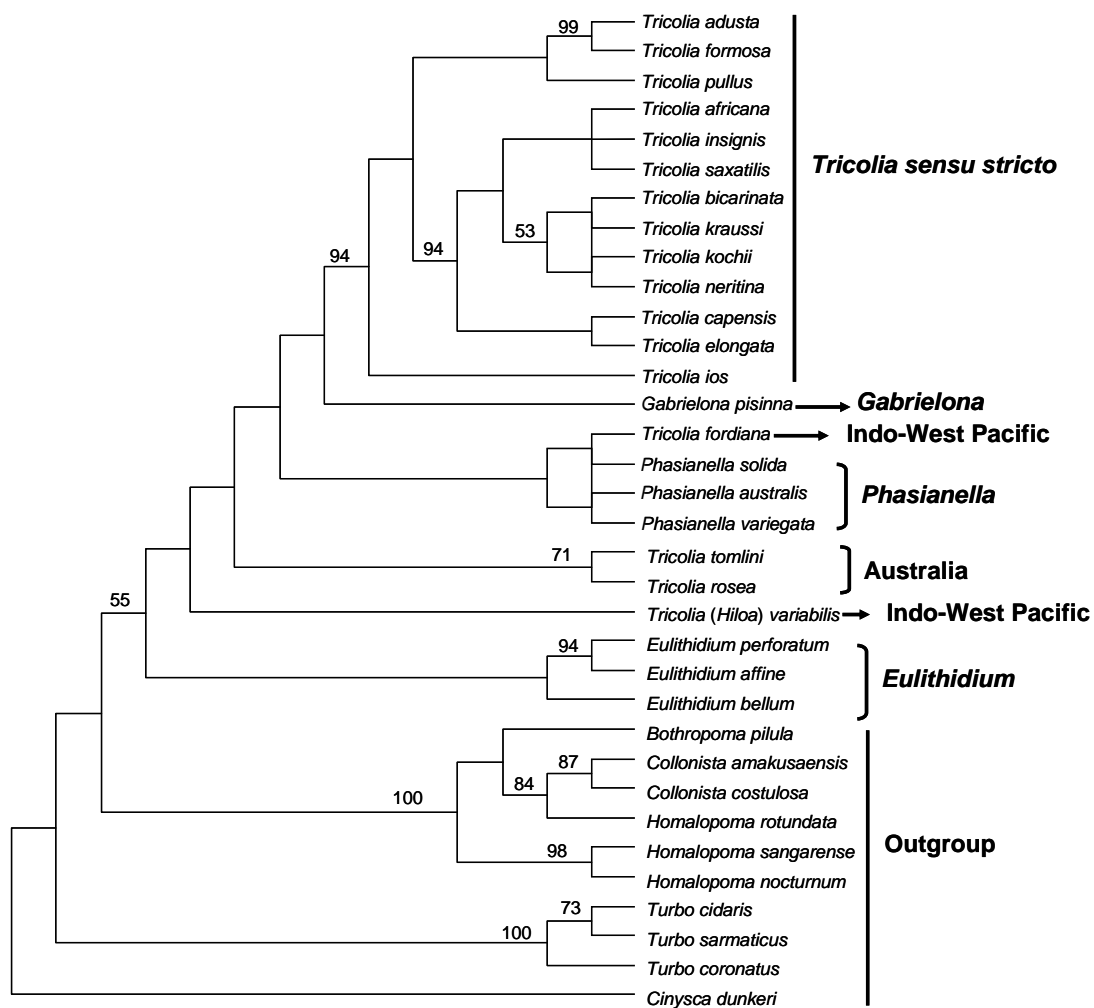


Figure 4.6.a. A strict consensus tree recovered using combined nDNA (28S rRNA +18S rRNA) sequence data. Numbers above nodes are bootstrap values.

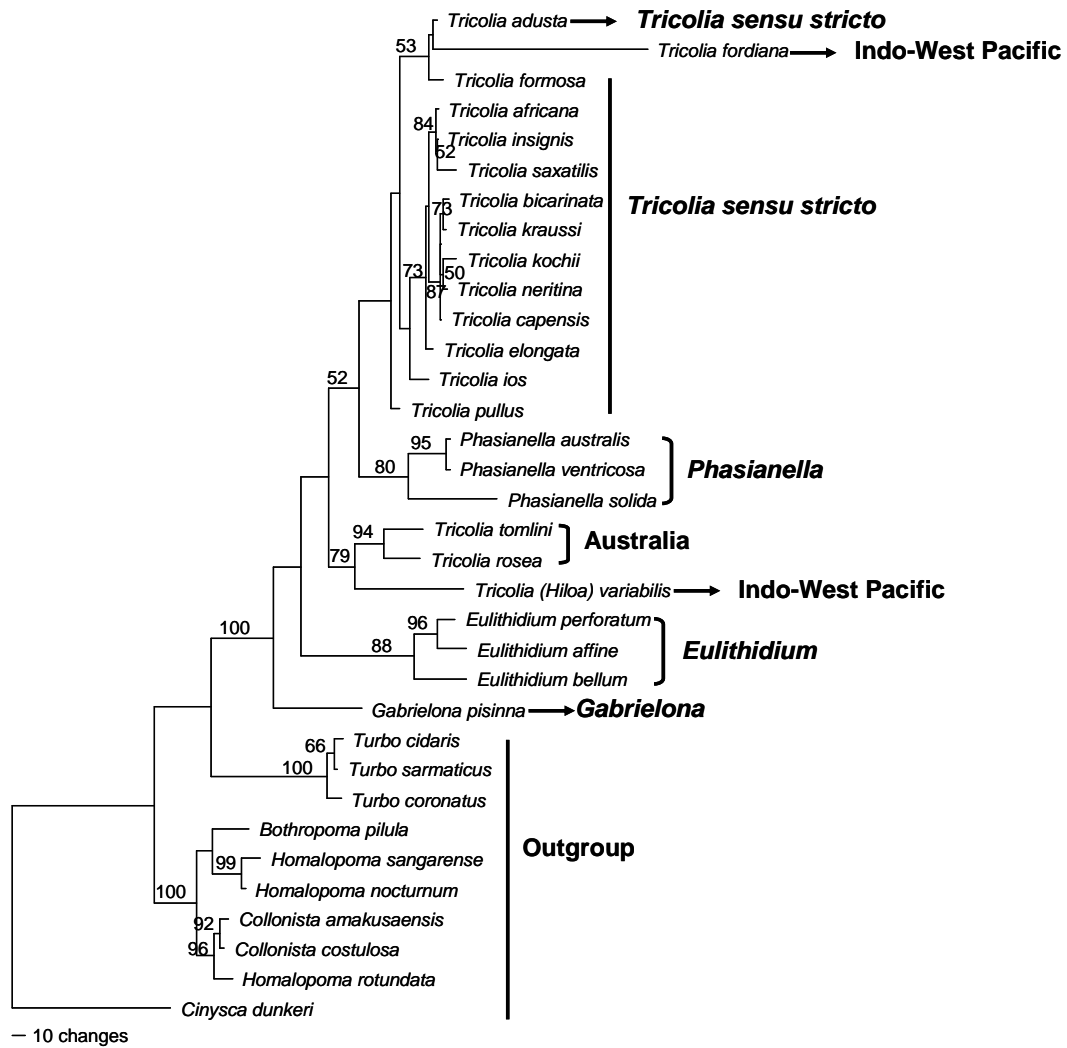


Figure 4.6.b. Best maximum likelihood of the combined nDNA (28S + 18S rRNA) sequence data. Numbers above nodes are bootstrap values.

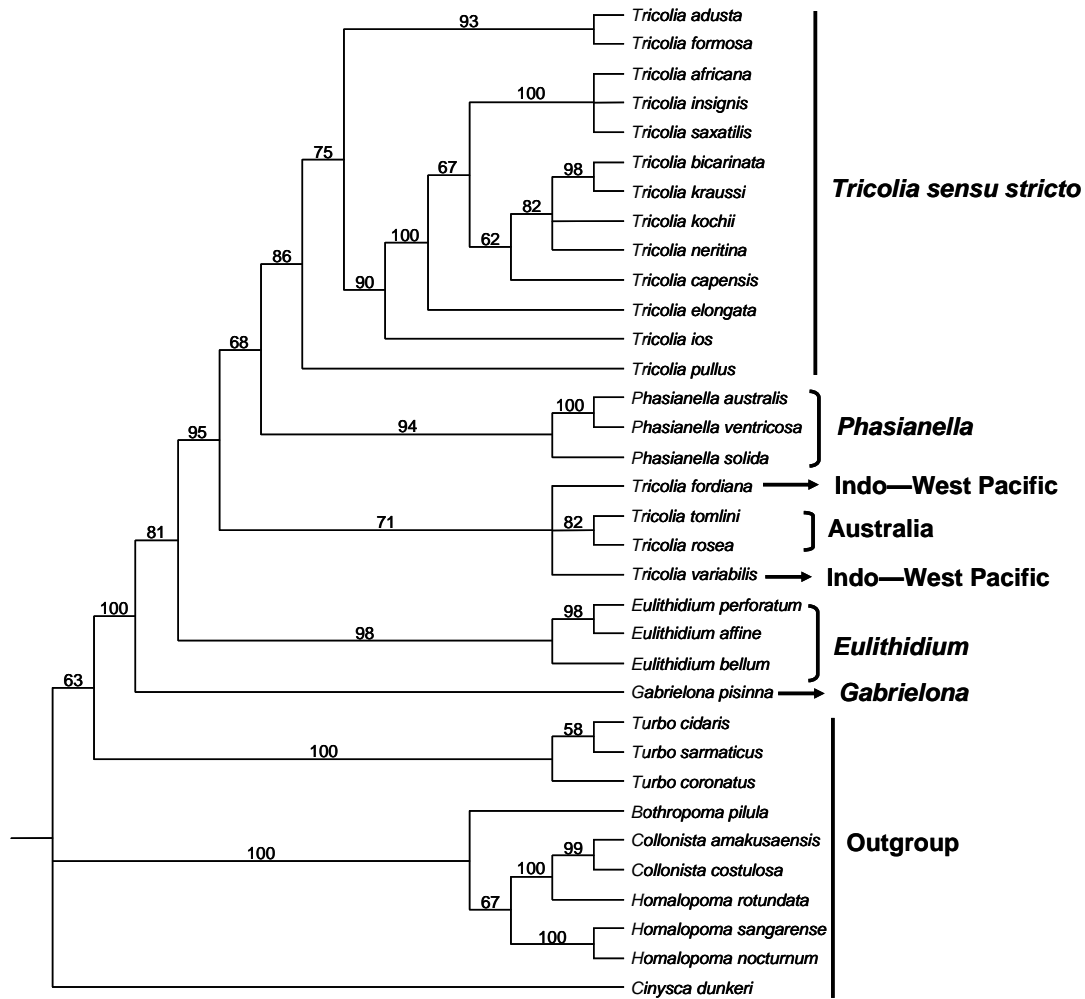


Figure 4.6.c. A 50% majority rule consensus tree recovered using bayesian inference of combined nDNA (28S + 18S) sequence data. Posterior probability values are shown for each clade.

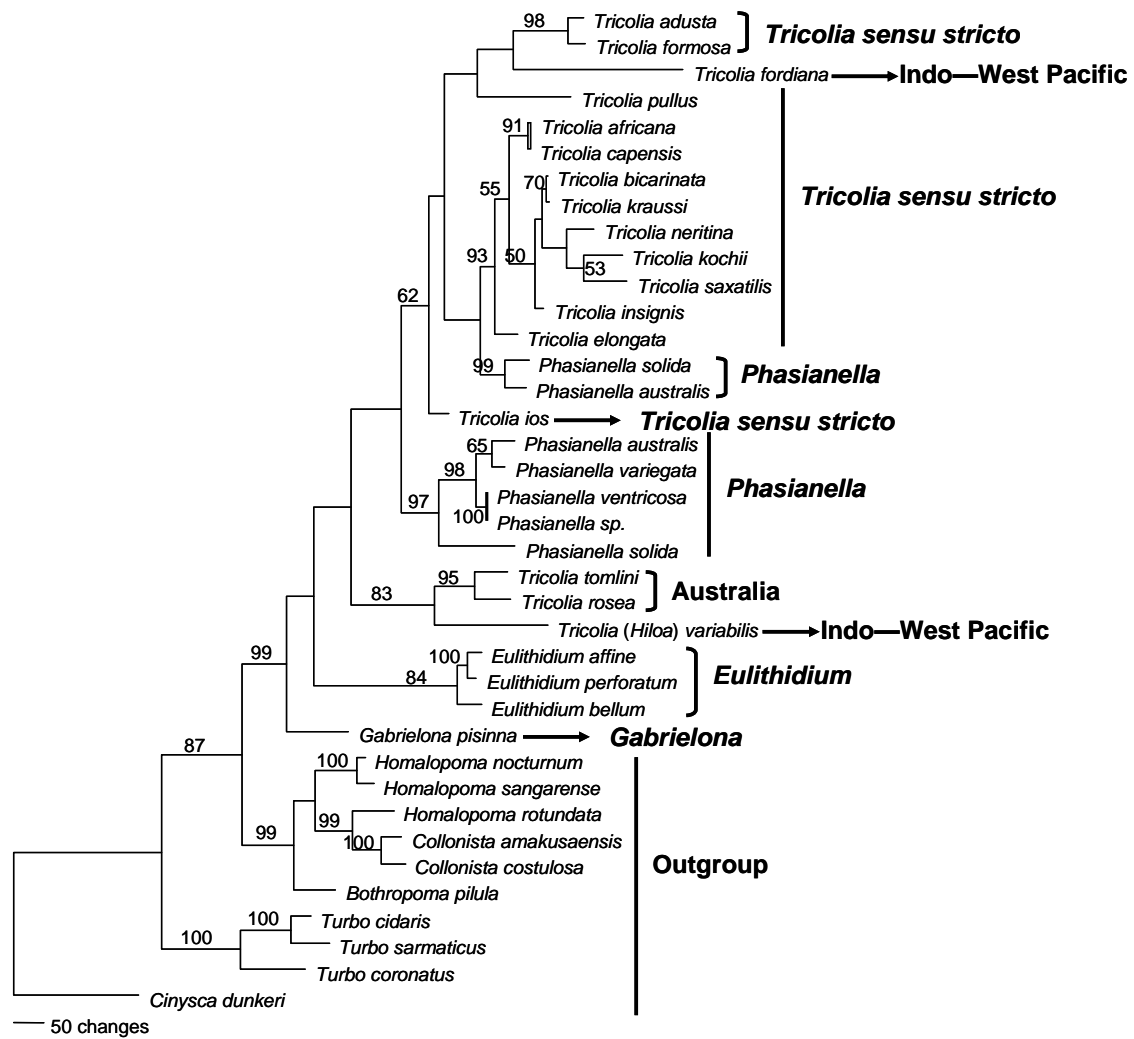


Figure 4.7.b. Best maximum likelihood tree of the combined mtDNA and nDNA sequence data of four genes (COI, 16S, 28S and 18S). Numbers above nodes are bootstrap values.

4.4. DISCUSSION

4.4.1. Phylogenetic relationships between the southern African *Tricolia* species

Phylogenetic analysis of the endemic southern African *Tricolia* species suggest that these taxa do not comprise a single monophyletic group. Instead, two major clades were recovered (A and B). Clade A is composed of *T. adusta* and *T. formosa* and clade B is composed of all the other endemic southern African *Tricolia* species and the East African *T. ios*. However, in most analyses the endemic African taxa form a monophyletic group and this is the sister clade to the type species, *T. pullus*, although levels of support are generally low.

4.4.1.1. The southern African clade A

The separation of *T. adusta* and *T. formosa* from other southern African *Tricolia* species is supported by morphological characters of the radula and external anatomy. Morphological synapomorphies include: the inner marginal teeth of the radula having one strong undivided ectocone, and one sense organ at the base of the anterior epipodial tentacle on the right.

4.4.1.2. The southern African clade B

The majority of species grouped in clade B differ from clade A in having two sense organs at the base of the anterior epipodial tentacle on the right, and also because the ectocone of the inner marginal teeth is bifid or notched, and interlocks with two notches at the base of the cusp of the adjacent outer tooth. Morphological characteristics of this clade resemble that of the type species, *T. pullus*.

Even though the monophyly of this clade was strongly supported in the phylogenetic analysis, the relationship among the species was not well established. It is possible that the lack of resolution within this clade is genuine and could be explained by a “burst of speciation” – an event where cladogenesis has occurred over a short period of time and are still busy diverging from each other. If this is the case then the lack of resolution could also indicate that the neutral genetic markers used are evolving too slowly to distinguish between species. It is possible that better resolution could be obtained by using longer DNA sequences, or by using faster evolving nuclear markers such as microsatellites, or highly variable sites of the nuclear genome such as ITS2.

4.4.2. Global relationships

4.4.2.1. Southern African and Eastern Atlantic species

The combined data analysis support the relationship between the southern African *Tricolia* species and the Eastern Atlantic species, *T. pullus* although with varying levels of support. The molecular results are congruent with morphology. *Tricolia pullus* is morphologically most closely related to the southern African clade B. The Eastern Atlantic and southern African species represent *Tricolia sensu stricto*.

Given that it is thought that *Tricolia* originated in the Tethys Sea (Adams *et al.* 1983, Robba 1987 *in* Herbert 1994), three possible hypotheses can be put forward in relation to the origins and phylogenetic composition of the southern African *Tricolia* fauna. The first hypothesis is that *Tricolia* radiated from Europe into southern Africa via the eastern Atlantic/west Africa. Once it reached southern Africa it then divides into two distinct clades (A and B). The second hypothesis is that the radiation of *Tricolia* species from Europe into southern Africa happened twice, giving rise to two separate clades in which case further study may reveal representatives of both clades in the Mediterranean. The third hypothesis is that the spread happened in two ways prior to the closing of the Tethys Sea, a vicariant event which happened in the Lower Miocene (Burdigalian) or Mid-Miocene (Badenian) (Adams *et al.* 1983, Robba 1987 *in* Herbert 1994), either via the west coast (Atlantic Ocean) or via the east coast (Indian Ocean) leading to two morphologically and genetically distinct lineages. In this case the divergence of the A and B clades must pre-date the eastern closure of the Tethys.

However, there is insufficient information to argue one way or the other and more data is needed to test these hypotheses. Specifically, we need molecular data from the 10 European species that were not available here, i.e., the large Eastern Atlantic species such as *T. speciosa*, *T. tenuis*, *T. miniata* and *T. petiti*, and the small Mediterranean species such as *T. nordsiecki*, *T. algoidea*, *T. tingitana*, *T. entomocheila*, *T. punctura*, and *T. deschampsi* to investigate monophyly of *Tricolia sensu stricto*. In addition, more surveys need to be done along the west African coast to find if there are any or more *Tricolia* species in this region and also to establish links between the North East Atlantic and the southern African *Tricolia* fauna.

Morphological and molecular data suggest that the southern African *Tricolia* species have close affinities with the Eastern Atlantic species of this genus. In other studies, it has been repeatedly shown that the southern African marine vertebrates and invertebrates, particularly snails and fishes, have sister taxon relationships with southern Australian species (Bowen & Grant 1997, Williams *et al.* 2003) and Australia represents the centre of origin for many taxa (Fell 1962). However, this is not the case in this study where the southern African *Tricolia* are more closely related to the Eastern Atlantic species belonging to the same genus. Sister taxon relationships between the southern African marine taxa and those from the Eastern Atlantic has been found in other marine organisms such as pipefish and *Siphonaria*, however, these studies are not yet published (M. Mwale 2007, P. Teske 2007, personal communication).

4.4.2.2. Southern African and Indo–West Pacific species

Even though the position of *Hilola variabilis* is unclear in the phylogenetic analyses, it stands apart from the *Tricolia sensu stricto* radiation. Morphological characters of the shell, operculum and radula also support the separation of this taxon from *Tricolia sensu lato*. Morphological autapomorphies include: exerted and narrowly rounded apex, a coarsely granulated operculum surface, and three pairs of lateral teeth per transverse row. As opposed to other *Tricolia* species, *Hilola variabilis* retains the basic radula plan in having a cusped rachidian tooth and the number of lateral teeth of the radula is reduced to three instead of five. This species has already been placed under another supra-specific name *Hilola* by Pilsbry (1917) and morphological and molecular data strongly suggest that it is indeed a distinct genus, and should be ranked separately from *Tricolia*. Williams and Ozawa (2006) found the genus *Tricolia* to be paraphyletic, but this is due to the fact that they did not take into consideration profound morphological differences that exist between *Tricolia* and *Hilola*, and included the latter taxon as part of *Tricolia*.

The position of *Tricolia fordiana* is also unclear in the phylogenetic trees, but it too repeatedly falls outside *Tricolia sensu stricto*. However, this species resembles the southern African, East African and the Eastern Atlantic *Tricolia* species in terms of the operculum and radula features. With the amount of data available at present, no conclusion can be drawn about the phylogenetic status of this species. Molecular data from two Indo–West Pacific species, *T. indica* and *T. tristis* are needed in further studies.

4.4.2.3. Southern African and southern Australian species

The two southern Australian species studied, *T. tomlini* and *T. rosea*, are also grouped outside *Tricolia sensu stricto* in a well supported clade. This separation is also supported by morphological characters of the shell, protoconch, radula and external anatomy. Morphological synapomorphies include: periostracum on the shell surface, protoconch with strong spiral cords, rachidian tooth is reduced to a narrow vestige, and the middle epipodial tentacle is more or less similar in size to the posterior and anterior epipodial tentacles. Again, the phylogenetic position of this southern Australian clade is unresolved, but it is evident that it may well represent a distinct lineage. The third southern Australian species, *T. gabiniana* needs to be included in further studies.

In conclusion, the position of the southern Australian and Indo–West Pacific (excluding the East African *T. ios*) *Tricolia* species as well as taxon *Hiloa* is unclear in the phylogenetic trees. They repeatedly fall outside *Tricolia sensu stricto* and this suggests that the inclusion of other members of the Phasianelloidea (i.e., genera *Eulithidium*, *Phasianella* and *Gabrielona*) could prove *Tricolia sensu lato* not to be monophyletic. It is possible that the southern Australian and the Indo–West Pacific (*T. fordiana*) may represent distinct genera separate from *Tricolia*. Thorough taxonomic revision on the Indo–West Pacific and the southern Australian *Tricolia* species is needed, including additional taxa mentioned above.

4.4.3. Family–level relationships

4.4.3.1. The family Tricoliidae

Tricolia sensu stricto is not monophyletic, the southern Australian (*T. tomlini* and *T. rosea*) species are placed outside the genus, and the Indo–West Pacific (*T. fordiana*) is placed close to clade A. Traditionally, the southern Australian and the Indo–West Pacific *Tricolia*, as well as *Hiloa* and *Eulithidium* have been grouped under *Tricolia sensu lato*. However, molecular data strongly suggest that they are distinct and each represent a distinct lineage. This distinction is also supported by morphological characters of the shell, operculum, radula and external anatomy.

The position of the Indo–West Pacific and the southern Australian *Tricolia* species remained unclear. Undoubtedly, the Indo–West Pacific and the southern Australian species are not part of *Tricolia sensu stricto*. Their exclusion from the Tricoliinae seems to be supported only in the combined nDNA bayesian inference analysis. It is logical to deduce that the southern Australian species belong to an undescribed genus since they exhibit atypical character states and molecular data placed them outside *Tricolia sensu stricto*. Unfortunately no phylogenetic conclusion can be drawn on the taxonomic and phylogenetic status of *T. fordiana*. However, it is highly recommended that future studies should include additional taxa from the Indo–West Pacific region (i.e., *T. indica* and *T. tristis*) in order to identify its position within the Phasianelloidea and its phylogenetic relationship with other members of the Tricoliidae.

The fact that *T. pullus* (the type species of *Tricolia*) is placed as a sister taxon to the southern African *Tricolia* species does not automatically indicate that other species from the Eastern Atlantic/Mediterranean region may group as such. Thus, additional Eastern Atlantic/Mediterranean *Tricolia* species are needed. We also need to establish if there are any clades A representative in the Eastern Atlantic/Mediterranean. The sister taxon relationship between the Eastern Atlantic and the southern African species is interpreted based on three biogeographical hypotheses. It was speculated that *Tricolia* might have originated in the Tethys (Hickman & McLean 1990). If the Tethys closed after the South African species split from the Eastern Atlantic *Tricolia* lineage, then the South African species could still have been derived from the Eastern Atlantic ones via West Africa or East Africa.

Morphological data presented in chapter 2 has already indicated that *Hilola* is a distinctive taxon and that it stands apart from the main *Tricolia* radiation. Molecular data presented in this chapter further confirms this. I therefore propose to rank this taxon as a full genus, based on both molecular and morphological evidence. Morphological features characteristic of *Hilola* include: apex exserted and narrowly rounded, rachidian tooth of the radula well-developed with prominent cusp, operculum coarsely granulated on the external surface, and radula with three pairs of lateral teeth per transverse row. However, the subfamily into which *Hilola* should be placed is still unknown, suggesting that further analyses with additional members of the Phasianelloidea from other genera are required.

Although members of *Eulithidium* form a well supported monophyletic group in the combined nDNA bayesian analysis (PP=1.00, Fig. 4.6c) and all data combined bayesian inference analysis (PP=100, Fig. 4.7c), phylogenetic relationships between them and other pheasant shell genera (*Tricolia*, *Phasianella* and *Gabrielona*) are not clear. The separation of *Eulithidium* from the Tricoliinae is also supported by morphological characters of the operculum, radula and external anatomy, as well as by geographical distribution. Morphological features characteristic of *Eulithidium* include: external surface of operculum with radiating ridges near labral margin, two pairs of epipodial tentacles on each side, radula with four pairs of lateral teeth per transverse row.

It was previously suggested that the radula character may have a phylogenetic and zoogeographic significance, and all the American species (W. Atlantic and E. Pacific) may have been derived from one stock missing the outermost lateral tooth (Robertson 1958). On the basis of these morphological characteristics, Hickman & McLean (1990) had recognized *Eulithidium* as a distinct genus separate from *Tricolia*. In this study, there is strong support from some analyses suggesting that *Eulithidium* groups outside *Phasianella* and *Tricolia* and should be placed in a subfamily of its own, separate from the Tricoliinae. However, this requires further study.

4.4.3.2. The family Phasianellidae

Phylogenetic analyses of the combined nuclear dataset strongly support the monophyly of *Phasianella* (BS=94 and 80%, Figs 4.6b, c), but its sister taxon relationship to *Tricolia sensu stricto* is not supported. The separation of *Phasianella* from other pheasant shells is also supported by morphological evidence. Morphological features characteristics of *Phasianella* include: radula without a functional rachidian tooth, colour pattern including spiral capillary lines, cephalic lappets present and well-developed, and one shell muscle present (Hickman & McLean 1990).

The closure of the Tethys in the east which cut the Mediterranean off from the Indo–West Pacific could have separated *Hiloa*, *T. fordiana*, *Phasianella* and *Gabrielona* species from the Eastern Atlantic and the southern African species. The two endemic south–western Australian *Phasianella* species (*P. australis* and *P. ventricosa*) represent a recent split from an older Indo–West Pacific stock (*P. solida*).

4.4.3.3. The family Gabrielonidae

The position of *Gabrielona* is unclear in the phylogenetic analysis. This could be due to long-branch attraction as only one member of the genus (1 species – *G. pisinna*) was included in the phylogenetic analysis. However, *Gabrielona* should remain a distinct genus within the Phasianelloidea pending further analysis with additional samples. Furthermore, morphological characteristics of the shell and the external surface of operculum are distinct. Morphological features characteristic of *Gabrielona* include: a globose shell shape, very low spire, granulated protoconch, external surface of operculum concave, right and left neck-lobes smooth. To identify the position of this genus and its phylogenetic relationship to other members of the Phasianelloidea, we need additional sequence data from four taxa that were not available for this study.

4.4.3.4. The superfamily Phasianelloidea

Monophyly of the Phasianelloidea was strongly supported in the 16S parsimony and maximum likelihood analyses (BS=99%, Fig. 4.2a, b), 18S rRNA maximum likelihood analysis (BS=100%, Fig. 4.4b), 28S maximum likelihood analysis (BS=87%, Fig. 4.5b), the combined nDNA bayesian analysis (PP=1.00, Fig. 4.6c), all data combined maximum likelihood analysis (BS=99%, Fig. 4.7b), all data combined bayesian analysis (PP=97%, Fig. 4.7c), although some of the internal nodes received little support. However, monophyly of the Phasianelloidea was not supported in most of the analyses. The relationship between the four subfamilies (Eulithidiinae, Tricoliinae, Phasianellinae and Gabrieloninae) is not clear due to the lack of resolution between *Gabrielona*, and the southern Australian and the Indo-West Pacific species of *Tricolia*. It is recommended that further analyses are required including all members of the Phasianelloidea, or at least to include 50% of species from each of the five genera.

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Appendix 4.1. mtDNA COI sequence alignment using the Multiple Sequence Alignment programme MAFFT version 6.

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Appendix 4.2. mtDNA 16S rRNA sequence alignment using the Multiple Sequence Alignment programme MAFFT version 6.

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Appendix 4.3. nuDNA 18S rRNA sequence alignment using the Multiple Sequence Alignment programme MAFFT version 6.

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GENERAL DISCUSSION

The Phasianelloidea though not highly diverse, is an interesting and distinctive group of marine gastropods but previously its systematics, zoogeography and phylogeny was poorly understood. This study contributed greatly in resolving its taxonomic complexity in terms of number of species, number of endemic species as well as hot-spots, diversity and biogeographical patterns along the South African coastline. During the course of this study, three additional taxa have been described from this region namely *T. adusta* Nangammbi & Herbert, 2006; *T. saxatilis* Nangammbi & Herbert, 2006 and *T. retrolineata* Nangammbi & Herbert, 2008. It is possible that more pheasant shell species may be found along the South African coastline and future research should focus on the conduct of more field work in this area. Morphological and molecular data have strongly proved that the name *Chromotis* is a junior synonym of *Tricolia sensu stricto*.

Most of the available museum specimens are either dried shells or relaxed into MgCl₂ prior to preservation into 70% ethanol. As a result, these specimens are not suitable for DNA sequencing. Due to global trends and new techniques that have recently become available for DNA sequencing, it is recommended that museum specimens should be preserved into absolute ethanol (96-100%). Thereafter, such specimens should be stored in the best possible condition for DNA sequencing and anatomical observations. Some of the described species such as *T. striolata* were not found alive and therefore not present in the phylogenetic analysis. This is because there was no information about the precise habitat of this species in the original description, and also there were no living specimens in the Natal Museum marine collection. The use of additional morphological characters such as those of the operculum, protoconch, radula and external anatomy as well as ecological and distribution data is highly recommended when describing new taxa. From the point of existing knowledge, what follows is what I consider to be the major contribution from my research.

The first major finding of the study is that, morphological characteristics alone are not enough to differentiate between species. For example *T. capensis* and *T. africana* were originally described as two distinct species based on morphological characteristics of the shell. This study also showed that the two species differ in terms of ecological (habitat preferences) and geographical range. Further evidence provided by molecules suggests that

the two species are genetically indistinguishable (0.00% maximum sequence divergence from both COI and 16S rRNA markers).

Similar results have been observed in *T. bicarinata*, *T. insignis* and *T. kraussi*. The mitochondrial COI and 16S rRNA markers are variable and are used to resolve intraspecific relationships. As a result, these markers were also used in the present study to resolve species level relationships, and provided good evidence that species identified on conchological grounds are in fact real entities. However, they both failed to discriminate between *T. africana* and *T. capensis*, as well as among *T. bicarinata*, *T. insignis* and *T. kraussi*. It has been suggested that the COI gene may not provide resolution at the species level, particularly in certain marine species (⁵D Colgan 2007, personal communication). This may also suggest that these species are likely to be phylogenetically inseparable with any conventional genetic markers, unless using rapidly evolving nuclear markers such as microsatellites. Consequently, very little population level work using these markers have been done so far. Future studies could determine whether the mtDNA lineages identified in this study are reproductively isolated (either by performing crossbreeding experiments in the laboratory or by performing translocation experiments where juvenile specimens of both *T. bicarinata* and *T. insignis* are placed in False Bay environmental conditions to see if their strong spiral ridge sculpture on the shell surface will develop into a fine spiral threads sculpture of *T. kraussi*); or whether there are previously unnoticed morphological differences. However, the logistics of actually performing these experiments can be problematic. A more sensible conclusion provided if all the proposed ideas failed could be that these species may have undergone recent speciation with rapid morphological and ecological divergence coincident with geographical separation.

The second major contribution of the study is that the southern African *Tricolia* radiation is represented by two major distinct clades that are easily separated by morphological characters of the radula and external anatomy and DNA sequence data. The East African species *T. ios* should be considered part of the southern African *Tricolia* radiation as it was constantly grouped within the southern African clade A. Both morphological and molecular data suggest that the southern African *Tricolia* fauna has close affinities with the Eastern Atlantic species of the same genus. Future studies could do more intensive field collecting or surveys along the west coast since very few *Tricolia* taxa are known from this region. By so

⁵ Dr D Colgan, Evolutionary Biology Unit, The Australian Museum, 6 College St., Sydney 2010

doing, this could also help to establish if there are any links between the Eastern Atlantic and the southern African *Tricolia* species.

The third major contribution made by this study is that the southern Australian and the Indo–West Pacific *Tricolia* species are not part of *Tricolia sensu stricto* and should probably be placed into separate genera pending further analysis with additional data from other members of the Tricoliinae such as the small Mediterranean, Eastern Atlantic, Northern Japan, Amsterdam and St. Paul Islands, southern Australia and the Indo–West Pacific. Morphological and molecular data have proved beyond any reasonable doubt that *Hiloa* should be treated as a distinct genus within the Phasianelloidea. However, both datasets have shown that *Hiloa* falls outside the Tricoliinae. Future research could investigate the subfamily in which this genus should be placed.

The fourth major finding made by this study is that the relationship of *Gabrielona* to other genera within the Phasianelloidea is not clear. Because only one species of this genus was present in this phylogenetic analysis, future studies could investigate the relationship of *Gabrielona* to other genera by obtaining additional sequences from species that were not available i.e., *G. hadra*, *G. nepeanensis*, *G. raunana* and *G. roni*. The radula of the type species (*G. nepeanensis*) is similar to that of the genera *Hiloa* and *Eugabrielona*. This further support *Gabrielona* as a member of this superfamily.

The fifth major finding made by this study is that *Eulithidium* should be placed into its own subfamily, separate from the Tricoliinae. Currently, there is not sufficient evidence from molecules to place this genus into a separate subfamily. As a result, additional sequence data of *Eulithidium* species from both sides of America (Eastern Pacific and Western Atlantic) is required.

A new species of pheasant shell from the south-western Indian Ocean (Mollusca: Gastropoda: Vetigastropoda: Phasianellidae: *Tricolia*)

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ABSTRACT

Tricolia retrolineata sp. n. is described from off-shore reef habitats in southern Mozambique and north-eastern South Africa. The smooth, glossy shell with bright, variegated colour pattern, as well as the convex, paucispiral, calcareous operculum and lack of interior nacre clearly place this species in the family Phasianellidae. The bulimoid shape of the shell, combined with its small size and lack of capillary lines in the colour pattern are typical of the genus *Tricolia* s.l.

KEY WORDS: Mollusca, Phasianellidae, *Tricolia*, pheasant shells, new species, subtropical, Indian Ocean, subtidal, coral reef.

INTRODUCTION

On-going research on phasianellid diversity and systematics in southern Africa has already brought to light two new species of the genus *Tricolia* from subtidal habitats off the east coast (Nangammbi & Herbert 2006). We here describe an additional species from southern Mozambique and north-eastern South Africa, which has recently been recognised amongst specimens previously identified as *T. alfredensis* (Turton, 1932), itself a junior synonym of *T. elongata* (Krauss, 1848) (Nangammbi unpubl. data), a species known only from the southern Cape.

MATERIAL AND METHODS

The material discussed was isolated during a re-evaluation of the phasianellid material in the Natal Museum Mollusca collection. Most of the specimens were obtained through the museum's SCUBA diving programme of the 1980s and 1990s. Additional material was obtained from dredge samples and beach-drift. Photographs of shells were taken using a Nikon D70 camera with 55 mm AF Micro Nikkor lens and extension tubes, or a Leica MZ16 stereomicroscope with auto-montage camera. The external surface of the operculum was examined at 15 kV accelerating voltage in a Philips XL30 Environmental Scanning Electron Microscope. The distribution map was plotted using ArcView GIS, Version 3.1.

The following acronyms are used:

NMDP – Natal Museum Dredging Programme;

NMSA – Natal Museum, Pietermaritzburg, South Africa;

NPB – Natal Parks Board (now Ezemvelo KwaZulu-Natal Wildlife).

TAXONOMY

Family Phasianellidae Swainson, 1840

Genus *Tricolia* Risso, 1826***Tricolia retrolineata* sp. n.**

Figs 1–12, 15–17

Etymology: From Latin *retro* (backward) and *lineata* (lined), referring to the opisthocline lines which usually form a conspicuous element of the colour pattern.

Diagnosis: Shell small, bulimiform; whorls lacking distinct keel or angulation, but noticeably more strongly rounded below periphery; body whorl relatively large in proportion to the rest of shell; suture relatively shallow; surface smooth and somewhat glossy; fresh specimens translucent with variable coloration, but typically yellowish brown patterned with numerous, fine, close-set, sinuous, orange-red, opisthocline lines, and with bold, white, red or dark brown blotches or zigzag axial lines on adapical surface of each whorl; apical whorls lacking subsutural spots.

Description:

Shell small, bulimiform, with up to 3.5 teleoconch whorls; body whorl relatively large in proportion to the rest of shell (*ca* 80 % of total length); whorls lacking a distinct keel or angulation, but noticeably more strongly rounded below periphery; suture relatively shallow. Shell usually smooth and glossy, lacking spiral sculpture, marked only by fine growth-lines. Aperture ovate-circular, outer lip thin; interior without nacre and colour pattern visible internally; inner lip concave and slightly reflected over umbilical region; umbilicus closed in most specimens, but occasionally remaining as a narrow chink. Shell translucent with variable coloration; ground colour yellowish, typically patterned with numerous, fine, close-set, sinuous, orange-red, opisthocline lines, and commonly with bold white and red or dark brown blotches on adapical surface (Figs 1, 2, 7, 8), or with alternating darker orange-red and paler zigzag axial lines (Figs 3–6); in some specimens the opisthocline lines anastomose, creating a darker reddish network with yellowish orange spots (Figs 9, 10); umbilical region often bordered by a broad white band traversed by the red opisthocline lines which by this stage appear almost axial; apical whorls lacking white subsutural spots (Fig. 15).

Protoconch: Unknown (shell apex worn in all the material available, no specimens suitable for SEM).

Operculum (Fig. 16): Calcareous, thick and convex; paucispiral with eccentric nucleus; exterior somewhat eroded in the single operculum available, but clearly showing a narrow peripheral groove underlying labral margin.

Radula and external anatomy: Unknown.

Measurements (mm): Holotype (Figs 1, 2) – length 6.4, width 3.5; largest specimen – length 7.4, width 4.1. Length:width ratio 1.2–1.3 (N=10).

Habitat: On the available evidence, *T. retrolineata* is a subtidal species inhabiting off-shore reefs; the bulk of material has been collected from swash accumulations of dead shells in coral reef gulleys, suggesting that the animals were living on the reefs themselves. The single live-collected specimen was found on a coral-dominated reef between 7 and 11 m. Empty shells have also been collected on more algae-dominated reefs and



Figs 1–12. *Tricolia retrolineata* sp. n., variation in shell colour and pattern: (1, 2) holotype, length 6.5 mm, width 3.5 mm, NMSA L5938/T2238, Ponta do Ouro, Mozambique; (3, 4) paratypes: (3, 4) length 5.8 mm, width 3.3 mm, NMSA S2851/T2242, between Bhanga Nek and Kosi Bay, KwaZulu-Natal; (5, 6) length 7.1 mm, width 3.8 mm, NMSA L7357/T3339, Ponta do Ouro, Mozambique; (7, 8) length 6.0 mm, width 3.4 mm, NMSA L6904/T2240, Malongane, Mozambique; (9, 10) length 6.5 mm, width 3.4 mm, NMSA W1935/T2243, Mzamba, Eastern Cape; (11, 12) length 7.4 mm, width 4.1 mm, NMSA E2476/T2241, Leadsman Shoal, KwaZulu-Natal.

this may be the principal habitat at southern localities where coral-dominated reefs are absent.

Comparison: The smooth, glossy shell with bright, variegated colour pattern, as well as the convex, paucispiral, calcareous operculum and lack of interior nacre clearly place this species in the family Phasianellidae. The bulimiform shape of the shell, combined

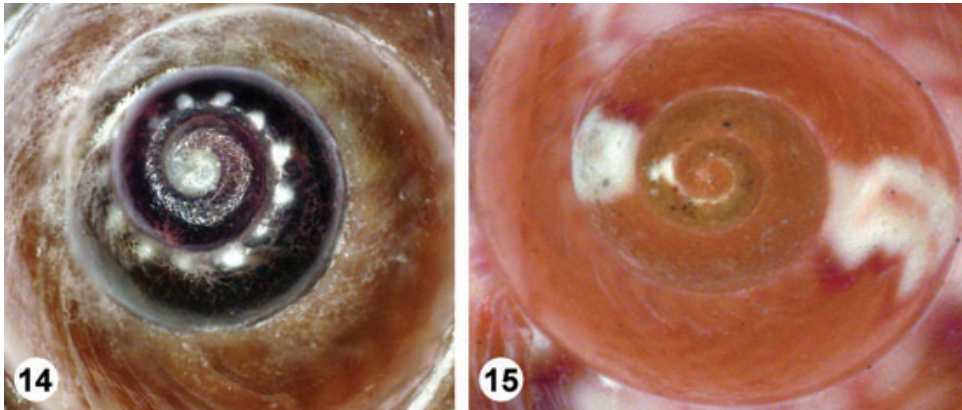


Fig. 13. *Tricolia elongata* (Krauss, 1848), length 12.7 mm, width 6.9 mm, NMSA W4769, Cape Agulhas, Western Cape.

with its small size and lack of capillary lines in the colour pattern are typical of the genus *Tricolia* s.l. (Robertson 1985; Hickman & McLean 1990).

Specimens of this new taxon were previously identified under the name *Tricolia alfredensis* (Turton, 1932), primarily on account of their bulimiform shape and distinctive colour pattern of sinuous opisthocline lines. However, *T. alfredensis* is now considered to represent nothing more than a colour form of the variable *T. elongata* (Krauss, 1848) (Nangammbi unpubl. data). Although *T. retrolineata* resembles *T. elongata* more than it does any other southern African *Tricolia* species, it differs from this in attaining a smaller size (maximum length 7.4 mm vs 13.7 mm in *T. elongata*) and in having a thin, translucent shell. This species is represented by a sample size of more than 100 specimens in the Natal Museum collection, and the probability of adult shells being represented in this sample would be high. *Tricolia elongata* (Figs 13, 14) also differs from *T. retrolineata* (Fig. 15) in having a spiral row of white, subsutural spots on second teleoconch whorl. However, this is only visible in fresh specimens of this species.

Furthermore, the two species differ in their habitat preferences. *T. retrolineata* is a subtidal species, whereas *T. elongata* occurs commonly in the rocky intertidal zone, living among seaweed at low spring tide level. Unfortunately, prior to this species being identified as an undescribed taxon, the body of the single live-collected specimen was used for DNA extraction in relation to phylogenetic studies of the southern African *Tricolia* radiation. However, the DNA was not successfully extracted, possibly due to relaxation of the specimen in $MgCl_2$ prior to preservation. Comparative data on the radula and external anatomy are therefore not available.



Figs 14, 15. Apices of *Tricolia elongata* (Krauss, 1848) and *T. retrolineata* sp. n.: (14) *T. elongata* showing white, sub-sutural spots on second teleoconch whorl, NMSA W4769, Cape Agulhas, Western Cape; (15) *T. retrolineata* sp. n. lacking spots on apical region, NMSA L5938/T2238, Ponta do Ouro, Mozambique.

Holotype: MOZAMBIQUE: Ponta do Ouro (26.850°S:32.917°E), subtidal reef, hand-dredged sand, ca 20 m, 14.iv.1997, dived D. Herbert (NMSA L5938/T2238).

Paratypes: MOZAMBIQUE: 25 specimens, same collection data as holotype (NMSA L7357/T3339); 15 specimens, Malongane (24.798°S:32.890°E), coral reef north, hand-dredged sand, 10–20 m, 16.iv.1997, dived D. Herbert (NMSA L6904/T2240). SOUTH AFRICA: *KwaZulu-Natal*: 2 specimens (one alive), Leadsman Shoal (27.800°S:32.867°E), main portion of coral reef, 7–11 m, 14.v.1988, dived D. Herbert & NPB (NMSA E2476/T2241, Figs 11, 12, 16); 1 specimen, between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), algal portion, 5–9 m, underwater pump, 03.v.1990, dived D. Herbert & K. Bloem (NMSA S2851/T2242). *Eastern Cape*: 26 specimens, Mzamba (31.100°S:30.183°E), x.1979, J.P. Marais (NMSA W1935/T2243).

Other material examined (all NMSA): MOZAMBIQUE: off Malongane, coral reef ca 5 km, north of Ponta do Ouro, hand-dredged sand, 15–20 m, v.1994, dived D. Herbert (V1501). SOUTH AFRICA: *KwaZulu-Natal*: between Bhanga Nek and Kosi Bay (26.433°S:32.900°E), reef off marker 13 north, near pinnacles, 10–12 m, hand-dredged sand, 12.v.1990, dived D. Herbert (S2427); same locality, ca 8 m, underwater pump, 06.v.1990, dived D. Herbert & K. Bloem (S2737); off Lala Nek (27.227°S:32.822°E), 75 m, coarse sand, sandstone, coral, dredged NMDP, Stn. ZDD4, 08.vi.1990 (S9014); “B.J.’s Reef”, off Hibberdene (30.583°S:30.600°E), 18–26 m, 15.xi.1992, dived D. Herbert (V1833). *Eastern Cape*: Mzamba (31.100°S:30.183°E), beach-drift, 12–30.v.1986, R. Kilburn & D. Herbert (D2933).

Distribution and Biogeography (Fig. 17): *T. retrolineata* is a subtropical species endemic to south-east Africa, ranging from just north of the South Africa–Mozambique border (Malongane) south to the extreme north-east of Eastern Cape Province, South Africa (Mzamba).

The southern distribution limit of *T. retrolineata* lies approximately 300 km to the north of the known range of *T. elongata*. However, a gap of similar extent occurs within the range of *T. retrolineata*, namely between Leadsman Shoal and Hibberdene. The significance of these gaps differs. The interval within the range of *T. retrolineata* occurs in the Natal Bight and is probably caused by lack of suitable habitat in this area. A number of large, sediment-laden rivers enter the sea here (Umfolosi, Thukela, Umgeni, Umkomaas) and rocky subtidal habitats are scarce in this region, re-appearing again in number only off the KwaZulu-Natal south coast, to the south of Scottburgh. Many subtropical reef species and tropical stragglers exhibit a similar hiatus in distribution records in this region and the shore at Mzamba is well known as a site where shells of

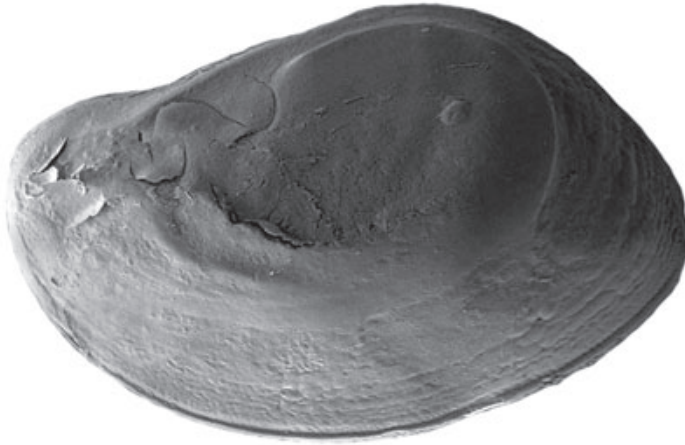


Fig. 16. Scanning electron micrographs of the external surface of operculum of *Tricolia retrolineata* sp. n., showing distinct peripheral groove underlying labral margin, paratype, maximum diameter 2.9 mm, NMSA E2476/T2241.

unusual tropical taxa regularly wash ashore, e.g. *Tonna perdux* (Linnaeus, 1758), *Agagus agagus* Jousseaume, 1894, *Strombus gibberulus* Linnaeus, 1758, *Conus obscurus* Sowerby, 1833, *Talparia talpa* (Linnaeus, 1758), and *Latirus turritus* (Gmelin, 1791). It is thus quite possible that shells of a species such as *T. retrolineata*, which is known from reefs off the KwaZulu-Natal south coast (as recorded at Hibberdene), could also wash ashore at Mzamba. The gap in its distribution in the Natal Bight is thus typical rather than exceptional for such warm-water taxa. Furthermore, the Natal Bight is also known to be impacted by the upwelling of cold, nutrient-rich water (Meyer *et al.* 2002), which may well be of significance to tropical/subtropical species accustomed to warmer water with lower nutrient content.

The similar sized gap between the southern population of *T. retrolineata* and the northern limit of *T. elongata* is of a very different nature. The southern African coastline is divided into three marine biogeographical provinces namely a subtropical east coast province, a warm-temperate south coast province and a cold-temperate west coast province (Stephenson & Stephenson 1972; Brown & Jarman 1978; Day & Grindley 1981; Emanuel *et al.* 1992; Bustamante 1994; Turpie *et al.* 2000; Harrison 2003). The boundaries between these provinces are defined by changes in species composition and water temperatures. The precise position of the interchange between the subtropical and the warm-temperate provinces on the east coast of South Africa appears to vary with the taxon under consideration and has been cited as Port St Johns (Stephenson & Stephenson 1972), Port Edward (Brown & Jarman 1978; Turpie *et al.* 2000), Great Kei River (Day & Grindley 1981), East London (Emanuel *et al.* 1992), and Mdumbi estuary (Harrison 2003). For the pheasant shells (Phasianellidae) of southern African this boundary lies between the Mbashe River and East London (Nangammbi unpubl. data). Thus the region separating the distributions of *T. retrolineata* and *T. elongata* has in many cases been identified as a region of major faunal turnover and biogeographic significance. In this context, *T. retrolineata* is a subtropical east coast species, whereas *T. elongata* is a warm-temperate south coast taxon.

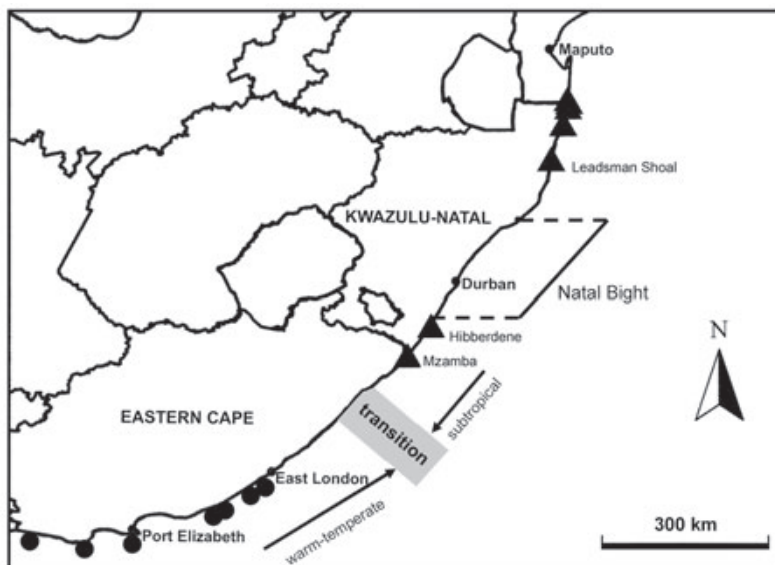


Fig. 17. Distribution of *T. retrolineata* sp. n. (▲) and *T. elongata* (●).

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