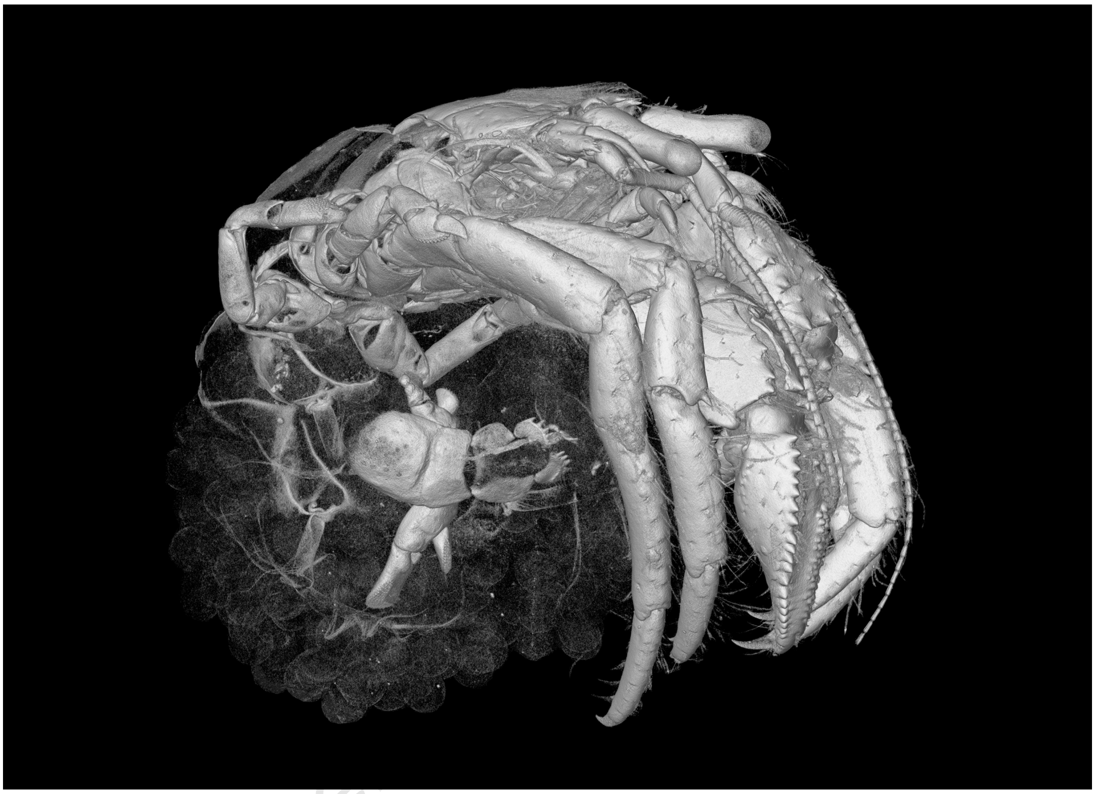
Contributions to the taxonomy of South African hermit crabs (Crustacea: Decapoda: Paguroidea) – integrating microCT scanning and barcoding



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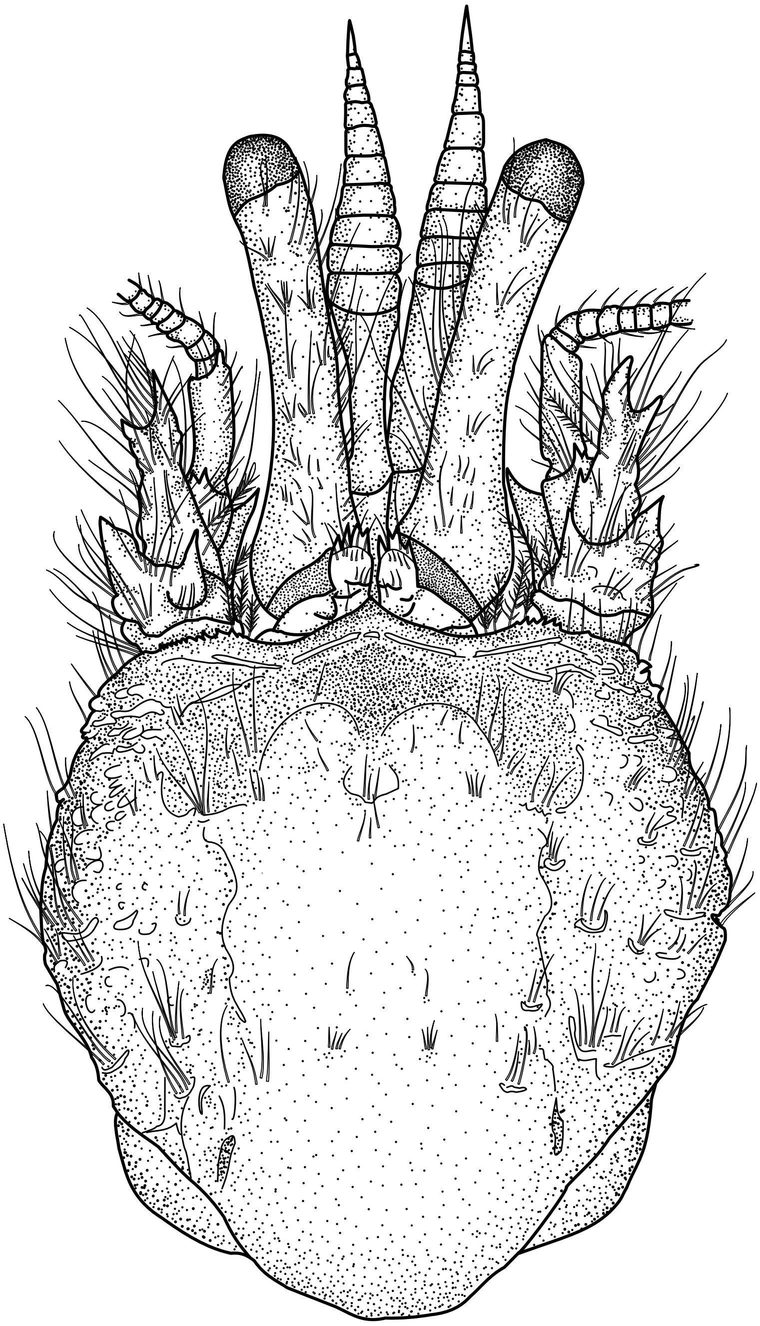

Title page: MicroCT scanning image of *Pagurus* n.sp., ovigerous ♀ paratype 2.4 mm shield length (SAMC MB-A066770).

Input page: Shield and cephalic appendages of *Cancellus macrothrix* Stebbing, 1924, specimen with both male and female secondary sexual characters, 9.8 mm shield length (USNM 1292096).

AUTHOR'S DECLARATION

I, Jannes Landschoff, hereby declare that I know the meaning of plagiarism, and that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise), for which I have received, beyond the normal guidance by my supervisor, no assistance except as stated below. Neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I authorise the University of Cape Town to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever. Several of the chapters in this thesis have been published or have been submitted to research journals in co-authorship with the other researchers listed below. The contributions made by the candidate, and each of the co-authors to each of these joint-papers/chapters, are stated below.

Author's abbreviations

JL: Jannes Landschoff
TK: Tomoyuki Komai
GG: Gavin Gouws
DLR: Dwi Listyo Rahayu
RL: Rafael Lemaitre
ADP: Anton du Plessis
CLG: Charles Llewellyn Griffiths

Chapter 2, published as:

Landschoff, J., Lemaitre, R., 2017. Differentiation of three common deep-water hermit crabs (Crustacea, Decapoda, Anomura, Parapaguridae) from the South African demersal abundance surveys, including the description of a new species of *Paragiopagurus* Lemaitre, 1996. *ZooKeys* 676, 21–45.

Author's contributions: JL conceived the paper with RL. JL collected the data, examined the specimens, produced all figures and wrote the first description and manuscript under the guidance of RL. RL edited or revised the manuscript.

Chapter 3, submitted as:

Landschoff, J., Rahayu, D. L., in press. A new species of the hermit crab genus *Diogenes* (Crustacea: Decapoda: Diogenidae) from the coast of KwaZulu-Natal, South Africa. *Zootaxa* [accepted with minor revisions on 2 Nov 2017].

Author's contributions: JL conceived the paper and prepared the manuscript. DLW helped with the taxonomy, edited or revised the manuscript and contributed valuable comments.

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Anomura: Paguridae), with selection of three-dimensional type data. *PLOS One* [submitted on 7 Aug 2017].

Author's contributions: JL conceived the paper, collected the data, examined the specimens, and wrote the initial manuscript. TK helped with and revised the taxonomic section. ADP and JL produced the microCT scans and ADP edited some of the text. GG provided the barcodes and edited the genetic sections of the manuscript. CLG's, and all co-author's comments, helped to improve the manuscript by valuable suggestions.

Chapter 5, published as:

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Author's contributions: JL conceived the paper with RL. JL collected the data and examined the specimens. Together, RL and JL wrote the manuscript.

Chapter 6, submitted as:

Landschoff, J., du Plessis, A., Griffiths, C. L., in press. A micro X-ray computed tomography dataset of South African hermit crabs (Crustacea: Decapoda: Anomura: Paguroidea), containing scans of two rare specimens and of three recently described species. *GigaScience* [accepted with minor revisions on 25 Sep 2017].

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Author's contributions: JL conceived the paper and study design, and wrote the manuscript. ADP prepared the data for upload and contributed to the writing of the technical section. CLG edited the manuscript and contributed valuable comments.

SIGNED: Signed by candidate DATE: **14th February 2018**

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ACKNOWLEDGEMENTS

The path to handing in this PhD thesis was long and filled with obstacles. If I had any doubts as to how much science depends on communal support structures, hermit crabs have certainly now taught me this lesson. By expressing my dearest gratitude to everyone who has been on this journey with me, in the following account I will venture the utterly impossible task to give adequately equal attentiveness to everyone involved. The order in which people are acknowledged is also not indicative of how much their support has meant for achieving the goal of writing this thesis. During the past three years so many exceptional people have influenced me, contributed to my life, or supported me in invaluable ways. These ways can be measured or expressed by words with some difficulties only.

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ACRONYMS

μCT	micro computed tomography.
♀♀	females.
♀	female.
♂♂	males.
♂	male.
3D	three-dimensional.
ACEP	African Coelacanth Ecosystem Programme.
BG	Barcoding Gap.
BOLD	Barcode of Life Data System.
brood.	brooding.
CBM	Natural History Museum and Institute, Chiba, Japan.
COI	cytochrome *c* oxidase subunit I.
coll.	collected by.
DAFF	South African Department of Agriculture, Forestry and Fisheries.
DEA	Department of Environmental Affairs.
DST	National Department of Science and Technology.
E. C.	Eastern Cape.
EEZ	Exclusive Economic Zone.
ESUs	evolutionary significant units.
GigaDB	GigaScience Database.
ICZN	International Code of Zoological Nomenclature.
juv.	juvenile.
K2P	Kimura 2-parameter.
KZN	KwaZulu-Natal.
n. sp.	new species.
NJ	Neighbour-Joining.
NRF	South African National Research Foundation, Pretoria, South Africa.
NTOU	National University of Taiwan.

numts	nuclear mitochondrial DNA segments.
ORI	Oceanographic Research Institute.
ovig.	ovigerous.
PCR	Polymerase Chain Reaction.
PDF	portable document format.
pers. comm.	personal communication.
pers. obs.	personal observation.
ROV	remotely operated underwater vehicle.
SAEON	South African Environmental Observation Network.
SAIAB	South African Institute for Aquatic Biodiversity.
SAMC	Iziko South African Museum, Cape Town.
SANBI	South African National Biodiversity Institute.
SCDSA	South Coast Demersal Survey Autumn.
SCDSS	South Coast Demersal Survey Spring.
Scuba	Self-contained underwater breathing apparatus.
SEAKY	SeaKeys.
SL	shield length.
sta	station.
STL	Stereolithography.
TRR	taxonomic resolution ratio.
U3D	Universal 3D.
UCT	University of Cape Town.
UCT E. S.	University of Cape Town Ecological Survey.
unpubl.	unpublished.
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D. C..
vs.	versus.
W. C.	Western Cape.
WCDSS	West Coast Demersal Survey Summer.
ZMB	Museum für Naturkunde Berlin, Germany.
ZRC	Lee Kong Chian Natural History Museum, Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore.

ABSTRACT

Hermit crabs form an important component of the marine benthos and globally more than 1,200 species have been described. In the unique bioregion of South Africa, hermit crabs are poorly known, and the last taxonomic revision of the group was that of K. H. Barnard in 1950, who recorded only 32 species. This study combines morphological taxonomy, three-dimensional (3D) micro-computed tomography (μCT) visualisations, and molecular barcoding to add to, revise, and provide an updated listing of, the regional fauna. The first section of the thesis comprises four chapters, each giving a detailed account of a species either new to science, or to the region. The pagurid hermit crab *Goreopagurus poorei*, a new species and genus record to the country, is reported and described from deep sea habitats along the Agulhas Shelf, extending the distribution by >10,000 km across the Indian Ocean. Furthermore, three species are described as new to science, one each from the three most common families. The first of these, a deep-water species from a genus of the family Parapaguridae that was previously unknown to South Africa, *Paragiopagurus atkinsonae* n. sp., is fully described and illustrated, and compared with two other parapagurids that each play a dominant role in the regional benthic offshore invertebrate community. The other two species new to science, *Diogenes* n. sp. from the family Diogenidae, and *Pagurus* n. sp. from the family Paguridae, inhabit coastal reefs in subtidal waters off southern KwaZulu-Natal. For the first time in crustacean taxonomy, species descriptions, particularly the one of *Pagurus* n. sp., are informed by, or based on, μCT imagery of calcified body parts. Following on this technique, Chapter 6 is a short presentation of the 3D raw dataset of seven μCT scans of types and rare museum specimens used in this thesis, which is made publicly available for download. The taxonomic use of the scanning method, with disseminating volumetric data of hermit crabs, is discussed briefly. The final section investigates the fauna as a whole. In Chapter 7, 194 cytochrome *c* oxidase subunit I gene segments (COI ‘barcodes’) of 43 nominal species plus 12 additional putative species (n = 55 species-like units) were used to validate morphological identifications. Testing this dataset revealed high barcoding efficacy, with nearly 99% identification success rates, and with the best Kimura 2-parameter distance to safely delimit species of hermit crabs of about 3.5%. Chapter 8 updates the regional fauna and provides taxonomic accounts for 62 nominal species which have either been added subsequent to the previous monographic review, or which have undergone taxonomic revision since that time. Of these, 12 are added for the first time here, increasing the number of known South African hermit crab species to 72, an expansion of 56% since Barnard, and about 20% since a recent species list published by W. Emmerson in 2016. Because colour images are provided for 51 out of 72 species, Chapter 8 can also be used as a preliminary guide. However, this study has shown that the hermit crabs of South Africa are by far more diverse than originally thought, and the summary, which includes only the 72 nominal taxa and none of the additional 10 putative species included in the barcoding dataset, is speculated to be only 60–70% complete. Future taxonomic work, especially in the genera *Diogenes* and *Paguristes*, will most likely result in many more species descriptions. Therefore, this current study is to be seen as important step towards a fully illustrated taxonomic catalogue on the South African hermit crabs to be produced in the near future.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Motivation and background

Hermit crabs, or paguroids, are familiar animals, most commonly observed in tidal pools or shallow subtidal waters, where they are well-known for their intriguing behaviour of colonising discarded gastropod shells. Some semiterrestrial species have also found controversial popularity in the pet market. In reality, however, hermit crabs are highly diverse in both their body form and habitat (McLaughlin et al. 2010). While a few species can tolerate estuarine conditions, or even occur in fresh water (McLaughlin and Murray 1990), the vast majority of species are fully marine and occur from the polar to tropical regions and from the supralittoral to the abyss (Mclaughlin 1983, McLaughlin 2003). Hermit crabs belong to the particularly conspicuous, and also commercially important, group of decapod Crustacea, of which about 15,000 extant species have been described (De Grave et al. 2009), and are further placed within the infraorder Anomura. A little less than half of the 2,500 anomuran species are hermit crabs (Lemaitre and McLaughlin 2009). Although the position of the king crabs in the family Lithodidae within the Anomura has caused considerable debate and phylogenetic research (Cunningham et al. 1992, Richter and Scholtz 1994, Tudge 1997, McLaughlin and Lemaitre 1997, 2000, Harvey 1998, Morrison et al. 2002, McLaughlin et al. 2004, Tsang et al. 2008, 2011, Ahyong et al. 2009, Bracken-Grissom et al. 2013, Keiler et al. 2016), the consensus suggests that king crabs have evolved from hermit crabs, but are currently given their own superfamily rank, Lithoidea (Lemaitre and McLaughlin 2009). Hermit crabs, comprising the superfamily Paguroidea (*sensu* McLaughlin et al. 2007a), therefore currently consist of about 1,200 species in over 130 genera and six families (McLaughlin and Türkay 2017). Nearly 95% of all species are to be found in the three most diverse families, the Diogenidae, Paguridae and Parapaguridae (Table 1.1).

Commonly, paguroids are known to shelter within gastropod shells, but many in fact dwell in other types of housing objects, such as bivalve shells (Anker and Paulay 2013), scaphopod shells or polychaete tubes, as well as sponges, pieces of wood or hollow rocks (Caine 1980, Forest 1987a, Forest et al. 2000, Lemaitre et al. 2009), or even inhabit living corals or parts thereof (McLaughlin and Lemaitre 1993, Igawa and Kato 2017). The largest paguroid species, the coconut crab *Birgus*

Table 1.1: Numbers of genera and species of Paguroidea of the world, compiled after McLaughlin et al. (2010), McLaughlin and Türkay (2017), and with assistance from R. Lemaitre.

Family	**Author**	**Genera**	**Species**
Coenobitidae	Dana, 1851	2	18
Diogenidae	Ortmann, 1892	21	462
Paguridae	Latreille, 1802	88	587
Parapaguridae	Smith, 1882	10	91
Pylochelidae	Bate, 1888	10	47
Pylojacquesidae	McLaughlin and Lemaitre, 2001	2	2
	Total	133	1207

latro (Linnaeus, 1767), is fully calcified most of its life and lives without any shelter from an early subadult age (Drew et al. 2010). However, this life-style is the rare exception among hermit crabs, and all other paguroids require some form of cover that serves to protect their soft pleon, the hind body part. By cleaning, maintaining, and preventing their homes from being swept around by currents, or being buried in the sediment, paguroids also provide a stable but mobile habitat for many associated organisms. As a result, a great number of hermit crab species have developed commensal, or even mutual, relationships with other invertebrates (Williams and McDermott 2004, McDermott et al. 2010). One of the most profound examples can be seen in deep sea environments, where large sea shells are a scarce resource. Here, mutualistic relationships with shell-building zoanthids have evolved and these construct a 'carcinoecium' – a shell-type structure for the hermit to live in (Dunn et al. 1980, Fautin 1987, Gusmão and Daly 2010, Crowther et al. 2011, Schejter and Mantelatto 2011). Released from the limitations of shell availability that constrain population densities in other hermit species, deep-water hermit crabs can thus reach impressive abundances and therefore play an important ecological role in deep sea benthic communities (Landschoff and Lemaitre 2017b). In shallower waters, hermit crabs have also been shown to be ecologically important predators and opportunistic scavengers (e.g. Whitman et al. 2001). Given this diversity of life forms and behavioural patterns, hermit crabs can thus form an important component of the marine benthos in a wide range of habitats.

In South Africa, there has been little scientific focus on paguroids as a group, and the taxonomy is poorly known. The earliest and very scattered taxonomic accounts that include some mention of hermit crabs (Krauss 1843, Stimpson 1858, Studer 1883, Henderson 1888, Stebbing 1908, 1910, 1914, 1917a, 1920, 1924, Balss 1912), were summarised in the 'Descriptive catalogue of South African decapod Crustacea' by Barnard (1950). This catalogue listed 32 valid paguroid species as occurring in South African waters and it remains the only comprehensive monographic revision of hermit crabs for the region. Thereafter, and despite this being a diverse and attractive group, taxonomic studies on South African paguroids continued to be erratic. Forest (1954) revised and described several South African taxa in his studies on the genus *Paguristes* Dana, 1851 found along the African coasts, McLaughlin (1998, 2004) revised the regional species of *Nematopagurus* A. Milne-Edwards and Bouvier, 1892, and McLaughlin and Forest (1999) provided a revision for the South African species in the genus *Pagurus* Fabricius, 1775. Several specimens from South African waters were also included in global revisions on deep-water hermit crabs by Lemaitre (1999, 2004a,b). The only other comprehensive treatments, other than Barnard (1950), were the species list by Kensley (1981), and recently another species list provided in the multi-volume guide on the Decapoda of Namibia, South Africa and Mozambique by Emmerson (2016a,b,c). However, because both lists contain taxonomic issues and inaccuracies, and especially because the organisation and presentation of Emmerson's books is problematic (Griffiths 2017), they are both merely a starting point for the identification of decapod crustaceans. In the absence of better information, Barnard's (1950) catalogue has therefore remained the main taxonomic reference on South African paguroids. However, this monograph is now seriously out-dated, both in terms of nomenclature and morphological terminology, and it includes far less than half of the current fauna, as well as lacking comprehensive illustrations and images, making it difficult to use.

The lack of taxonomic knowledge of species-rich groups such as hermit crabs is particularly unsettling in the light of the special geography of the South African region, as South Africa's marine realm is remarkably intriguing for biodiversity analyses (Awad et al. 2002, Griffiths et al. 2010, Teske et al. 2011, Scott et al. 2012). The country has a linear, but long coastline of 3,650 km, with a mainland Exclusive Economic Zone (EEZ) of over 1 million km^2. While depth strata play a major role in the offshore community assemblies, the inshore species distributions are strongly influenced by contrasting temperature regimes around the coastline. The West Coast is dominated by the cold Benguela upwelling system, whereas in the east the warm Agulhas Current brings tropical water from the Indian Ocean southwards. These two mighty ocean currents act as major species boundaries to the east and west, resulting in high rates of endemicity along the southern coast that is located between them (Awad et al. 2002). Furthermore, for many widespread Indo-Pacific species South Africa is the southeastern-most range extension. Hence species information from this region is valuable in determining the global distribution patterns of many widespread Indo-Pacific species.

With major benthic groups such as hermit crabs being poorly known, biodiversity studies are facing a major methodological limitation, as imperfect taxonomy will inevitably cause uncertainties due to erroneous assumptions on species distributions. While it is well accepted that particularly inconspicuous groups are poorly studied and therefore hardly represented in South African biodiversity analyses (Scott et al. 2012), Griffiths et al. (2010) remarked that the Crustacea, including Decapoda, were relatively well documented. However, this statement must be interpreted in the light of the almost complete absence of knowledge on some other groups. In fact, the vast majority of South African marine decapod Crustacea, including hermit crabs, have hardly been studied in the past 70 years. Descriptions of the majority of species therefore most often even pre-date the time at which colour photographs were commonly used. The resulting lack of illustrational photographs of species makes identifications in the field virtually impossible. This adds further uncertainty to studies that aim to document biodiversity, and also adds uncertainty to data needed for marine spatial planning, for example to plan and establish a representative network of marine protected areas. The lack of knowledge on the hermit crabs of the region also means it is impossible to gauge the diversity, rates of endemicity, etc., of the fauna for global comparisons. Lastly, poor taxonomic information is one obvious explanation to why so few ecological studies have addressed the biology of this group. Indeed only very few papers have examined aspects of the biology of just a few well-known paguroid species of the country (Emmerson and Alexander 1986, Walters and Griffiths 1987, Reddy and Biseswar 1993, Nakin and Somers 2007, Wait and Schoeman 2012).

There is thus an immense need for a faunal update that provides better taxonomic resolution on South African paguroids, which are an important or sometimes even dominant group across several depth ranges. Since the review by Barnard (1950), morphological taxonomy of hermit crabs has been massively advanced (e.g. McLaughlin 2003, McLaughlin et al. 2010), and modern molecular tools can be invaluable in helping to delimit taxonomic units in paguroids (Poupin and Malay 2009, Malay and Paulay 2010, Negri et al. 2014, Rahayu et al. 2016, Mantelatto et al. 2009, Olguín and Mantelatto 2013). In an integrated framework, classical morphology, molecular tools, as well as high-resolution photography and imaging techniques, should be applied together to increase the information on the South African hermit crab fauna. Such work will also feed up the biodiversity knowledge chain to support future biodiversity research, marine spatial planning and ecosystem classifications or assessments.

1.2 Aims and objectives

The Paguroidea of South Africa are poorly studied. The only existing monographic treatment by Barnard (1950) is seriously out-dated, and the available species lists published by Kensley (1981) and Emmerson (2016c) are not linked to specimen vouchers or images and hence have no taxonomic validation. They are also incomplete or inaccurate, and give no or little information on the identification of species. Furthermore, none of the mentioned literature is confined to South Africa in terms of geographic coverage, which makes a clear assessment of the national fauna a challenging task. Another problem is that Barnard included only diagnoses and few illustrations that are confined to identification characters that he deemed to be important at that time. Thus, by today's understanding of hermit crab taxonomy, his accounts are mostly insufficient for accurate species-level identifications. Although live photographs of a few common species have been published in local field guides (Branch and Branch 1992, King and Fraser 2014, Branch et al. 2016), the number of species for which illustrations or photographs exist is a small fraction of the actual fauna. Because there is currently no guide to the hermit crabs of South Africa, the first proposals of this thesis included the compilation of a complete national field guide. However, with the growing number of species discoveries during the course of the project and with the increasing taxonomic issues involved, it quickly became apparent that such an objective would lie beyond the scope of a three years study period. Although this did not change the overall theme of the initial objective, the scope and aims of this study have been amended to the following.

The main objective of this study was to add to, revise, and provide an updated taxonomic listing of the Paguroidea of South Africa. This objective was achieved through an integrated framework combining morphological taxonomy with high-resolution macro photography, classical manually-drawn illustrations, and three-dimensional (3D) micro computed tomography (μCT) imaging techniques, and also affirmed by molecular barcoding. Practically, this was accomplished by means of the following aims and goals:

- To sample hermit crabs in South African waters and add as many records as possible.
- To examine existing museum material of paguroids (mostly at the collections of the Iziko South African Museum, Cape Town), and to identify, report or update misidentified or unidentified material.
- If found, to describe species as new to science.
- To explore the use of μCT imaging techniques for hermit crab taxonomy.
- To acquire genetic barcodes for as many species as possible (ideally at least 5–10 per species), and to test the resulting dataset for barcoding efficacy in hermit crabs.
- To address taxonomic issues both using morphological and genetic tools, and to add taxonomic knowledge for poorly-known species.
- To provide an updated taxonomic listing of the regional fauna, with colour images and barcodes, parts or the sum of which can be used as a preliminary tool for the identification of South African hermit crabs.

1.3 Chapter outline

To meet the aims and objectives stated above, and for the reason of scientific efficiency in publishing the results, this thesis is presented in the form of individual chapters, which are formatted as free-standing papers. Except for Chapters 1 and 9, each of the chapters in this thesis has been prepared as a manuscript for submission and publication in a variety of scientific journals. This required that each introduction mentions the available literature, and that each component chapter states similar sampling methods and imaging or molecular techniques, thus making some repetition inevitable. Furthermore, a few differences in formatting and style, due to different journal requirements, were unavoidable. For example and also for the purpose of different sorting approaches, the organisation of the specimen data in the material examined sections vary slightly between different chapters. However, in the preparation of this final thesis, format and style differences were reduced to the minimum, so that this document acts as coherent script, with one single reference list in the end. Where possible, abbreviations and acronyms were also used consistently for the entire document, but unfamiliar acronyms are usually repeated and written out in full length once in the beginning of each chapter. Abstracts are included for each of Chapter 2–8, in which abbreviations are usually given in full when mentioned for the first time. Of the three species that are being described as new to science, one species description, that of *Paragiopagurus atkinsonae* n. sp. Landschoff and Lemaitre, 2017b, has already been published and the new name was thus available to be included in this thesis. The other two descriptions are pending publication and thus the species are referred to as "n. sp." in this document. The thesis consists of the following chapters (short title versions given for Chapter 2-8):

Chapter 1: General introduction

This chapter provides a general background and motivation for the study, sets the aims and objectives, and gives a general outline of the chapters.

Chapter 2: Differentiation of three common deep-water hermit crabs

During the course of this study it became apparent that a third and new species of deep-water hermit crabs from the family Parapaguridae lay undiscovered among the two recognised parapagurid hermit crabs common amongst the invertebrate bycatch of the offshore fishery surveys. This chapter describes this new species, *Paragiopagurus atkinsonae* n. sp., as new to science. Furthermore and to better distinguish the new species in the field, taxonomic updates are also given on the two other common parapagurids that are trawled in great abundances in the research surveys and potentially play important roles in the offshore benthic communities. This chapter was prepared as a manuscript published in the journal *Zookeys*.

Chapter 3: A new species of the hermit crab genus *Diogenes*

Diving and sampling in an understudied and biodiverse region of southern KwaZulu-Natal near Port Shepstone revealed a small and uniquely coloured, ovigerous female specimen assignable to the genus *Diogenes*. This species proved to be distinctively different from all other known species. This chapter describes this species as new to science and provides high-resolution macro photographs and μCT images, as well as a molecular barcode for the holotype. This chapter was prepared as a manuscript for publication in the journal *Zootaxa*.

Chapter 4: MicroCT imaging applied to the description of a new species of *Pagurus*

Sampling hermit crabs in southern KwaZulu-Natal also resulted in the discovery of a new species in the genus *Pagurus* from the family Paguridae. This chapter describes this species as new to science, and for the first time in crustacean taxonomy, explores μCT scanning and 3D imaging techniques for the purpose of illustrating identification characters of calcified body parts. The species is also compared to two similar species from Australia and Thailand and Taiwan. This chapter was prepared as a manuscript for publication in the journal *PLOS ONE*.

Chapter 5: Crossing the Indian Ocean: a range extension for *Goreopagurus poorei*

The pagurid hermit crab *Goreopagurus poorei* Lemaitre and McLaughlin, 2003, previously known only from off eastern Tasmania, was discovered along the continental shelf edge of southeastern South Africa, greatly extending the range of this species by 10,100 km to the west. This chapter reports on this large range extension, along with providing the first live colour information for the species, as well as noting morphological variations to complement the original description. This chapter was published in the journal *Zootaxa*.

Chapter 6: A micro X-ray computed tomography dataset of South African hermit crabs

The μCT 3D raw data produced during the course of this study, which were used to inform the taxonomy predominantly of the new species, are made publicly available for download from the GigaScience database repository. This chapter presents the dataset and provides aspects of the quality and re-use potential. The use of μCT scanning for hermit crab and crustacean taxonomy, with the benefit of disseminating virtual type data instead of, or as an addition to, the shipping of valuably physical specimens, is discussed briefly. This chapter was prepared as both a manuscript and a dataset for publication in the journal *GigaScience* and the data repository *GigaDB*.

Chapter 7: DNA barcoding as a tool to facilitate hermit crab taxonomy

Genetic barcoding using the mitochondrial cytochrome *c* oxidase subunit I (COI) gene segment has gained considerable popularity and has become an integrative part of taxonomic work. During the course of this study, barcodes were collected for 194 specimens of hermit crabs, predominantly from South African waters. This chapter presents and analyses this dataset and also acts as validation of the morphological identifications. Furthermore, the dataset is tested for barcoding efficacy in this group. Although limited to the results of a single mitochondrial marker, this chapter also discusses phylogenetic relationships among the represented hermit crabs.

Chapter 8: Taxonomic revisions and additions to the hermit crab fauna of South Africa

This chapter summarises the most recent available species information of the regional hermit crab fauna, reports on existing material, and accounts for all new findings made. This is achieved by taking Barnard's (1950) catalogue as the general baseline, and incorporating all additions and taxonomic changes to the regional fauna that have taken place since that time. Species accounts are provided for 62 species of the total of 72 species now recognised to comprise the South African fauna. A complete species list is given, as well as colour images for 52 of the taxa. Thus this chapter can be used not only as a taxonomic reference, but also as a preliminary guide to the local fauna.

Chapter 9: Synthesis

This section is a short synopsis of the thesis, remarks on the significance of the findings, and gives an outlook on remaining research gaps and future areas of research.

CHAPTER 2

DIFFERENTIATION OF THREE COMMON DEEP-WATER HERMIT CRABS (CRUSTACEA: DECAPODA: PARAPAGURIDAE) FROM THE SOUTH AFRICAN DEMERSAL ABUNDANCE SURVEYS, INCLUDING THE DESCRIPTION OF A NEW SPECIES OF *Paragiopagurus* LEMAITRE, 1996

2.1 Abstract

Deep-water hermit crabs of the family Parapaguridae can be abundant (up to 20 kg or 1,000 hermit crab individuals per haul) in the trawl bycatch collected during South African demersal abundance research surveys. Until recently, only two parapagurid species had been recognised in the bycatch; *Parapagurus bouvieri* Stebbing, 1910, and *Sympagurus dimorphus* (Studer, 1883). Detailed examination of numerous samples of parapagurid specimens from research surveys revealed the existence of a third, undescribed species previously confounded with *S. dimorphus*, but in fact belonging to a different genus. This new species, *Paragiopagurus atkinsonae* n. sp. is the 25th in the genus *Paragiopagurus* Lemaitre, 1996, and has been found only in a small region on the West Coast shelf of South Africa, at depths of 199–277 m. The species is herein fully described and illustrated, including colour images, micro computed tomography (μCT) scans of selected body parts, and cytochrome *c* oxidase subunit I (COI) barcode data. The new species is morphologically most similar to *P. ventilatus* Lemaitre, 2004c, a species associated with hydrothermal vents, but differs in armature of the fourth antennal segment (armed with a spine on the dorsolateral distal angle vs. unarmed in *P. ventilatus*); setation of the antennal flagella (nearly naked vs. with dense setae in *P. ventilatus*); plumose setation on the third maxillipeds and basal segments of chelipeds (absent vs. present in *P. ventilatus*); number of rows of scales on the propodal rasp of pereopod 4 (two or three rows vs. one row in *P. ventilatus*); and degree of telson asymmetry (weakly asymmetrical vs. strongly asymmetrical in *P. ventilatus*). *Paragiopagurus atkinsonae* n. sp. is superficially similar to *S. dimorphus*, with males of the two species showing the same extreme degree of sexual dimorphism on the right cheliped, general light orange colouration, and frequent

use of colonial zoanthid carcinoecia for pleonal protection. To aid in future identfications and to facilitate data gathering during surveys, a comparison of *P. atkinsonae* n. sp. with *S. dimorphus* is provided, along with descriptions of colouration and photographs of live specimens of all three parapagurid species. Information on the taxonomy of the species is summarised, as well as knowledge of their distribution in the demersal research survey regions of South Africa.

2.2 Introduction

The South African Department of Agriculture, Forestry and Fisheries (DAFF), formerly Department of Environmental Affairs and Tourism, has conducted biannual demersal fishery surveys since 1986. To assess the stock status of commercial fish species such as South African hake (*Merluccius* spp.), two 'demersal surveys' are usually conducted every austral summer (West Coast) or autumn (South Coast). In some years, the two surveys are repeated during the winter or spring. Each survey conducts between 100–120 trawls, the majority of these take place between the 100–500 m isobaths, but some trawls extend to depths >1,000 m (Yemane et al. 2009). Among the invertebrate bycatch retained in research trawls, deep-water hermit crabs of the family Parapaguridae are particularly common and occasionally, remarkably abundant, although they have not always been adequately monitored. On the West Coast, a trawl can contain up to 20 kg (about 1,000 individuals) of parapagurids per haul, and these can make up the vast majority of all invertebrates retained in the research trawls (Figure 2.1; L. Atkinson, pers. comm.). Such parapagurid abundance is an indication of their ecological importance on the South African continental shelf. The exact role, however, that these anomuran crustaceans might play in the benthic community remains to be studied.

Since 2011, invertebrate bycatch, including parapagurids, has been monitored more consistently in research surveys, as part of DAFF's commitment to developing an ecosystem approach to management. Based on limited benthic taxonomic literature from the region, biologists identified only two abundant parapagurid species, *Sympagurus dimorphus* (Studer, 1883) and *Parapagurus bouvieri* Stebbing, 1910. However, during the January 2012 West Coast survey on the R. V. *Africana*, an unfamiliar male parapagurid specimen with "green eyes" was noticed and collected by Dr. L. Atkinson, a researcher with the South African Environmental Observation Network (SAEON), leading the invertebrate monitoring component. The individual male specimen was sent for identification to Dr. R. Lemaitre, who concluded that the specimen might represent an undescribed species of *Paragiopagurus* Lemaitre, 1996, but without additional specimens he was unable to make a final determination. Subsequently, during the 2015 and 2016 DAFF West Coast demersal surveys, numerous additional specimens were collected, and proved to be conspecific with the first male specimen obtained by Dr. Atkinson. A detailed taxonomic study of all these specimens showed that indeed, they represent a new species of *Paragiopagurus* that co-occurs with the two common parapagurid species in the DAFF demersal research surveys, although in a comparatively confined area on the West Coast. Herein this new species is fully described and illustrated, including colour photographs. Furthermore, to improve understanding of the parapagurid fauna occurring on the South African continental shelf, this new species is compared with the other two co-existing parapagurids, *S. dimorphus* and *P. bouvieri*. For the first time, live colour information is provided for the latter two hermit crab species. In combination, this diagnostic information on the three most common South African deep-water hermit crabs will facilitate improved accuracy in identification of the species, as well as future monitoring and ecological studies.

The systematics and taxonomy of deep-water hermit crabs of the family Parapaguridae has been revised in a number of broad studies over the last three decades. The family currently includes 91 species classified in 10 genera, of which five are monotypic (Lemaitre 1989, 1993, 1996, 1999, 2004a,b, 2013, 2014, Osawa 1995, McLaughlin et al. 2010). The new species described herein within *Paragiopagurus* Lemaitre, 1996, is the 25th known for this genus. The other two genera represented in the bycatch of demersal research surveys, *Parapagurus* Smith, 1879, and *Sympagurus* Smith, 1883, each contain 17 species. Although many species of parapagurids are known to occur in the western Indian Ocean and vicinity of the east African coast, only eight species in four genera have previously been documented specifically from South Africa: *Oncopagurus africanus* (de Saint Laurent, 1972), *Parapagurus andreui* Macpherson, 1984, *P. bouvieri, P. richeri* Lemaitre, 1999, *P. stenorhinus* Lemaitre, 1999, *Strobopagurus sibogae* (de Saint Laurent, 1972), *Sympagurus dimorphus*, and *S. trispinosus* (Balss, 1911). In a recent catalogue of decapods, Emmerson (2016b,c) did list 13 species of parapagurids from the broad region that encompasses Namibia, South Africa and Mozambique, including two species of *Paragiopagurus*; however, the two latter species have only been reported from the Valdivia Bank, off Namibia. Thus, the new species of *Paragiopagurus* described herein represents the first report of a species of *Paragiopagurus* in waters of South Africa.

Several earlier reports of parapagurids from South Africa have been corrected in various taxonomic revisions of species in this family, as follows. Lemaitre (1989, 1999) concluded that reports by Kensley (1969, 1974, 1977) of *Parapagurus pilosimanus* Smith, 1879 actually represent *P. bouvieri*. The subspecies *Parapagurus pilosimanus bouvieri* proposed by de Saint Laurent (1972) in her division of the genus *Parapagurus*, and listed by Kensley (1981) in his zoogeographic study of Southern African decapods, was elevated to species status by Lemaitre (1989, 1999). *Parapagurus kilburni* Kensley, 1973, was determined by Lemaitre (2004a) to be conspecific, and thus a junior synonym, of *Strobopagurus sibogae*.

2.3 Materials and methods

Since 2011, targeted invertebrate specimens retained in the research trawl nets were collected during the DAFF demersal research abundance surveys, using a German otter trawl design with various configurations, and a 75 mm mesh cod-end fitted with a 35 mm mesh liner. Trawls were deployed for 30 minutes (bottom time) over all feasible habitats on the South African shelf (for detailed methods see Atkinson et al. 2011). During the 2015 research surveys, hermit crabs were pre-sorted on board by scientific staff, and all specimens of *S. dimorphus* and *P. bouvieri* were separated. Three male specimens with “green eyes” were obtained during the 2015 surveys. During the 2016 research surveys, a subsample of approximately 100 hermit crab specimens from each trawl were separated and frozen for further identification at the University of Cape Town (UCT). Three additional males and 23 females with "green eyes" were obtained from trawls at two West Coast stations during the 2016 surveys. All specimens with "green eyes" were found to be the new species of *Paragiopagurus* herein described. No specimens with "green eyes" were found in trawls from the South Coast. Live images of *S. dimorphus* and *P. bouvieri* were taken in the laboratory at UCT, and in a photographic tank on board of the R. V. *Africana* during an additional South Coast spring survey in September/October of 2016.

The micro computed tomography (μCT) scan of the holotype of the new species of *Paragiopagurus* was performed at the 'CT Scanner Facility' at Stellenbosch University, South Africa, using a General Electric Phoenix V|Tome|X L240 with NF180 option (du Plessis et al. 2016). The specimen was defrosted and placed on top of a plastic rod with dense polystyrene foam as a platform, and consecutively scanned at an X-ray voltage of 100 kV and 100 μA, and a resolution of 35 μm. Images were recorded in 3,200 steps in one full rotation of the sample averaging two image acquisitions at every step. Using a detector shift function between images reduced ring artefacts. The projection images were reconstructed using the system-supplied General Electric Datos reconstruction software, which were subsequently utilised for the visualisation of the right cheliped using Volume Graphics VGStudioMax 3.1. (Heidelberg, Germany).

Illustrations were drawn using a Wild stereomicroscope equipped with a camera lucida, and digitally traced in Inkscape 0.91 (www.inkscape.com). Colour photographs were processed in Gimp 2.8 (www.gimp.com).

Specimens examined in this report are deposited in the Iziko South African Museum, Cape Town (SAMC), the United States National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM) as well as in the Lee Kong Chian Natural History Museum, Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC). Morphological terminology for parapagurids is that used by Lemaitre (2013). Measurements of specimens, in mm, listed in the material examined sections are for shield length (SL), taken from the tip of the rostrum to the midpoint of the posterior margin of the shield. Other acronyms or abbreviations used are: male (♂); female (♀); ovigerous (ovig.); South Coast Demersal Survey Autumn (SCDSA); South Coast Demersal Survey Spring (SCDSS); West Coast Demersal Survey Summer (WCDSS); station (sta); and in the material examined sections, months are abbreviated by the first three letters.

Muscular tissue, usually from the merus of the right cheliped, was extracted from freshly frozen specimens, placed in 96% ethanol, and sent to the South African Institute for Aquatic Biodiversity (SAIAB). At SAIAB, DNA extractions were carried out using a standard "salting out – ethanol precipitation" protocol (Sunnucks and Hales 1996), followed by the amplification of the 'barcoding' (Hebert et al. 2003) fragment of the cytochrome *c* oxidase subunit I (COI) gene for each sample by Polymerase Chain Reaction (PCR), using the universal invertebrate primers (LCOI-1490 and HCOI-2198) of Folmer et al. (1994), or their degenerate variants (dgLCO1490 and dgHCO2198;

Meyer 2003). PCR recipes and conditions followed Meyer (2003) and Gouws et al. (2015), with annealing performed at 48°C for the latter. Successful amplification was determined by visualising products under UV light, following electrophoresis in 1% agarose gels, stained with ethidium bromide, in a TBE buffer. PCR products were purified with an Exonuclease I – Shrimp Alkaline Phosphate (Exo/SAP, ThermoFisher Scientific) protocol (Werle et al. 1994), sequenced in both the forward and reverse directions using BigDye v3.1 (Applied Biosystems, Austin, Texas) terminator chemistry and analysed on an ABI-Hitachi 3500 Genetic Analyser (Applied Biosystems) at SAIAB. The resulting sequences were checked against their chromatograms for misreads and sequencing errors using ChromasLITE (Technylesium). Sequences were aligned, edited and the consensus DNA barcode compiled using Lasergene SeqMan Pro 9 (DNASTAR, Madison, Wisconsin). Barcodes were uploaded to the SeaKeys (SEAKY) project on the Barcode of Life Data System (BOLD) (www.boldsystems.org; Ratnasingham and Hebert 2007) and were submitted to GenBank. For a number of specimens, tissues were submitted to the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, for barcoding. These data were also uploaded to SEAKY on BOLD. For future reference and studies, the database gene codes are included under each species.

2.4 Systematic account

2.4.1 Family Parapaguridae Smith, 1882

2.4.1.1 Genus *Paragiopagurus* Lemaitre, 1996

***Paragiopagurus atkinsonae* n. sp.**

http://zoobank.org/833540CC-B266-4010-A401-E7CA010CDE6A

Figures 2.2–2.6, 2.8

Type material. *Holotype*: ♂ 7.0 mm, South Africa, West Coast, WCDSS2016, CCH008, sta D00723-3243, S 31° 52.81’, E 16° 57.12’, 265 m, 11 Mar 2016 (USNM 1292083).

Paratypes: South Africa, West Coast. WCDSS2012, AFR279: 1 ♂ 7.6 mm [with zoanthid symbionts], sta A32208-3233, S 31° 39.79’, E 17° 02.79’, 259 m, 24 Jan 2012, coll. L. Atkinson (USNM 1292086). WCDSS2015, AND004: 1 ♂ 7.6 mm, sta C0416-3258, S 32° 08.05’, E 17° 08.52’, 230 m, 26 Feb 2015 (USNM 1292080); 1 ♂ 7.0 mm (USNM 1292084), 1 ♂ 6.2 mm (SAMC MB-A066814), sta C430-3237, S 31° 42.07’, E 16° 58.53’, 277 m, 1 Mar 2015. WCDSS2016, CCH008: 1 ♂ 6.8 mm, sta D00724, S 32° 03.18’, E 17° 03.11’, 243 m, 11 Mar 2016 (SAMC MB-A066815); 1 ♂ 7.8 mm (USNM 1292082), 3 ♀♀ 6.4–7.0 mm (USNM 1292081), 4 ♀♀ 5.9–7.1 mm (USNM 1292085), 1 ovig. ♀ 6.8 mm (SAMC MB-A066809), 1 ovig. ♀ 5.9 mm (SAMC MB-A066810), 1 ovig. ♀ (SAMC MB-A066811), 3 ovig. ♀♀ 6.6–7.2 mm, 7 ♀♀ 7.2–8.0 mm (SAMC MB-A066812), 2 ovig. ♀♀ 6.7–7.3 mm (SAMC MB-A066813), 1 ovig. ♀ 6.4 mm (SAMC MB-A066816), sta D00726-2446, S 32° 22.98’, E 17° 27.78’, 199 m, 11 Mar 2016.

Figure 2.1: Abundance of deep-water hermit crabs in South African demersal research survey, Agulhas Bank, South Africa, Nan2007 401, sta 1294-008, S 35° 24.40', E 19° 10.70', 227 m, 12 Jan 2007: **A** contents of one trawl showing catch **B** close-up of parapagurid specimens and anthozoan symbionts (colonies of *Epizoanthus* sp.) in same. (Photographs by K. Sink).

Description. Eleven pairs of biserial (Figure 2.2 A), or at most weakly divided quadriserial gills. Shield (Figure 2.2 B, 2.6 C) about as broad as long; dorsal surface nearly naked or with scattered short setae, with weakly- to moderately-calcified median region extending from anterior margins of rostrum, anterior and lateral projections, to about proximal 0.2 length of shield; anterior, lateral and posterior margins with short setae. Rostrum broadly rounded, with short mid-dorsal ridge. Anterior margins weakly concave. Lateral projections subtriangular, armed with short terminal spine. Anterolateral margins sloping. Ventrolateral margin usually with small spine. Posterior margin broadly rounded. Anterodistal margin of branchiostegite rounded, unarmed, setose.

Ocular peduncles (Figure 2.2 B) about half, or slightly more than half, length of shield, each with longitudinal row of short setae on dorsal surface. Corneas weakly dilated. Ocular acicles subtriangular, about 0.3 as long as ocular peduncles, each terminating in strong, simple spine; separated basally by about 0.6 the width of 1 acicle.

Antennular peduncles exceeding distal margin of corneas by 0.8–0.9 length of ultimate segment; ventral flagellum with 5–7 articles. Ultimate segment twice, or more than twice, as long as penultimate, with scattered setae dorsally. Basal segment with strong ventromesial spine; lateral face with distal subrectangular lobe armed with 1 or 2 spines, and strong spine proximally.

Antennal peduncles (Figure 2.2 C) reaching to about distal margin of corneas. Fifth segment unarmed, with longitudinal row of setae on lateral and mesial margins. Fourth segment with strong spine on dorsolateral distal angle. Third segment with strong ventromesial distal spine. Second segment with dorsolateral distal angle produced, terminating in strong, simple spine extending to about half length of acicle and having 2 or 3 small spines dorsally; mesial margin with spine on dorsodistal angle. First segment with lateral surface armed with small spine; ventromesial angle not strongly produced, armed with 1–3 small, blunt spines. Antennal acicle slightly curved outward (dorsal view), overreaching proximal margin of cornea, but not exceeding distal margin of cornea, terminating in strong spine; mesial margin with row of about 10 strong spines of similar size and set at about 45° to longitudinal axis of acicle. Flagellum exceeding distal margin of extended right cheliped, nearly naked, or with scattered, short setae less than 1 flagellar article in length.

Mandible (Figure 2.3 A) with 3-segmented palp. Maxillule (Figure 2.3 B) with external lobe of endopod moderately-well developed, internal lobe with 1 long setae. Maxilla (Figure 2.3 C) with endopod well exceeding distal margin of scaphognathite. First maxilliped (Figure 2.3 D) with endopod exceeding distal margin of exopod. Second maxilliped (Figure 2.3 E) without distinguishing characters. Third maxilliped (Figure 2.3 F) with crista dentata with about 10 corneous teeth, decreasing in size distally; basis with 1 dorsomesial corneous tooth; coxa with 1 or 2 mesial teeth.

Chelipeds markedly dissimilar, proportions strongly affected by size and sexual dimorphism, males growing distinctly longer right chelipeds with narrower chela, than females. Right cheliped (Figures 2.4 A–D, 2.6 A–B) massive; in males, about 1.5 times as long as left cheliped and 4.3 times as long as SL; in females, about 1.3 times as long as left cheliped and 3 times as long as SL; dorsal

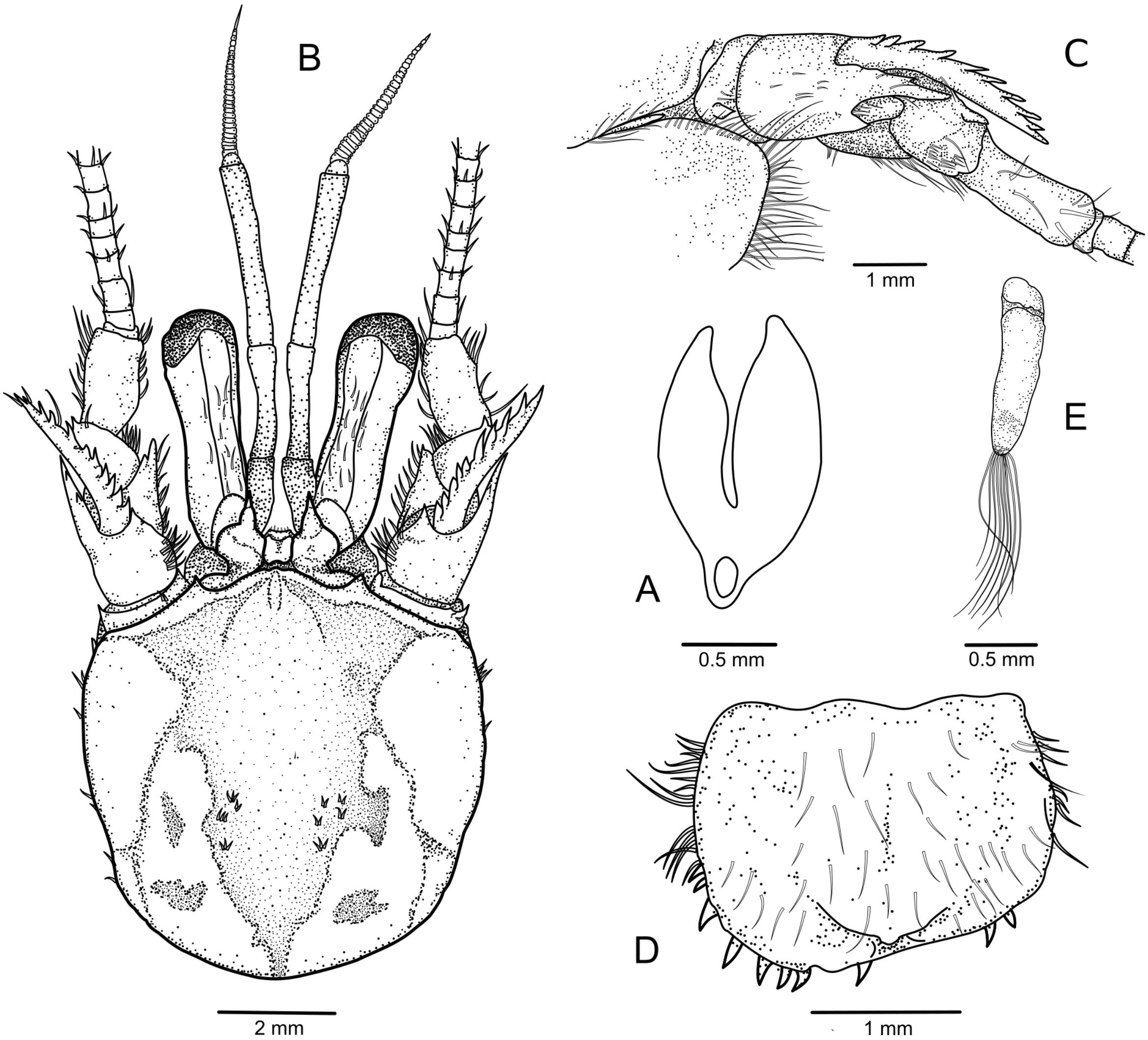

Figure 2.2: ***Paragiopagurus atkinsonae*** **n. sp., South Africa, West Coast, A ♂ paratype 7.0 mm, WCDSS2015 (USNM 1292084), B–E ♂ holotype 7.0 mm, WCDSS2016 (USNM 1292083): A** gill lamella of posterior-most arthrobranch **B** shield and cephalic appendages, dorsal view **C** right antennal peduncle and branchiostegite, lateral view **D** telson, dorsal view **E** left pleopod 2, lateral view.

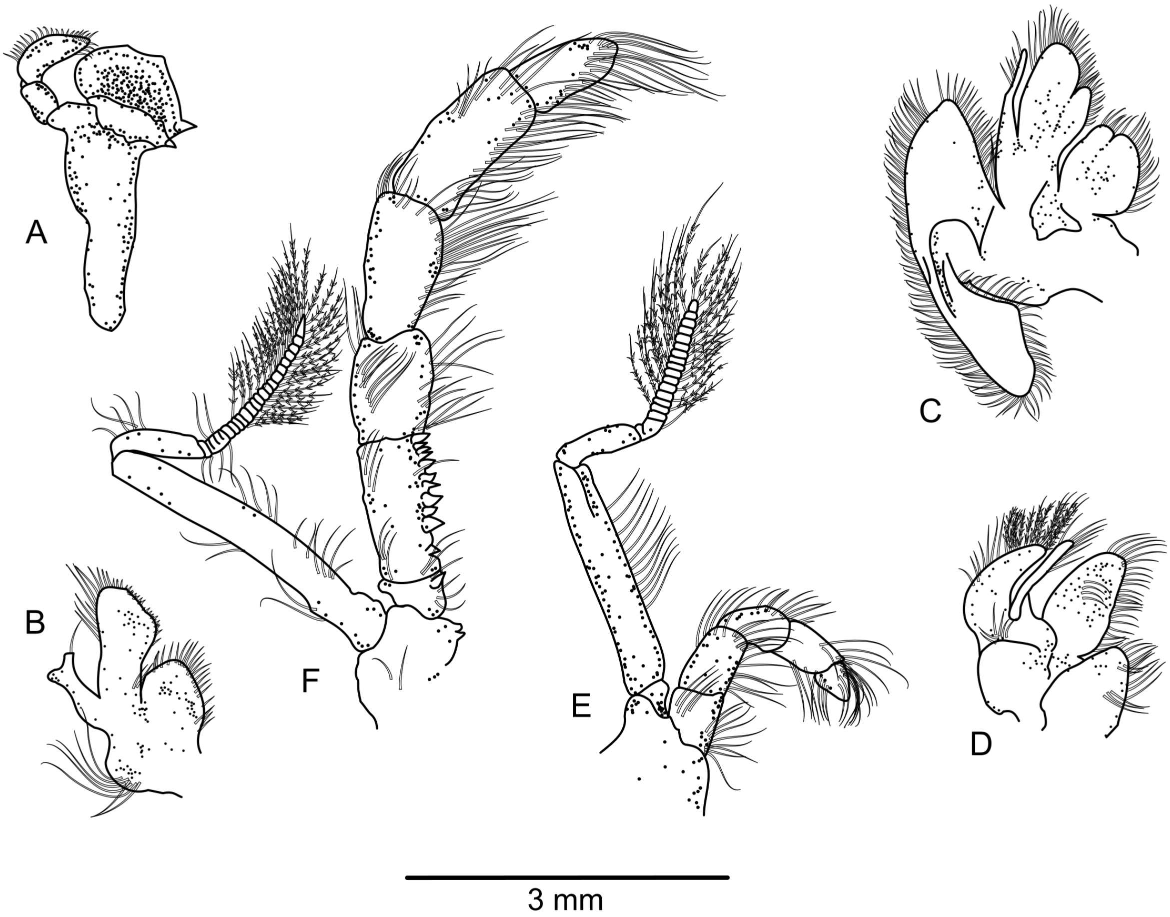

Figure 2.3: ***Paragiopagurus atkinsonae*** **n. sp., South Africa, West Coast, ♂ paratype 7.0 mm, WCDSS2015 (USNM 1292084). Left mouthparts, internal view: A** mandible **B** maxillule **C** maxilla **D** first maxilliped **E** second maxilliped **F** third maxilliped.

surfaces covered with sparse or inconspicuous short, simple or plumose setae. Chela operculate, somewhat dorsoventrally flattened, less so in males; males about twice as long as wide, or in females about 1.3 times as long as wide. Fingers moderately curving mesioventrally, each terminating in small corneous claw, dorsal surfaces covered with numerous small, blunt to sharp tubercles or spines, ventral surfaces covered with small tubercles; cutting edge of dactyl with 2 larger calcareous teeth and several small teeth in between, distal row of small fused corneous teeth; cutting edge of fixed finger with 2 large, rounded calcareous teeth and several small calcareous teeth distally and proximally. Dactyl longer (female), or shorter (male), than mesial margin of palm, set at oblique angle to longitudinal axis of palm; mesial margin well defined by longitudinal row of spines or tubercles; proximal half of ventromesial face strongly concave. Fixed finger basally much broader in females than in males. Palm distinctly broader than long in females, or usually distinctly longer than broad in males; dorsal surface covered with numerous small tubercles or spines; lateral margin well defined by row of small tubercles or spines; dorsomesial margin with row of irregular spines (less strong in males); mesial face strongly sloping, slightly concave (less so in males), covered with small tubercles; ventromesial margin weakly delimited (less so in males)

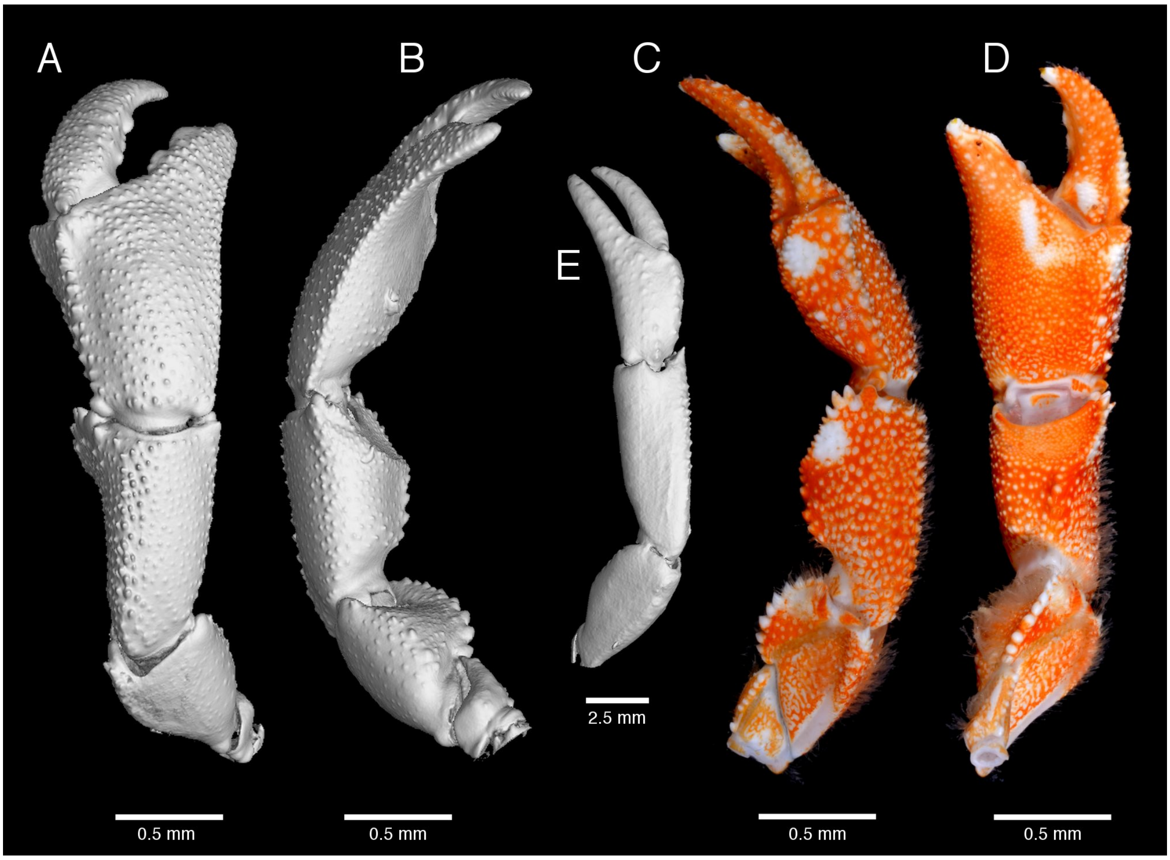

Figure 2.4: *Paragiopagurus atkinsonae* n. sp., South Africa, West Coast, A–B, E μCT scans, ♂ holotype 7.0 mm, WCDSS2016 (USNM 1292083), C–D photographs, ♂ paratype 6.8 mm, WCDSS2016 (SAMC MB-A066815): Right cheliped **A** dorsal view **B** lateral view **C** mesial view **D** ventral view. Left cheliped **E** dorsal view.

by row of low tubercles or spines; ventral surface nearly flat or weakly convex, with small tubercles or spines less numerous than on dorsal surface. Carpus similar to chela in general armature and setation, subtriangular in cross-section, longer in males than in females; dorsal surface covered with numerous small tubercles or spines, generally spines sharper in females than in males; dorsal margin with irregular row of spines, dorsodistal margin armed with strong (females) or weak (males) spines, increasing in size mesially; ventrolateral margin well defined (more so in females) by row of spines increasing in size distally; ventromesial distal margin somewhat expanded, wing-like, armed with row of strong spines. Merus subtriangular in cross-section, dorsal margin unarmed, or with low tubercles and row of short setae, and strong dorsodistal spine; lateral surface with minute tubercles; ventrolateral margin with row of blunt spines distally; mesial surface flat, unarmed, ventromesial margin with row of strong, mostly blunt spines; ventral surface smooth or with very low tubercles. Ischium with ventrolateral row of small spines, and moderately long setae mesioventrally. Coxa with row of small spines on ventrolateral distal margin and ventrodistal row of long setae.

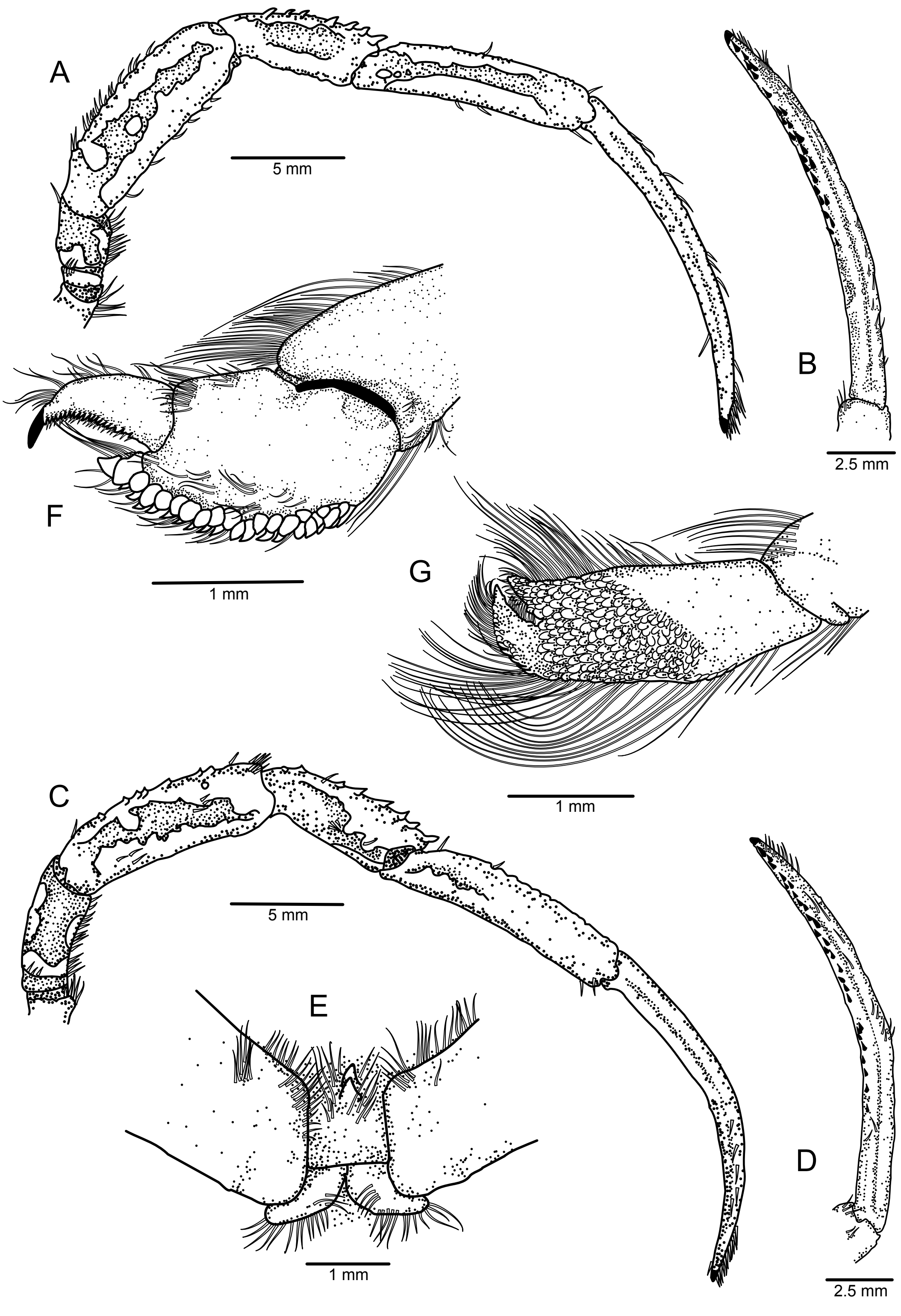

Figure 2.5: ***Paragiopagurus atkinsonae*** **n. sp., South Africa, West Coast, ♂ holotype 7.0 mm, WCDSS2016 (USNM 1292083):** **A** right pereopod 2, lateral view **B** dactyl of same, mesial view **C** right pereopod 3, lateral view **D** dactyl of same mesial view **E** sternite XII and basal portion of coxae of pereopods 3, ventral view **F** propodus and dactyl of left pereopod 4, lateral view **G** propodus and dactyl of left pereopod 5, lateral view.

Left cheliped (Figures 2.4 E, 2.6 A–B) generally well calcified, reaching to base of dactyl (females), or midlength of palm (males), of right cheliped. Fingers weakly bent lateroventrally, gaping slightly when closed, each terminating in sharp corneous claw; dorsal and ventral surfaces unarmed, except for few tufts of short setae; cutting edges each with closely-set small, corneous teeth. Dactyl slightly longer than palm; proximal half of ventromesial face slightly concave. Palm longer than wide; dorsal surface with two median rows of small, low tubercles, and sparse tufts of short setae, somewhat depressed medially; dorsomesial margin with row of small tubercles or spines; dorsolateral margin rounded; ventral surface unarmed except for scattered setae. Carpus with moderately dense setation on dorsal, lateral and mesial surfaces; dorsal margin with irregular row of small tubercles or spines, and strong dorsodistal spine; lateral and mesial faces unarmed except for setae, and strong spine on lateroventral distal angle; ventral surface smooth, at most with tufts of sparse setae. Merus unarmed except for minute tubercles on lateral, mesial and ventral faces, and dense setation on dorsal ventromesial margins. Ischium unarmed and smooth except for dense setae on ventral surface. Coxa at most with minute spines on ventromesial distal margin and row of setae on ventrodistal margin.

Ambulatory legs or pereopods 2 and 3 (Figures 2.5 A–D, 2.6 A–B) similar from right to left, except for slightly longer meri on right; usually exceeding right cheliped by about 0.2 length of dactyl of legs when fully extended. Dactyl about 1.5–1.9 as long as propodus, broadly curved, terminating in sharp corneous claw; dorsal margin mostly with short setae, except for distal row of bristle-like setae; ventromesial margin (Figure 2.5 B, D) armed with 2 or 3 irregular rows of short, corneous spinules and usually terminating as single row near claw; lateral and mesial face with shallow, longitudinal sulcus on proximal half, deeper on mesial face. Propodus nearly naked; dorsal margin with setae usually arising from low tubercles. Carpus nearly naked, or with sparse short setae; dorsal margin armed with row of distinct, well-spaced small spines (stronger on pereopod 2) increasing slightly in size distally, and small dorsodistal spine. Merus unarmed except for scattered setae on dorsal margin. Ischium with dorsal and ventral row of setae. Coxa unarmed except for 1 or 2 minute spines on ventromesial proximal angle (pereopod 2 only) and ventromesial row of setae. Anterior lobe of sternite XII (of pereopods 3; Figure 2.5 E) subtriangular, setose, and terminating in simple or more frequently bifid spine.

Pereopod 4 (Figure 2.5 F) subchelate. Dactyl broadly curved, terminating in sharp, corneous claw, with ventrolateral row of small corneous teeth increasing in size distally. Propodus longer than wide; rasp consisting of 2 or 3 rows of rounded scales. Carpus with long setae on dorsal margin. Merus with rows of long setae on dorsal, ventromesial and ventrolateral margins.

Pereopod 5 (Figure 2.5 G) chelate. Propodal rasp extending slightly beyond midlength of segment. Dactyl with row of minute, rounded scales on ventrolateral surface.

Uropods and telson asymmetrical. Telson (Figure 2.2 D) lacking transverse sutures separating anterior and posterior lobes; dorsal surface with scattered short setae; lateral margins with moderately long (left) and short (right) setae; posterior lobes separated by narrow, median cleft, terminal margins rounded, armed with row of 8–15 (left lobe) or 10–12 (right lobe) short corneous

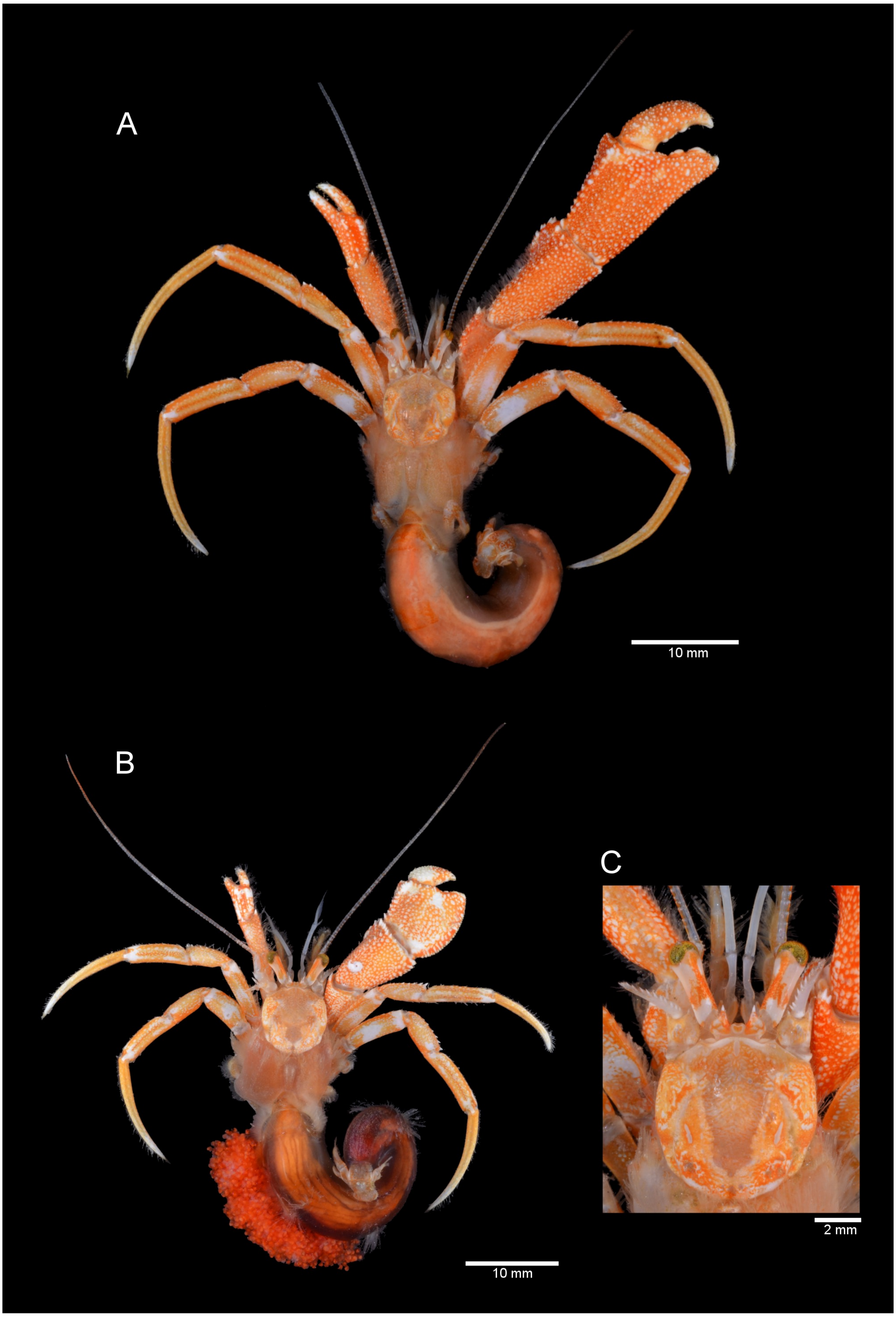

Figure 2.6: Colouration (in life or fresh). ***Paragiopagurus atkinsonae*** **n. sp., South Africa, West Coast: A** ♂ holotype 7.0 mm, WCDSS2016 (USNM 1292083) **B** ovig. ♀ 6.4 mm, WCDSS2016 (SAMC MB-A066816) **C** ovig. ♀ 6.8 mm, WCDSS2016 (SAMC MB-A066809), shield and cephalic appendages, dorsal view.

spines, some slightly curved.

Males lacking first gonopods; with unpaired left pleopods 2–5, of which pleopod 2 (Figure 2.2 E) is 2-segmented, uniramous, and other pleopods biramous. Females with unpaired pleopods 2–5, with well-developed rami on pleopods 2–4, and short endopod on pleopod 5.

Colour (in life; Figures 2.4 C–D, 2.6 A–C). Shield and cephalic appendages mottled orange and cream to white. Ocular peduncles white with basally and distally broadened dorsomedian orange stripe; orange pattern extending to ventromesial face just below midlength of ocular peduncle. Corneas usually green. Ocular acicles mottled orange with white spines. Chelipeds orange-red, with white tubercles and spines. Right chela often with dactyl and fixed finger each with cream patch proximally at about midline, fingertips white; propodus, merus and carpus with distinct cream to white spot on dorsomesial distal angle. Left chela with cream patches of different size, fingertips white. Ambulatory legs orange overall; dactyl light orange, distally cream; propodus with cream patch on distolateral and distomesial angles, lateral face with dark orange stripe; carpus orange overall, with lighter orange medially on lateral face. Merus with white band distally, large white patch on proximal half of lateral face, and darker orange on dorsodistal margin. Uropods and telson mottled orange and cream. Pleon orange, in some females dark red ventrally due to gonads with unspawned eggs. Eggs bright red.

Habitat. Occupying shells created by colonies of *Epizoanthus* sp. that incorporate sand grains in their tissue and form a carcinoecium that completely covers a minute gastropod shell. This *Epizoanthus* sp. appears the same to that frequently used by *Sympagurus dimorphus* in the South African region.

Distribution (Figure 2.8). Known so far only from a small portion of the West Coast of South Africa, between S 31°42’ and S 32°23’, in a depth range of 199–277 m.

Etymology. This species is named after Dr. Lara Atkinson, a researcher from SAEON, Egagasini Node for marine-offshore systems, who first noticed the presence of this new species and collected the first specimen. The name honours her research efforts to understand the benthic marine fauna of South Africa, and acknowledges the major role she played in organising sampling of additional material of this new species.

Common name. “Green-eyed hermit crab”.

Genetic data. Sta D00723-3243, S 31° 52.81’, E 16° 57.12’, 265 m, ♂ 7.0 mm (holotype), BOLD: SEAKY1181-17 (USNM 1292083). Sta D00726-2446, S 32° 22.98’, E 17° 27.78’, 199 m, ovig. ♀ 6.8 mm, BOLD: SEAKY1181-17 (MB-A066809); ovig. ♀ 5.9 mm, BOLD: SEAKY1183-17 (MB-A066810); ♂ 6.8 mm, BOLD: SEAKY1180-17 (MB-A066815).

Variations. In males with SL >7.0 mm, the right cheliped (merus to dactyl) ranges from 3.6–4.8 times as long as the shield, and the chela varies from 1.7–2.4 as long as wide. In females with SL >5.9 mm, the right cheliped (merus to dactyl) ranges from 2.6–3.2 times as long as the shield, and the chela varies from 1.3–1.6 as long as wide. The spination of both right and left chelae tends to be sharper, and stronger in females.

Remarks. Three characters present in *Paragiopagurus atkinsonae* n. sp. exemplify the morphological evolutionary tendencies that in general are observed (Lemaitre 2013) in species of *Paragiopagurus.* These three characters are: biserial gills that are, at most, weakly divided distally; the drastic sexual dimorphism exhibited on the right cheliped; and in males, the complete loss of paired first and second pleopods modified as gonopods. In sharing these three characters, this new species is most similar to *P. ventilatus* Lemaitre, 2004c, a northwestern Pacific species that is known to associate with hydrothermal vents in the northeastern coast of Taiwan and the Mariana Trough (Lemaitre 2004c, Komai et al. 2010). Additionally, both species share a rare armature condition in parapagurids for the ventromesial margin of the dactyls of the ambulatory legs, being armed in this new species with two or three irregular rows of numerous corneous spinules instead of a single regular row of relatively few spines, as in other species of this genus. In other respects, however, these two species are markedly different. In *P. atkinsonae* n. sp. the fourth antennal segment is armed with a spine on the dorsolateral distal angle, whereas in *P. ventilatus* the fourth segment is unarmed; the antennal flagella is nearly naked or with scattered short setae, whereas in *P. ventilatus* the flagella are densely covered with long setae; the third maxillipeds and basal segments of the chelipeds lack dense plumose setae, whereas in *P. ventilatus* these are present; the propodal rasp of pereopod 4 has two or three rows of ovate scales, whereas in *P. ventilatus* the rasp has only one row of ovate scales; the telson is weakly asymmetrical, whereas in *P. ventilatus* the telson is strongly asymmetrical. Furthermore, *P. atkinsonae* n. sp. is not associated with hydrothermal vent habitats, whereas *P. ventilatus* has been found exclusively in or close to vent habitats (Lemaitre 2004c, Komai et al. 2010).

In addition to *Paragiopagurus atkinsonae* n. sp., there are seven other species of *Paragiopagurus* in which the male lacks paired first and second gonopods: *P. trilineatus* Lemaitre, 2013, *P. bicarinatus* (de Saint Laurent, 1972), *P. hirsutus* (de Saint Laurent, 1972), *P. acutus* (de Saint Laurent, 1972), *P. ruticheles* (Milne-Edwards and Bouvier, 1891), *P. hobbiti* (Macpherson, 1983), and *P. ventilatus.* The complete pleopod condition in the male for all these species is the same, i.e., presence of left unpaired pleopods 2–5. Pleopod 2 is uniramous, 2-segmented, with a short distal segment, and pleopods 3–5 are biramous. In both sexes of *P. atkinsonae* n. sp., the propodal rasp of pereopod 4 has two or three rows of ovate scales, a condition similar to that of three other congenerics: *P. trilineatus, P. pilimanus* (Milne-Edwards, 1880), and *P. tuberculosus* (de Saint Laurent, 1972). Other than the development of pleopods in the male, and the number of rows of scales on the propodal rasp of the pereopod 4, *P. atkinsonae* n. sp. differs markedly from all those species (see Lemaitre 2013).

When using Lemaitre's (2013) species identification key for specimens of *Paragiopagurus atkinsonae* n. sp., the user will reach couplet 19. To accommodate this new species to that key, couplet 19 can be replaced with the following two new couplets 19 and 20 (and changing the numbers of Lemaitre’s couplets 20–23 by +1):

19. Ventromesial margins of ambulatory legs (pereopods 2, 3) armed with several irregular rows of numerous corneous spinules **20**

– Ventromesial margins of ambulatory legs (pereopods 2, 3) armed with single, regular row of corneous spinules **21**

20. Propodal rasp of pereopod 4 with 2 or 3 rows of ovate scales; antennal flagella naked or with scattered short simple setae; fourth antennal segment armed with spine on dorsolateral distal angle; telson weakly asymmetrical .... ***Paragiopagurus atkinsonae* n. sp.**

– Propodal rasp of pereopod 4 with 1 row (at least distally) of ovate scales; antennal flagella densely covered with long mostly plumose setae; fourth antennal segment lacking spine on dorsolateral distal angle; telson strongly asymmetrical .... ***P. ventilatus***

2.4.1.2 Genus *Sympagurus* Smith, 1883

***Sympagurus dimorphus* (Studer, 1883)**

Figure 2.7 A–B, 2.8

Primary synonymy: *Eupagurus dimorphus* Studer, 1883: 24, Figs 11–12 (type locality: South Atlantic Ocean, South Africa, off Cape of Good Hope, S.M.S. *Gazelle*, S 34° 13.6', E 15° 00.7', 211 m).

Parapagurus brevimanus Balss, 1911: 4, Fig 5.

Eupagurus modicellus Stebbing, 1914: 255, Pl 26, Fig D (see "General distribution").

Sympagurus var. *arcuatus johnstoni* Hale, 1941: 279, Fig 13a–d.

Sympagurus var. *arcuatus mawsoni* Hale, 1941: 280, Fig 14a–c.

Material examined. *South Africa, West Coast.* WCDSS2012, AFR279: 4 ♂♂ 9.5–12.0 mm, 1 ovig. ♀ 8.1 mm, sta A32144-4116, S 32° 18.26', E 16° 18.53', 369 m, 11 Jan 2012 (SAMC MB-A066808). WCDSS2015, AND004: 1 ovig. ♀ 9.7 mm [inside stomach of Monk fish], sta C0400-3330, S 33° 55.08', E 17° 39.26', 285 m, 20 Jan 2015 (SAMC MB-A066807); 4 ♂♂ 10.0–12.0 mm, 5 ovig. ♀♀ 7.7–9.1 mm, 1 ♀ 9.4 mm, sta C0367-3336, S 33° 58.11', E 17° 52.51', 220 m, 9 Feb 2015 (SAMC MB-A066801); 1 ♂ 7.4 mm, sta C0379-3130, S 36° 34.74', E 20° 38.10', 12 Feb 2015 (SAMC MB-A066805); 1 ♀ 7.1 mm, sta C0458-5008, S 29° 57.54', E 14° 49.40', 448 m, 8 Mar 2015 (SAMC MB-A066803). WCDSS2016, CCH008: 1 ♂ 7.8 mm, sta D00640, S 31° 28.02', E 16° 05.64', 470 m, 21 Feb 2016 (SAMC MB-A066806); 1 ♂ 11.2 mm, sta D00726-2446, S 32° 22.98', E 17° 27.78', 199 m, 11 Mar 2016 (SAMC MB-A066492).

South Africa, South Coast. SCDSA2015, AND005: 1 ♂ 14.6 mm, sta D0520-4071, S 36° 27.78', E 21° 53.58', 401 m, 20 Apr 2015 (SAMC MB-A066839); 1 ♂ 12.0 mm (SAMC MB-A066840), 1 ♂ 13.2 mm (SAMC MB-A066841), sta D00521-4043, S 36° 25.50', E 21° 27.12', 192 m, 20 Apr 2015; 1 ♂ 4.9 mm, sta D00540-6542, S 35° 21.30', E 22° 49.98', 585 m, 26 Apr 2015 (SAMC MB-A066833); 1 ♂ 12.7 mm, sta D00561-6671, S 34° 05.22', E 26° 55.68', 466 m, 1 May 2015, (SAMC MB-A066818);

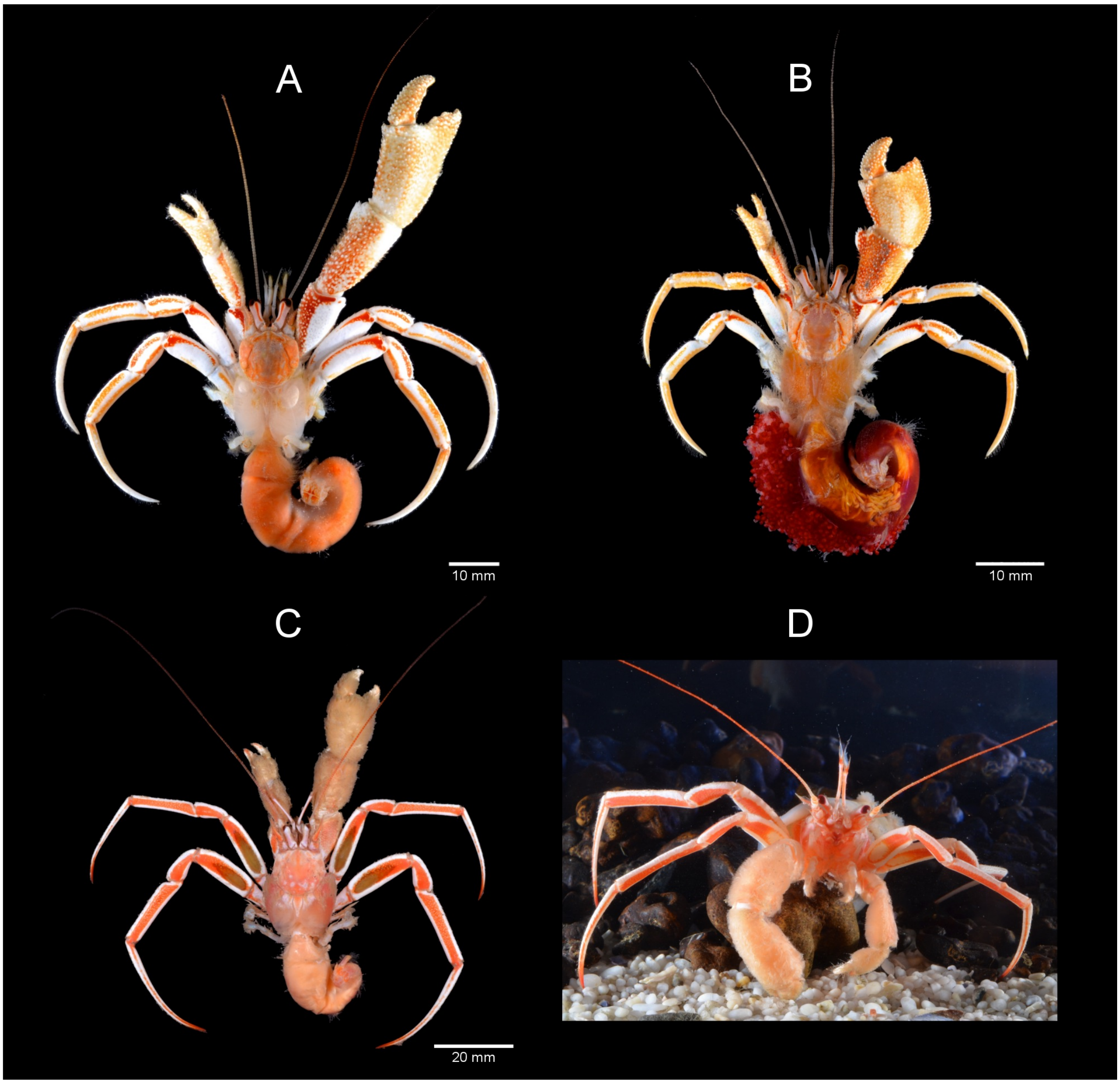

Figure 2.7: A–B *Sympagurus dimorphus* (Studer, 1883), South Coast, C–D *Parapagurus bouvieri* Stebbing, 1910, West Coast (C), South Coast (D): A ♂ 11.2 mm SCDSA2016 (SAMC MB-A066492) **B** ovig. ♀ 9.4 mm SCDSA2016 (SAMC MB-A066491) **C** ♂ 12.2 mm, WCDSS2016 (SAMC MB-A066432) **D** ♂ 10.6 mm, SCDSS2016 (SAMC MB-A066794), front view of live specimen in aquarium, using zoanthid (*Epizoanthus* sp.) carcinoecium.

1 ♂ 10.3 mm, sta D00565-4224, S 34° 10.20', E 26° 46.38', 425 m, 2 May 2015 (SAMC MB-A066823); 1 ♂ 6.5 mm, 1 ♀ 7.5 mm, sta D00582-4153, S 34° 54.96', E 23° 22.08', 210 m, 7 May 2015 (SAMC MB-A066820). SCDSA2016, CCH009: 1 ♂ 11.3 mm, sta D00757-4020, S 36° 49.19', E 20° 33.72', 538 m, 4 May 2016 (SAMC MB-A066802); 2 ♂♂ 10.1–10.4 mm, 3 ovig. ♀♀ 6.8–7.6 mm, sta D00812-4174, S 34° 46.80', E 24° 12.30', 196 m, 19 May 2015 (SAMC MB-A066804); 1 ♂ 8.8 mm (SAMC MB-A066490), 1 ovig. ♀ 9.4 mm (SAMC MB-A066491), sta D00819, S 34° 52.32', E 23° 35.70', 195 m, 21 May 2016.

Diagnosis, taxonomy, larval and juvenile morphology. See Lemaitre (1989, 1990, 1996, 2000, 2004b), Lemaitre and McLaughlin (1992), and Poore (2004).

Colour (in life; Figure 2.7 A–B). Until now, information on colour of *Sympagurus dimorphus* had been based on three published photographs taken of live specimens inside their gastropod housing (Lemaitre 2000, Pl 7; 2004b, Fig 35a; Poore 2004, Pl 17c), and formalin-preserved specimens with patterns still visible (Lemaitre 2004b). Although the basic colour pattern can be discerned in those photographs, the specimens used have only partially visible body parts, and furthermore, the exposures of the images show somewhat distorted colour tones. The photographs presented herein are the first high quality colour photographs of the entire body removed from it's housing of a freshly caught male and of an ovigerous female specimen (Figure 2.7 A–B), which accurately show complete colour tones and patterns. The photographs show that the background colour of the body is white, or white and light amber on the chelae. The shield has orange and reddish patches arranged more-or-less symmetrically on the calcified portions. The ocular peduncles are white, each with an orange-red stripe on the dorsal face, and a light orange ventral face. The antennular peduncles are semi-transparent. The antennal peduncles each have a light orange-red patch on the laterodistal face of the second segment, and an orange stripe on the lateral faces of the fourth and fifth segments; the flagella are semitransparent or light orange. The right cheliped has the chela mostly light amber with white spines or tubercles, and white patches medially; the carpus is orange dorsally, with white spines or tubercles; the merus is red dorsally, with bright white lateral and mesial faces. The colour pattern of the left cheliped is similar to that of the right cheliped. The ambulatory legs have mostly white dactyls except for a light orange proximally; the propodus and carpus are white except for two light orange stripes (one dorsolateral, and one ventrolateral) on the lateral face of both segments, and the mesial face of both segments are similar to the lateral face; the merus is bright white except for a dorsolateral red stripe broadening distally near the distal margin; the ischium is white with a dorsolateral light orange stripe. The pleon is orange or reddish. The uropods and telson are white with light orange.

General distribution Reported from the southern hemisphere from S 22° to S 57°, depth range 91–1995 m. As discussed by Lemaitre (2004b), *Eupagurus modicellus* Stebbing, 1914 from Ascencion Island, was believed by Manning and Chace (1990) to represent *S. dimorphus.* However, Stebbing's taxon was based on a juvenile specimen that likely does not represent *S. dimorphus.* Thus, the presence of this species as far north as Ascencion Island in the South Atlantic is considered questionable.

South African distribution (Figure 2.8). Highly abundant all along the West Coast, common on and along the shelf of the Agulhas Bank on the South Coast, extending to offshore areas off East London; depth range of material in this study is 170–585 m.

Common names. "Monkey-nut hermit crab", "Cloaked hermit crab".

Habitat. Found living in gastropod shells, usually with actinian or zoanthid polyp attached to the shell, or in carcinoecia formed by colonies of *Epizoanthus* sp.; young have been found in scaphopod shells Lemaitre (2004b). On the South Coast of South Africa, commonly found in gastropod shells that are not covered by anthozoan symbionts.

Genetic data. Sta D0520-4071, S 36° 27.78', E 21° 53.58', 401 m, ♂ 14.6 mm, BOLD: SEAKY962-15 (MB-A066839), ♂ 13.2 mm, BOLD: SEAKY876-15 (MB-A066841).

2.4.1.3 Genus *Parapagurus* Smith, 1879

Parapagurus bouvieri Stebbing, 1910

Figure 2.7 C–D 2.8

Parapagurus bouvieri Stebbing, 1910: Pl 17 (Crustacea Pl 43) (type locality: South Africa, s. s. *Pieter Faure*, sta 153, Buffalo River, NW 1/2W, 19 miles, 549 m).

Material examined. *South Africa, West Coast.* WCDSS2012, AFR279: 2 ♀♀ 8.6–11.0 mm, sta A32144-4116, S 32° 18.26', E 16° 18.53', 369 m, 11 Jan 2012 (SAMC MB-A066800); 3 ♂♂ 10.4–13.1 mm, sta A32147-5079, S 32° 01.87', E 16°17.43', 458 m, 11 Jan 2012 (SAMC MB-A066799). WCDSS2015, AND004: 8 ♂♂ 7.5–14.3 mm, 3 ovig. ♀♀ 9.2–11.8 mm, 1 ♀ 8.9 mm, sta C0372-5140, S 35° 41.28', E 19° 09.82', 551 m, 11 Feb 2015 (SAMC MB-A066793); 1 ♀ 9.4 mm, sta C0407-5104, S 33° 01.92', E 17° 01.98', 436 m, 21 Feb 2015 (SAMC MB-A066795); 2 ♂♂ 6.1–12.5 mm, sta C0420-5078, S 31° 59.88', E 16° 17.64', 812 m, 27 Feb 2015 (SAMC MB-A066796). WCDSS2016, CCH008: 1 ovig. ♀ 10.0 mm (SAMC MB-A066429), 1 ♂ 14.0 mm (SAMC MB-A066430), 1 ovig. ♀ 9.3 mm (SAMC MB-A066431), 1 ♂ 12.2 mm (SAMC MB-A066432), 1 ovig. ♀ 10.0 mm (SAMC MB-A066433), sta D00716, S 30° 46.14', E 15° 28.44', 387 m, 9 Mar 2016.

South Africa, South Coast. SCDSA2015, AND005: 1 ♂ 11.8 mm, sta D00570-6628, S 34° 40.95', E 25° 09.15', 556 m, 3 May 2015 (SAMC MB-A066797); 2 ♂♂ 10.0–12.7 mm, sta D00573-6592, S 34° 58.42', E 24° 18.37', 758 m, 4 May 2015 (SAMC MB-A066798). SCDSS2016, AFR289: 2 ♂♂ 7.4–10.6 mm, sta A32823-96971, S 35° 14.95', E 22° 50.80', 511 m, 5 Oct 2016 (SAMC MB-A066794).

South Africa, East Coast. African Coelacanth Ecosystem Programme (ACEP) (no cruise name): 4 ♂♂ 7.9–12.2 mm, sta ACEP 3-6, S 29° 29.10', E 31° 54.36', 563–569 m, 20 Mar 2010 (ZRC 2013.0548).

Diagnosis, taxonomy. See Lemaitre (1990, 1999, 2000), and Poore (2004).

Colour (in life; Figure 2.7 C–D). Until now, colour information on this species has been based only on Barnard's (1950: 451, as *Parapagurus pilosimanus*) description of specimens from South

Africa, and a photograph by Poore (2004, Pl 17b) only partially showing the body of a live specimen in a zoanthid carcinoecium. Herein, colouration of this species is described in detail for the first time, and colour photographs are presented of the entire body of a fresh specimen removed from it's housing and with it's anthozoan housing (Figure 2.7 C–D). Shield light orange with small white patches on posterior half, and white near anterior margin. Ocular peduncles white dorsally, turning light orange on lateral faces; corneas black to dark brown. Antennules white with light orange flagella. Antennal penduncles white except for orange lateral faces of second segments, and orange acicles; flagellum light orange except for white basal portion. Colour of chelipeds hidden by dense light brown setation, surfaces white except for some orange tint distally on fingers. Ambulatory legs white with broad orange stripe on lateral faces of meri, carpi, and propodi; dactyls orange distally and with narrow orange stripe on lateral face; weakly calcified region on lateral face of meri brownish.

General distribution. Southeastern Atlantic, from Angola to South Africa, and southwestern Indian Ocean to KwaZulu-Natal (South Africa); western Pacific, from off the southern and southeastern coast of Australia, from the South Australian Bight and Queensland (Lemaitre 1999; Poore, 2004), depth range 247–990 m.

South African distribution (Figure 2.8). Highly abundant on the West Coast, common on the shelf of the Agulhas Bank on the South Coast, and extending to the eastern coast off KwaZulu-Natal; depth range of material in this study from 369–812 m.

Common name. “Hairy-clawed hermit crab”.

Habitat. With extremely rare exceptions, exclusively found living in carcinoecia formed by zoanthids, probably *Epizoanthus* species.

Genetic data. Sta ACEP 3-6, S 29° 29.10’, E 31° 54.36’, 563–569 m, ♂ 12.2 mm, BOLD: SEAKY1174-17 (ZRC 2013.0548-2). Sta D00716, S 30° 46.14’, E 15° 28.44’, 387 m, ♂ 12.2 mm, BOLD: SEAKY1169-17 (MB-A066432); ovig. ♀ 10.0 mm, BOLD: SEAKY1167-17 (MB-A066429); ovig. ♀ 9.3 mm, BOLD: SEAKY1168-17 (MB-A066431).

Remarks. As pointed out by Lemaitre (1990, 1999, 2000), this species is unique among species of *Parapagurus* in several characters. In *P. bouvieri* the corneas are weakly dilated, and the overall length of the ocular peduncles are atypically long, being distinctly more than half the length of the shield, whereas in other species of the genus the corneas are reduced, not wider than the distal width of the ocular peduncles, and the ocular peduncles are short, less than half the length of the shield. The most striking and distinctive character of this species is the presence of a weakly-calcified area on the lateral and mesial faces of the propodi of the ambulatory legs. In live specimens this area is brownish in colour (Figure 2.7 C), and that tone is similarly retained even in specimens that have been preserved for a long time.

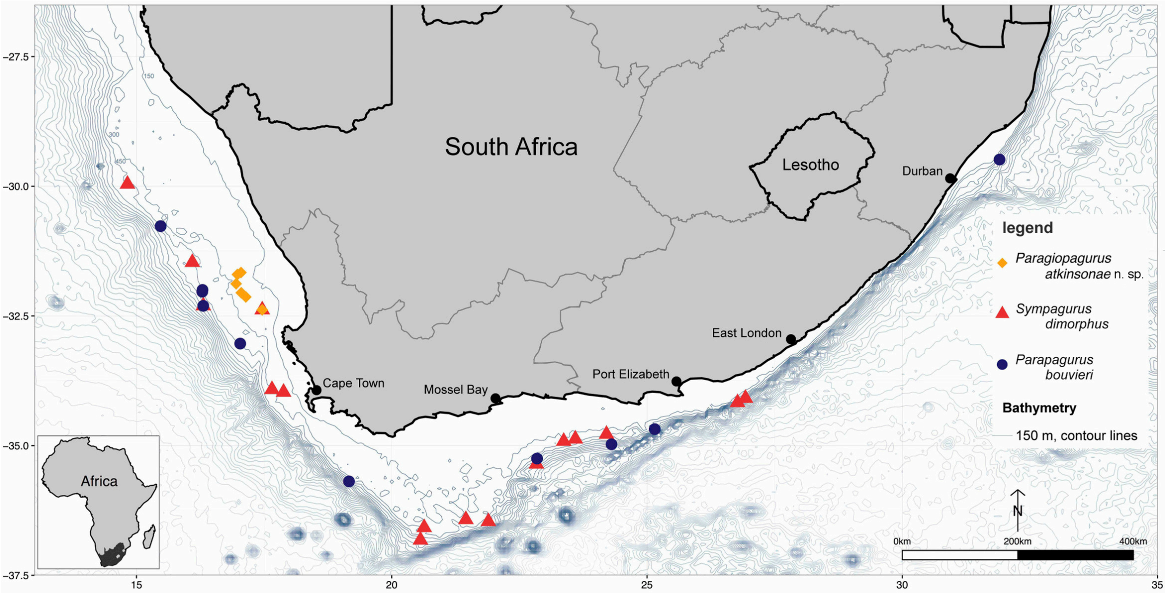

Figure 2.8: South African distribution of three parapagurid species based on specimens found during South African Department of Agriculture, Forestry and Fisheries demersal research surveys.

2.5 Discussion

Sympagurus dimorphus and *Paragiopagurus atkinsonae* n. sp. are superficially similar and could be confused if the morphology is not carefully examined. Given the scarcity of taxonomic information on South African parapagurids, it is therefore not surprising that until now the latter new species has been confounded with the former. In addition, the two species co-exist and are trawled in large numbers from the same benthic environments, and both species utilise a similar housing strategy for protection, i.e., a carcinoecium formed by potentially the same species of zoanthid polyps (in South Africa, *S. dimorphus* is also often found inhabiting shells). Morphologically, both species exhibit a marked sexual dimorphism that is expressed most visibly in males by having a long and often slender right cheliped, whereas in females the right cheliped is stout, with a broad, operculate chela. The variations in males and females of *S. dimorphus* have been documented in detail by Lemaitre (1989, 1996, 2004b). The general tone of the colouration of *S. dimorphus* and *P. atkinsonae* n. sp. is also superficially similar, i.e., white in background with orange or red stripes. However, that is where the similarity ends, as the two species differ in fundamental generic characters as defined by Lemaitre (2004b) for *Sympagurus*, and Lemaitre (2013) for *Paragiopagurus*. Most significantly, species of *Sympagurus* are the only among parapagurids that posses a vestigial pleurobranch on each side of the eighth thoracic somite, above each fifth pereopod (see Lemaitre 2004b: 89, Fig 2). Furthermore, in *S. dimorphus* the gills are quadriserial, deeply divided, whereas in *P. atkinsonae* n. sp. the gills are at most weakly divided distally. In addition, the condition of pleopods in males of these two species differ drastically, the males in *S. dimorphus* having well developed, paired first and second pleopods modified as gonopods, whereas the males in *P. atkinsonae* n. sp., lack first pleopods and only have unpaired left second pleopods. Aside from fundamental generic differences, however, in the field these two species can be best identified by differences in colouration pattern (Figures 2.6 A–D, 2.7 A–B). In *P. atkinsonae* n. sp. the corneas are greenish (Figure 2.6 C), whereas in *S. dimorphus* they are dark brown or black; the general background colouration is more orange, whereas in *S. dimorphus* it is mostly white; the chelipeds are almost entirely orange with white tubercles or spines, whereas in *S. dimorphus* most of the chelae and lateral faces of carpi are white or light amber, and the meri are bright white except for a red dorsal face; the carpi, propodi and dactyls of the ambulatory legs have three orange stripes on a light orange background, whereas in *S. dimorphus* those segments have two orange stripes on often bright white background; the meri have a large white patch on the proximal half of the lateral face and a dark orange dorsal margin, whereas in *S. dimorphus* the lateral face of the merus is almost entirely bright white, except for a red-orange stripe dorsodistally.

Even without sufficient familiarity with the other taxonomic characters that define species of parapagurids, *P. bouvieri* can also be easily separated from the other two most commonly co-occurring parapagurid species encountered in the South Africa demersal surveys, by the relative length of the antennal peduncles (peduncle and acicle distinctly exceeding distal margins of the corneas), the more slender, longer, and dorsally unarmed meri and carpi of the ambulatory legs, and shape (stout propodus and short dactyl) and armature of propodus and propodal rasp (with conical scales) of the fourth pereopod, all of which can be easily compared in the publications cited herein for each of the three parapagurid species encountered in the demersal surveys. Compared to *P. atkinsonae* n. sp. and *S. dimorphus*, *P. bouvieri* inhabits different carcinoecia formed by different zoanthid species. Whereas the carcinoecia are firm, rigid, stabilised by imbedded grains of sand, and usually dark brown in the former two species, the carcinoecia inhabited by *P. bouvieri* are softer and gelatinous, grey to rosy in colour and almost neutrally buoyant in sea water. Additionally, the colour photographs (Figures 2.4 C–D, 2.6 A–C, 2.7 A–D) presented for *P. bouvieri*, *Sympagurus dimorphus*, and *Paragiopagurus atkinsonae* n. sp., complete the set of morphological comparisons that should enable biologists to identify these three species.

Despite the considerable sampling effort along the entire extent of the South African offshore demersal survey grounds, *P. atkinsonae* n. sp. was confined to a small area on the West Coast, where it appears to be common. The distribution, being restricted to an area of only 43 nautical miles in the north-south, and only 25 nautical miles in the east-west direction, is unusual for any parapagurid species, which normally have widespread distributions (e.g. Lemaitre 1999, 2004b, 2013, 2014). For example, in the South African benthic abundance surveys, the distributions of *S. dimorphus* and *P. bouvieri* extend from the westernmost fishing grounds from the Namibian boarder to the easternmost sites west of Port Elizabeth. Using the newly provided identification information, future studies should monitor the occurrence of *P. atkinsonae* n. sp. in the demersal abundance surveys. Should it be confirmed that *P. atkinsonae* occurs exclusively in the small area of the South African West Coast then this area should be given more research attention. The area does not obviously appear oceanographically or biologically distinct, but more detailed sampling of the benthic invertebrate community and ecosystem might reveal that it provides specific habitat conditions that could be important to both study, and also protect from future anthropogenic impacts.

CHAPTER 3

A NEW SPECIES OF THE HERMIT CRAB GENUS *Diogenes* (CRUSTACEA: DECAPODA: DIOGENIDAE) FROM THE COAST OF KWAZULU-NATAL, SOUTH AFRICA

3.1 Abstract

A new diogenid hermit crab with bright-white chelae, *Diogenes* n. sp., is described and illustrated, based on a single ovigerous female collected from KwaZulu-Natal, South Africa. The new species is compared to morphologically similar species, in particular to *D. holthuisi* and *D. dorotheae*, from which it is distinguishable by the shape and armature of the telson; and also to the superficially-similar South African *D. extricatus*, from which it differs by having unarmed dorsal margins of the propodi and meri of the pereopods, as opposed to being armed by rows of strong spines. The unusually white chelae are similar in colour to those of *D. takedai*, but the colouration of all other parts is different in these two species. High quality macro photographs, a high-resolution micro computed tomography scan of the whole animal, and the reference to the repository of the molecular barcode of the new species are provided.

3.2 Introduction

Species of the hermit crab genus *Diogenes* Dana, 1851 are primarily defined by the presence of an intercalary rostriform process centred between the ocular acicles. Currently 65 species are assigned to *Diogenes* globally (McLaughlin and Türkay 2008). These species are distributed from the east Atlantic to the west Pacific, but the vast majority (62 species) are found in the Indo-West Pacific (Asakura and Tachikawa 2010, Komai et al. 2012, 2013, McLaughlin et al. 2010, Rahayu 2012, 2015, Xiao et al. 2015). Although well studied in the latter region (Rahayu 2015), information on *Diogenes* from southern Africa is scarce and out-dated.

The species of *Diogenes* of South Africa have received little to no taxonomic attention for almost 70 years, but a revision of the local fauna lies beyond the scope of this study. Current knowledge on South African members of *Diogenes* is based on earlier accounts of Krauss (1843), Henderson (1893), Stebbing (1910), Balss (1912, 1921), and Barnard (1947, 1950), as well as on the species lists compiled by Kensley (1969, 1981). Two of the better known and illustrated species, *Diogenes brevirostris* Stimpson, 1858 and *D. extricatus* Stebbing, 1910, appear to be endemic to South Africa (Barnard 1950). Although the reproduction of *D. brevirostris* was studied in southern Mozambique (Litulo and Tudge 2005), this occurrence requires validation as there is currently no taxonomic record of the species outside South Africa. Barnard (1950) also compiled a diagnosis for South African specimens referred to *Diogenes costatus* Henderson, 1893, that was considerably detailed for its time. Moreover, he recorded *Diogenes senex* Heller, 1865, collected from Durban, KwaZulu-Natal, during the University of Cape Town Ecological Survey, 1946. Kensley (1969) reported *Diogenes custos* (Fabricius, 1798) from KwaZulu-Natal, but without comment excluded his record from his 1981 zoogeography of southern African decapod Crustacea. Probably relying on the later list, Emmerson (2016b,c) overlooked Kensley's earlier record of *D. custos* from South Africa. There are thus currently five species of *Diogenes* formally reported from within the national borders of South Africa, although more as yet undetermined species certainly occur in the region (pers. obs.).

A recent collection trip to Pumula near Port Shepstone, KwaZulu-Natal, on the east coast of South Africa, revealed a single small and uniquely coloured, ovigerous female specimen assignable to *Diogenes* that proved to be distinctively different from all other known species and is herein illustrated and described as new to science. High quality macro photographs taken *in situ*, as well as photographs of the specimen extracted from its shell will aid recognising the species should it be found again in the field. Molecular barcodes, and a high-resolution micro computed tomography (μCT) scan complement the species description, with the genetic data to support potential future studies of genetic relationships among populations and species of *Diogenes*.

3.3 Methods

The single specimen of the new species was collected during a 20 m Scuba dive off Pumula on 14 October 2015, where it was found along the nearly vertical slope of an approximately 5–6 m high rocky reef wall. The specimen was photographed alive from various angles *in situ* in a photographic tank, then anaesthetised in a 0.125 $\frac{\text{mL}}{\text{L}}$ clove-oil seawater solution and frozen prior to shell extraction, photographed again from all angles, and then preserved in 96% ethanol. Several eggs were taken as tissue samples for the sequencing of the cytochrome *c* oxidase subunit I (COI) gene barcoding fragment, carried out at the South African Institute for Aquatic Biodiversity, as described in Landschoff and Lemaitre (2017b). Genetic data were made available through the SeaKeys project on the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007), and were submitted to GenBank. Drawings were initially made under a M5 Wild stereomicroscope with attached camera lucida. Pencil drawings were then digitally traced using inkscape (www.inkscape.com). For the μCT scan the specimen was taken out of ethanol and carefully wrapped in parafilm (Bemis NA, Neenah, WI, United States), mounted on rigid foam, which itself was glued to the top of a plastic rod, and scanned at 6 μm voxel resolution at the CT Scanner Facility at Stellenbosch University, South Africa (du Plessis et al. 2016). The raw data of the scan are publicly available from the GigaScience Database (GigaDB) repository (Landschoff et al. 2017). In a datanote (see Chapter 6, Landschoff et al. in press) give detailed information on the acquisitioning of the data. The 3D visualisation movie was rendered using Volume Graphics VGStudioMax 3.1. (Heidelberg, Germany).

The specimen is deposited at the Iziko South African Museum, Cape Town (SAMC MB-A066353). Morphological terminology follows Rahayu (2012, 2015). Measurement of the shield length (SL) is given in millimetres (mm) and was taken from the tip of the rostrum to the midpoint of the posterior margin of the shield. Coordinates are given using the Degrees Decimal Minutes system.

3.4 Systematic account

3.4.1 Family Diogenidae Ortmann, 1892

3.4.1.1 Genus *Diogenes* Dana, 1851

Diogenes n. sp.

Figures 3.1–3.3, Suppl. Material Video 3.1

Material examined. Holotype. Ovig. ♀ 2.0 mm (SAMC MB-A066353), from rocky reef off Pumula, KZN, South Africa, S 30° 38.34’, E 30° 32.94’, Scuba, 20 m, 14 October 2015, coll. J. Landschoff.

Description of holotype. Shield (Figure 3.1 A) as long as broad, dorsal surface somewhat smooth medially, with minutely rugose tubercles and short to moderately long fine setae on lateral and anterolateral regions, with 1 or 2 small anterolateral spines; rostral lobe broadly rounded, weakly produced. Lateral projections triangular, slightly exceeding tip of rostral lobe, each with small, prominent anterior spine. Branchiostegites membraneous, except for dorsal margin being well calcified, bearing 5 or 6 small spines; anterior angle rounded to weakly truncate, unarmed (left) or with 2 small spines (right); surface with long and finely plumose setae increasing in density towards dorsal and anterior margins.

Ocular peduncles (Figure 3.1 A) inflated, somewhat bulbous in proximal portion, distal half cylindrical, about 0.7 length of shield, with few short setae dorsally and mesially. Corneas at most very weakly dilated, their diameter about 0.2 of peduncular length, including cornea. Ocular acicles longer than broad, subtriangular, their mesioproximal angles almost touching at base, with two large mesial spines in addition to row of 2–5 spinules and few fine setae on mesial 0.6 of terminal margin. Intercalary rostriform process simple at tip, not reaching tips of mesial spines of ocular acicles.

Antennular peduncles (Figure 3.1 A), when fully extended, overreaching corneas by 0.5 length of ultimate segment. Ultimate and penultimate segments unarmed, dorsally with few short to moderately long and fine setae. Ultimate segments distally dilated. Basal segment unarmed.

Antennal peduncles (Figure 3.1 A) overreaching distal margins of corneas by 0.2–0.3 length of fifth segments; fifth segments unarmed, ventrally with row of long setae; fourth segments with triangular dorsodistal margin and mesiodistal tuft of short setae, and with single long seta on ventrodistal margin; third segments short, with few medium-long setae mesially, and single long seta ventrally; second segments each with dorsolateral distal angle produced into prominent spine accompanied by tuft of finely plumose medium-long setae, dorsomesial distal angle with tiny spinule, mesial margins with very short setae, laterodistal margin subtriangular, bearing few short to medium-long finely plumose setae, distally with small spine or spinule, ventrodistal angle with prominent spine laterally and spinule ventrally; first segments unarmed, or at most with few tubercles on dorsolateral distal angle, with scattered short setae, mesially with very short plumose setae. Antennal acicles reaching to half length of third segment of antennal peduncles, with row of 5 or 6 irregular spines and medium-long setae on mesial margin, lateralmost spine strongest. Antennal flagella, when fully extended, reaching tip of left cheliped, each article proximally with lateral and mesial long and minutely plumose seta, sometimes with additional short seta dorsally.

Chelipeds unequal and dissimilar, left markely larger than right. Left cheliped (Figure 3.1 B) with very narrow hiatus between dactyl and fixed finger. Dactyl about 0.7 length of palm measured along dorsal margin; cutting edge with row of irregularly sized and spaced, blunt, calcareous teeth, and 2 or 3 single or tufts of short setae, distally terminating in calcareous claw; outer surface convex to straight, regularly to irregularly covered by small, distally acute to minutely crenulate, rounded tubercles, with row of larger tubercles or spines near outer margin interspersed by scattered short setae, subdistally with tuft of very short setae, tubercles less developed near cutting edge; upper margin with 1 or 2 irregular rows of distally subacute or minutely crenulate tubercles or spines, with 1 or 2 short setae; inner surface somewhat smooth, with broad longitudinal sulcus on upper half, and with weakly elevated median ridge bearing 1 or 2 rows of very low, rounded tubercles, with 3 tufts of short setae near cutting edge. Fixed finger with outer surface covered by tubercles as on dactyl, distally with scattered very short setae; cutting edge forming nearly straight line, with 3 major regular calcareous teeth larger than of movable finger, and 2 or 3 single or tufts of short setae, terminating in calcareous small claw; lower margin convex; inner surface nearly smooth, with 1 or 2 single or tufts of short setae near cutting edge, and with tuft of longer setae at midlength near lower margin. Palm with outer surface covered by distally minutely crenulate tubercles, distally convex to straight, proximally with larger tubercles or spines on slightly elevated median ridge, spaces either side of median ridge shallowly concave, near upper margin with 1–4 irregular rows of stronger tubercles or spines; upper margin with row of distally-curved, prominent spines; lower margin delimited by 1 or 2 irregular rows of subacute tubercles extending onto fixed finger; inner surface distally with round, proximally with subquadrate very low, flattened

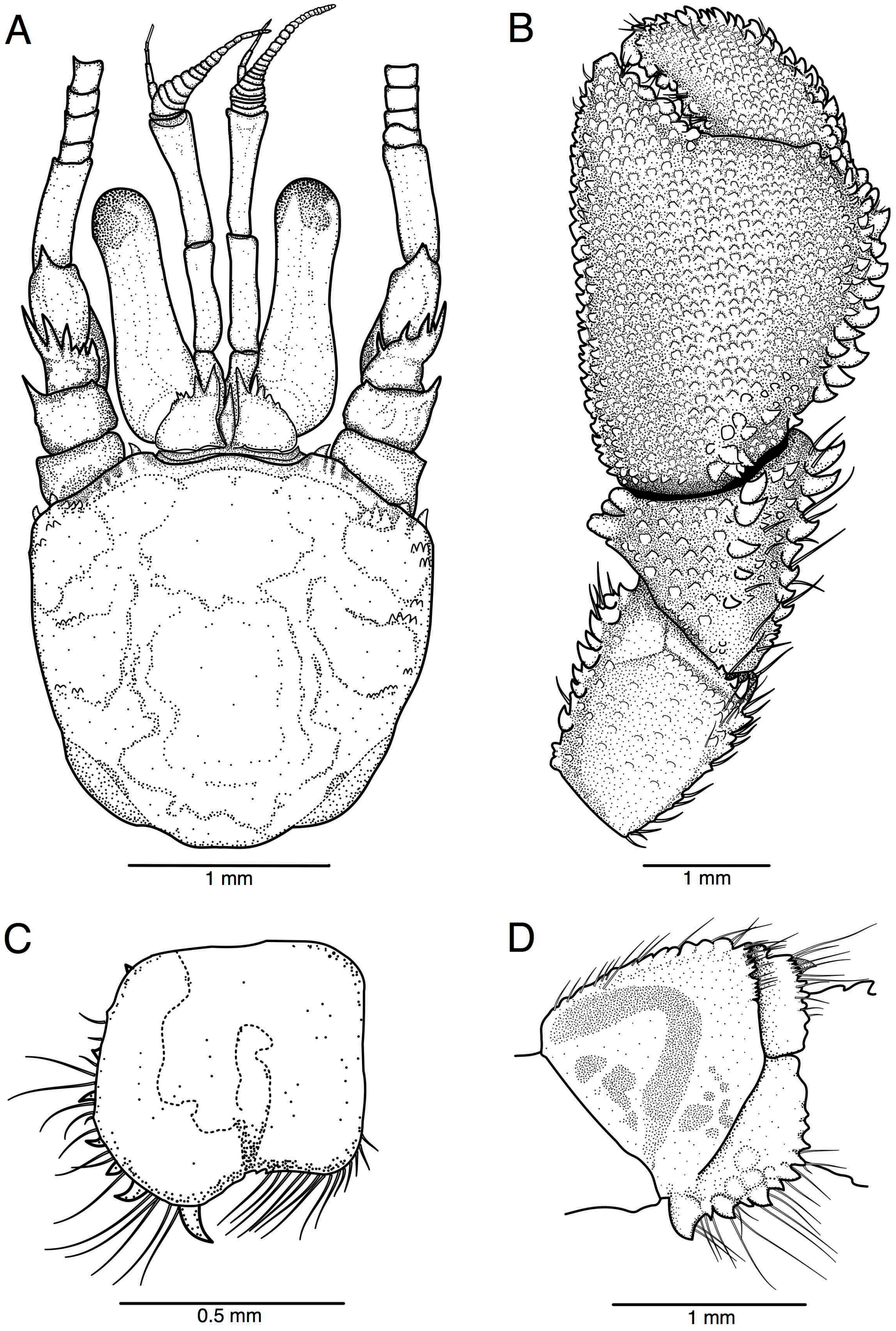

Figure 3.1: ***Diogenes* n. sp., Pumula, South Africa, holotype, ovig. ♀ 2.0 mm SL (SAMC MB-A066353):** **A** shield and cephalic appendages, dorsal view (setae omitted) **B** dactylus, propodus, carpus and merus of left cheliped, lateral view **C** telson, dorsal view **D** merus of left cheliped, mesial view.

tubercles of irregular size arranged in somewhat transversal bands, near upper margin with 2–4 rows of larger tubercles or spines, uppermost row with sparse short setae. Carpus approximately 0.5 length of palm; outer surface with longitudinal, irregular row of spines near midline increasing in size towards distal, upper outer surface flattened, with 1 or 2 irregular rows of larger tubercles or spines, lower surface tuberculate; upper margin with row of strong distally-curved spines, increasing in size distally, and at distal base giving rise to tufts of short to medium-long setae; lower margin distally with protuberances, bearing small acute tubercles; inner surface strongly convex, sparsely covered by fine, medium-long plumose setae, low and rounded tubercles arranged in somewhat transversal bands, forming row on distal margin, slightly larger and acute tubercles or small spines forming 1 or 2 rows near upper margin accompanied by short to medium-long setae. Merus subtriangular in dorsal view; dorsodistal margin with several spines of different sizes and medium-long to long setae or bristle-like setae, subdistally delimitated by shallow transversal furrow proceeding onto lateral and mesial faces; dorsal surface in distal half with small, elongated, round or acute tubercles or spines and tufts of short setae, in proximal half with low tubercles and medium-long fine, plumose setae; lateral face with very low tubercles and somewhat appearing smooth, ventrally with some blunt low tubercles; ventrolateral margin with irregularly spaced, distally-curved spines accompanied by sparse short setae; mesial face (Figure 3.1 D) with weakly-calcified V to U-shaped patch, distally divided by transversal furrow dorsally bearing denticulate protuberances and row of short setae, distal section further separated into dorsal and ventral lobes by median cleft; dorsal lobe with distal margin bearing small spines and short to medium-long setae, medially rounded; ventral lobe with distal margin also medially rounded, ventrally with large spines, and with medium-long, fine, plumose setae. Ischium with row of minute denticulation on ventral margin; ventrolateral face with sparse setae.

Right cheliped (Figure 3.2 A) slightly overreaching upper dorsodistal angle of carpus of left cheliped; slight hiatus between dactyl and fixed finger. Dactyl 1.3 times length of palm, moderately arched; upper margin with row of small acute spines; outer surface with several small acute tubercles or spines arranged in 2 irregular rows, and also covered by moderately dense, long setae, individual setae minutely plumose; cutting edge with row of small calcareous teeth, distally terminating in strong and sharp claw overlapped by fixed finger; inner surface with 2 rows of tufts of short setae near cutting edge. Fixed finger with outer surface covered by minute blunt or acute tubercles, and also by long fine setae, distally becoming more bristle-like; lower margin with small acute tubercles or spines, distally with tufts of long setae; cutting edge straight to convex distally, with row of calcareous teeth terminating in sharp claw; inner surface with 2 rows of tufts of short setae near cutting edge, subdistally with small corneous spine. Palm with small acute spines on upper margin, increasing in size towards distal and interspersed by long setae; outer surface with irregularly to regularly spaced blunt or acute tubercles or spines, and also with moderately dense long, fine setae; lower margin with acute tubercles or small spines and long setae; inner surface with single or tufts of long setae. Carpus triangular from dorsal view, with row of equally large spines on upper margin interspersed by long setae, upper outer surface flattened to concave and

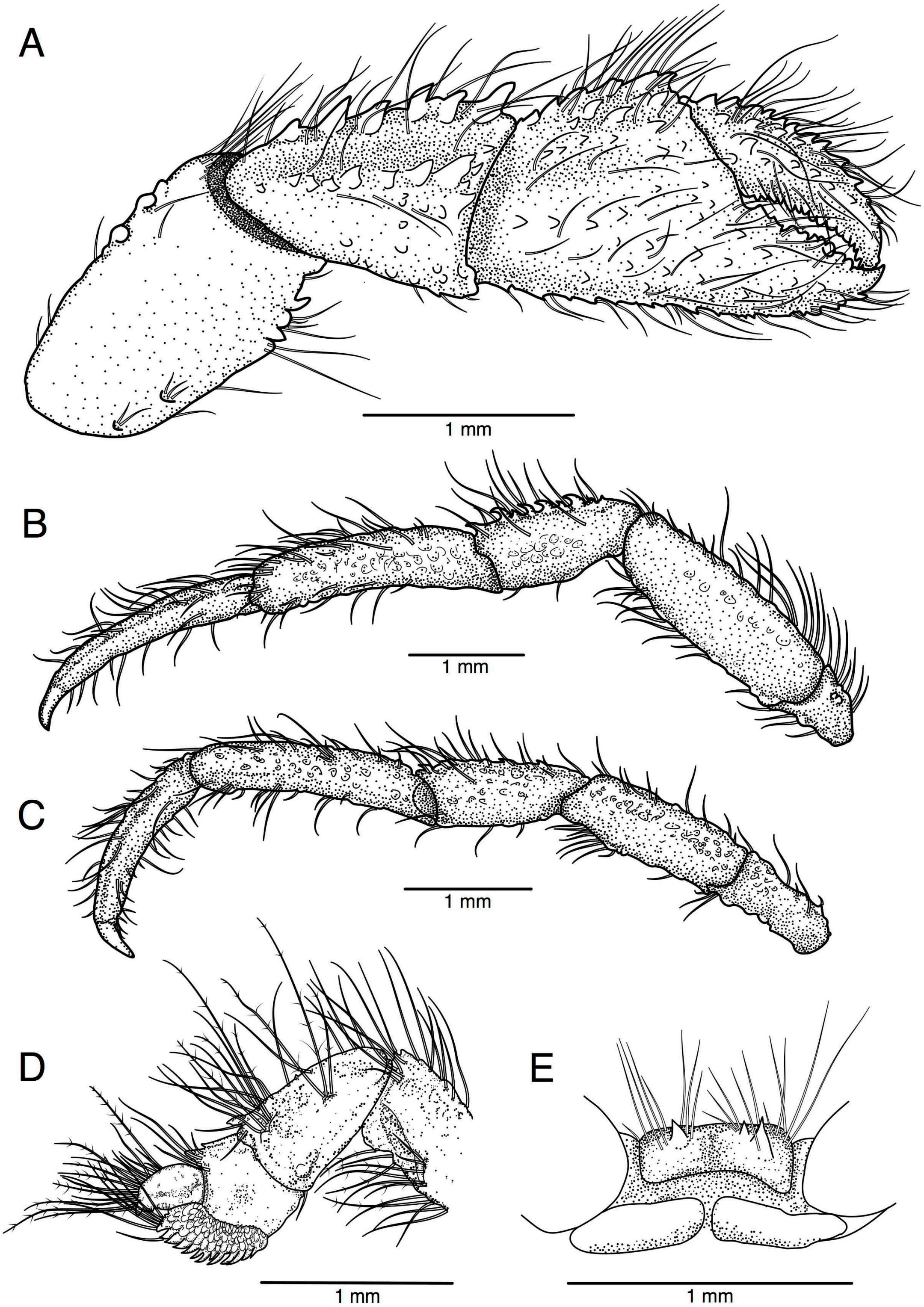

Figure 3.2: *Diogenes* n. sp., Pumula, South Africa, holotype, ovig. ♀ 2.0 mm SL (SAMC MB-A066353): **A** dactylus, propodus, carpus and merus of right cheliped, lateral view **B** second left pereopod, lateral view **C** third left pereopod, lateral view **D** dactylus, propodus, carpus and merus (in part) of fourth left pereopod, lateral view **E** sternite XII and basal portion of coxae of third pereopods, ventral view.

smooth, distal margin with blunt tubercle; outer surface with longitudinal row of small spines, increasing in size distally; lower outer surface somewhat smooth with few blunt or acute tubercles and few medium-long setae; lower margin not delimited, with at most few short setae. Merus with low tubercles or protuberances on dorsal margin accompanied by sparse short setae, dorsodistally with row of long straight setae; ventrolateral margin with short and medium-long, fine setae, in distal half with acute tubercles or spines; ventromesial margin with short simple setae arising from few tubercles; ventral surface flattened, distally with medium-long plumose setae. Ischium with row of setae and row of minute spinules or tubercles on ventromesial margin; ventrally with row of small spines and short setae along articulation with merus.

Second and third pereopods slender (Figure 3.2 B–C). Second pereopods with dactyls 1.1 times longer than propodi, slightly curved ventrally but not twisted in dorsal view, terminating in long corneous claw, 0.1–0.2 length of dactyl; dorsal and ventral surfaces each with lateral and mesial rows of fine, medium-long setae or tufts of few setae; lateral surface with longitudinal shallow sulcus; mesial surface sparsely covered by fine, medium-long setae. Propodi 1.5 times longer than carpi; dorsal margin with minute, low tubercles, and with single or tufts of fine, medium-long setae; ventral margin with sparse tufts of 2–3 shorter setae; lateral and mesial surfaces smooth, with sparse fine setae. Carpi 0.7 length of meri; dorsal margin each with row of very small spines (distalmost strongest) and long and medium-long setae or tufts of setae; ventral margin unarmed, but on left with row of short setae on ventrodistal margin; surface of lateral face on left with very shallow dorsal sulcus resulting in slightly elevated, broad longitudinal ridge near midline, less developed on right; mesial face smooth. Meri each with row of short to long setae on dorsal margin; ventral margin with low tubercles or protuberances and sparse long, fine setae; lateral face somewhat smooth. Ischia with low tubercles or protuberances and row of medium-long fine setae on dorsal and ventral margins. Third pereopods with dactyls similar as in second pereopods, but 1.2–1.3 times longer than propodi. Propodi each with dorsal row of low tubercles, left with fine short to medium-long setae, right with less and shorter setae on dorsal margin; ventral margin of left with tufts of 2 or 3 setae or medium-long single setae, right almost non-setose; lateral faces smooth or at most with very low tubercles. Carpi 0.8–0.9 length of meri; dorsal margin with row of very small acute tubercles or minute spines and sparse short to medium-long setae; ventral margin unarmed, ventrodistal margin with row of short setae; lateral surface as in second pereopods. Meri and ischia unarmed, or at most with small tubercles and sparse setae on dorsal and ventral margins.

Fourth pereopods semichelate (Figure 3.2 D). Dactyls dorsodistally with long, dense plumose setae on left, and with long, predominantly simple setae on right. Propodi and carpi each with small dorsodistal projection covered by tufts of long setae and terminating in single spine; propodal rasp with 5–7 rows of oval corneous scales. Anterior lobe of sternite of third pereopods (Figure 3.2 E) with 1 or 2 small spines on each side of anterior margin. Female with paired gonopores.

Telson (Figure 3.1 C) with indistinct shallow median cleft; left lobe moderately longer and round, terminal margin with two large spines and long setae, continued on lateral margin, spines decreasing in size towards anterior; right lobe subquadrate, terminal margin with 2 minute spines and long setae, not continued onto lateral margin.

Colour (in life; Figure 3.3). General background white, with orange-red and dark brown or black dots, patches and stripes. Shield white, with two major longitudinal orange lines. Anterior carapace transparent to deeply orange towards branchiostegites. Ocular peduncles sprinkled white, with small red to brown dots of different sizes, orange at base; corneas black; ocular acicles white, orange at base. Antennular peduncles white-transparent, with small orange and red to brown dots. Antennal peduncles white to transparent; first segments with two major red-brown patches; second segments orange at base and with small red to brown dots; antennal acicles and fourth segments with few small red to brown dots and each with one large dorsolateral dot subdistally, third and fourth segments also with large ventrodistal red to brown dots; fifth segments transparent and with laterodistal red to brown dots; flagella with red to brown band about every fourth article. Mouthparts with second and third maxillipeds bearing red to brown dots on endopods, exopods with narrow black and yellow to white bands. Left cheliped with entire surface of dactyl and propodus brightly white, at most minute red dots and with orange patch on base of dactyl and propodus on inner surface; integument between propodus and carpus with orange vertical bands; carpus with upper outer surface orange, tubercles, spines and lower surface white; inner surface with median white patch surrounded by orange areas, tubercles white; integument between carpus and merus orange; merus similar to carpus. Right cheliped similar to left, with dactyl and palm white with orange base; carpus with upper surface orange, more pronounced distally, orange at base, spines and tubercles white. Second and third pereopods white, with orange and black bands and orange longitudinal stripes; dactyls each with white tip, broad orange band subdistally and broad orange to dark-orange band in proximal half, dorsoproximally each with weak black spots; propodi each with orange longitudinal stripes on dorsal margin and on median line of lateral faces, dark orange bands at base, and dorsoproximally each with pronounced dark spots; carpi laterally each with two longitudinal stripes; meri laterally each with longitudinal stripe on median line, dorsally each with proximal black spot, and also with larger black spot on proximal side of proximal half. Fourth and fifth pereopods mostly white. Pleopods transparent to white. Eggs deeply orange, with yellow yolk. Pleon deeply orange. Telson, uropods and pleonal tergites white.

Distribution. Known only from the type locality off Pumula, KwaZulu-Natal, South Africa.

Habitat. Rocky reef, in worn gastropod shell of subadult *Favartia maculata* Reeve.

Genetic data. Pumula, South Africa, 20 m reef, holotype, ovig. ♀ 2.0 mm SL, BOLD: SEAKY1091-16 (SAMC MB-A066353).

3D μCT data. The species description is complemented by a rotation movie clip of the holotype in the supplemental material (Video 3.1). While the scan was performed at a high resolution of

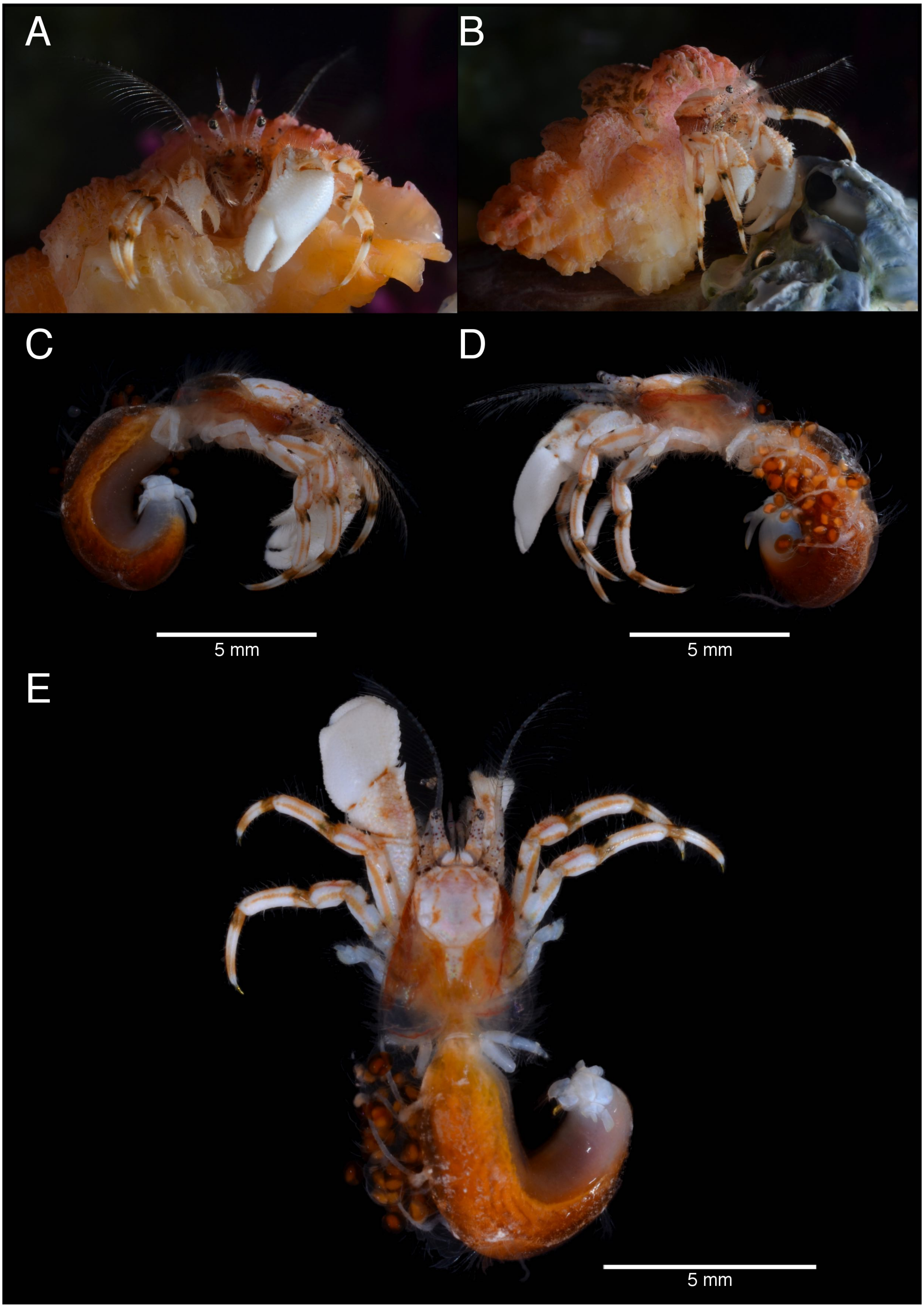

Figure 3.3: *Diogenes* n. sp., Pumula, South Africa, holotype, ovig. ♀ 2.0 mm SL (SAMC MB-A066353), colouration (in life or fresh): A–B *in situ* in worn shell of *Favartia maculata* Reeve **C** extracted from shell, right lateral aspect **D** same, left lateral aspect **E** same, dorsal aspect.

6 μm voxel size, image artefacts of the wrapping material that prevented the specimen from drying out during the scan had a similar density to the soft tissue of the sample (setation, pleon, etc.) and hence were not easily separated from the latter. In the movie clip visualisation, and in order to remove the majority of the unwanted artefacts, the focus was placed on the presentation of the main surfaces of the calcified body parts (majorly chelipeds and the pereopods). This was achieved by lowering the density/brightness threshold, which had the side effect of also eliminating weakly calcified body parts of the sample. Also, using this approach as a compromise for the visualisation, one area of scanning artefacts (beam hardening plus wrapping material) remained present on the upper outer surface of the palm of the left cheliped that can still be seen in Video 3.1. Further lowering of the brightness threshold would have cleared it, but would also have removed more other material of the sample. Should more information (e.g. on the soft tissue) be needed, the raw data of the μCT scans can be consulted, which are publicly available for download from the GigaDB data repository (Landschoff et al. 2017). Data acquisition and quality of the data are also separately discussed in more detail in an accompanying datanote (Chapter 6, Landschoff et al. in press).

The μCT-derived 3D data alone do not show all, but do illustrate many, characters needed to describe and identify the new species. By a hypothetical definition (Faulwetter et al. 2013b) the data therefore do not qualify as 'cybertypes', and are precautiously referred to as '3D virtual type data'.

3.5 Taxonomic remarks

Within the diverse genus *Diogenes*, *Diogenes* n. sp. belongs to the *'edwardsi'* group as defined by Asakura and Tachikawa (2010). This group is characterised by a simple intercalary rostral process, and by antennal peduncles that exceed the ocular peduncle and have long flagella. Among the species of this group, five, *D. dorotheae* Morgan and Forest, 1991, *D. guttatus* Henderson, 1888, *D. tirmiziae* Siddiqui and McLaughlin, 2003, *D. holthuisi* Asakura and Tachikawa, 2010, and *D. takedai* Rahayu, 2012, have short antennal acicles that reach only to the midlength of the fourth segment of the antennal peduncles. *Diogenes* n. sp. has short antennal acicles, the longest spine of each acicle does not reach the midlength of the fourth peduncular segment. Moreover, with the basally inflated ocular peduncles and slightly dilated corneas, it most closely resembles *D. holthuisi* and *D. dorotheae*. The most obvious character to distinguish these three species is the shape of the telson. The telson of *D. dorotheae* has unequal subtriangular lobes (left much larger) separated by a distinct median cleft, and the posterior and posterolateral margins of the lobes are armed by several strong spines. The telson of *D. holthuisi* is subtriangular, armed with two small spines on each posterior lobe, which are separated by a broad median cleft. In the new species the telson is subquadrate, the median cleft is indistinct, and the posterior margin of the left lobe armed with two strong spines. The posterolateral and posterior margin of the right lobe has only minuscule spines. Furthermore, the left cheliped of *D. holthuisi* bears small tubercles or rows of spines on the palm, the palm of *D. dorotheae* bears numerous acute tubercles and four large spines along a short longitudinal row from the proximoventral angle, while the palm of the new species is covered by small, rounded, acute or multi-dentate tubercles with a short proximal row of stronger tubercles at the midline. The surface of the palm of *D. tirmiziae* is also different, in that it does not have drop-like tubercles. As stated by Siddiqui and McLaughlin (2003), *D. guttatus* is distinguished from all other *Diogenes* species by the mushroom-shaped tubercles on the chelipeds. The white colouration of the chelipeds of *Diogenes* n. sp. resembles in general that of *D. takedai*, however, the remaining colouration differs markedly between the two species. *Diogenes takedai* has dark brown or black bands on the ocular peduncle and the second and third pereopods, while *Diogenes* n. sp. has light and dark orange bands and longitudinal stripes on the second and third pereopods.

Compared to the known local species in South Africa, *Diogenes* n. sp. is readily identifiable by the short antennal acicles. Even if it shares some similarities with *D. extricatus* in the shape and armature of the chelipeds (rows of spines on the dorsal surface of the carpus), apart from length ratios of the cephalic appendages it is also easily distinguished from *D. extricatus* by the armature of the pereopods (propodi and meri without spines vs. with spines in the latter), as well as by its small adult size (2 mm SL vs. >8 mm SL), and by colour in life (white with orange vs. pale-yellow colour; Figure 3.3, Chapter 8 Figure 8.10 F).

So far, only a single individual of *Diogenes* n. sp. was found in the coastal area of southern KwaZulu-Natal. Reefs at diving depths of this area are poorly sampled. Further sampling may well lead to the discovery of other undescribed species, as well as more specimens of *Diogenes* n. sp. that will reveal the distribution along the coast of KwaZulu-Natal and provide characters for males.

CHAPTER 4

MICROCT IMAGING APPLIED TO THE DESCRIPTION OF A NEW SPECIES OF *Pagurus*, FABRICIUS, 1775 (CRUSTACEA: DECAPODA: PAGURIDAE), WITH SELECTION OF THREE-DIMENSIONAL VIRTUAL TYPE DATA

4.1 Abstract

A new species of hermit crab, *Pagurus* n. sp. (family Paguridae) is described from rocky subtidal reefs off KwaZulu-Natal, South Africa, and illustrated using both conventional drawings and colour photographs, and via three-dimensional (3D) X-ray micro computed tomography (μCT). Because of the limitation μCT has in detecting very fine and soft structures, a novel approach of manually drawing setation and spinulation into the two-dimensional images of the μCT-visualisations was used to illustrate pereopods 2 and 3. Character presentations are also complemented by an interactive figure embedded into the portable document format (PDF) version of this document. The 3D raw data of the virtual types are downloadable from the GigaScience Database repository. The new species is the sixth offcial species of *Pagurus* Fabricius, 1775 reported from South Africa and is closely allied to the Indo-Pacific *P. boriaustraliensis* Morgan, 1990 and *P. pitagsaleei* McLaughlin, 2002, from which it differs by its shorter ocular peduncles, by the armature of the carpus of the right cheliped, and also in colouration. Colour photographs and molecular barcodes are provided, and the latter compared to *P. pitagsaleei*, as well as to three additional South African members of the genus. This is the first description of a hermit crab in which a majority of taxonomic details are illustrated through 3D volume-rendered illustrations. However, the μCT derived 3D data alone do not show all distinguishing characters. By the current standing definition they therefore do not qualify as 'cybertypes' and are referred to as '3D virtual type data'.

4.2 Introduction

With over 170 species worldwide the genus *Pagurus* Fabricius, 1775 is the most species-rich genus in the hermit crab family Paguridae (McLaughlin et al. 2010), although its heterogeneous nature has been pointed out (e. g. Forest and de Saint Laurent 1968, McLaughlin 1974, Komai 1998). Of all South African paguroids (*sensu* McLaughlin et al. 2007a) the genus *Pagurus* is one of the taxonomically best known. McLaughlin and Forest (1999) reviewed all earlier accounts of South African species, reported as *Eupagurus* Brandt, 1851 by Stebbing (1910, 1920, 1924) and Odhner (1923), as well as the eight species listed by Barnard (1950) (as *Eupagurus* and one as *'Incertae sedis'*). Moreover, those authors used newly available material, primarily collected during the 1982–1986 R. V. *Meiring Naudé* cruises on the eastern coast, to take up questions about the true identifications of South African species raised by Forest (1955). They came to the conclusion that five species of *Pagurus* occur in South African waters, *P. carvicarpus* (Paul'son, 1875), *P. cuanensis* Bell, 1846, *P. emmersoni* McLaughlin and Forest, 1999, *P. liochele* (Barnard, 1947), and *P. prideaux* Leach, 1815, plus a sixth undescribed species, of which only a single juvenile male had been found.

Recent Scuba collections from the eastern coast of South Africa revealed another species assignable to *Pagurus* that was common on subtidal reefs off Pumula and Hibberdene, KwaZulu-Natal. This species was clearly not referable to any known South African species, but it shows certain similarities to *Pagurus boriaustraliensis* Morgan, 1990, and *Pagurus pitagsaleei* McLaughlin, 2002. It is herein fully described as new to science and compared with the latter two. For the first time in hermit crab taxonomy, it is illustrated by three-dimensional (3D) micro computed tomography (μCT) imaging techniques for major body parts, using 3D-visualisations in interactive portable document format (PDF), rotation videos, and 3D still images overlaid with manually drawn setae and corneous spines. The use of μCT for crustacean taxonomy is discussed briefly as benefits and limitations are exemplified for the description of this new species of hermit crab. In addition, full colour information, as well as molecular barcodes, are provided, and the latter are compared to three other South African species (*P. cuanensis*, *P. emmersoni*, and *P. liochele*) and to specimens from Taiwan of the morphologically-similar *P. pitagsaleei*.

4.3 Material and Methods

4.3.1 Sampling and photography

Specimens of *Pagurus* n. sp. were collected during two days of diving on near-shore reefs off Pumula and Hibberdene, approximately 100 km south of Durban, KwaZulu-Natal, South Africa. Back on land, the specimens were photographed alive in a photographic tank, then anaesthetised in a 0.125 $\frac{\mathrm{mL}}{\mathrm{L}}$ clove-oil seawater solution and frozen. After defrosting and extraction from their shells, colour images of the whole animals were taken in the laboratory of the University of Cape Town. All specimens were preserved in 96% ethanol. The South African specimens of *P. cuanensis*, *P. emmersoni*, and *P. liochele* used for genetic comparison were collected on various sampling occasions in 2015–2016 (see specimen data in section on genetic comparison). Specimens are deposited at the Iziko South African Museum, Cape Town (SAMC) with two paratypic specimens also deposited at the Natural History Museum and Institute, Chiba, Japan (CBM). The two specimens of *Pagurus pitagsaleei* McLaughlin, 2002 used for genetic comparison are located in the collections of the National University of Taiwan (NTOU). Measurements of specimens are given for shield length (SL) in mm taken from the tip of the rostrum to the midpoint of the posterior margin of the shield.

4.3.2 MicroCT scanning and illustrations

X-ray μCT scans were performed at the CT Scanner Facility at Stellenbosch University, South Africa (du Plessis et al. 2016). Two specimens of *Pagurus* n. sp. were scanned in three scans, using a General Electric Phoenix Nanotom S (Wunstorff, Germany). The holotype (♂ 2.7 mm, SAMC MB-A066790) was placed on rigid foam in a small container filled with ethanol and scanned whole at 11 μm voxel resolution. Because the left cheliped had broken off during previous handling, a 4.5 μm resolution scan of the left cheliped alone was also obtained, applying the same method as before, but in order to acquire a higher magnification, the sample has to be positioned closer to the X-ray source of the scanner, hence a smaller container was used. Later, in the rendering of the computer software, the two scans were overlaid, putting the left cheliped virtually back into its place. In addition, a paratype (ovig. ♀ 2.4 mm, SAMC MB-A066770) was wrapped in parafilm (Bemis NA, Neenah, WI, United States), mounted on rigid foam, which itself was glued to the top of a plastic rod, and scanned at 5 μm voxel resolution. Detailed information on data acquisition and processing for species descriptions are given in a separate datanote (Chapter 6, Landschoff et al. in press).

The 3D-visualisations were carried out using Volume Graphics VGStudioMax 3.0. (Heidelberg, Germany). As described in du Plessis et al. (2017), various parameters had to be optimised to obtain high quality data. Data processing was achieved using a combination of ‘Isosurface’ and ‘Phong’ rendering. To remove noise from the 3D rendered images, a first-level surface determination was used, followed by an ‘opening/closing’ function applied to the region of interest determined as the surface. Cropping removed unwanted material, often most efficiently used by applying the ‘Polyline3D’ function from various angles. Moreover, this function was used for separation of the chelipeds and pereopods from the whole animal. Contrary to most μCT data, image filtration did not improve the visualisations, and especially setae and fine textures were lost when filtering was attempted. The process to select the region of interest for visualisation as described above, could be continued with many more iterations of fine improvements, but with little improvement to the overall image. Hence, a good compromise was found between quality of the image and the processing time used.

Once selected, the object of interest was exported in the form of Stereolithography (STL) data, typically used for 3D printing. By loading these data into free software called MeshLab (www.meshlab.net), the data were converted to a Universal 3D (U3D) compressed format to be embedded in Adobe PDF files, or viewed online as interactive 3D files.

Drawings were initially made under a M5 Wild stereomicroscope with attached camera lucida. Pencil drawings were then digitally traced using inkscape (www.inkscape.com). For the illustrated pereopods and dactyli of pereopods, the setae and spinules of the drawings were overlayed with the 3D rendered image of the μCT scan. All figures were assembled in Gimp 2.8 (www.gimp.org).

4.3.3 Genetic comparison

Genetic barcodes of the cytochrome *c* oxidase subunit I (COI) mitochondrial DNA fragment were generated for four specimens of *Pagurus* n. sp. at the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, using a methodology described previously (Landschoff and Lemaitre 2017b). Tissue was either taken from eggs of ovigerous females, or, for small specimens, from the coxae and ischia of different pereopods. Tissue of the other species of *Pagurus*, for comparison, was primarily taken from eggs or the chelae and carpus of the right cheliped. DNA extraction, Polymerase Chain Reaction amplification of the COI fragment, purification of amplicons, fluorescently-labelled terminator cycle sequencing and sequence analysis proceeded as documented by Landschoff and Lemaitre (2017b). One specimen each of *P. cuanensis* and *P. liochele* were barcoded by the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, Canada. Sequences of the two specimens of *P. pitagsaleei* from Taiwan were kindly made available by Prof. Dr. Tin-Yam Chan (Institute of Marine Biology, National Taiwan Ocean University). Sequences of the South African specimens were uploaded to the SeaKeys project on BOLD (Ratnasingham and Hebert 2007), and were submitted to GenBank. All COI barcodes were aligned in ClustalX 2.1 (Larkin et al. 2007) and subsequently analysed in MEGA7 (Kumar et al. 2016), where a Neighbour-Joining (NJ) (Saitou and Nei 1987) tree was constructed and nodal support was determined using 1000 bootstrap replicates (Felsenstein 1985). Pairwise distances, corrected using a Kimura 2-parameter (K2P) model of sequence evolution, were calculated between individuals and species.

4.4 Systematic account

4.4.1 Family Paguridae Latreille, 1802

4.4.1.1 Genus *Pagurus* Fabricius, 1775

***Pagurus* n. sp.**

Figures 4.1–4.7, (4.1 interactive), Suppl. Material Videos 4.1–4.3

Type material. Holotype, ♂ 2.7 mm (SAMC MB-A066790), from off Hibberdene, KZN, South Africa, S 30° 34.92’, E 30° 34.86’, Scuba, 20 m reef, 15 Oct 2015.

Paratypes, all from KZN, South Africa. 14 Oct 2015, off Pumula, S 30° 38.34’, E 30° 32.94’, Scuba, 20 m reef, 1 juv. ♂ 1.4 mm (SAMC MB-A066408), 1 ♂ 2.1 mm (SAMC MB-A066410), 1 ♀ 2.4 mm (SAMC MB-A066407), 1 ♀ 2.0 mm (SAMC MB-A066411), 1 ovig. ♀ 1.2 mm (SAMC MB-A066409); 15 Oct 2015, off Hibberdene, S 30° 34.92’, E 30° 34.86’, 20 m reef, Scuba, 1 ♂ 1.9 mm, 1 ♀ 2.3 mm (CBM-ZC 14133), 1 ovig. ♀ 2.4 mm (SAMC MB-A066770).

Other material. Aug 2015, Vetch’s Pier, KZN, Durban, S 29° 52.02’, E 31° 03.00’, Scuba, 6 m, one specimen not collected (photographed *in situ* by G. Jones).

Description. Eleven pairs of biserial gills.

Carapace flattened dorsoventrally. Shield (Figures 4.1, 4.2 A) about as broad as long; dorsal surface nearly flat except for sloping lateral parts, with scattered low, blister-like tubercles (only visible when stained with methylene blue) and rows of tufts of short, distally plumose setae along rather distinct paragastric grooves; anterior margin between rostrum and lateral projections shallowly concave; anterolateral margins sloping, very weakly concave or straight; posterior margin roundly truncate. Rostrum broadly rounded or very broadly triangular, not reaching (or just reaching) level of lateral projections; dorsal surface usually with few short paired setae. Lateral projections roundly triangular, each armed with minute spine or unarmed. Posterior carapace (Figure 4.1, Video 3.1, in part) slightly shorter than shield and about half as long as wide, cardiac region flanked by sulci cardiobranchiales slightly calcified, with scattered low, blister-like tubercles; branchiostegite to branchial regions membranous, with sparse tufts of short to moderately-long plumose setae.

Ocular peduncles (Figures 4.1, 4.2 A) including cornea about 0.75 length of shield, weakly inflated in proximal half; cornea weakly dilated, its width about 0.25 length of peduncular length; dorsal surface mesially with 3 or 4 tufts of setae, ventromesial surface also with 1 or 2 individual setae, or tufts of few setae. Ocular acicles suboval, separated basally by 0.5 width of 1 acicle, each with a small submarginal spine and some short setae on distal margin and dorsal surface; dorsal surface shallowly-concave. Interocular lobe fully exposed, visible in dorsal view, medially concave.

Antennular peduncles (Figures 4.1, 4.2 A), when fully extended, overreaching distal corneal margins by 0.3–0.5 length of ultimate segment. Ultimate segment about twice as long as penultimate segment, widened distally, with sparse setae increasing in length distally on dorsal surface to dorsolateral distal angle. Penultimate segment with few short setae. Basal segment with setose, rounded laterodistal lobe; statocyst lobe with small distal spine; ventromesial distal angle unarmed.

Antennal peduncles (Figures 4.1, 4.2 A), when fully extended, overreaching distal corneal margins by 0.5 length of fifth segment. Fifth and fourth segments with few short setae on lateral and mesial faces (mesial setae on fourth segment stiff). Third segment unarmed on ventromesial distal angle, but with tuft of short to long stiff setae. Second segment with dorsolateral distal angle produced, reaching to about midlength of fourth segment, terminating in simple spine partially

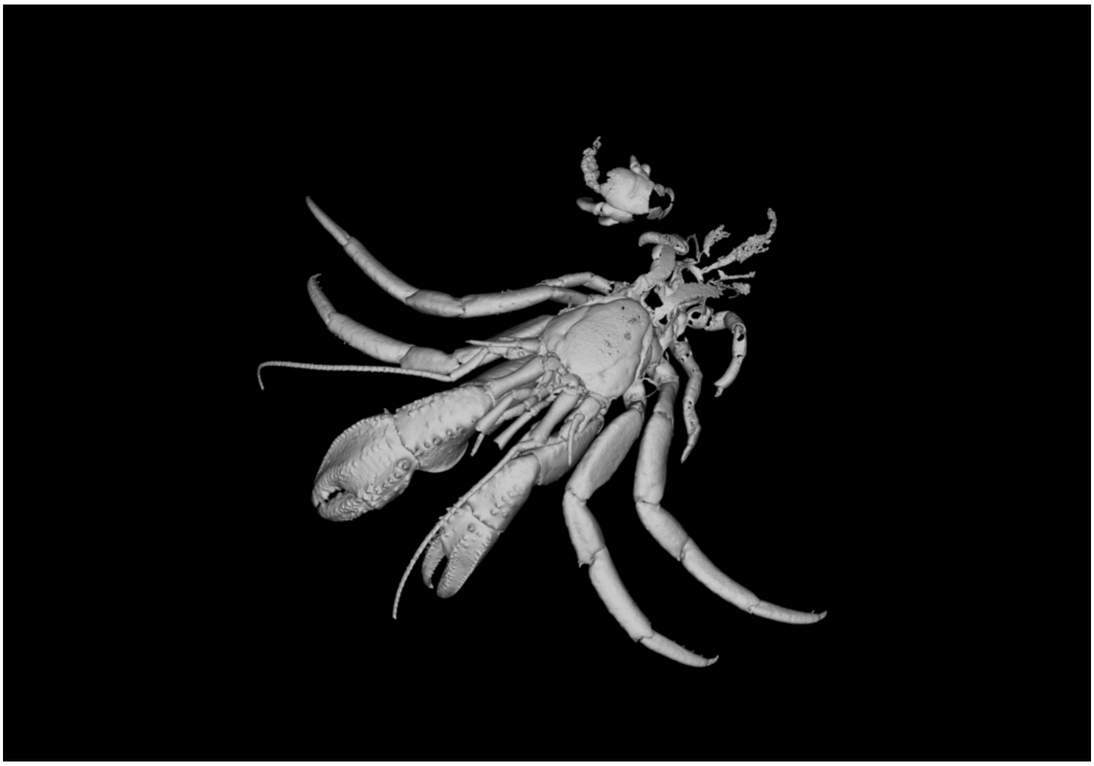

Figure 4.1: Interactive 3D, μCT derived volume reconstruction of *Pagurus* n. sp., ♂ holotype (SAMC MB-A066790): Note that only well-calcified structures are illustrated, as scan limitations and data processing to remove scanning artefacts reduced the possibilities of visualising soft body parts (pleon, posterior carapace, membranous structures like gills and setation). Small, calcified characters like tiny spines are also not displayed in this low-resolution version, but high-resolution rotation videos are provided in the supplemental material of this thesis. Clicking on the image activates the interactive 3D-mode, allowing the viewer to move, rotate and zoom into the character of choice (requires recent version of Adobe Acrobat Reader).

obscured by tuft of short to long, stiff setae, with few minute spinules on dorsomesial margin; dorsomesial distal angle with small spine; mesial margin with short to long setae. First segment with very small laterodistal spine; ventrodistal margin mesially with small process distally with excretory pore. Antennal acicle reaching to midlength or distal margin of cornea, moderately arcuate, terminating in simple spine encircled and partially obscured by long stiff setae; dorsomesial margin with row or tufts of moderately-long to long, often distally plumose setae. Antennal flagellum more than 3 times length of shield; each article with some short setae on distal margin, length of setae 0.5–1.0 times length of 1 article.

Mouthparts as figured. Majority, but particularly mandible (Figure 4.3 A) and second maxilliped (Figure 4.3 E), not showing distinguishing features. Maxillule (Figure 4.3 B) with external lobe of endopod moderately well developed, triangular, not recurved; internal lobe well produced, with 1 apical seta. Maxilla (Figure 4.3 C) with endopod exceeding anterior margin of scaphognathite; endopod basally with small lobe. First maxilliped (Figure 4.3 D) with endopod reaching level of distal third of exopod. Third maxilliped (Figure 4.3 F) moderately stout, setation normal;

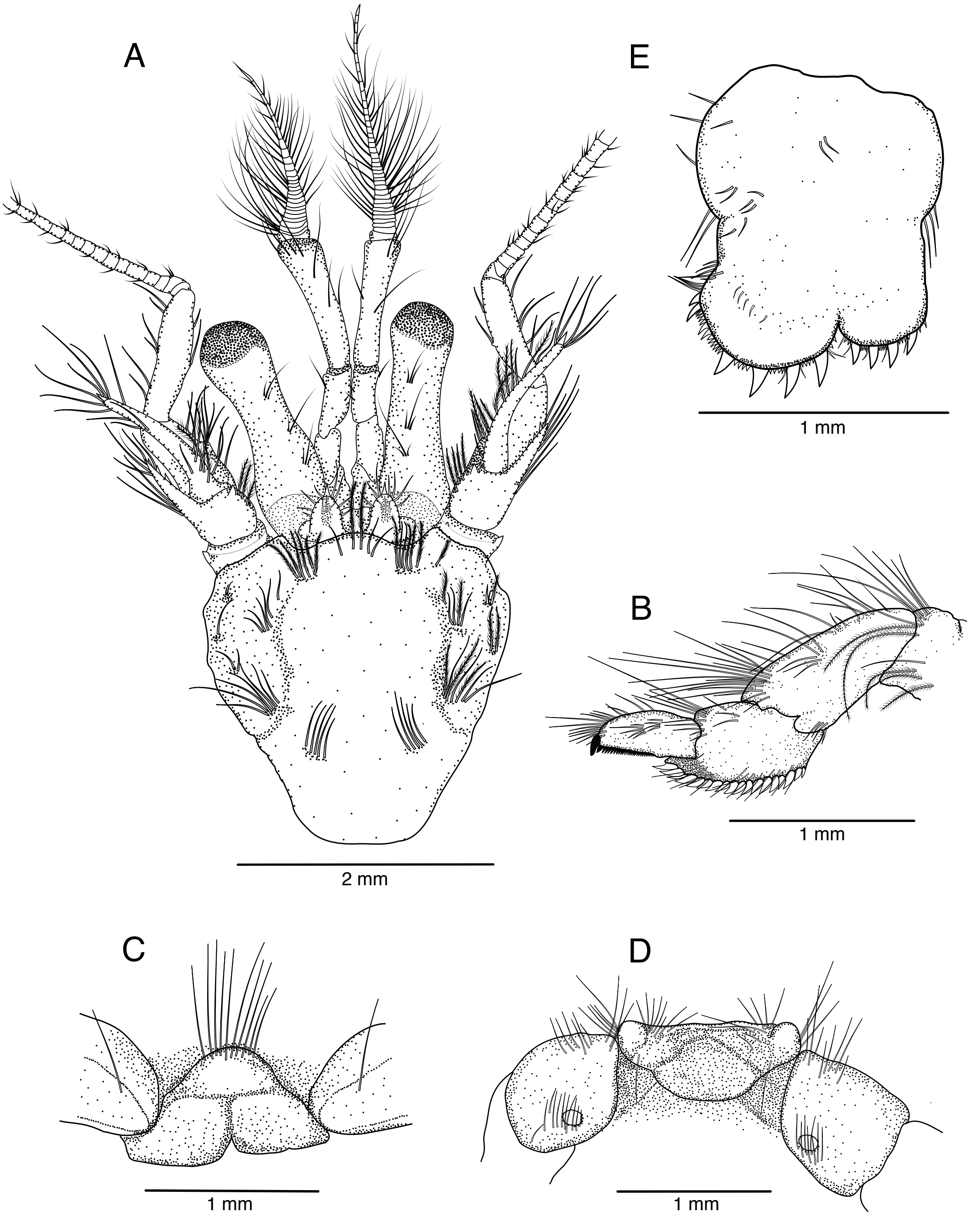

Figure 4.2: ***Pagurus* n. sp.:** **A** Ovig. ♀ paratype 2.4 mm (SAMC MB-A066770), shield and cephalic appendages, dorsal view **B–E** ♂ holotype 2.7 mm (SAMC MB-A066790), dactylus, propodus, carpus and merus (in part) of fourth left pereopod, lateral view (B), thoracic sternite 6 (third pereopods), ventral view (C), coxae of fifth pereopod and thoracic sternite 8, ventral view (D), telson, dorsal view (E).

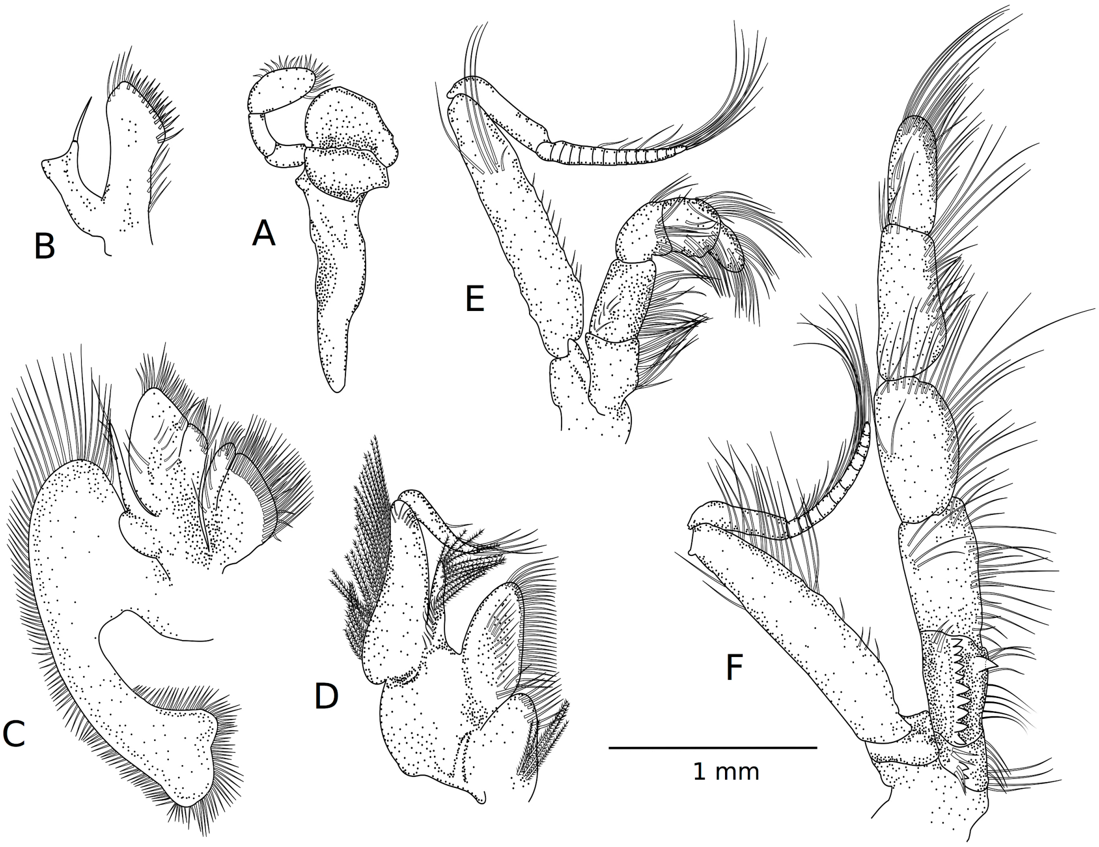

Figure 4.3: *Pagurus* n. sp., left mouthparts (internal view), ♀ paratype 2.4 mm (SAMC MB-A066407): A Mandible **B** maxillule **C** maxilla **D** first maxilliped **E** second maxilliped **F** third maxilliped.

dactyl about 0.5 length of propodus; carpus unarmed; merus also without conspicuous armature; ischium with crista dentata with about 10 corneous teeth increasing in size and more widely spaced proximally, and with 1 strong accessory tooth; basis with 2 minute denticles on mesial margin; exopod exceeding midlength of carpus.

Chelipeds unequal and dissimilar, right appreciably stronger than left. Right cheliped (Figure 4.4 A–D) moderately stout, not particularly elongated, even in males. Chela subovate in dorsal view, about 1.4 times as long as wide. Dactyl subequal in length to palm (measured along mesial margin), not overlapped by fixed finger when closed; dorsal surface slightly elevated along midline, bearing 1–3 irregular longitudinal rows of tubercles and sparse tufts of short stiff setae, and also with longitudinal row of stiff setae along cutting edge; mesial surface with irregular double row of small tubercles decreasing in size distally and with tufts of stiff, simple or plumose setae becoming shorter distally; ventral surface nearly smooth, with 2 rows of tufts of stiff setae; cutting edge with row of 5 rounded or bluntly-triangular calcareous teeth in proximal 0.8 and short row of minute corneous teeth in distal 0.2, terminating in small corneous claw. Palm 0.75 times as long as carpus; dorsolateral margin slightly elevated, clearly delimited with row of small, rounded tubercles extending onto fixed finger (tubercles becoming smaller distally) and bearing tufts of long, thick plumose setae not extending onto fixed finger; dorsomesial margin also slightly elevated, delimited with double row of small to moderately small spines and tufts of long, densely plumose setae; dorsal surface with broad, blunt ridge extending from midlength of palm onto fixed finger, leading proximally to row of small, simple or multifid tubercles; surface of median ridge covered with small, low, rounded tubercles; spaces either side of median ridge very shallowly concave, with sparse minute tubercles; lateral surface nearly perpendicular, without conspicuous armature, with longitudinal row of rows or tufts of short to moderately-long plumose setae adjacent to dorsal margin; mesial face with several short, obliquely transverse ridges or elevations each bearing row or tuft of long setae (setae on dorsal side thickly plumose, those on ventral side generally simple); ventral surface slightly convex, smooth, with few tufts of simple setae. Cutting edge of fixed finger with 3–4 prominent calcareous teeth, terminating in small corneous claw. Carpus moderately widened distally, 1.1–1.2 length of merus; dorsal surface with very low, small, distally multidenticulate protuberances, each bearing short to long stiff plumose setae, arranged in 2 rows; dorsomesial margin clearly delimited with row of small spines increasing in size distally and becoming blunt and low proximally, and tufts of long stiff setae; dorsolateral margin at least distally armed by 1–3 irregular rows of acute small tubercles or tiny spines, and also with row of tufts of long, stiff setae decreasing in length proximally, in smaller specimens rounded and undelimited; dorsodistal margin with row of long, stiff, often plumose setae partially obscuring proximal part of palm; lateral surface nearly flat, perpendicular, smooth, with few short setae; mesial face slightly concave, with scattered tufts of short to long, simple setae, ventromesial margin sharply crested, somewhat flared, visible in dorsal aspect; ventral surface convex, with scattered tufts of short to moderately long setae. Merus subtriangular; dorsal surface almost smooth, with few short setae and low subdistal ridge extending onto lateral and mesial faces, dorsodistal margin with small spine partially obscured by adjacent stiff setae; lateral surface only with few short setae, ventrolateral distal margin minutely denticulate; mesial surface with scattered stiff setae distally, ventromesial margin crested with prominent tubercle proximally, ventromesial distal angle produced into subtriangular plate, its ventral margin minutely denticulate distally or less produced, rounded, bearing few minute tubercles; ventral surface with tiny, low tubercles and few tufts of setae, but without conspicuous tubercle or spine. Ischium unarmed. Coxa with few low, blister-like tubercles on ventral surface and tufts of setae on ventromesial distal angle.

Left cheliped (Figure 4.5 A–E) moderately long and slender, reaching to level of midlength of dactyl of right cheliped; setae stiff, those of dorsal surface of palm particularly densely plumose. Chela elongate subovate in dorsal view, 1.9 times as long as wide (measured at greatest width at base of dactyl). Fingers leaving narrow hiatus in proximal third when closed. Dactyl gently curving ventrally, 1.6–1.9 times as long as palm; dorsal surface slightly elevated along midline, bearing row of tiny tubercles in proximal 0.4 and tufts of setae extending to tip (setae of proximal tufts longer, thickly plumose, those of distal tufts becoming shorter, thin and simple); dorsomesial margin not delimited; mesial face with row of tufts of setae along midline (setae of proximal 2 or 3 tufts long, plumose, those of distal tufts shorter and simple), bases of setal tufts (in particular those of 2 most proximal) forming small tubercles; ventral surface smooth, with tufts of

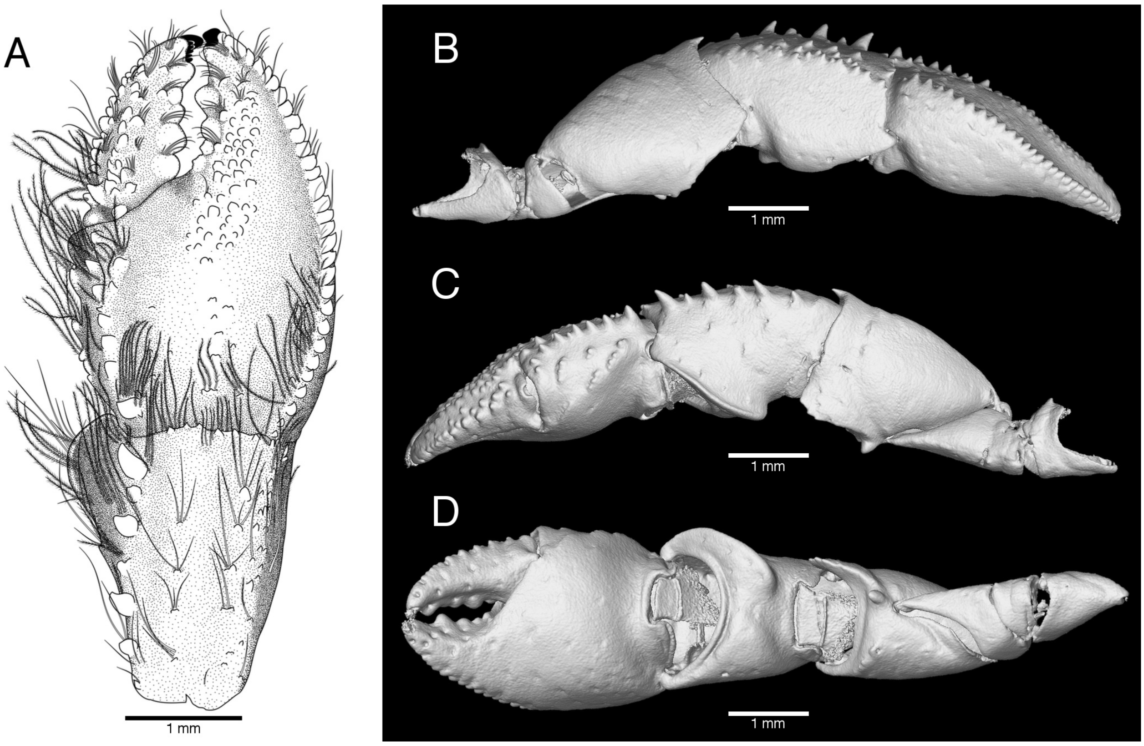

Figure 4.4: *Pagurus* n. sp., drawing (includes setation) and μCT images (only calcareous structures) of right cheliped of ♂ holotype 2.7 mm (SAMC MB-A066790): A Drawing of chela and carpus, dorsal view **B** μCT image of right cheliped, lateral view **C** same, mesial view **D** same, ventral view.

short setae arranged in 2 rows; cutting edge with row of minute, calcareous tubercles in proximal half and row of minute, corneous teeth in distal half, terminating in strong corneous claw. Palm approximately half length of carpus; dorsolateral margin distinctly delimited with row of tiny tubercles extending onto midlength to proximal 0.3 of fixed finger and tufts of long, plumose setae; dorsomesial margin rounded, but with row of 4 small spines or tubercles; dorsal surface medially with tiny tubercles arranged in irregular 2 rows and extending from proximal part of palm to midlength of fixed finger and prominent tufts of long plumose setae, and with longitudinal row of blunt tubercles and prominent tufts of long, plumose setae mesial to midline; lateral surface nearly perpendicular, smooth, with few tufts of short setae; mesial surface smooth, with few tufts of setae; ventral surface slightly convex, with few tiny tubercles laterally at base of fixed finger, and with scattered tufts of long setae; fixed finger with cutting edge with row of tiny, triangular calcareous teeth, terminating in strong, spooned corneous claw; ventral surface with 2 rows of tufts of setae. Carpus subequal in length to merus; dorsal surface slightly depressed or nearly flat, smooth or with very small tubercles, with several short, simple and long, plumose setae; dorsomesial margin with 3 small spines increasing in size distally, and sometimes followed by 2 or 3 tiny tubercles or low protuberances proximally, all accompanied with tufts of simple or plumose, long setae; dorsolateral margin unarmed or with tubercles or small spines increasing in size distally, all spines or tubercles bearing tufts of short to long setae; lateral surface with few low protuberances and tufts of setae dorsally, otherwise smooth; mesial surface with scattered tufts of long setae, distomesial angle triangularly produced; ventral surface strongly convex, with scattered tufts of short to long setae. Merus with row of sparse setae on dorsal margin and with short transverse ridge subdistally, dorsodistal margin unarmed; lateral surface almost smooth, only with few setae, ventrolateral margin with few minute denticles; mesial surface also smooth, with few setae, ventromesial margin unarmed distally, proximally with blunt tubercle; ventral surface with scattered tuft of short to long setae, but without conspicuous spines or tubercles. Ischium with ventromesial margin faintly denticulate; surfaces with scattered tufts of short, thin setae. Coxa similar to that of right cheliped.

Ambulatory legs (Figure 4.6 A–D) similar from left to right, moderately stout, with tufts of long, stiff or slightly shorter, plumose setae predominantly along dorsal and ventral margins, right second pereopod slightly overreaching tip of extended right cheliped. Dactyli approximately as long as propodi and about 5 times longer than broad, in dorsal view straight, in lateral view gently curving ventrally, terminating in moderately long (0.15–0.25 of entire length of each dactylus), curved corneous claw; dorsal surfaces each with sparse row of tufts of setae; lateral and mesial faces sparsely setose, latter without corneous spinules; ventral margins each with row of 5 or 6 (rarely 4) corneous spines, increasing in size and becoming more widely spaced distally, and row of tufts of plumose setae (setae most prominent in left third pereopod). Propodi slightly curved ventrally, 1.2–1.4 length of carpi; dorsal surfaces each with single or double row of tufts of long setae; lateral and mesial faces smooth, only with few very short setae; ventral surfaces each with 1–3 corneous spinules, including one at distal margin and row of tufts of short to long setae (distal setae plumose). Carpi each with dorsodistal spine; dorsal surface with row of tufts of long setae; lateral surface also with 2 rows of tufts of short to long, plumose setae with minute setules; ventral surface with few tufts or individual setae. Meri each without conspicuous spines or tubercles (2 right usually with minute denticle on ventrolateral distal angle); dorsal and ventral margins each with row of long, plumose setae (with very short setules); lateral faces smooth, with only few short setae. Ischia with few tufts of short to long setae on dorsal and ventral margins; without conspicuous spines or tubercles. Females with paired gonopores on coxae of third pereopods.

Fourth pereopods (Figure 4.2 B) semichelate, subequal in length from left to right, with subterminal tuft of short setae on dorsal margin of dactyli, stiff long setae and tufts of setae on dorsal margin of propodi to meri and ventromesial margin of meri. Dactyli nearly straight, with convex dorsal margin, terminating in small, strongly-curved corneous claw; ventral margin with closely set, microscopic corneous teeth; no preungual process. Propodal rasp consisting of a single row of corneous scales.

Fifth pereopods chelate, propodal rasp extending slightly beyond midlength of segment. Coxae of male (Figure 4.2 D) each with gonopore partially masked by tuft of setae.

Sternite of somite XII (thoracomere 6, third pereopods, Figure 4.2 C) with subsemicircular, wide anterior lobe, bearing several setae on anterior surface. Sternite of somite XIV (thoracomere 8, fifth pereopods, Figure 4.2 D) wide, with row of short setae on anterior margin; anterolateral

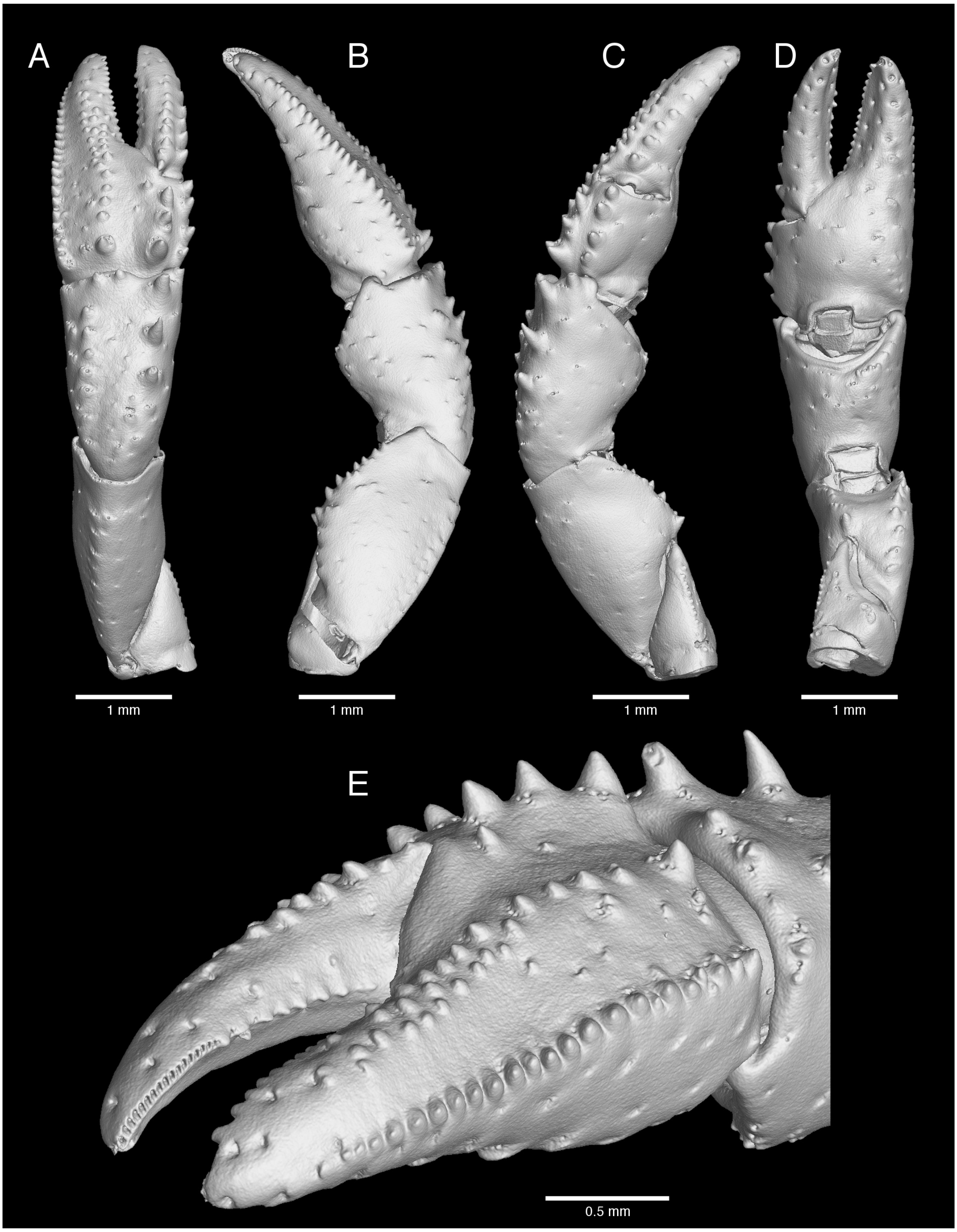

Figure 4.5: *Pagurus* n. sp., μCT images of left cheliped of ♂ holotype (SAMC MB-A066790), setation and corneous teeth and claw not illustrated: **A** Dorsal view **B** lateral view **C** mesial view **D** ventral view **E** chela and part of carpus, laterofrontal view.

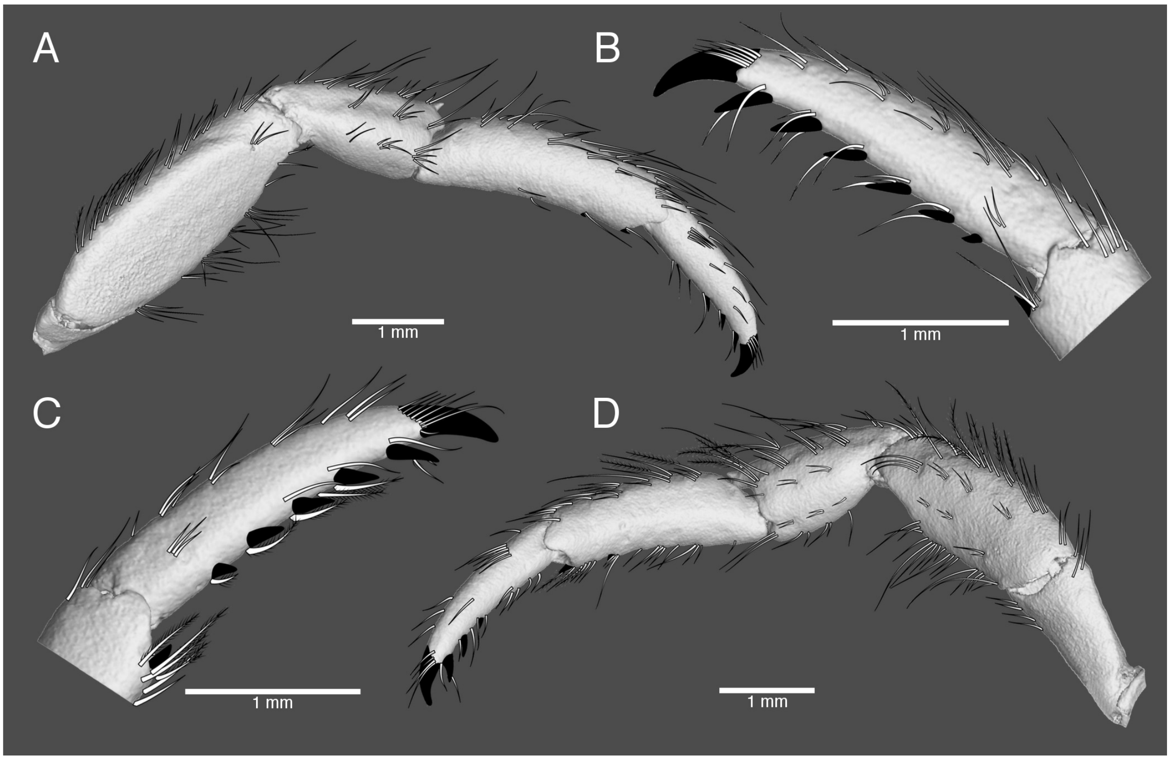

Figure 4.6: *Pagurus* n. sp., μCT images with manually drawn setation and spinules, as well as claw of pereopods of ♂ holotype (SAMC MB-A066790): **A** Second right, lateral view **B** same, dactylus and distal part of propodus of second right, mesial view **C** third left, dactylus and distal part of propodus, mesial view **D** same, lateral view, drawing.

lobes widely separated, slightly produced.

Pleon dextrally twisted. Male with 3 (third to fifth) unpaired, unequally biramous left pleopods. Female with slightly unequally biramous second to third pleopods; fourth pleopod unequally biramous with reduced endopod; fifth pleopod with endopod greatly reduced, exopod well developed.

Uropods and telson asymmetrical. Telson (Figure 4.1, in part, Figure 4.2 E) with distinct lateral indentations separating anterior and posterior lobes; posterior lobes rounded to subrectangular, unequal, with deep V-shaped median cleft; right posterior lobe more rounded and about twice as large as left one; terminal margins each with 4–6 (left usually with 4) prominent spines interspersed by minute spines and very short setae; lateral margins with rows of stiff setae.

Colouration (in life or fresh; Figure 4.7 A–D.) Shield pink to maroon and mottled cream to white, usually darker anteriorly. Posterior portion of carapace pink mottled cream, branchiostegites usually dark-brown and mottled cream. Ocular peduncle sky-blue with two bright orange transverse bands, one distally just proximal to base of cornea not extending to ventral surface, and one in second quarter from proximal; cornea yellow golden with very small red dots. Antennular peduncle with penultimate segment sky-blue in proximal and bright orange in distal half, ultimate segment azure and with bright orange band distally; flagella bright orange. Antennal peduncle cream with maroon stripes and bands, fifth segment with lateral and mesial longitudinal maroon stripe accompanied by small, white spots; flagellum in proximal half laterally and mesially with intermitted longitudinal maroon stripes leading distally into broadly transverse bands. Chelipeds similar in colouration, cream with maroon bands mottled cream; dactyl and fixed finger with weak pale brown band in distal half and maroon band or patch in proximal half, palm with irregular maroon patterns; carpus and merus proximally with transverse band of irregular maroon pattern. Ambulatory legs similar to chelipeds; dactyl with pale brown band in distal half and proximal transverse maroon band mottled cream; transverse maroon bands occurring along ambulatory legs with equal distances to each other, with one band each near middle of propodus, proximal portion of carpus, at midlength of merus, proximal portion of merus and distal half of ischium. Uropods and telson cream to mottled pink. Pleon orange to pink. Eggs deep maroon.

Distribution. Known from rocky reefs off Pumula and Hibberdene, near Port Shepstone, KZN, South Africa, and from a photographic record from Vetch's Pier, Durban, South Africa; 6–20 m depth.

Parasites. Host of an unknown parasitic bopyrid isopod probably of *Pseudionella* spp. (Figure 4.7 D), and of a second unidentified parasitic isopod, *Pseudione* sp., both inhabiting the branchial chamber.

Taxonomic remarks. The new species is clearly not referable to any of the known South African species presently referred to *Pagurus*, but appears close to *P. boriaustraliensis* from northern and northwestern Australia, and *P. pitagsaleei* from Thailand and Taiwan. All three species share strong similarities in the shape and ornamentation of the shield and cephalic appendages, characteristically ridged palms of the chelipeds, sharply crested, flared ventromesial margins of the carpus and merus of the right cheliped at least in males, and general shape of the eighth thoracic sternite and telson. However, morphological characters that separate *Pagurus* n. sp. from the other two species are the shorter ocular peduncles, which are exceeded by approximately half the length of the ultimate article of the antennular peduncle (only slightly exceeded in *P. boriaustraliensis* and *P. pitagsaleei*), the meri of the chelipeds that lack distinct tubercles on the proximal ventral surface (distinct tubercle(s) occur in both the other species), and the unarmed ventral margin of the merus of the right second pereopod (armed with one or more spines in *P. boriaustraliensis*, and with one spine in *P. pitagsaleei*). Furthermore, in *P. pitagsaleei* the dorsolateral margin of the carpus of the right cheliped is sharply delimited by a row of prominent spines (Rahayu and Komai 2000, McLaughlin 2002, McLaughlin et al. 2007b), in *P. boriaustraliensis* it is less strongly delimited, but bears considerably large spines (Morgan 1990). In *Pagurus* n. sp. the dorsolateral margin of the carpus of the right cheliped is armed with 1–3 irregular rows of acute tubercles or tiny spines. Furthermore, a strong asymmetry in the dimensions of the fourth pereopods, present (Rahayu and Komai 2000) in *P. pitagsaleei*, is absent in the new species.

In addition to the morphological characters, living colouration is useful to differentiate the new species from the other two species (Morgan 1990, Rahayu and Komai 2000, McLaughlin 2002,

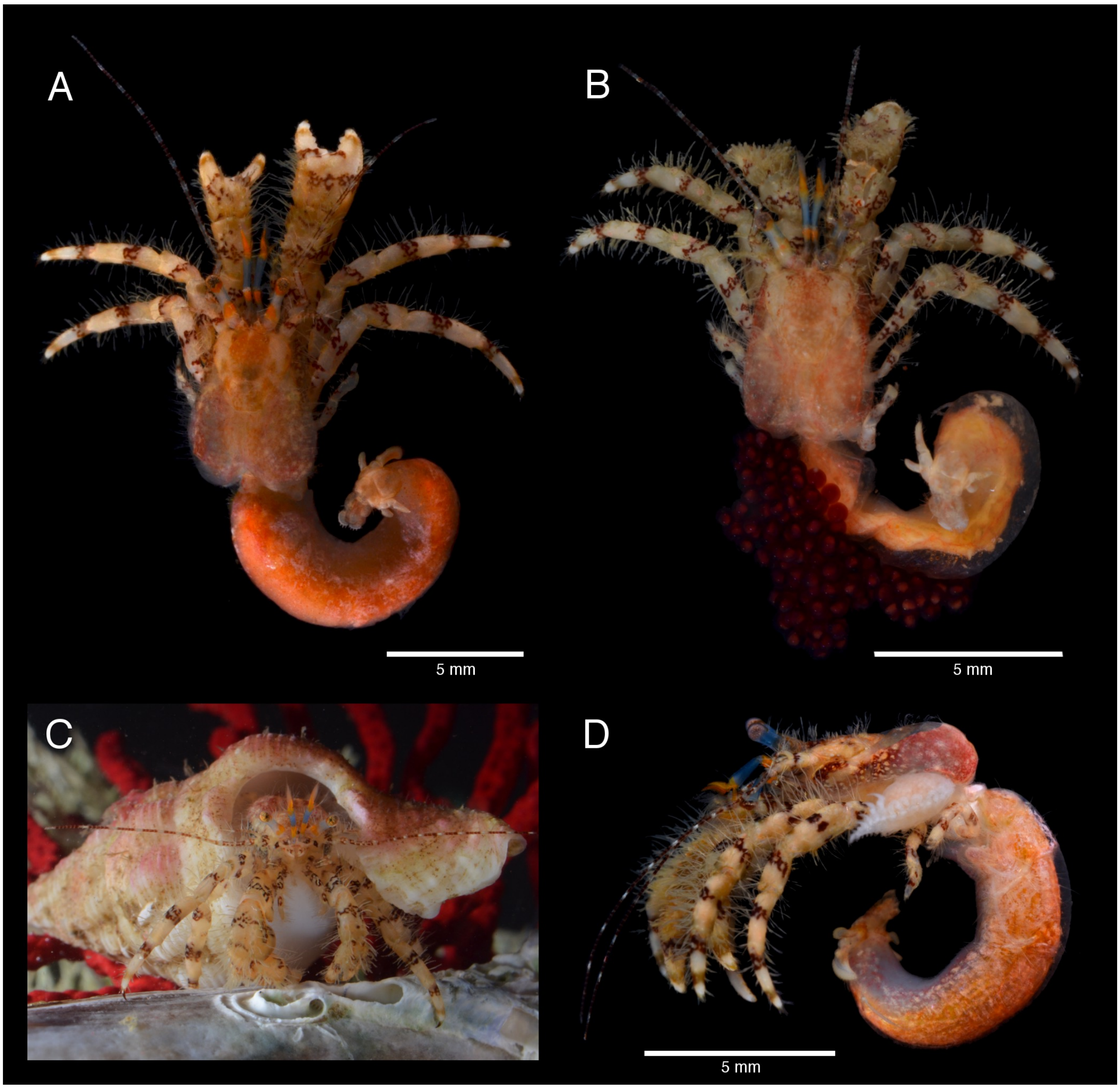

Figure 4.7: ***Pagurus*** **n. sp., colouration in life or fresh: A** ♂ holotype 2.7 mm (SAMC MB-A066790), dorsal view **B** ovig. ♀ paratype 2.4 mm (SAMC MB-A066770), dorsal view **C** holotype, frontal view, in shell **D** ♀ paratype 2.4 mm (SAMC MB-A066407), left lateral view, parasitised by undescribed parasitic gills isopod *Pseudionella* sp..

McLaughlin et al. 2007b). The ocular peduncles of *P. boriaustraliensis* and *P. pitagsaleei* were reported as cream and gray-white respectively, and have longitudinal stripes, whereas in *Pagurus* n. sp. they are sky-blue with two bright orange transverse bands, and without longitudinal stripes. The antennular peduncles are described as generally cream (the penultimate segment with dark stripes, and the flagellum bright orange) in *P. boriaustraliensis* and generally grayish-white (with dark-red stripes and patches, ultimate segment orange distally) in *P. pitagsaleei*, whereas in the new species they are sky-blue to azure with bright orange bands and bright orange flagellum, but not with longitudinal stripes or dark patches. Similar differences can be seen in the colours of chelipeds and ambulatory legs. While the chelipeds and pereopods in *P. boriaustraliensis* are cream-brown with dark-brown lines and in *P. pitagsaleei* grayish-white and black with short black or reddish-black stripes, in the new species they are cream with maroon bands mottled cream, and do not have longitudinal stripes.

In South Africa, *Pagurus* n. sp. is easily distinguishable from all other local species presently referred of *Pagurus* by the characteristic shape, armature, and setation of the chelipeds, pereopods, and telson. Among South African representatives of the genus, *Pagurus* n. sp. is perhaps morphologically most similar to *P. liochele*, with which it shares general characters of the right cheliped, such as some delimitations of the dorsolateral and dorsomesial margins, as well as the wing-like projection of the ventromesial face of the merus and carpus. However, for example, *Pagurus* n. sp. differs from *P. liochele* by having a characteristic median ridge on the palm of the right cheliped, the less evenly distributed, less rounded and slightly more acute tubercles on the dorsal surface of the right palm, and by having long and densely plumose setae in many places of the chelipeds (both chelipeds in *P. liochele* are at most covered with short setae). In life, the two species can readily be identified by the colour, as *Pagurus* n. sp. has maroon bands around the chelipeds and pereopods, and *P. liochele* has longitudinal orange stripes on the dactyli and a sienna band on the propodi proximally (see Chapter 8).

Key to known South African species of *Pagurus*, adapted after McLaughlin and Forest (1999):

1a Dorsal surface of palm of chelipeds armed with spines 2

1b Dorsal surface of palm of chelipeds unarmed or armed only, or majorly, with granules or small tubercles 4

2a Right second pereopod with dorsal row of spines on propodus 3

2b Right second pereopod without dorsal row of spines on propodus .... *Pagurus* sp. (see McLaughlin and Forest 1999)

3a Ocular peduncles short, stout. Dorsal surface of palm of right chela with small tubercles or spines, strongest mesially and laterally; carpi of chelipeds each, or at least right, usually with prominent foramen on ventral surface .... *Pagurus carvicarpus* (Paul'son, 1875)

3b Ocular peduncles moderately long and slender. Dorsal surface of palm of right chela with rows of spines, strongest in midline; carpi of chelipeds each, or at least right, without prominent foramen on ventral surface .... *Pagurus cuanensis* Bell, 1846

4a Dactyls of ambulatory legs shorter to only slightly longer than propodi 5

4b Dactyls of ambulatory legs at least 1.5 length of propodi .... *Pagurus prideaux* Leach, 1815

5a Ventromesial face of merus and carpus of right cheliped developed as wing-like projection in both sexes 6

5b Ventromesial face of merus and carpus of right cheliped not developed as wing-like projection in either sex.......................... *Pagurus emmersoni* McLaughlin and Forest, 1999

6a Dorsal surface of right palm and merus evenly covered by blunt tubercles, surface of palm convex, not forming a longitudinal elevation in distal half ....
. ... *Pagurus liochele* (Barnard, 1947)

6b Dorsal surface of right palm and merus medially unevenly covered with majorly blunt tubercles, surface of palm mesially and laterally concave, medially forming a longitudinal elevation in distal half extending onto fixed finger .... *Pagurus* n. sp. (Figures 4.1–4.7)

3D μCT virtual type data. The 3D data of the holotypic and one paratypic specimens derived from μCT scans are presented as interactive PDF (Figure 4.1), still images (Figures 4.4 B–D, 4.5), or still images overlaid with manually drawn morphological characters such as the setation or corneous spinules (Figure 4.6), as well as video clips viewable in the supplemental material of this thesis (Videos 4.1–4.3). Data processing, as described in the materials section, was used to remove noise and unwanted features, while maintaining the original data as reference. Because this cleaning process has advantages (revealing a nice and clean surface, illustrating calcified, well-defined taxonomic characters) and disadvantages (removing important information such as minute spines, corneous spinules, and setation), for presentation purposes it was applied to the holotype (Figures 4.1, 4.4 B–D, 4.5, Videos 4.2–4.3), but not to the female paratype (Video 4.1). The scan-visualisations of the combined holotype in an interactive image (Figure 4.1) allow the viewer to move, rotate and zoom into characters of interest. This interactive 3D image is limited to isosurface views and is reduced to information on relative grey values, e. g. lowering the possible quality of the image especially for fine features. It shows the calcified parts of the holotype as a whole and offers a rapid 3D overview of the specimen that includes the real size dimensions, such as relationships of *in situ* taxonomic characters from any possible angle. Its resolution is not sufficient for the study of finer structures such as small spines or setae. If more detailed information is needed the suite of other illustrations can be consulted. The 3D still images of the right cheliped (Figure 4.4 B–D) complement the line drawing of the dorsal view of the dactylus, propodus and carpus of the right cheliped (Figure 4.4 A). Although the setation is not visualised in these images, the scan reconstructions provide 3D details in lateral, mesial and ventral view that outplay the surface details of the drawing in accuracy. Being scanned separately, the high resolution scan of the left cheliped made it possible to show the minute cavities from which each setae arises (Figure 4.5). While this does not provide information about the setae itself (setation is well described in the description section), it precisely reveals the location of each seta on the cheliped. The 3D images of the pereopods (Figure 4.6) are surface renderings overlaid with manual drawings of the setation, the corneous spinules and of the claw. In addition, three video clips are provided if more 3D views are needed. Video 4.1 shows the female paratype in a μCT reconstruction in which the 'noise' was not removed. Being wrapped and scanned in parafilm it includes scanning artefacts, but in return also a majority of setation, parts of the pleon and the eggs carried on the pleopods are all visible. Videos 4.2 and 4.3 are rotation clips of isosurface rendered separations of the holotypic right and left chelipeds. They resemble the scan images in Figure 4.4 and Figure 4.5. Because in Paguridae the chelipeds have significant identification characters, through the rotation videos the viewer can gain even more insights into the armature and appearance. Furthermore, all scan raw data are publicly available for download from the GigaScience Database online depository (Landschoff et al. 2017), and more detailed information on scanning parameters and data quality can be retrieved from the accompanying datanote (Chapter 6, Landschoff et al. in press).

4.5 Genetics

Material with COI barcodes. *Pagurus* n. sp., off Pumula, KwaZulu-Natal (KZN), South Africa, S 30° 38.34', E 30° 32.94', 20 m reef, ♂ 1.4 mm, BOLD: SEAKY1146-16, GenBank: MF695076 (paragenetype) (SAMC MB-A066408), ovig. ♀ 1.2 mm, BOLD: SEAKY1147-16, GenBank: MF695072 (paragenetype) (SAMC MB-A066409), ♂ 2.1 mm, BOLD: SEAKY1148-16, GenBank: MF695073 (paragenetype) (SAMC MB-A066410), ♀ 2.0 mm, BOLD: SEAKY1149-16, GenBank: MF695068 (paragenetype) (SAMC MB-A066411). *Pagurus cuanensis*, Roman Rock, False Bay, South Africa, S 34° 10.80', E 18° 27.48', 20 m, ovig. ♀ 6.6 mm, BOLD: SEAKY931-15, GenBank: MF695069 (SAMC MB-A066192). *Pagurus emmersoni*, off Pumula, KZN, South Africa, S 30° 38.34', E 30° 32.94', 20 m reef, ♂ 4.6 mm, BOLD: SEAKY1139-16, GenBank: MF695070 (SAMC MB-A066401). *Pagurus liochele*, Algoa Bay, Port Elizabeth, South Africa, S 33° 50.10', E 25° 57.00', 50 m, ovig. ♀ 5.7 mm, BOLD: SEAKY878-15, GenBank: MF695074 (SAMC MB-A066845), ♂ 7.1 mm, BOLD: SEAKY879-15, GenBank: MF695075 (SAMC MB-A066846); Buffels Bay, 34° 05.40', E 22° 58.68', intertidal, ♂ 5.5 mm, BOLD: SEAKY863-15, GenBank: MF695071 (SAMC MB-A066246). *Pagurus pitagsaleei*, Haikou, Kending, Pingtung County, Taiwan, 8 September 2005, 1 ♂ 4.1 mm, 1 ovig. ♀ 4.3 mm, GenBank: MF667024, MF667023 (NTOU A01441).

Comparision of COI barcodes. In the NJ tree, barcodes of the four specimens of *Pagurus* n. sp. formed a monophyletic unit with 100% bootstrap support (Figure 4.8). The new species clustered closest to *P. pitagsaleei* and the sister-taxa relationship was well-supported (99%). *Pagurus cuanensis*, *P. emmersoni* and *P. liochele* formed a second, well-supported clade. Pairwise comparisons revealed that *P. liochele* and *P. emmersoni* to be genetically much closer (0.039–0.044) to each other than to the morphologically very similar *Pagurus* n. sp. and *P. pitagsaleei* (0.110–0.114, Table 4.1).

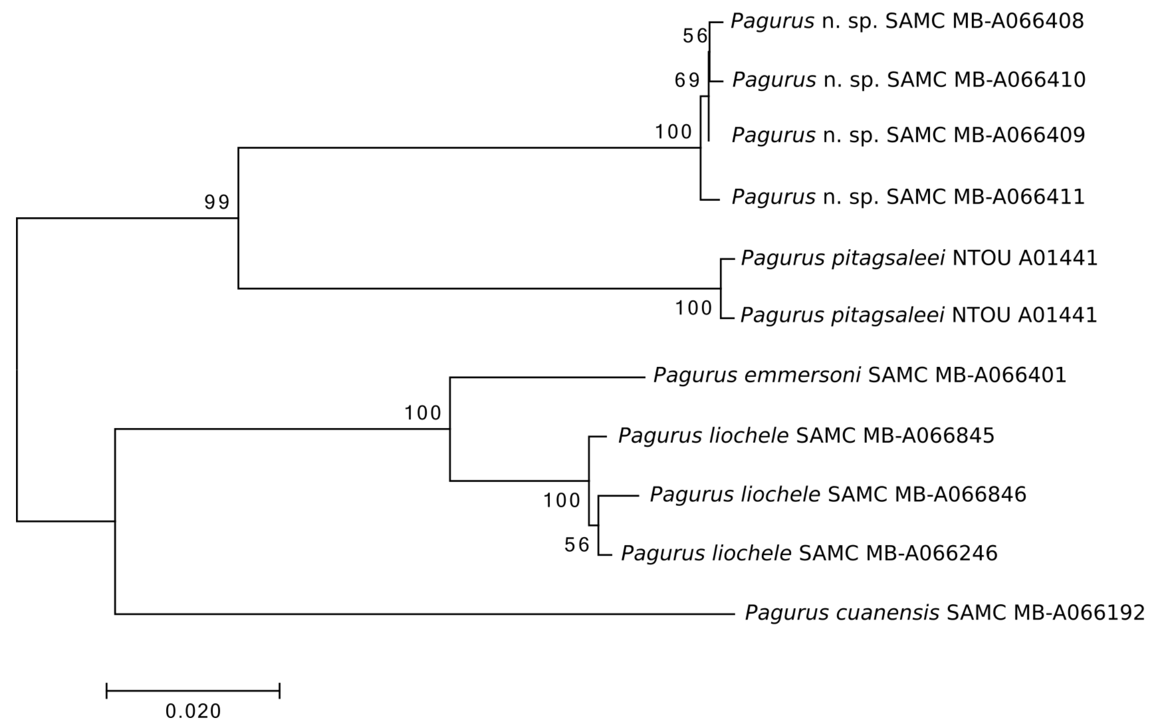

Figure 4.8: NJ tree based on Kimura 2-parameter (K2P) distances, showing relationships among mitochondrial cytochrome *c* oxidase subunit I (COI) barcode sequences of *Pagurus* n. sp. and four other species of *Pagurus*. Nodal support from 1000 bootstrap replicates indicated above the branches.

Table 4.1: Pairwise Kimura 2-parameter (K2P) distances matrix among mitochondrial cytochrome *c* oxidase subunit I (COI) barcode sequences of *Pagurus* n. sp. and four other species of *Pagurus*; values highlighted in bold for comparisons of *Pagurus* n. sp. with *P. pitagsaleei*, as well as for *P. liochele* with *P. emmersoni*.

		1	2	3	4	5	6	7	8	9	10
1	*Pagurus* n. sp., (SAMC MB-A066408)										
2	*Pagurus* n. sp., (SAMC MB-A066409)	0.002									
3	*Pagurus* n. sp., (SAMC MB-A066410)	0.003	0.002								
4	*Pagurus* n. sp., (SAMC MB-A066411)	0.005	0.003	0.005							
5	*Pagurus liochele*, (SAMC MB-A066845)	0.153	0.151	0.153	0.151						
6	*Pagurus liochele*, (SAMC MB-A066846)	0.157	0.155	0.157	0.155	0.006					
7	*Pagurus liochele*, (SAMC MB-A066246)	0.151	0.149	0.151	0.149	0.006	0.006				
8	*Pagurus emmersoni*, (SAMC MB-A066401)	0.155	0.153	0.155	0.157	**0.039**	**0.044**	**0.044**			
9	*Pagurus cuanensis*, (SAMC MB-A066192)	0.163	0.161	0.163	0.161	0.129	0.133	0.133	0.131		
10	*Pagurus pitagsaleei*, (NTOU A01441)	**0.114**	**0.112**	**0.114**	**0.114**	0.137	0.141	0.139	0.150	0.174	
11	*Pagurus pitagsaleei*, (NTOU A01441)	**0.112**	**0.110**	**0.112**	**0.112**	0.139	0.142	0.141	0.152	0.174	0.003

4.6 Discussion

In South Africa, *Pagurus* is the one of the only two genera of hermit crabs that has been the subject of a relatively recent revision (McLaughlin and Forest 1999), with *Nematopagurus* A. Milne-Edwards and Bouvier, 1892 being the other one (McLaughlin 1998). With the discovery of *Pagurus* n. sp. in shallow waters on the southern coast of KwaZulu-Natal, there are now six (plus one undescribed) species of *Pagurus* reported in the region. Of these, *P. emmersoni*, *P. liochele*, as well as *Pagurus* n. sp. appear to be national endemics.

Delimitating *Pagurus* n. sp. morphologically and based on the available molecular data shows that genetic divergence between species in this genus can be reasonably high (>10% *Pagurus* n. sp. to *P. pitagsaleei*), even when morphological characters seem similar (Figure 4.8, Table 4.1). In comparison, the genetic difference between *P. emmersoni* and *P. liochele* (3.9%–4.4%) is small, yet these two South African species are well distinguishable by both morphological characters and colouration (McLaughlin and Forest 1999). Colouration has frequently been shown to be reliable and sufficient for the identification of many hermit crab species (e. g. Rahayu and Forest 1992, Komai 2003a,b, Asakura 2006b, Komai and Osawa 2006, Malay and Paulay 2010, Lemaitre 2013), as natural selection presumably accelerates colour differentiation (Malay and Paulay 2010). This is again evident from the considerable differences in colour patterns between *Pagurus* n. sp., *P. boriaustraliensis* and *P. pitagsaleei*, species which show few distinguishing features in terms of their structural morphology. In fact, the distinctively coloured ocular acicles, antennae and ambulatory legs shown by *Pagurus* n. sp. were the characteristics which initially motivated this study and led to the suspicion that this might be a new species. Only later did this lead to morphological examination and the detection of morphological differences with its relatives.

4.6.1 Taxonomy

The species-rich and heterogeneous genus *Pagurus* is systematically poorly understood (Komai and Rahayu 2014), and requires revision (Ingle 1985, Olguín and Mantelatto 2013). The results of this study suggest a close relationship of *Pagurus* n. sp. to *P. boriaustraliensis* and *P. pitagsaleei*. Both of the two latter species have been discussed as potential allies of the '*Pagurus anachoretus*' group cf. Forest (1978) (Komai and Osawa 2001, Komai and Rahayu 2004). At present, this group formerly includes the following 12 species: *P. anachoretus* (Risso, 1827) from the Mediterranean, *P. anachoretoides* Forest, 1966, *P. gordonae* (Forest, 1956), *P. laurentae* Forest, 1978, *P. souriei* (Forest, 1952), from the tropical eastern Atlantic, *P. liochele* (Barnard, 1947), *P. emmersoni* McLaughlin and Forest, 1999 from South Africa, and *P. decimbranchiae* Komai and Osawa, 2001, *P. fungiformis* Komai and Rahayu, 2004, *P. hedleyi* (Grant and McCulloch, 1906), *P. kulkarnii* Sankolli, 1962, and *P. moluccensis* Haig and Ball, 1988 from the Indo-West Pacific (Forest, 1978, Forest and Ngoc-Ho, 1992, McLaughlin and Forest, 1999, Komai and Rahayu, 2004). In addition, four more species from the tropical eastern Atlantic fit well into the general definition of the *anachoretus* group, but have a different cheliped form. These species are *P. alcocki* (Balss, 1911), *P. dartevellei* (Forest, 1958), *P. fimbriatus* Forest, 1966, and *P. triangularis* (Chevreux and Bouvier, 1892) (McLaughlin and Forest 1999). Predominantly based on the presence of low, blister-like tubercles, which are darkly stained by methylene blue, Komai and Rahayu (2004) assessed all the species formerly assigned to the *anachoretus* group (McLaughlin and Forest, 1999), except for the two South African species *P. liochele* and *P. emmersoni*, as well as three species from the latter subgroup (*P. dartevellei*, *P. fimbriatus*, and *P. triangularis*). Since all of the tested species carried such blister-like tubercles, and because these tubercles are currently not known from any other group (Komai and Rahayu, 2004), they (Komai and Rahayu) assumed that this character is useful to define a homogenous assemblage within the heterogeneous genus *Pagurus*. Strengthening this assumption, during the course of this study the presence of tubercles were confirmed for both the additional South African species *P. liochele* and *P. emmersoni*. Therefore, of this group *P. alcocki* remains the last to be tested to determine whether it shares character.

Both *Pagurus* n. sp. and *P. pitagsaleei* have blister-like tubercles predominantly on the shield that stain darkly in methylene blue. Because no specimens were available for examination, it is unknown if *P. boriaustraliensis* has such tubercles. Given the close relationship to *Pagurus* n. sp. and *P. pitagsaleei*, it seems likely. However, whether *P. boriaustraliensis*, *P. pitagsaleei* and *Pagurus* n. sp. should be assigned to the *anachoretus* group remains questionable. Morgan (1990) compared *P. boriaustraliensis* with *P. hedleyi* and *P. kulkarnii*, McLaughlin (2002) discussed the affinities of all these three species with *P. pitagsaleei*, Komai and Osawa (2001) suggested a close relationship between *P. boriaustraliensis*, *P. decimbranchiae*, *P. moluccensis* and *P. pitagsaleei* (as *P.* cf. *boriaustraliensis*), but none of the authors made a final determination of formal assignment. One of the main characteristics of the *anachoretus* group is the shape of the right cheliped, with the dorsal surface of the palm being more or less rounded (Forest and Ngoc-Ho 1992). Later, McLaughlin and Forest added one supplemental character of the fourth pereopod consisting of a single row of scales (McLaughlin and Forest 1999), and Komai and Rahayu (2004) added two supplemental characters of the presence of low, blister-like tubercles on the calcified integuments of the body and pereopods, as well as the widely separated anterolateral lobes on the eighth thoracic sternite. Moreover, Komai and Osawa (2001) noted that members of the *anachoretus* group and their allies share the uniting feature of the terminal margins of the telson usually being armed with some spines interspersed by smaller spines or spinules. While *Pagurus* n. sp. and *P. pitagsaleei* (and *P. boriaustraliensis* partially, but presumably fully) agree with all these additional characters, they differ somewhat in the shape of the right cheliped. In particular, all three species share a remarkably similar right cheliped with the dorsal surface of the chela mesially and laterally concave, medially bearing a broadly elevated, tuberculated ridge extending onto the fixed finger, and also with tufts of long plumose setae.

Although analyses were confined to a single mitochondrial marker, *Pagurus* n. sp. and *P. pitagsaleei* formed a clade with well-supported sister-groups, underpinning their close relationship (Figure 4.8). Furthermore, *P. liochele* and *P. emmersoni* clustering together with *P. cuanensis* (herewith confirmed to not have blister-like tubercles) as a second well-supported clade to the former might suggest that the group of *Pagurus* n. sp., *P. pitagsaleei*, (and *P. boriaustraliensis*) is indeed a homogeneous assemblage outside of the *anachoretus* group. However, these results are preliminary, as COI alone may not be sufficient in resolving phylogenetic relationships. More extensive research and molecular work are needed to elucidate the phylogeny within this group of *Pagurus*. Nevertheless, the current morphological observations lead to the speculation that the three species *P. boriaustraliensis*, *Pagurus* n. sp., and *P. pitagsaleei* may be a distinct and homogeneous subgroup.

4.6.2 Three-dimensional visualisations

As one of the most powerful tools for generating 3D illustrations, X-ray μCT is gaining popularity in taxonomy and morphological studies of various invertebrate animal groups, such as planarians (Carbayo et al. 2016), oligochaetes (Fernández et al. 2014), insects (Wipfler et al. 2011, Simonsen and Kitching 2014, Sarnat et al. 2016, Garcia et al. 2017), arachnids (Michalik and Ramírez 2013), myriapods (Stoev et al. 2013, Akkari et al. 2015), and gammarid amphipods (Haug et al. 2011). Amongst others, it has also been applied to marine invertebrates including sponges (Faulwetter et al. 2013a), cnidarians (Holst et al. 2016), polychaetes (Dinley et al. 2010, Faulwetter et al. 2013b, 2014), rhizocephalans (Noever et al. 2016), bivalves (Faulwetter et al. 2013a), ophiuroids (Landschoff and Griffiths 2015, MacKinnon et al. 2017), and echinoids (Ziegler 2012). In higher taxa of Crustacea, the technique has been used to study sexual reproductive organs or internal anatomy (Gardner et al. 1998, Hayer et al. 2016, Köhnk et al. 2017), such as the lung complexity of terrestrial fiddler crabs (Paoli et al. 2015), or the vascular system and inner anatomy in Anomura (Keiler et al. 2013, 2015, 2016). The latter, for example, brought new insights into the evolution of the hermit crab-derived king crabs. Nevertheless, μCT has not seen many applications in taxonomy of higher crustaceans, although (Landschoff and Lemaitre 2017b) and (Landschoff and Rahayu in press, Chapter 3) included single μCT images or videos of calcified characters to inform the species description of paguroids. In contrast, the present description of *Pagurus* n. sp. is the first to use a larger set of characters illustrated by μCT scan reconstructions, including an interactive PDF of the calcified structures of the holotype (Figure 4.1), a video of a female paratype as a whole (Video 4.1), high-resolution images and videos of the holotypic chelipeds (Figures 4.5 B–D, 4.5, Videos 4.2–4.3), as well as still images of 3D reconstructions of the pereopods overlaid by manually-drawn setation and corneous spinules (Figure 4.6). However, with the difficulties that emanate from soft tissue visualisations, at present μCT scans of hermit crabs do not provide the same information as the physical material. For this reason, the provided scans also do not qualify as 'cybertypes' as hypothetically defined by Faulwetter et al. (2013b). Neither does the International Code of Zoological Nomenclature (ICZN) depict the concept of cybertypes. Therefore, for the species description of *Pagurus* n. sp., and until virtual specimen data are better classified, the μCT data are inexplicitly referred to as '3D virtual type data'.

This present study introduces a holistic species description of a pagurid hermit crab, linking classical taxonomic practices with DNA molecular barcodes, as well as μCT data that are publicly available for download. Moreover and for the first time, μCT 3D images are combined with line drawings to show high-resolution surface structures in parallel with fine characters and setation. In their recent description of a millipede species that was for the first time accompanied by the deposition of cybertypes as virtual figures, Akkari et al. (2015) noted both how taxonomic science has progressed into a modern era, and how cybertypes will facilitate the spirit of data sharing. While this current description of *Pagurus* n. sp. certainly falls into the same category of advancing modern taxonomy, the definition and therefore the application of cybertypes for μCT scanning in taxonomy, however, and particularly for the group of hermit crabs, has to be explored further.

CHAPTER 5

CROSSING THE INDIAN OCEAN: A RANGE EXTENSION FOR *Goreopagurus poorei* LEMAITRE AND MCLAUGHLIN, 2003 (CRUSTACEA: DECAPODA: PAGURIDAE)

5.1 Abstract

Goreopagurus poorei Lemaitre and McLaughlin, 2003, a hermit crab of the family Paguridae previously known only from off eastern Tasmania in the Tasman Sea, has been discovered in the western Indian Ocean off the coast of South Africa, extending considerably the range of this species by 10,100 km to the west. While this finding represents a large range extension, similar wide ranges are frequent and well known in other deep-water decapods including paguroids. Colour information and minor morphological variations are presented to complement the morphological information provided in the original description. References to genetic sequence data are also provided for future use in phylogenetic and biogeographic studies.

5.2 Introduction

The four species currently in the genus *Goreopagurus* McLaughlin, 1988a, stand out by the unusually large and sexually dimorphic right cheliped. The morphology of the carpus in particular, is quite striking in having an unusually expanded ventral portion and a flared dorsomesial margin armed with spines, both features being much more pronounced in males than in females. Among other diagnostic characters, the females of species of *Goreopagurus* have well developed, paired first pleopods modified as gonopods, whereas males may or may not have paired short sexual tubes emanating from the gonopores on the coxae of the fifth pereopods. The genus was established by McLaughlin (1988a) for *Pagurus piercei* Wass, 1963, a western Atlantic species now known to range in the Gulf of Mexico and southeastern coast of the United States (Felder et al. 2009). Subsequently, two more species were described from the coast of the Americas: *G. garthi* McLaughlin and Haig, 1995, from the eastern Pacific, off Baja California; and *G. lemaitrei* Nucci and de Melo, 2007, from the southwestern Atlantic, off Fortaleza, Brazil. A fourth species of this genus, *G. poorei* Lemaitre and McLaughlin, 2003, was surprisingly discovered in the western Pacific, off the coast of eastern Tasmania, considerably expanding the distribution of *Goreopagurus*.

Herein we report the presence of *Goreopagurus poorei* on the western side of the Indian Ocean, off the coast of South Africa, based on specimens collected during studies sponsored by the South African Department of Agriculture, Forestry and Fisheries (DAFF) and the Department of Environmental Affairs (DEA). During the spring 2015 DAFF demersal research survey a single specimen was collected from a trawl on board the R. V. *Africana*. At the same time numerous specimens were dredged on board the R. V. *Algoa* during the 2016 Deep Secrets Cruise, a collaborative project enabled through the African Coelacanth Ecosystem Programme (ACEP). All specimens were collected along the edge of the Agulhas Shelf, from south of the Cape Agulhas to off the coast of Jeffreys Bay. The discovery of *G. poorei* in South African waters represents a large and significant range extension for this species. Furthermore, the colour photographs obtained of live specimens provide the opportunity to describe complete and accurate information on the colouration of *G. poorei*. Some morphological variations observed in the South African specimens are also described. Genetic data has been obtained as part of the South African SeaKeys project and is reported, in order to make it available for subsequent studies of phylogenetic relationships or genetic exchange among populations across the wide range of distribution of *G. poorei*.

Taxonomic knowledge of the Paguroidea (*sensu* McLaughlin et al. 2007a) from South Africa remains inadequate. A summary of the history of decapod collecting and research from the 19th to the late 20th century was provided by Kensley (1981), and to recent times by Emmerson (2016a). The most prominent earlier attempts at comprehensive treatments of the South African paguroid fauna are in the catalogues by Stebbing (1910) on the Crustacea, and Barnard (1950) on the Decapoda, although hermit crab classification and nomenclature used in both these works is now severely out-dated. Forest (1954) included specimens from the South African coast in his detailed report on the species of the diogenid genus *Paguristes* Dana, 1851, and remarked on the scarcity of samples and poor knowledge of the hermit crabs from this region. Kensley (1969) provided taxonomic information on a few hermit crab species from the South African region, although subsequently in his study on the zoogeography of decapods from the region, he (Kensley 1981) presented a long list of hermit crab species. Recently, Emmerson (2016a,b,c) published a multivolume guide to the decapods from South Africa and Mozambique, in which 70 paguroid species are included, but not confined to South African territories. Among the diverse family Paguridae, a number of species from South Africa have been discussed in various taxonomic studies: McLaughlin and Haig (1989) re-examined the only known South African specimen of *Pylopaguropsis zebra* (Henderson, 1893); García-Gomez (1994) redescribed the South African endemic *Anapagurus hendersoni* Barnard, 1947; Lemaitre and McLaughlin (1996) discussed the type specimens from South Africa of *Manucomplanus ungulatus* (Studer, 1883); McLaughlin (1998) described three new species of *Nematopagurus* that occur in South Africa, *N. crosnieri, N. kosiensis*, and *N. meringae*; and McLaughlin and Forest (1999) revised six species of Pagurus from South African waters, and redescribed *Propagugurus deprofundis* (Stebbing, 1924). Despite all these studies, however, the fact remains that the South African hermit crab fauna remains woefully understudied and undersampled, with many species still known based on a few specimens. Recent sampling efforts and ongoing studies of paguroid specimens collected in shallow to moderately deep waters, are revealing many previously unreported or undescribed species from the South African coast (J. Landschoff and R. Lemaitre, pers. obs.). As surmised by Griffiths et al. (2010), many discoveries are still to be made in the marine invertebrate communities of South Africa, particularly in deep sea habitats that are notoriously under-sampled.

Specimens used in this report are deposited in the Iziko South African Museum, Cape Town (SAMC), South Africa, with duplicates at the United States National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM). Morphological terminology follows Lemaitre and McLaughlin (2003). Measurements in mm of specimens listed in the material examined sections are for shield length (SL), taken from the tip of the rostrum to the midpoint of the posterior margin of the shield. Station coordinates are given using the Degrees Decimal Minutes system.

5.3 Systematic account

5.3.1 Family Paguridae Latreille, 1802

5.3.1.1 Genus *Goreopagurus* McLaughlin, 1988a

***Goreopagurus poorei* Lemaitre and McLaughlin, 2003**

Figures 5.1–5.4

Goreopagurus poorei Lemaitre and McLaughlin, 2003: 222, Figs 1–3. – McLaughlin et al., 2010: 29.

New material. Agulhas Shelf. South Coast Survey spring 2016, AFR289: 1 ♂ 4.5 mm, sta A32823-076, S 35° 14.94', E 22° 50.82', 520 m, 5 Oct 2016 (USNM 1292090). Deep Secrets Cruise, ALG230: 1 ♂ 3.9 mm, sta DSC027 DSCS-INV-422, S 34° 43.74', E 25° 09.06', 622 m, 15 Oct 2016 (USNM 1292091); 1 ♀ 3.7 mm (USNM 1292088), 1 ♀ 4.5 mm (USNM 1292089), sta DSC006 DSCS-INV-154, S 36° 45.54', E 21° 12.72', 516 m, 1 Oct 2016; 1 ♀ 2.8 mm (damaged), sta DSC012 DSCS-INV-280, S 35° 07.20', E 23° 02.76', 334 m, 6 Oct 2016 (USNM 1292093); 1 ♀ 5.7 mm (USNM 1292087), 1 ♀ 4.0 mm (SAMC MB-A066772), sta DSC003 DSCS-INV-97, S 36° 01.92', E 19° 42.24', 463 m, 30 Sep 2016; 2 ♂♂ 4.1–4.7 mm (SAMC MB-A066784), sta DSC003 DSCS-INV-98, S 36° 01.92', E 19° 42.24', 463 m, 30 Sep 2016; 1 ♂ 3.5 mm, 2 ovig. ♀♀ 2.6–3.1 mm (USNM 1292092), 2 ovig. ♀♀ 2.6–2.9 mm (SAMC MB-A066771), sta DSC057 DSCS-INV-568, S 34° 47.10', E 24° 45.60', 388 m, 22 Oct 2016.

Description. See Lemaitre and McLaughlin (2003).

Colouration (in life; Figure 5.1). General background orange. Shield light orange fading to white

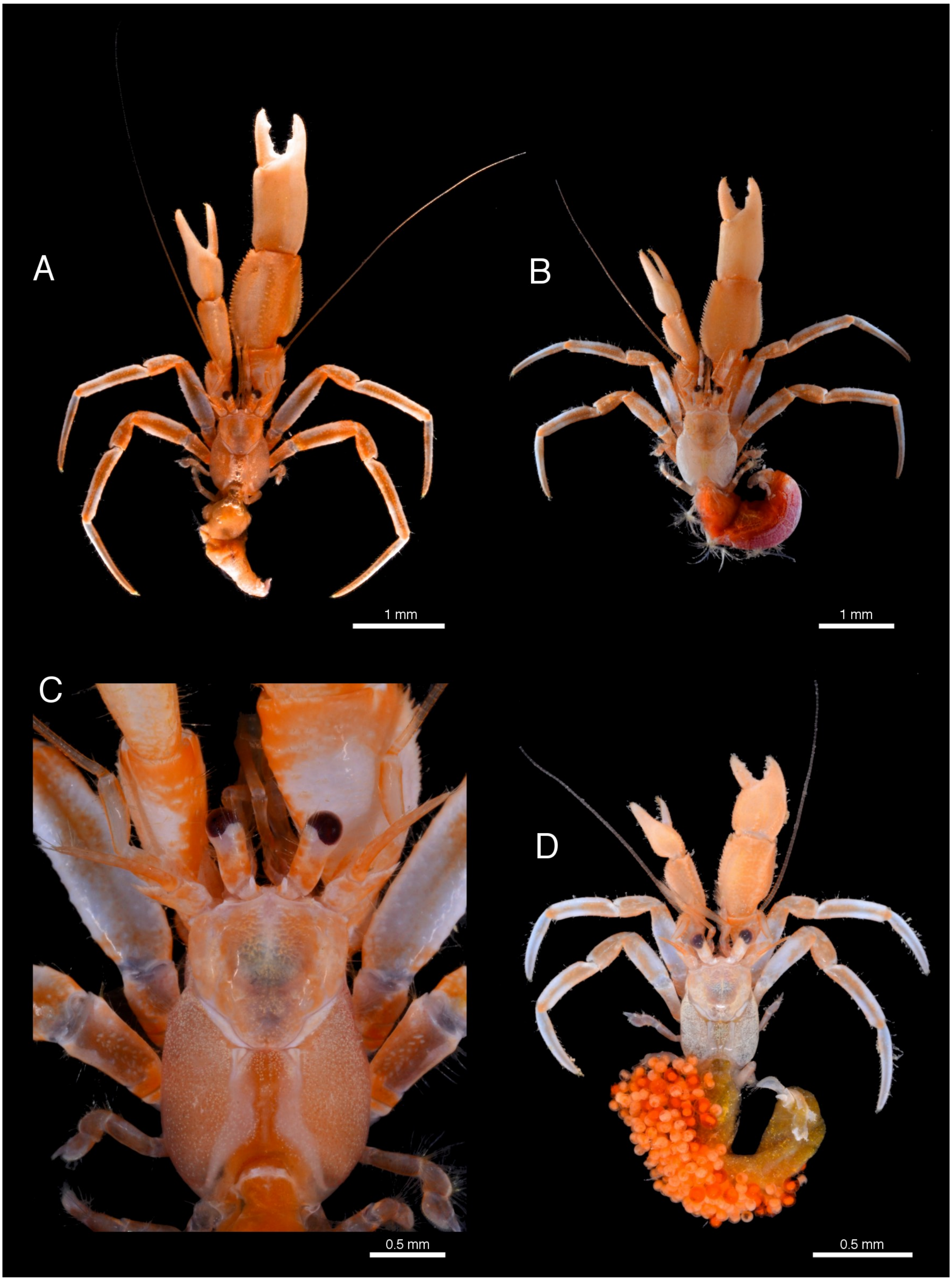

Figure 5.1: *Goreopagurus poorei* Lemaitre and McLaughlin, 2003, Agulhas Shelf, fresh specimens after capture, dorsal view: A ♂ 4.5 mm, South Coast Survey spring 2016, sta A32823-076 (USNM 1292090) **B** ♀ 5.7 mm, Deep Secrets Cruise, ALG230, sta DSC003 DSCS-INV-98 (USNM 1292087) **C** same ♂ as A, shield and cephalic appendages, and posterior carapace **D** ovig. ♀ 3.1 mm, Deep Secrets Cruise, ALG230, sta DSC057 DSCS-INV-568 (USNM 1292092).

medially and near rostrum, anterior and anterolateral margins. Carapace with lateral lobes adjacent to posterolateral margins white. Posterior carapace with branchiostegites orange with numerous minute white punctae; posteromedian plate orange; posterolateral plates white. Ocular acicles white with small orange portion basally on mesial side. Ocular peduncles mottled orange and white on proximal half, distal half mostly white distally except for two orange patches mesially. Chelipeds mostly orange on dorsal, lateral and mesial surfaces, and much lighter orange tone on chela and even lighter on fingers; ventral surfaces nearly white; carpus with light orange tone dorsomedially; merus dorsal surface, lateral and mesial surfaces light orange to white medially, and darker orange distally and proximally. Ambulatory legs each with dactyl white dorsally and light orange ventrally; propodus with weakly defined orange stripe on lateral and mesial faces, otherwise white dorsally and ventrally; carpus mostly orange with undefined white areas dorsally; merus with weakly defined orange stripe on lateral and mesial faces, orange all around distally and mesially, otherwise white dorsally and ventrally; ischium orange.

Distribution. From off eastern Tasmania, Australia, in the western Tasman Sea, and the Agulhas Shelf, off South Africa (see Figure 5.4 for South African distribution, depth range 334–1,300 m.

Genetic data. Sta DSC006 DSCS-INV-154, S 36° 45.54', E 21° 12.72', 516 m, ♀ 3.7 mm, BOLD: SEAKY1190-17 (USNM 1292088), ♀ 4.5 mm, BOLD: SEAKY1189-17 (USNM 1292089). Sta A32823-076, S 35° 14.94', E 22° 50.82', 520 m, ♂ 4.5 mm, BOLD: SEAKY1187-17 (USNM 1292090). Sta DSC027 DSCS-INV-422, S 34° 43.74', E 25° 09.06', 622 m, ♂ 3.9 mm, BOLD: SEAKY1188-17 (USNM 1202091). Sta DSC012 DSCS-INV-280, S 35° 07.20', E 23° 02.76', 334 m, ♀ 2.8 mm, BOLD: SEAKY1191-17 (USNM 1292093).

5.4 Taxonomic remarks

Goreopagurus poorei had not been reported since its original description by Lemaitre and McLaughlin (2003), which was based exclusively on specimens collected off the Freycinet Peninsula and seamounts of the Southeast Cape, eastern Tasmania. Thus, the presence of this species in South African waters represents a huge range extension to the west and across the Indian Ocean, of approximately 10,100 km (5,400 nautical miles). The specimens in the original description were collected at a depth range of 500–1,300 m, whereas the new specimens herein reported from South Africa were collected at a shallower depth range of 334–622 m. The broad distribution of this species across such an immense expanse of oceans, covering from the western Indian Ocean to the Tasman Sea in the western Pacific, might appear to be unusual. However, a good number of deep-water paguroids, such as various species in genera of the families Paguridae and Parapaguridae that live at similar depth ranges along the continental slopes, are known to also have the same or even wider distributions in the Indo-West Pacific region (e. g., McLaughlin 1997, 2002, 2004, Lemaitre 1999, 2004a,c, 2013, 2014). Moreover, parallel distribution patterns from southern Australia to southeastern Africa were recently recorded for the caridean shrimp *Leontocaris bulga* Taylor and Poore, 1998, and the squat lobster *Munidopsis pyrochela* Ahyong, 2014. Whether or not *G. poorei* will be found between Tasmania and South Africa, across

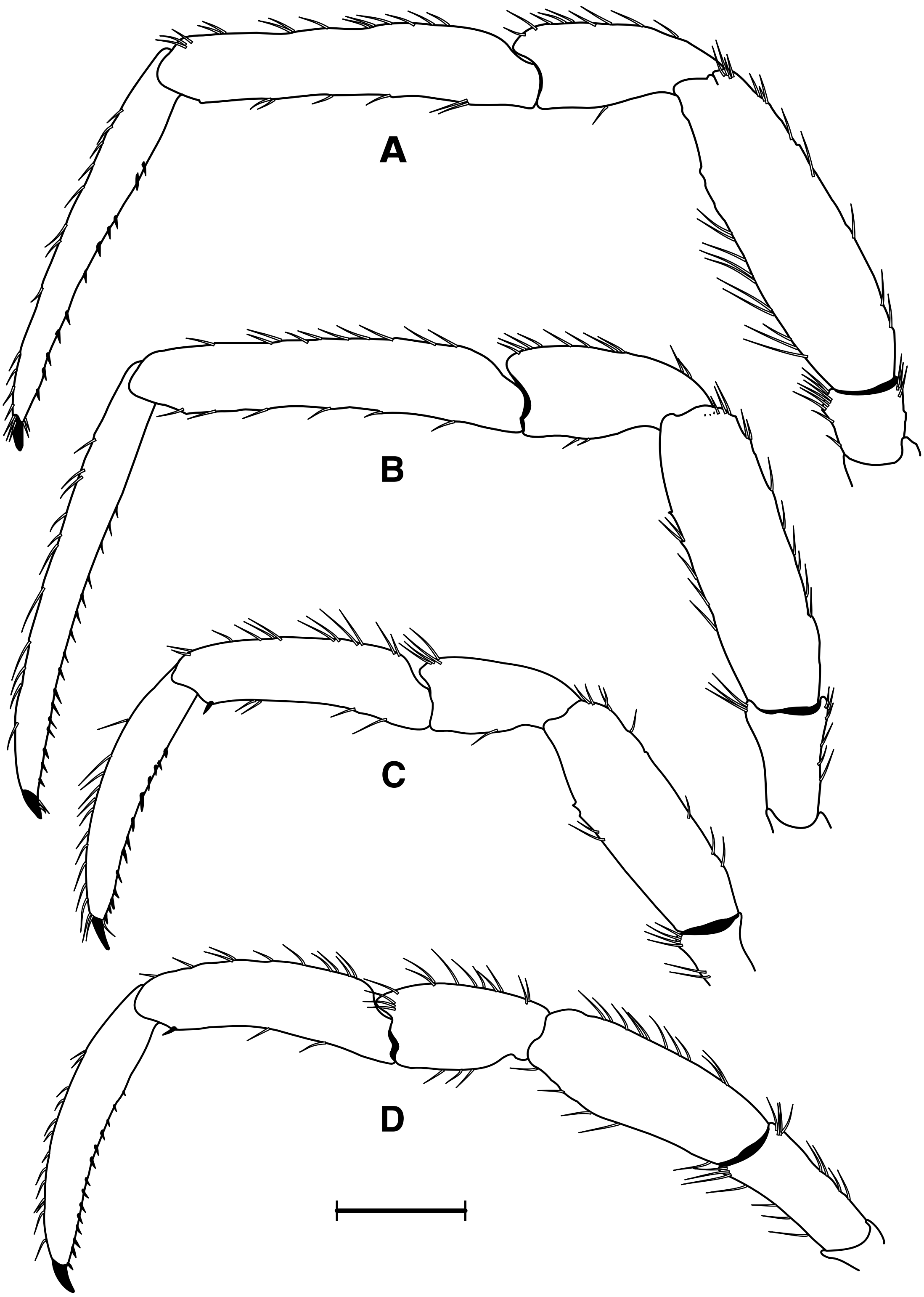

Figure 5.2: ***Goreopagurus poorei*** **Lemaitre and McLaughlin, 2003, left ambulatory legs (pereopods 2 and 3), lateral view: A–B** ♂ 4.5 mm, South Coast Survey spring 2016, sta A32823-076 (USNM 1292090) **C–D**, ♀ 2.8 mm, Deep Secrets Cruise, ALG230, sta DSC012 DSCS-INV-280 (USNM 1292093). **A, C** pereopod 2 **B, D** pereopod 3. Scale = 2 mm (A, B), and 1 mm (C, D).

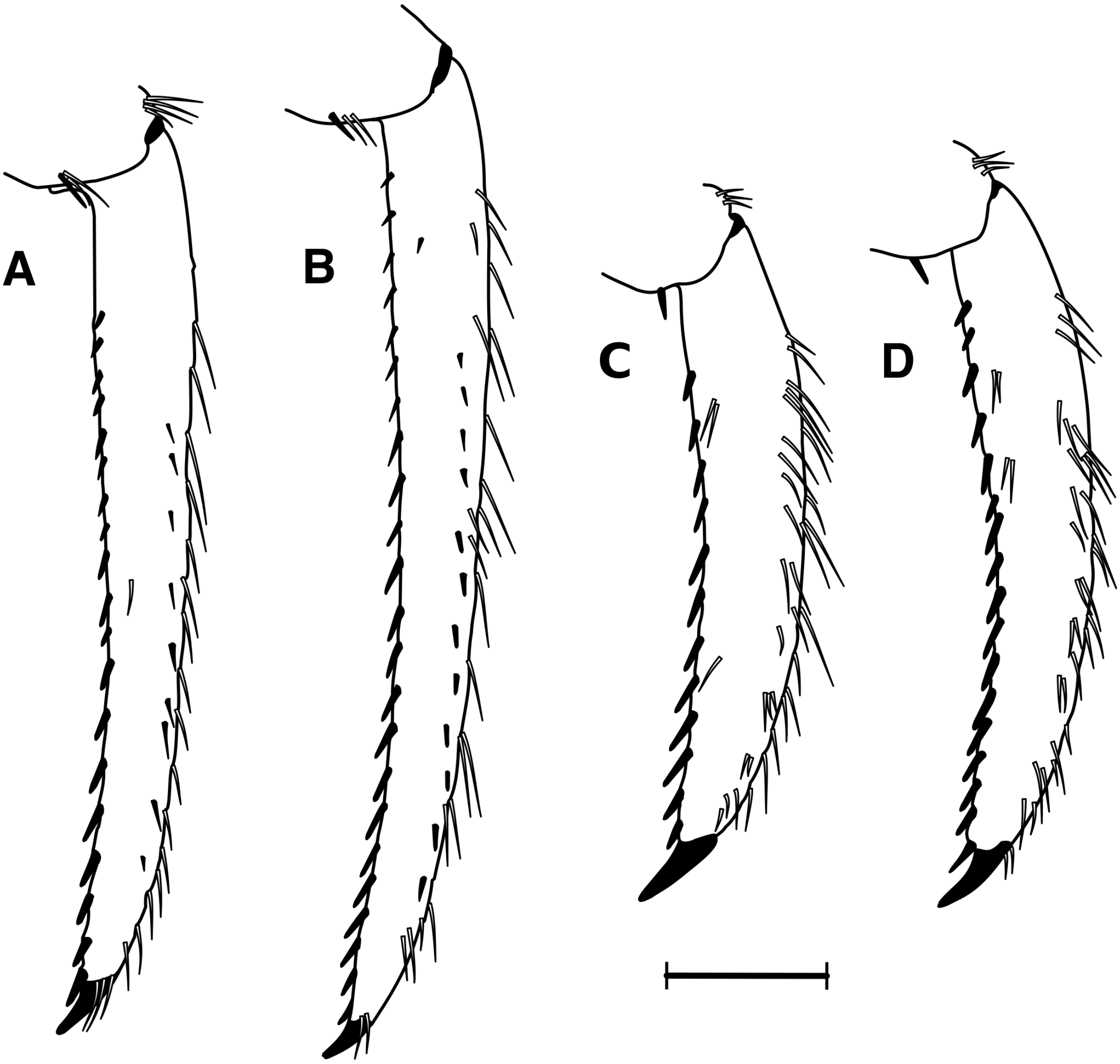

Figure 5.3: *Goreopagurus poorei* Lemaitre and McLaughlin, 2003, dactyls of left ambulatory legs (pereopods 2 and 3), mesial view: A–B ♂ 4.5 mm, South Coast Survey spring 2016, sta A32823-076 (USNM 1292090) **C–D** ♀ 2.8 mm, Deep Secrets Cruise, ALG230, sta DSC012 DSCS-INV-280 (USNM 1292093). **A, C** pereopod 2 **B, D** pereopod 3. Scale = 1 mm.

the vast Indian Ocean, can only be determined by more sampling of the varied deep-water habitats that exist in this oceanic region.

Morphological variations of species of *Goreopagurus* have been sufficiently documented in each of the original descriptions of the four species currently known of this genus (McLaughlin 1988a, McLaughlin and Haig 1995, Lemaitre and McLaughlin 2003, Nucci and de Melo 2007). Variations are particularly visible on the expansion of the carpus and length of the chela of right cheliped, which in some species can be attributable to sexual dimorphism (*G. piercei*, *G. garthi*) or allometric growth (*G. poorei*). In the specimens herein reported from South Africa of *G. poorei*, variations in the ambulatory legs (pereopods 2 and 3) were noted related to sex that do not occur

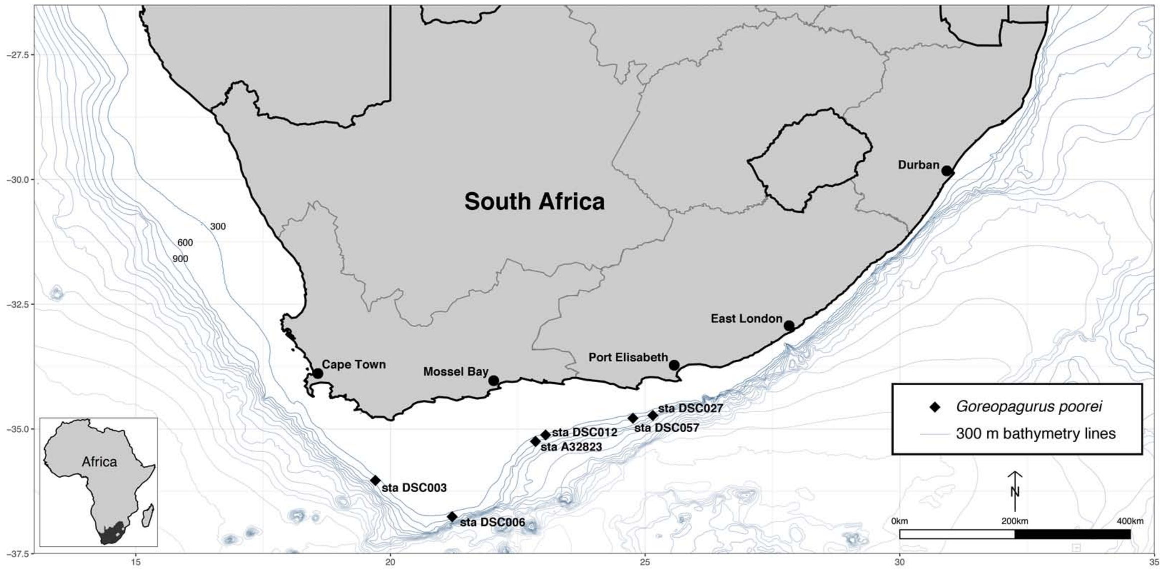

Figure 5.4: Distribution of *Goreopagurus poorei* Lemaitre and McLaughlin, 2003, along the edge of Agulhas Shelf, South Africa.

in other congeners or at least have not been discussed in the descriptions of species of *Goreopagurus*. In *G. poorei*, males tend to develop distinctly more slender ambulatory legs and longer dactyls than females (Figures 5.1–5.2), and some females can have distinctly stout segments on the ambulatory legs (Figure 5.2). The dactyls in males can be up to nine times as long as wide, whereas in females the dactyls can be short and wide, only about six times as long as wide.

The only appreciable morphological difference between the South African specimens of *G. poorei* and those from Tasmania used in the original description by Lemaitre and McLaughlin (2003), is in the armature of the dactyls of the ambulatory legs. The dactyls were described by Lemaitre and McLaughlin (2003) as having ventral margins armed with a range of 10–13 corneous spines, whereas the South African specimens reported herein have a range of 12–23 corneous spines. In addition, the preungual process on the dactyl of pereopod 4 is in some specimens obsolete.

The finding in South African waters of numerous specimens of *Goreopagurus poorei* during South African research surveys, suggests that this species is not rare. Individuals can grow to a relatively large size, and it is probably quite abundant. Thus, it seems this species has simply remained overlooked despite the various taxonomic studies and voluminous reports and catalogues on South African decapods spanning 100 years (Stebbing 1910, Barnard 1950, Kensley 1969, Emmerson 2016a,b,c). This discovery also clearly suggests that, like other invertebrates, the paguroid fauna from South Africa is understudied and requires attention.

CHAPTER 6

A MICRO X-RAY COMPUTED TOMOGRAPHY DATASET OF SOUTH AFRICAN HERMIT CRABS (CRUSTACEA: DECAPODA: PAGUROIDEA), CONTAINING SCANS OF TWO RARE SPECIMENS AND THREE RECENTLY-DESCRIBED SPECIES

6.1 Abstract

Background. Along with the conventional deposition of physical types at natural history museums, the deposition of three-dimensional (3D) image data has been proposed for rare and valuable museum specimens, such as irreplaceable type material.

Findings. Micro computed tomography (μCT) scan data of five hermit crab species from South Africa, including rare specimens and type material, depicted main identification characters of calcified body parts. However, low image contrasts, especially in larger (>50 mm total length) specimens did not allow sufficient 3D reconstructions of weakly-calcified or fine characters, such as soft tissue of the pleon, mouthparts, gills, or of the setation. Reconstructions of soft tissue were sometimes possible, depending on individual sample and scanning characteristics. The raw data of seven scans are publicly available for download from the GigaScience Database repository.

Conclusions. Calcified body parts visualised from μCT data can aid taxonomic validation and provide additional, virtual deposition of rare specimens. Using a non-destructive, non-staining μCT approach for taxonomy, reconstructions of soft tissue structures, microscopic spines and of setae depend on species characteristics. Constrained to these limitations, the presented dataset can be used for future morphological studies. However, virtual specimens will be most valuable to taxonomists who can download a digital avatar for 3D examination. Simultaneously, in the possible event of physical damage to, or loss of, the original physical specimen, this dataset serves as a vital insurance policy.

6.2 Motivation and background

X-ray micro computed tomography (μCT) is an emerging tool in taxonomy (Faulwetter et al. 2014). Besides being one of the most powerful methods to produce multidimensional scientific images, another benefit is the creation of a three-dimensional (3D) volumetric dataset, which not only acts as a virtual duplication of the physical museum types, but can much more easily be digitally stored and distributed. Such a dataset could act also as 'cybertype' (Faulwetter et al. 2013b), even if this terminology and definition remains to be defined for taxonomy. However, the increasing availability of μCT facilities, computing power, and online data repositories, is stimulating the use of 'virtual types', including cybertypes (Akkari et al. 2015, Garcia et al. 2017).

With about 1,200 species worldwide (McLaughlin and Türkay 2017), paguroid hermit crabs form the largest group of anomuran decapod crustaceans (McLaughlin et al. 2010). Hermit crabs mostly inhabit empty gastropod shells and their overall body plan has become modified to suit this specialised habitat. Body proportions have had to remain within certain dimensional limitations, while the pleon and most of the carapace have evolved to be soft, flexible and generally dextrally coiled such that they can be retracted into the spiral of the shell. Having a conservative and generally similar body plan, as well as having half the body parts membranous and for the most lacking identification characters, hermit crabs often remain taxonomically poorly understood. Correct identifications require careful examinations, and depend heavily on the quality of the original species descriptions and illustrations. Until now, when literature-based descriptions have proven inadequate, the only option has been to loan and examine physical museum material. However, loaning such material from globally-spread natural history museums is not only costly, but also a time-consuming undertaking. Permission to loan material may also be refused, especially where type specimens are involved.

The dataset presented in this study was primarily created to visually support descriptive taxonomic studies of hermit crabs (Landschoff and Lemaitre 2017b, Chapters 3 and 4), but the 3D raw data that are publicly made available here, can also be used for morphological comparisons, including species validations, without examining the physical specimen. To our knowledge, this is the first publicly-available 3D μCT dataset of hermit crabs and also of decapod crustaceans. It includes scans of the types of three recently described species and two scans of rare species, one of which is from a deep sea habitat at >500 m depths. While the inspection of virtual representations of a specimen does not entirely replace the examination of a physical sample, the dataset presented here will serve as an extra taxonomic tool that may be sufficient to confirm species identification and that can be consulted before the physical material has to be sourced from natural history collections. Through making this μCT dataset publicly available, taxonomists are potentially provided with more time and cost efficient options for specimen examination and character comparisons.

6.3 Sampling and specimens scanned

Scans of seven specimens of five species, belonging to three families of hermit crabs (Paguroidea *sensu* McLaughlin et al. 2007a) are presented: *Diogenes* n. sp. and *Cancellus macrothrix* Stebbing, 1924 (family Diogenidae), *Pagurus* n. sp. and *Goreopagurus poorei* Lemaitre and McLaughlin, 2003 (family Paguridae), as well as *Paragiopagurus atkinsonae* Landschoff and Lemaitre, 2017b (family Parapaguridae). All specimens were collected in South Africa during various sampling operations and physical specimens used in this study are deposited at the Iziko South African Museum, Cape Town (SAMC) and at the United States National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM). Detailed specimen information can be found in Table 6.1, where the standard size measurement for hermit crabs is given as shield length (SL), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield in millimetres. To give a better understanding of the overall size dimensions, 'total length' as given in the text refers to the length of a specimen when it is stretched out and measured from the distal-most tip of the respectively longer cheliped to the outer edge of the curvature of the pleon.

Specimens of *Diogenes* n. sp. and *Pagurus* n. sp. were collected on 14–15 October 2015 during Scuba dives at 20 m depth off Pumula (S 30° 38.34', E 30° 32.94') and Hibberdene (S 30° 34.92', E 30° 34.86'), respectively, on the southern coast of KwaZulu-Natal. Both these species are small reef inhabitants with a total length of about 20 mm. All samples were preserved in 96% ethanol. Although in good condition, the left cheliped of the male holotype of *Pagurus* n. sp. has broken off, but is still present in the sample. The specimen of *C. macrothrix* was collected on 13 May 2015 during a 20 m Scuba dive near Roman Rock in False Bay (S 34° 11.16', E 18° 25.63), and also preserved in 96% ethanol. The specimen is unusual in that it has both male and female gonopores on the coxae of the third and fifth pereopods. Due to previous tissue extraction for DNA barcoding the scan is missing the five distal-most segments of the second left pereopod, but the three distal-most segments are still present in the physical sample. Specimens of *G. poorei* and of *P. atkinsonae* were collected during research cruises conducted by the South African Department of Agriculture, Forestry and Fisheries (DAFF), where they were frozen onboard. The specimen of *G. poorei* was trawled on 15 October 2016 from 520 m at the shelf edge of the Agulhas Bank on the South coast (S 35° 14.94', E 22° 50.82'). This sampling event constituted the first record of *G. poorei* in South Africa and represents a remarkable range extension, as this species had previously been recorded only from Tasmania (see Chapter 5, Landschoff and Lemaitre 2017a). *Paragiopagurus atkinsonae* were trawled on 11 March 2016 from two nearby sampling stations on the West Coast (♂ holotype from 265 m, S 31° 52.80', E 16° 57.12', ♀ paratype from 199 m, S 32° 22.98', E 17° 27.78'). The female paratype was left in its original shell, which is a carcinoecium created by a mutualistic species of zoanthid (probably *Epizoanthus* spp.). *Cancellus macrothrix*, *P. atkinsonae* and *G. poorei*, are all medium-sized hermit crabs of about 50–70 mm total length.

Table 6.1: Scanning details of micro computed tomography dataset of South African hermit crabs.

Species	**Museum ID**	**Sex & Size (Shield Length)**	**Preservative, scanning medium**	**Isotropic voxel size (μm)**	**Voltage (kV) / current (μA) / filter**	**name of scan**
***Diogenes* n. sp.**	SAMC MB-A066353 (holotype)	ovig. ♀ (2.0 mm)	96% EtOH, wrapped in parafilm	6	100 / 240 / none	Diogenes_f_holotype
***Pagurus* n. sp.**	SAMC MB-A066790 (holotype)	♂ (2.7 mm)	96% EtOH, in solution	11	60 / 310 / none	Pagurus_ m_holotype
				4.5	60 / 310 / none	Pagurus_m_holotype
	SAMC MB-A066770 (paratype)	ovig. ♀ (2.4 mm)	96% EtOH, wrapped in parafilm	5	60 / 240 / none	Pagurus_f_paratype
Paragiopagurus atkinsonae	USNM 1292083 (holotype)	♂ (7.0 mm)	fresh, in air	20	100 / 100 / none	Paragiopagurus_atkinsonae_ m_ holotype
	SAMC MB-A066812 (paratype)	♀ (7.3 mm, in zoanthid shell)	fresh, in air	20	120 / 240 / 0.1 mm Cu	Paragiopagurus_atkinsonae_ f_ paratype
Cancellus macrothrix	SAMC MB-A066204	♂/♀ (9.0 mm)	96% EtOH, in solution	20.4	100 / 100 / none	Cancellus_macrothrix
Goreopagurus poorei	USNM 1292090	♂ (4.5 mm)	fresh, in air	35	100 / 100 / none	Goreopagurus_poorei_m

6.4 Scanning and quality control

Using several methods of sample preparation, all specimens were scanned using two systems at the CT Scanner Facility at Stellenbosch University, South Africa (du Plessis et al. 2016). The male holotype of *P. atkinsonae*, as well as the specimen of *G. poorei*, were defrosted, mounted on top of a plastic rod with dense polystyrene foam as a platform, and scanned fresh at 20 μm and 35 μm isotropic voxel resolution, respectively, using a General Electric Phoenix V|Tome|X L240 with NF180 option. The same method was applied to the paratypic female *P. atkinsonae* left in its carcinoecium shell, which was scanned at 20 μm isotropic voxel resolution. However, like in all other remaining scans listed below, this scan was performed using a General Electric Phoenix Nanotom S. For the scans of the holotype of *Pagurus* n. sp. and of *C. macrothrix*, specimens were each placed in a small plastic container filled with ethanol, in which the samples were supported by dense polystyrene foam. The containers were then mounted on a plastic rod using double-sided tape and placed in the scanner whole. *Cancellus macrothrix* was scanned at 20.4 μm isotropic voxel resolution, whereas the holotype of *Pagurus* n. sp. was scanned in two parts. Because the left cheliped had broken off during previous handling of the sample, the whole animal was scanned at 11 μm isotropic voxel resolution, while the individual scan of the left cheliped allowed for an isotropic voxel resolution of 4.5 μm, which resulted in the highest resolution scan of this dataset. As a last and slightly different method, the ovigerous female holotype of *Diogenes* n. sp. and the ovigerous female paratype of *Pagurus* n. sp. were taken out of ethanol, wrapped in parafilm (Bemis NA, Neenah, WI, United States), and again mounted on rigid foam, which itself was glued to the top of a plastic rod. They were subsequently scanned at 6 μm and 5 μm isotropic voxel resolution, respectively.

Parameter optimisation for all scans performed followed du Plessis et al. (2017), and included settings of X-ray spot sizes to not exceed the selected scan resolution, as well as good X-ray penetration indicated by high transmitted brightness values in the live digital X-ray images.

For the small species' *Diogenes* n. sp. and *Pagurus* n. sp., the scan parameters were set at 60 kV and 240 μA or 310 μA, using no filter. The parameters for the larger specimens of *P. atkinsonae*, *G. poorei*, and *C. macrothrix* were set at 100 kV and 100 μA, and also used no filter for the scans of the hermit crabs only. However, in order to allow for sufficient x-ray penetration through the carcinoecium shell the female paratype of *P. atkinsonae* was scanned at a higher voltage (120 kV) and current (240 μA), using a 0.1 mm copper beam filter to reduce potential beam hardening artefacts. Furthermore, background detector calibrations before each scan, as well as visual inspections of the reconstruction images, ensured high data quality and good image contrast. Image acquisition in all scans was between 333 and 500 ms per image, with average 1 and skip 1, as well as activated detector shift to minimise ring artefacts. Between 1,600 and 3,600 images were recorded in steps during one full sample rotation. Reconstructions of the acquired projection images were computed using the system supplied General Electric Datos software, and were consequently analysed using Volume Graphics VGStudio Max 3.0 (Heidelberg, Germany). One novel aspect of these data is the combination of scans of parts of the holotype of *Pagurus* n. sp., which were aligned and overlaid using the merge volumes function in VGStudio Max. The merged volume can therefore be downloaded as a single combined dataset.

6.5 Data quality and limitations

Scan quality varied, based on the resolution of the scans, size of the specimen scanned, but also on species characteristics and sample preparation. The scans of the larger species of *G. poorei* and *P. atkinsonae* showed major morphological structures, but did not reveal enough resolution to study fine details, such as the setation or corneous spinulation (Figure 6.1 A–D). The reason is that for larger samples a wider field of view invariantly compromises resolution. Hermit crabs are also a challenging taxon to study using μCT scanning, as a vast proportion of the body consists of soft tissue. With the lowest resolution of the presented scans, the data of *G. poorei* were only usable for visualisations of the well-calcified areas of the exoskeleton, for example like the chelipeds (Figure 6.1 A–B). Also, although being a fresh sample and not preserved in ethanol, the left second antenna moved slightly during the scanning process as the sample was drying (Figure 6.1 A). It was found that scanning specimens (particularly larger ones) in an airtight container to prevent them from drying out exacerbated the problem of having to move the sample further away from the X-ray source of the scanner, causing significant loss of resolution. Therefore, and because hermit crabs have many joints and flexible soft parts that are both prone to movements, the better compromise was to keep the scanning time short when the fresh samples were scanned while exposed to air.

The scans of *P. atkinsonae* are of better quality than the one of *G. poorei*: both were scanned with settings to keep the scanning time below 30 min. The quality of the latter allowed the visualisation of some soft tissue, like the pleon (Figure 6.1 C), and even some information on the gills are retrievable from the scan of the female (Figure 6.1 D). Further overcoming the problem of drying samples and sample movements during the scans, scanning the holotype of *Pagurus* n. sp.

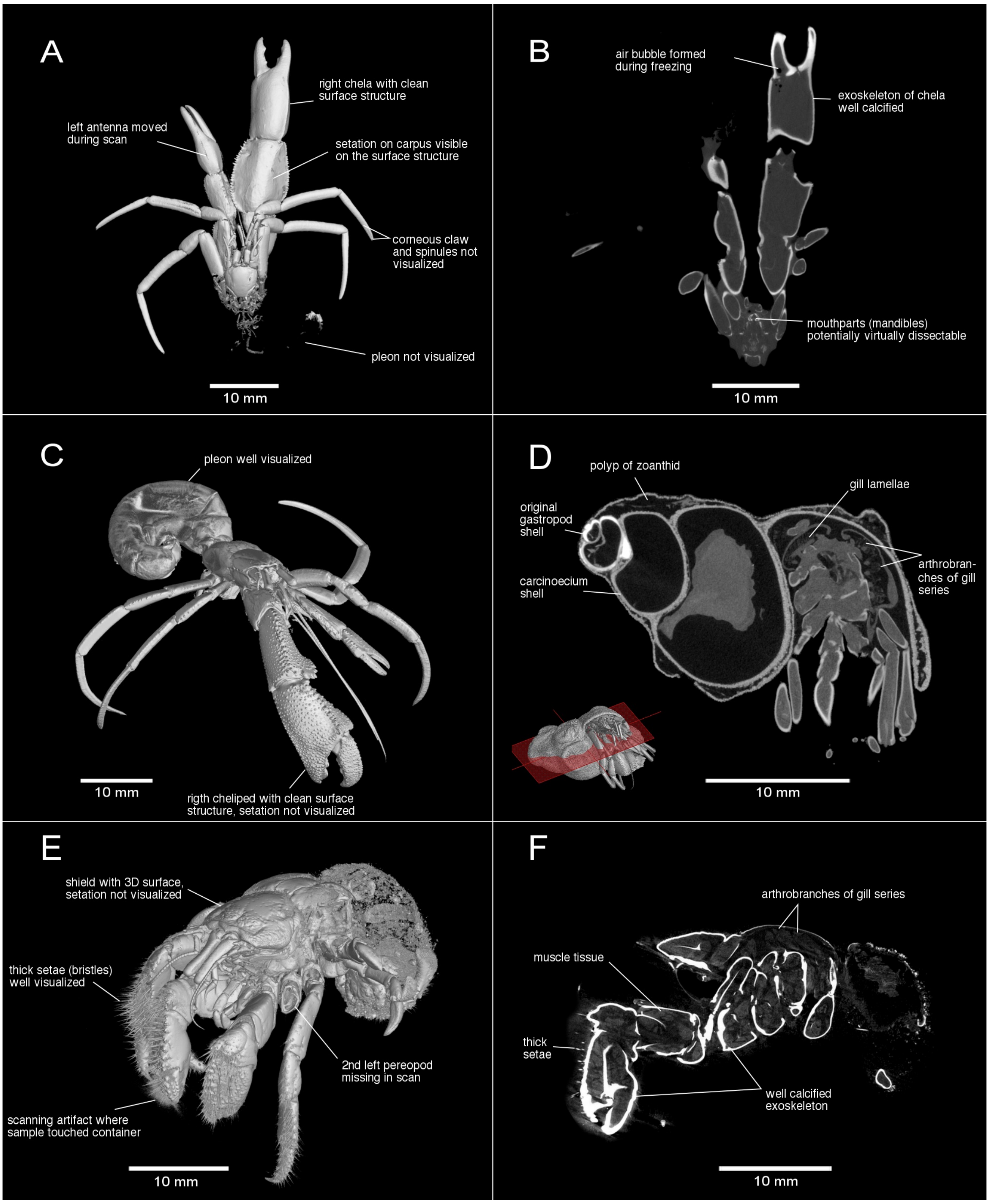

Figure 6.1: MicroCT scanning images (“two-dimensional”, B, D, F) and combination of surface and volume reconstructions (“three-dimensional”, A, C, E) of medium-sized hermit crabs (50–70 mm total length): A–B *Goreopagurus poorei*, ♂ 4.5 mm SL (USNM 1292090) **C** *Paragiopagurus atkinsonae*, ♂ holotype 7.0 mm SL (USNM 1292083) **D** *Paragiopagurus atkinsonae*, ♀ paratype (in carcinoecium shell, SAMC MB-A066812) **E–F** *Cancellus macrothrix*, ♂/♀ 9.0 mm SL (SAMC MB-A066204).

in ethanol resulted in a clean, high-resolution surface scan (Figure 6.2 A). Nevertheless, the decreased density difference between the sample and the surrounding medium hindered detection of fine, soft structures. It particularly ‘removed’ all setation, although some setae are visible in the highest resolution scan of the left cheliped, but only if the brightness contrast threshold in the 3D rendering is set very low. However, it is then almost impossible to separate the sample from ‘noise’ like the mounting material and to get a clean image (Figure 6.2 C).

Mostly because long-term effects on tissue by staining agents remain unknown (Faulwetter et al. 2013b), contrast enhancement techniques were not used in this study for these rare or type specimen scans. Moreover, a test scan using iodine as staining agent did not result in markedly better image contrast on taxonomically important features (scan not included in this dataset). Secondly, after sample preparation and the iodine-staining test scan, it was noticed that the eggs of the stained and scanned ovigerous female started to fall off the pleopods more easily. Although setation was difficult to visualise in the two separate scans of the holotype of *Pagurus* n. sp., particularly the scan of the left cheliped reveals exceptional quality of detail. It is, for example, possible to detect the exact position of each seta as a depression from which each seta arises on the exoskeleton surface (Figure 6.2 D–C). Combined, the two scans of this holotypic specimen show great detail, but predominantly of calcified body parts only. Scanned in the same way while being submerged in ethanol, the scan data of *C. macrothrix* are of high quality as well. In contrast to the in-ethanol-scans of *Pagurus* n. sp., they also reveal a number of details that include soft tissue or fine structures. For example, the very thick setae, as alluded to in the species name of *C. macrothrix*, are easily visible (Figure 6.1 E–F), highlighting that visualisations of soft tissue depend on sample characteristics.

Overall, the two scans (holotype *Diogenes* n. sp. and female paratype *Pagurus* n. sp.), which were performed with the samples wrapped in parafilm, potentially show the most detail of all scans (Figure 6.2 B, E–F). Not being placed in a container, the samples could be mounted extremely close to the X-ray source of the scanner, which markedly improved resolution of the scans. From these two scans it is therefore possible to retrieve information on many soft tissue parts, including the pleon and eggs attached to the pleopods, small corneous spinules, and setation. However, the quality of the data is still not sufficient, for example, to study the taxonomically highly important gills. Furthermore, this sample preparation had a disadvantage in that, wherever parafilm touched the specimen, this created unwanted scanning surface artefacts that are difficult to eliminate in the visualisations. Such scanning artefacts resulting from wrapping material can, for example, be found around the shield of the female *Pagurus* n. sp. (Figure 6.2 B), as well as on the left cheliped of *Diogenes* n. sp. (Figure 6.2 E–F), but also in the scan of *C. macrothrix* scanned in a small container in ethanol (Figure 6.1 E–F). Furthermore, in the scan of *Diogenes* n. sp., the parafilm also increased beam-hardening effects on the edge of the scan and ventrally of the specimen, but these are easily removed in the visualisation software. Lastly, the female paratype of *Pagurus* n. sp. has a slightly broken right cheliped, which might have been damaged

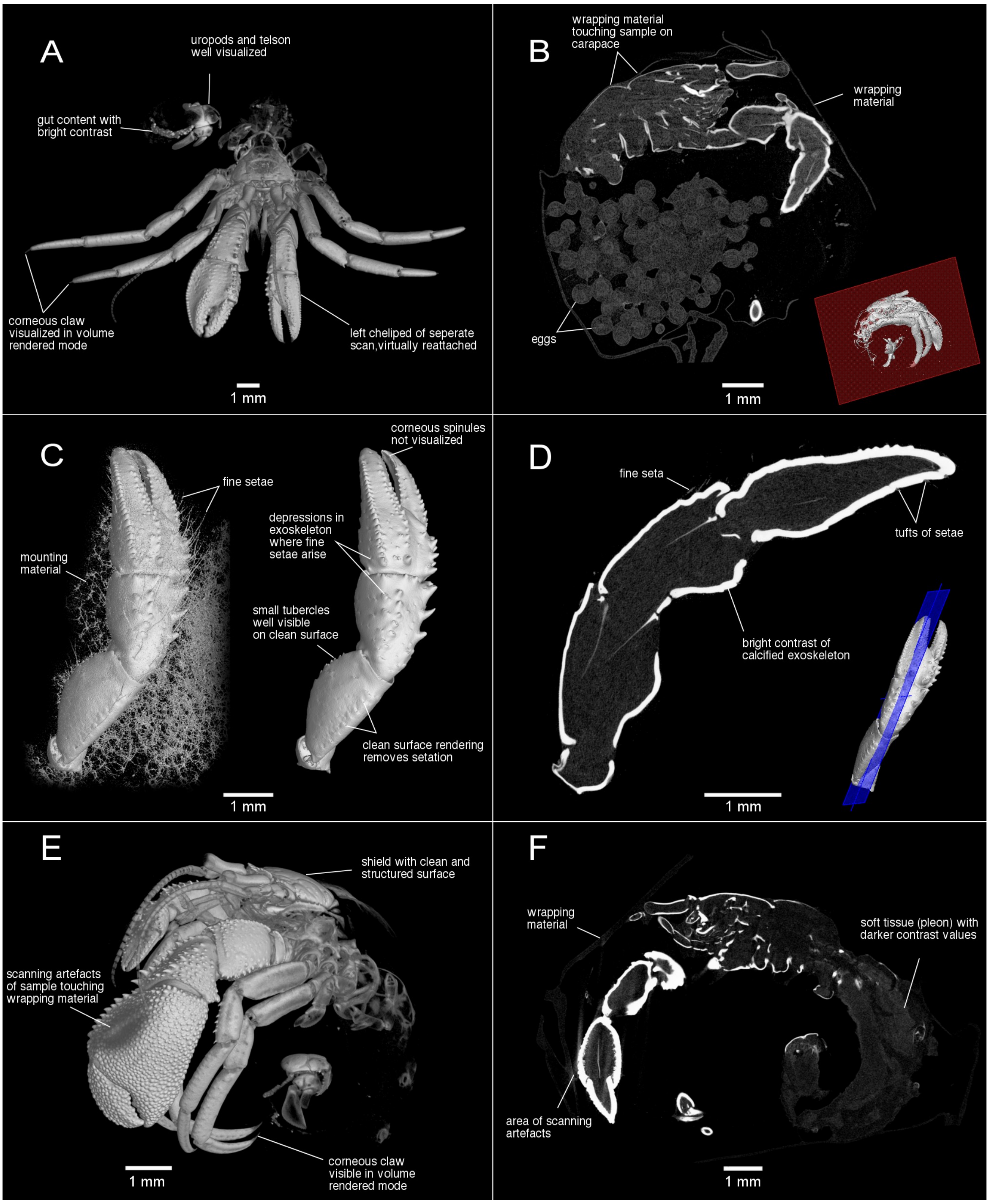

Figure 6.2: MicroCT scanning images ("two-dimensional", B, D, F) and combination of surface and volume reconstructions ("three-dimensional", A, C, E) of small-sized hermit crabs (20 mm total length): A *Pagurus* n. sp., ♂ holotype 2.7 mm SL (SAMC MB-A066790) **B** *Pagurus* n. sp., ovig. ♀ paratype 2.4 mm SL (SAMC MB-A066770) **C–D** left cheliped of same as A **E–F** *Diogenes* n. sp., ovig. ♀ paratype 2.0 mm SL (SAMC MB-A066353).

during collection. The cracks in the exoskeleton of the carpus are visible in the scan (not pictured in the figures), but are not a result of the scanning and are rather derived from the damaged sample. However, all major specimen characters can still be studied in great detail.

In conclusion, the quality of each scan in this dataset varied and is dependent on sample characteristics and scanning protocol. Due to a lower resolution from a wider field of view, the scans of the larger specimens show good surface details of the calcified body parts, but insufficiently depict information on small features. In contrast, the scans of the smaller specimens show better details including some soft tissue, mainly because their small size allowed scanning at a much higher resolution. Protocol optimisation for future studies includes the use of the smallest possible container in which the sample can be placed (in air, but without touching container and mounting material), and which can be mounted as close to the X-ray sources of the scanner as possible. However, in this study, a good compromise was found that secured high scanning quality, while keeping the effort of data collection reasonable.

6.6 Re-use potential

While the presented dataset can be used for morphological studies in general, any such research attempt would lie within the limitation of using information derived from the calcified parts of the specimens. As mentioned above, particularly the scans of the larger specimens of *G. poorei* and *P. atkinsonae* are too low in resolution to include analyses of soft tissue. The female paratype of *P. atkinsonae* is also still located in a carcinoecium shell of an anthozoan species (probably *Epizoanthus* spp.) that would have to be virtually removed prior to analysis. However, the scan can also be used to study the zoanthid shell itself, which remains a poorly known structure. Some soft tissue information will be retrievable from the higher resolution scans of the *Diogenes* n. sp. and *Pagurus* n. sp. specimens that allowed narrow field of view of the scanner, as well as of the medium-sized *C. macrothix*. This dataset was not designed for the analyses of internal anatomy and contains no or little information on internal organs. Instead, the value of the presented scans lies in the potential to download a 3D virtual copy of museum specimens that otherwise would have to be loaned. Shipment of specimens involves significant cost and effort, as well as the potential risk of damage, or even the entire loss of a specimen, while this dataset is freely available for download and can also be examined by an unlimited number of people simultaneously. At the same time, it serves as an insurance policy should the original specimens ever get damaged or lost.

Using this dataset, researchers who want to validate a species and examine the specimens for the comparison to other taxa are provided with a 3D virtual, interactive view that allows deriving character information of some soft tissue and a suite of calcified characters. These are mainly the shield and cephalic appendages, the chelipeds, the pereopods, as well as the uropods and the telson. Experts on hermit crab taxonomy might object to the absence of information on important soft structures, such as the gills. Nevertheless, even if the provided scans do not show all the important characters that are currently used in hermit crab taxonomy, they do show many such characters like the 3D shape of the chelipeds and pereopods, in an exceptional way. Furthermore, the digital third dimension allows for internal character examination, even of type material.

6.7 Availability of supporting data

The presented dataset is deposited in the GigaScience Database repository (Landschoff et al. 2017). In a previously published dataset on brittlestars, which is so far the only other available μCT dataset of South African invertebrates, the full raw data was provided as X-ray projection images from the scanner (Landschoff et al. 2015a,b). It was now realised that users would not use the projections from the scanner and that these data make the dataset unnecessarily large. Therefore, for the dataset here, each scan contains the reconstructed stack slice images both available as 16-bit tiff, and to compress the file sizes further, also as 8-bit jpg stacks. The stack slice images comprise the volume data of the region of interest and can be read by any 3D visualisation software package; slice images can also simply be viewed in any image viewer program. In addition, 3D interactive models are provided and can be viewed online to give the user a quick preview of the content of each scan.

CHAPTER 7

DNA BARCODING AS A TOOL TO FACILITATE HERMIT CRAB TAXONOMY (CRUSTACEA: DECAPODA: PAGUROIDEA)

7.1 Abstract

With the primary aim of creating an efficient identification tool to inform taxonomy, DNA barcoding has become an important component in biodiversity research. However, barcoding is largely ineffective without comprehensive databases that can relate molecular sequences to scientific names. Hermit crabs or paguroids are an important and diverse component of the marine benthos, and are vastly understudied in southern Africa, a poorly sampled, but globally important bioregion with high rates of endemism. As an integrative part of an ongoing morphology-based taxonomic revision of South African hermit crabs, this study provides a total of 194 cytochrome *c* oxidase subunit I (COI) barcode sequences (>550bp) of 43 nominal and 12 putative paguroid species from 20 genera and four families. Preliminary COI-based phylogenetic analyses suggested some overall pattern of monophyly in the Parapaguridae and in the genera *Paguristes* and *Dardanus*. However, large groups in the Diogenidae, such as the genera *Calcinus* and *Diogenes*, were recovered as poly- or paraphyletic. Testing the dataset for barcoding efficacy revealed that, in an integrated taxonomic framework for hermit crabs, the technique reaches barcoding identification rates near 100% success. A barcoding gap was apparent for all but one problematic taxon. The optimum threshold range to discriminate between species for this set of data was calculated at 3.7–3.9%, although the overall mean intraspecific distance was well below 1%. As another practical use of barcoding, glaucothoe larval forms of two deep-water paguroids could be matched to names in the newly available molecular library. However, in three problematic and unresolved species, *Areopaguristes* cf. *jousseaumei*, *Goreopagurus poorei* and *Pagurus cuanensis* the COI marker alone was insufficient to provide clear species identifications, indicating that more taxonomic and molecular work will be needed in these cases. Furthermore and despite the dataset being one of the most comprehensive barcoding libraries of hermit crabs for any bioregion, having considerable species coverage of 55 total taxa, the dataset is estimated to be only about 50% complete in terms of the total South African fauna. Future work should therefore increase the national species coverage, and also expand geographic coverage to outside South African waters for widely distributed species.

7.2 Introduction

Although the usefulness of single-gene DNA-fragments as a tool to aid classical taxonomy has created great controversy (Ebach and Holdrege 2005, Hickerson et al. 2006, Rubinoff 2006, de Carvalho et al. 2007, Roe and Sperling 2007, Ebach 2011), much of the earlier debate was fuelled by the bold promise that sequencing all earth's life forms alone would be sufficient to decipher the many complex problems taxonomists are confronted with (Sperling 2003, Meier et al. 2006). Over recent years, however, the initially rather theoretical discussion over the principle prospects of DNA taxonomy (Tautz et al. 2003), using DNA barcoding (Hebert et al. 2003), has streamlined into more empirical evaluations revealing both the benefits and limitations of the barcoding approach for biodiversity research (Meier et al. 2006, Costa et al. 2007, Hajibabaei et al. 2007, Ward 2009, Robe et al. 2012, Shackleton and Rees 2015). At the outset, DNA barcoding should be understood to be a complementary item in the taxonomist's toolbox (Stevens et al. 2011), and as such it primarily remains a mechanism to assist in species identification (DeSalle 2006, Collins and Cruickshank 2012). However, barcoding may fall short even in this aspect, depending on the taxon group studied and the study design (e. g. see Prendini 2005). Because the technique is vastly ineffective without barcode databases of sufficient species coverage and that are founded on verified, curated specimens (Funk and Omland 2003, Meyer and Paulay 2005), biologists are calling for increased integrative taxonomic knowledge (Will et al. 2005, Padial and De La Riva 2007, Boero 2010, Padial et al. 2010, Goldstein and DeSalle 2011, Cristescu 2014). On a global scale, such databases that contain adequate taxonomic and molecular coverage remain scarce (Kvist 2013), yet they are particularly needed for species-rich, taxonomically-ambiguous groups. In a carefully designed study and for taxa in which DNA barcoding achieves sufficient resolution, the tool can then support and help to refine taxonomic hypotheses on species delineations, as for example applied in anomuran decapod Crustacea by Puillandre et al. (2011).

Crustacea are one of the most diverse animal groups on the planet and are especially diverse in habitats that are explored the least, namely the oceans (Costello et al. 2010). Within the Crustacea, decapods such as crabs, shrimps, lobsters or hermit crabs are particularly large and recognisable, and form an ecologically and economically important group known to contain about 15,000 extent species (De Grave et al. 2009). Decapod crustaceans have been subject to successful barcoding studies (Lefébure et al. 2006, Costa et al. 2007, Radulovici et al. 2009, da Silva et al. 2011, Puillandre et al. 2011, Robe et al. 2012, Meyer et al. 2013, Bilgin et al. 2014, Raupach et al. 2015), showing the great potential of the technique for taxonomic biodiversity research in this group. However, compiling sufficient regional information that would enable the analysis of decapod diversity on a global scale remains an enormous challenge. Indeed da Silva et al. (2011) estimated that only 5.4% of all decapod species were represented in the available barcoding databases at that time. Another problem is that repository entries in barcoding libraries are often not identified by taxonomic experts, and that they are geographically biased towards those parts of the world that are scientifically well-funded (and generally biologically better studied). This leaves major gaps, particularly in marine habitats in the developing world, which includes some of the important biodiversity regions globally. Data are in fact particularly scarce across the entire continent of Africa. This study makes an attempt to fill this gap by compiling and analysing a taxonomically comprehensive barcoding dataset for the group of hermit crabs from this understudied part of the world, predominantly South African waters.

Most hermit crabs, or paguroids, maintain the remarkable life-style of inhabiting empty marine gastropod shells, and their body forms are evolutionarily-adapted to dwell into this unusual habitat (Hazlett 1981). Therefore, the hind body parts are almost entirely soft, forming few calcified characters that could be used to inform taxonomy. Yet, hermit crabs occupy many options of housing (McLaughlin 2015), and most species frequently use a vast suite of different types of shells (see Barnes 2003), with varying three-dimensional properties. This behaviour is known to influence and change growth rates in hermit crabs in different housings (Bertness 1981), resulting in and enhancing intraspecific variation (Blackstone 1985). Having half their body parts soft and being subject to high rates of intraspecific variation, these factors play a contributing role to why the taxonomy of many paguroids remains poorly understood. In an integrated taxonomic framework, barcoding could here provide additional resolution needed to identify and delineate species, particularly among closely-related species of difficult paguroid groups. With high success and promise, molecular sequencing of the mitochondrial cytochrome *c* oxidase subunit I (COI) marker has already been applied to paguroid hermit crabs, for example to inform the taxonomy of individual species of *Clibanarius* and *Coenobita* at a regional scale (Negri et al. 2014, Rahayu et al. 2016), as well on the entire genus *Calcinus* in an extensive, global study (Malay and Paulay 2010). However, no COI barcoding dataset of paguroids has been tested across a larger range of genera and species, or even families.

The primary aim of this study is to generate a DNA barcoding reference library for identified and curated hermit crab specimens from South African waters, and which reciprocally informs and supports morphology-based identifications in an ongoing nation-wide biodiversity assessment. In a second step, this database is herein, for the first time on a broader scale, tested for efficacy as an expert identification tool for hermit crabs. The results from the divergence analysis can also be used to refine knowledge and ideas of evolutionary speciation processes in the Paguroidea, or in Decapoda as a whole. Moreover, and given the almost entire absence of phylogenetic information on intrafamiliar paguroid relationships, some phylogenetic considerations are provided to give an overview within the limitations of the single mitochondrial marker. Aspects of previously unrecognised diversity, such as the presence of cryptic species, are discussed.

7.3 Methods

7.3.1 Sampling, specimen identifications and species concept

Sampling of South African marine invertebrates was carried out within the SeaKeys Project, a large collaborative marine biodiversity framework overseen by the South African National Biodiversity Institute (SANBI) and funded by the South African National Research Foundation, Pretoria, South

Africa (NRF) through their Foundational Biodiversity Information programme. Within the period of the Seakeys Project, from August 2014 to April 2017, hermit crabs were specifically targeted during multiple collection events around the South African coasts. In total, sampling yielded about 550 hermit crab specimens, and these were collected from all possible habitats, obtained using various collection methods (hand, diving, dredging, trawling). Except for some glaucothoe larvae, all specimens were identified *a priori* to species level by morphological examinations using both published identification literature (Barnard 1950, Forest 1954, McLaughlin 1998, McLaughlin and Forest 1999, Landschoff and Lemaitre 2017b,a) and resources that are currently being prepared as part of this study (see Chapter 8). Because identification expertise on the South African hermit crab fauna was mostly only developed in parallel and during the course of this study, specimens were frequently revisited, and in some instances morphology- and barcoding-based identifications were also reciprocally informed as sequences became available. For example, this was the case in some juvenile specimens with initially uncertain identifications, and also in four sequences derived from glaucothoe larvae. These sequences, matched to taxon names from the preliminary database, were thus included in the final analysis. Morphological separation of the putative species of *Diogenes* spp. and *Paguristes* spp., for which no identification literature existed, was primarily based on colouration patterns and the shape and armature of chelipeds and ambulatory legs. However, species entities in the text are referred to as ‘species’ when a certain level of morphological evidence justified the assignment of a taxon name from the literature, or are referred to as ‘putative species’ (sp.) when no morphological identification to an existing taxon name was possible. Although these general terms are often used in the text, it should also be mentioned that species entities were regarded and tested following the concept of ‘species-like-units’ (Collins and Cruickshank 2012). The general terms of ‘taxon’ or ‘taxa’ are used for unspecific groupings.

Depending upon availability, up to five specimens of each taxon were selected for barcoding, plus additional specimens were selected from different localities when a taxon was sampled over a wide geographic range, or when specimens seemed particularly interesting or taxonomically challenging (e. g. colour variations or juveniles). Fresh tissue was usually taken from unpreserved specimens after freezing/defrosting. Preferably, tissue was taken as eggs of ovigerous females or as muscular tissue, most often from the merus of the larger cheliped. In some smaller species, tissue was retrieved by dissecting one walking leg (ideally using a different leg for different specimens of a taxon) and then using the coxa for barcoding, while the remainder of the leg was retained with the sample. Also, in some abundant, very small taxa, larger body parts or even entire specimens were used. Some tissue was also taken from museum material following a similar protocol as for the fresh material. Tissue, placed in 96% ethanol, was sent to two different institutions for barcoding. The majority of the molecular work was carried out at the South African Institute for Aquatic Biodiversity (SAIAB), while other tissues were submitted to the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph. Most specimens are deposited at the Iziko South African Museum, Cape Town, South Africa, and a few are now in the collections of the United States National Museum of Natural History, Smithsonian Institution, Washington,

D. C., USA. Detailed sample information can be found in the supplemental material of this thesis.

7.3.2 DNA extractions and sequencing

At SAIAB, DNA was extracted using a standard “salting out – ethanol precipitation” protocol (Sunnucks and Hales 1996), followed by the amplification of the ‘barcoding’ (Hebert et al. 2003) fragment COI gene for each sample by Polymerase Chain Reaction (PCR), using the universal invertebrate primers (LCOI-1490 and HCOI-2198) of Folmer et al. (1994), or their degenerate variants (dgLCOI490 and dgHCO2198; Meyer 2003). PCR recipes and conditions followed Meyer (2003) and Gouws et al. (2015), with annealing performed at 48°C for the latter. Successful amplification was determined by visualising products under UV light, following electrophoresis in 1% agarose gels, stained with ethidium bromide, in a TBE buffer. PCR products were purified with an Exonuclease I - Shrimp Alkaline Phosphate (Exo/SAP, ThermoFisher Scientific) protocol (Werle et al. 1994), sequenced in both the forward and reverse directions using BigDye v3.1 (Applied Biosystems, Austin, Texas) terminator chemistry and analysed on an ABI-Hitachi 3500 Genetic Analyser (Applied Biosystems) at SAIAB. The resulting sequences were checked against their chromatograms for misreads and sequencing errors using ChromasLITE (Technylesium). Sequences were aligned, edited and the consensus DNA barcode compiled using Lasergene SeqMan Pro 9 (DNASTAR, Madison, Wisconsin). Barcodes were uploaded to the SeaKeys project on BOLD (www.boldsystems.org; Ratnasingham and Hebert 2007), using the BOLD inbuilt quality control functions for detecting stop-codons and annotating ambiguous bases. Sequences shorter than 550 basepairs (bp) were removed from the dataset.

7.3.3 Genetic analysis

7.3.3.1 Alignment and tree-building

Alignment of the COI barcodes was conducted in ClustalX 2.1 (Larkin et al. 2007). Neighbour-Joining (NJ) tree-building (Saitou and Nei 1987) of the aligned sequences was subsequently carried out in MEGA7 (Kumar et al. 2016), using a Kimura (1980) 2-parameter (K2P) model of sequence evolution using 1000 bootstrap replicates (Felsenstein 1985). Final trees were drawn in FigTree v1.4.3 (tree.bio.ed.ac.uk/software/figtree) and edited in Inkscape 0.91 (inkscape.org).

7.3.3.2 Distance analysis

All following analyses were conducted in the *R* 3.3.1 and *R* 3.4.3 statistical environments (*R* Core Team 2016) using the packages *spider* (Brown et al. 2012) and *sidier* (Muñoz-Pajares 2013) within the *Rstudio* interface (*RStudio* Team 2016). Inter- and intraspecific pairwise distances were calculated, again corrected using the K2P model, and statistics of mean, minimum and maximum distances were retrieved from comparisons of sequence pairs. To calculate the overlap of distances on species-genus and genus-family levels, these distances were also computed within or between congeneric and intrafamiliar taxa. The taxonomic resolution ratio (TRR) was calculated as defined as the quotient between congeneric interspecific and intraspecific divergences (Costa et al. 2007). The difference separating intra- and interspecific distances, also known as the Barcoding Gap (BG) (Meyer and Paulay 2005), was derived by subtracting the minimum interspecific from the maximum intraspecific distance (Meier et al. 2008, Robe et al. 2012). A second version of the BG, based on subtractions of the smallest interspecific from the largest intraspecific K2P distance value for each sequence (Brown et al. 2012) instead of the overall minimum and maximum values for the species, was also explored for this set of data.

7.3.3.3 Testing barcoding efficacy

Along with an analysis to find the best threshold that would separate hermit crab taxa in this study, the barcoding efficacy for the COI dataset was tested using both Meier's best close match (Meier et al. 2006), and the threshold-based analysis functions *threshID* and *threshOpt* provided by the *spider* package in *R*. Species boundary thresholds, as proposed in the literature (Hebert et al. 2003: 3%, Ratnasingham and Hebert 2007: 1.0% BOLD, 2013: 2%), and calculated for this set of data (Hebert et al. 2004: 8.1% [10x intraspecific divergence], Lefébure et al. 2006: 4.6% [assumption-free statistical approach], Meier et al. 2006: 3.0% [95% rule], Brown et al. 2012: 1.9% [*localMinima* method]), were tested for the highest identification success rates. Additionally, an optimal threshold range was calculated and tested after Brown et al. (2012).

7.4 Results

7.4.1 COI dataset and quality

A total of 194 COI barcode sequences (>550bp) of 43 nominal and 12 putative species from 20 genera and four families were retrieved and analysed. The majority of these taxa belonged to the family Diogenidae (39 taxa, 131 sequences), while the families Paguridae (9 taxa, 40 sequences) and Parapaguridae (6 taxa, 23 sequences) were less represented, and only one barcode of *Coenobita rugosus* from the family Coenobitidae was retrieved. Of the 55 total taxa, 16 were represented only by a single sequence, while on average each taxon was presented by four barcode sequences, and a maximum of 16 barcodes were sequenced for the widespread *Diogenes brevirostris* (Figure 7.1). Three sequences were derived from glaucothoe larval forms of *Sympagurus dimorphus*, and one of a glaucothoe form of *Parapagurus bouvieri* (Figure 7.1 D). Quality control detected stop codons probably indicating nuclear mitochondrial pseudogenes (numts) in the two sequences of *Calcinus guamensis*. The vast majority of 177 sequences consisted of the normal length of 658bp and had no ambiguities, but some were shorter and only one was below 600bp. Six sequences from three taxa (*Pagurus cuanensis*, *Clibanarius virescens*, and *Paguristes* sp.1) had >2 ambiguous nucleotide bases (4–7n). Because exploratory analyses carried out with or without sequences of lesser quality led to the same or very similar results, these sequences were included in the final dataset analysed, although respective data quality flags were retained (Figure 7.1 B–D).

7.4.2 Phylogentic aspects

The NJ tree of the 55 taxa supported monophyly at the species level (but see section on the divergence analysis for results on species identifications). Both the Paguridae and Parapaguridae were recovered as monophyletic, whereas the Diogenidae was poly- or paraphyletic (Figure 7.1). However, the clade forming the Paguridae had weak bootstrap support (21%), while the Parapaguridae were relatively well supported (93%) as a family. Within the Paguridae nodal support on generic levels was low, except for the sister-taxa relationship of *P. emmersoni* and *P. liochele*, which was well supported (100%, Figure 7.1 A, D). The polyphyly of the genus *Pagurus* became apparent (Figure 7.1 D). In contrast, nodal support within the Parapaguridae was higher, with *Paragiopagurus* standing at the base of this family. With only few taxa represented in the tree, *Parapagurus* was recovered as monophyletic, clustering within the poly- or paraphyletic *Sympagurus*.

The case of the Diogenidae was more complex, because *Clibanarius* clustered between the Paguridae and Parapaguridae (Figure 7.1 A), and the single sequence of *Coenobita rugosus* clustered within the genus *Calcinus*, making this family poly- or paraphyletic in this analysis limited to COI data. The genus *Diogenes* was recovered as polyphyletic (Figure 7.1 A–B), forming two distinct clades. As already mentioned, the well-represented genus *Calcinus* was found to be poly- or paraphyletic containing a member of *Coenobita*, but also the closely-related taxon *Ciliopagurus* (Figure 7.1 A–B). *Dardanus* was recovered to be monophyletic, and *Paguristes* formed the only monophyletic genus with high (100%) bootstrap support. As a second branch of the *Paguristes* clade, *Areopaguristes engyops* and *Pseudopaguristes* formed a well-supported sister-taxa relationship and was sister to the *Paguristes* clade, but notably distant from the other species of *Areopaguristes*, *A.* cf. *jousseaumei*. The positions of *Paguropsis* and *Cancellus* within the Diogenidae had little support (Figure 7.1 A–B).

7.4.3 COI divergence analysis

Mean, minimum and maximum intraspecific K2P distances for all taxa presented by more than one sequence are summarised in Table 7.1. At 0.0081 (± 0.0016 SE), the overall mean intraspecific distance was well below 1%, and 93.65% of the 441 intraspecific comparisons fell below 3%. The highest maximum distance resulted from intraspecific comparisons within *Anapagurus hendersoni* (3.5%), *Diogenes brevirostris* (3.5%), *Areopaguristes* cf. *jousseaumei* (4.3%), *Goreopagurus poorei* (5.0%) and *Pagurus cuanensis* (5.1%). Congeneric distances varied from a minimum of 3.9%, between *Pagurus emmersoni* and *P. liochele*, to maximum values of 27–28% when comparing congeneric sequences of *Calcinus*, *Dardanus* and *Diogenes* (Table 7.2). In these 1379 congeneric comparisons, 99.85% were above 4%. Furthermore, the intrafamiliar overlaps of interspecific, congeneric and intergeneric distances for the three main families are visualised in Figure 7.2. On the levels between species and genera, no overlap (or only marginal overlap in the Paguridae) was observed, but major overlaps were apparent on the intra-intergenera comparison levels in all three families; the latter being most apparent in the Diogenidae. The mean distance values

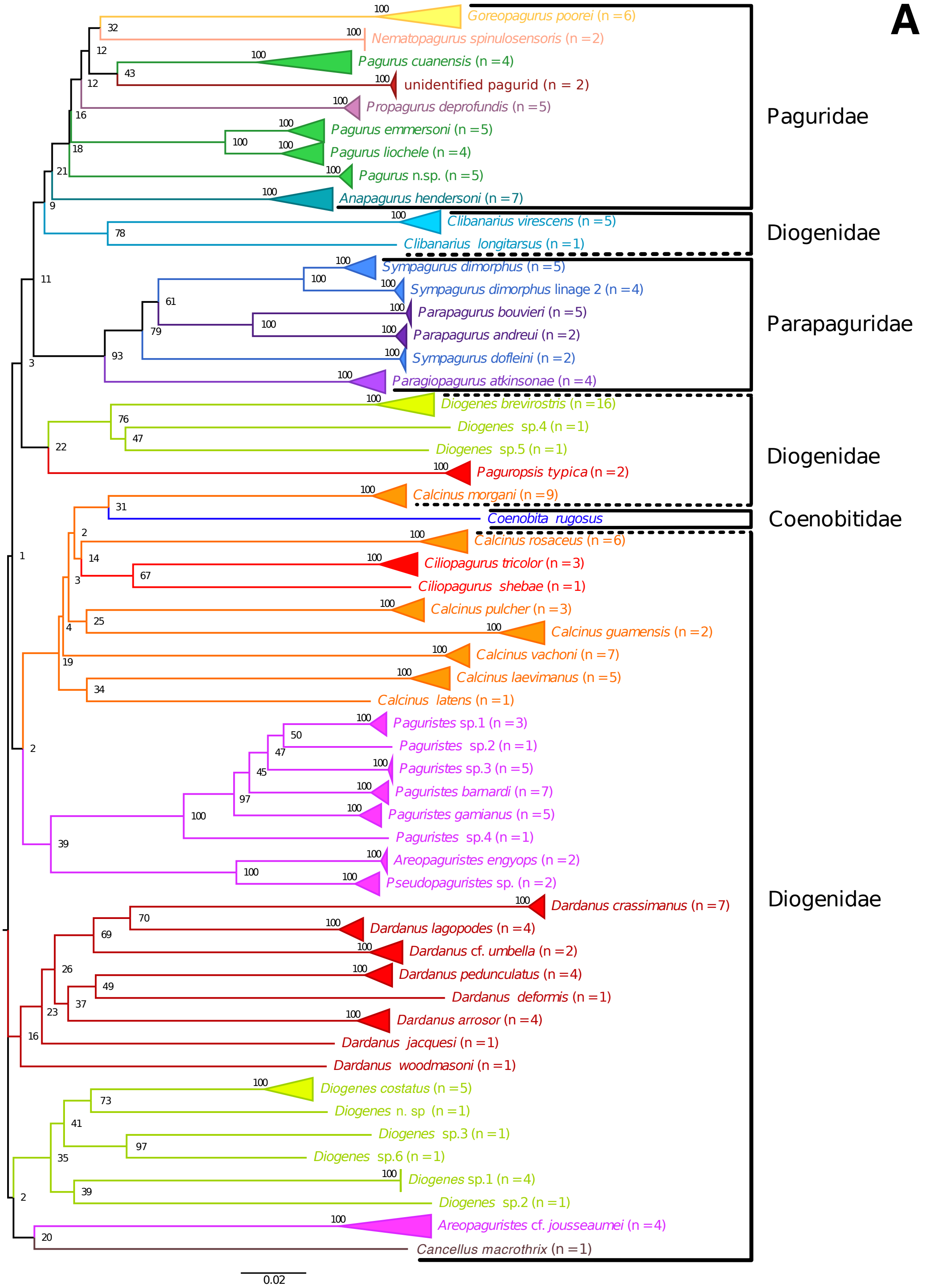

Figure 7.1: Neighbour-joining tree of hermit crabs predominantly from South African waters (except where elsewhere indicated), constructed using the cytochrome *c* oxidase subunit I (COI) barcoding fragment and corrected by a Kimura 2-parameter model (K2P): A Overview, followed by detailed subsections **B** Diogenidae 1 **C** Diogenidae 2 **D** Paguridae plus Parapaguridae. Bootstrap values based on 1000 replications, K2P distance values shown by scale bar (%), sample size (n =) given for each species in **A**, stop codons (*) and ambiguous bases (n) indicated in **C–D**, sequence length 658bp if not specified.

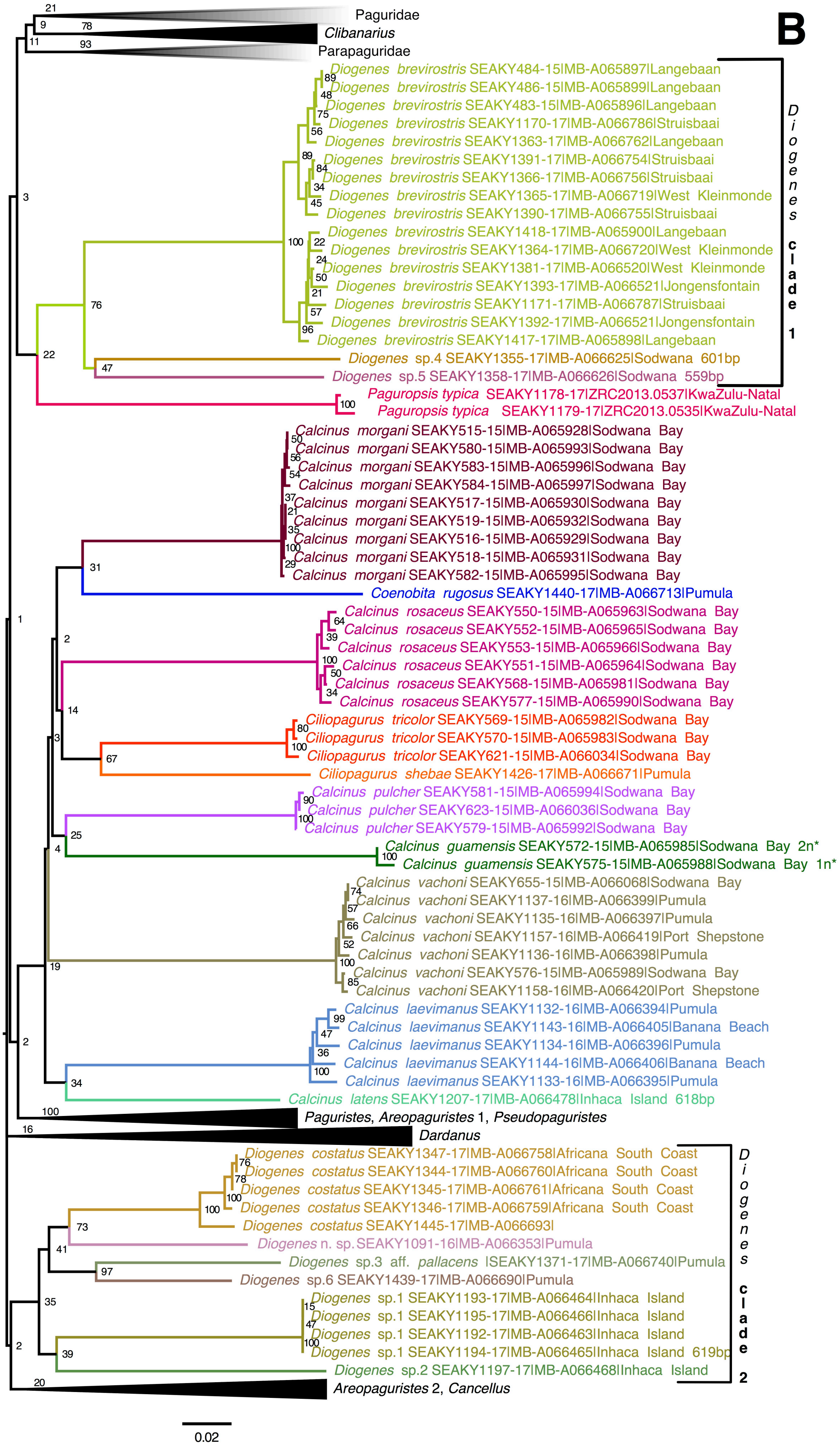

Figure 7.1 continued: Diogenidae 1 in detail.

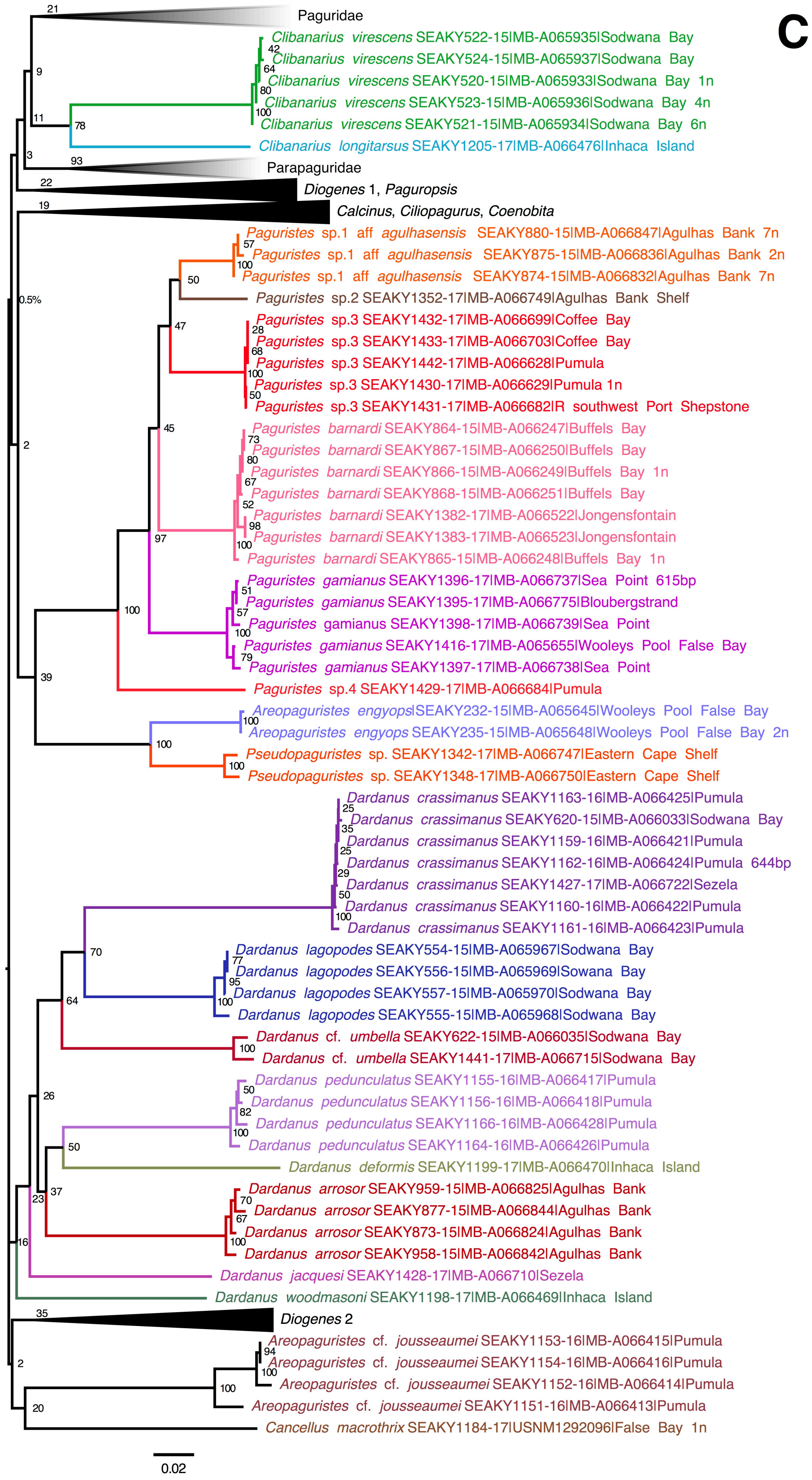

Figure 7.1 continued: Diogenidae 2 in detail.

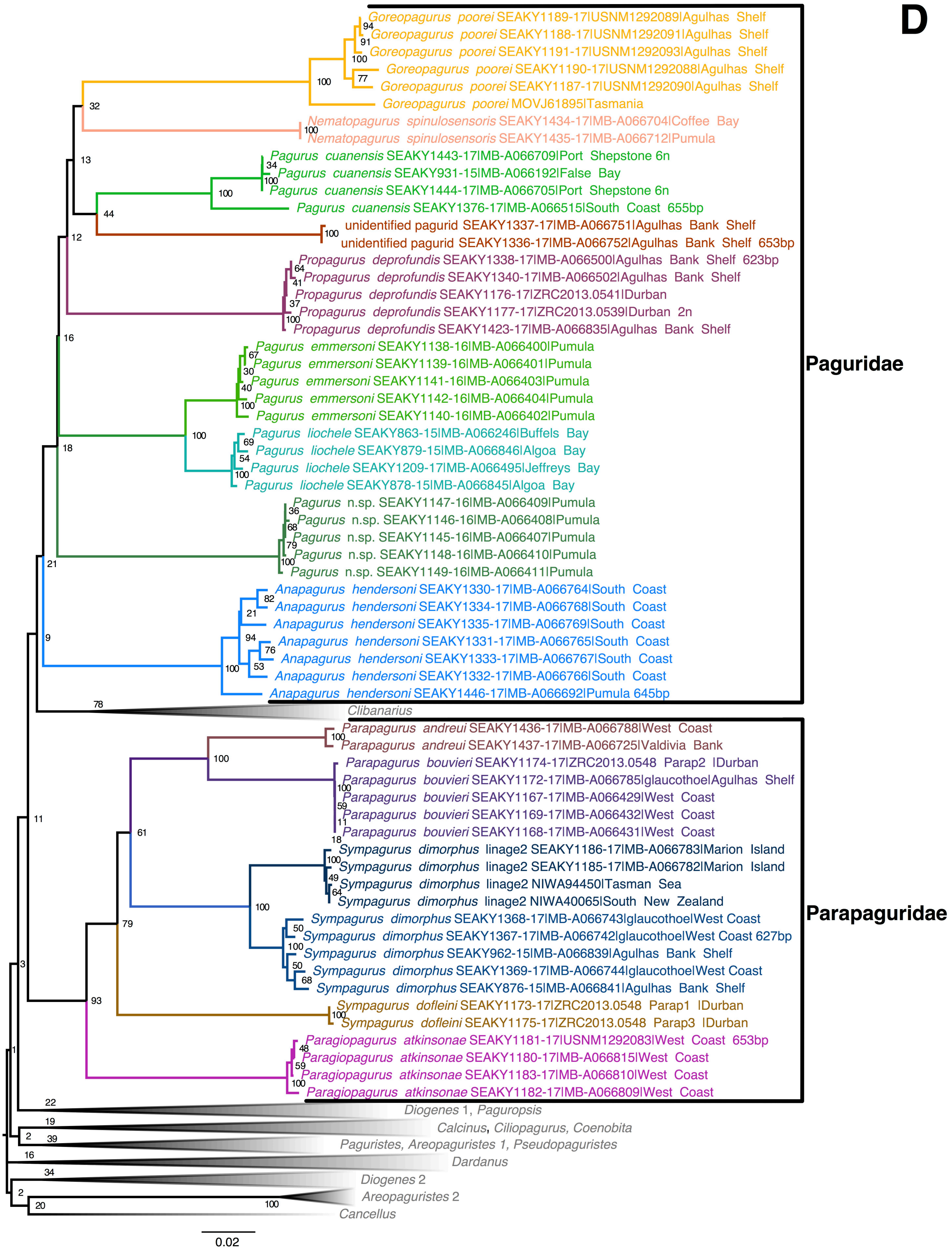

Figure 7.1 continued: Paguridae and Parapaguridae in detail.

of congeneric and intergeneric distances were also notably higher for the Diogenidae (about or >20%) than for the Paguridae or Parapaguridae (<20%).

Following the version of the BG by Brown et al. (2012), all specimens had a measurable barcoding gap. However, when averaging intra- and interspecific distances of each genus first, and then subtracting the minimum interspecific from the maximum intraspecific distance (Robe et al. 2012), a small barcoding gap (overlap by 1.2%) was found in the case of *Pagurus* (Table 7.2). Although present, the gap was also small in the genera *Sympagurus* (2.7%) and *Paguristes* (4.1%), while it was close to, or larger than, 10% for all other genera calculated. The TRR values were lowest in *Areopaguristes* (1.153) and highest in *Clibanarius* (113.125, Table 7.2).

7.4.4 Thresholds and dataset efficacy

Testing the dataset for various distance thresholds (1–8.1%) resulted in a range of success rates (2–39 cumulative errors) in false negative or false positive barcoding identifications (Table 7.3). For this set of data, Meier's best close match and the *spider* functions *threshID*/ *threshOpt*, had the same results. Sequences of the 16 species with only a single sequence present could not be matched and hence were "positively not identified" using the dataset. The smallest threshold of 1% tested resulted in 20 false positive barcoding identifications, whereas the largest threshold of 8.1%, corresponding to ten times the mean intraspecific divergence, resulted in 39 false negatives. The derived threshold from Lefébure et al.'s (2006) assumption-free statistical approach (Figure 7.3) resulted in 13 cumulative mis-identifications. With only three false positive errors Hebert et al.'s (2003) threshold of 3%, which also coincided with Meier et al.'s (2006) 95% rule, was close to the optimum thresholds of 3.7–3.9% that had a minimum of only two false positives and 192 correctly-identified sequences. Applying this optimal threshold range therefore resulted in a barcoding efficacy of 98.96%.

Table 7.1: Averages and ranges of Kimura 2-parameter (KP2) distance value (%) pairwise comparisons based on cytochrome *c* oxidase I (COI) nucleotides for hermit crab species represented in this study by more than one sequence.

Species	**No. of comparisons**	**Min distance**	**Mean distance ± std. err.**	**Max distance**
Anapagurus hendersoni	21	0.008	0.0218 ± 0.0018	0.035
Areopaguristes cf. *jousseaumei*	6	0.000	0.0222 ± 0.0074	0.043
Areopaguristes engyops	1	0.002	0.0020	0.002
Calcinus guamensis	1	0.005	0.0050	0.005
Calcinus laevimanus	10	0.008	0.0190 ± 0.0014	0.023
Calcinus morgani	36	0.000	0.0028 ± 0.0003	0.006
Calcinus pulcher	3	0.002	0.0023 ± 0.0003	0.003
Calcinus rosaceus	15	0.005	0.0099 ± 0.0007	0.015

Calcinus vachoni	21	0.000	0.0079 ± 0.0007	0.012
Ciliopagurus tricolor	3	0.003	0.0073 ± 0.0023	0.011
Clibanarius virescens	10	0.000	0.0016 ± 0.0004	0.003
Dardanus arrosor	6	0.006	0.0100 ± 0.0012	0.014
Dardanus cf. *umbella*	1	0.017	0.0170	0.017
Dardanus crassimanus	21	0.000	0.0032 ± 0.0004	0.006
Dardanus lagopodes	6	0.000	0.0070 ± 0.0026	0.014
Dardanus pedunculatus	6	0.006	0.0100 ± 0.0011	0.014
Diogenes brevirostris	120	0.000	0.0185 ± 0.0008	0.035
Diogenes costatus	10	0.000	0.0134 ± 0.0039	0.028
Diogenes sp.1	6	0.000	0.0000	0.000
Goreopagurus poorei	15	0.002	0.0249 ± 0.0044	0.050
Nematopagurus spinulosensoris	1	0.000	0.0000	0.000
unidentified pagurid sp.	1	0.002	0.0020	0.002
Paguristes barnardi	21	0.000	0.0050 ± 0.0007	0.011
Paguristes gamianus	10	0.002	0.0081 ± 0.0014	0.017
Paguristes sp.1 *aff. agulhasensis*	3	0.000	0.0013 ± 0.0007	0.002
Paguristes sp.3	10	0.000	0.0012 ± 0.0003	0.002
Paguropsis andersoni	1	0.009	0.0090	0.009
Pagurus cuanensis	6	0.000	0.0252 ± 0.0104	0.051
Pagurus emmersoni	10	0.002	0.0056 ± 0.0007	0.009
Pagurus liochele	6	0.006	0.0070 ± 0.0004	0.008
Pagurus n. sp.	10	0.000	0.0027 ± 0.0005	0.005
Paragiopagurus atkinsonae	6	0.002	0.0048 ± 0.0012	0.008
Parapagurus andreui	1	0.006	0.0060	0.006
Parapagurus bouvieri	10	0.000	0.0008 ± 0.0003	0.002
Propagurus deprofundis	10	0.002	0.0040 ± 0.0005	0.006
Sympagurus dimorphus	10	0.008	0.0122 ± 0.0010	0.017
Sympagurus dimorphus l2	6	0.002	0.0040 ± 0.0006	0.006
Sympagurus dofleini	1	0.002	0.0020	0.002
Total average	**11.6**	**0.0028**	**0.00871 ± 0.00167**	**0.0131**

Table 7.2: Pairwise comparisons of cytochrome *c* oxidase I (COI) nucleotide Kimura 2-parameter (K2P) distance averages and ranges (%) for the hermit crab genera in this study for which barcode sequences were available for more than one species. TRR = Taxonomic Resolution Ratio; BG = Barcoding Gap, negative value reflects absence of BG.

Genus	**No. of taxa**		**No. of comparisons**	**Min distance**	**Mean distance ± std. err.**	**Max distance**	**TRR**	**BG**
Areopaguristes	2	within	7	0.000	0.0193 ± 0.0069	0.043	1.153	**0.171**
		between	8	0.214	0.2225 ± 0.0017	0.229		
Calcinus	7	within	86	0.000	0.0072 ± 0.0006	0.023	30.500	**0.164**
		between	442	0.187	0.2196 ± 0.0010	0.280		
Ciliopagurus	2	within	3	0.003	0.0073 ± 0.0023	0.011	22.740	**0.151**
		between	3	0.162	0.1660 ± 0.0021	0.169		
Clibanarius	2	within	3	0.003	0.007 ± 0.0023	0.011	113.125	**0.173**
		between	5	0.176	0.1810 ± 0.0018	0.184		
Dardanus	8	within	40	0.000	0.0062 ± 0.0007	0.017	34.919	**0.152**
		between	236	0.169	0.2165 ± 0.0017	0.272		
Diogenes	9	within	136	0.000	0.0173 ± 0.0008	0.035	12.578	**0.095**
		between	329	0.130	0.2176 ± 0.0017	0.271		
Paguristes	6	within	44	0.000	0.0046 ± 0.0006	0.017	19.587	**0.041**
		between	187	0.058	0.0901 ± 0.0015	0.145		
Pagurus	4	within	32	0.000	0.0086 ± 0.0023	0.051	15.291	**-0.012**
		between	121	0.039	0.1315 ± 0.0037	0.179		
Parapagurus	2	within	11	0.000	0.0013 ± 0.0006	0.006	72.462	**0.088**
		between	10	0.094	0.0942 ± 0.0001	0.095		
Sympagurus	3	within	17	0.002	0.0087 ± 0.0012	0.017	11.287	**0.027**
		between	38	0.044	0.0982 ± 0.0082	0.159		

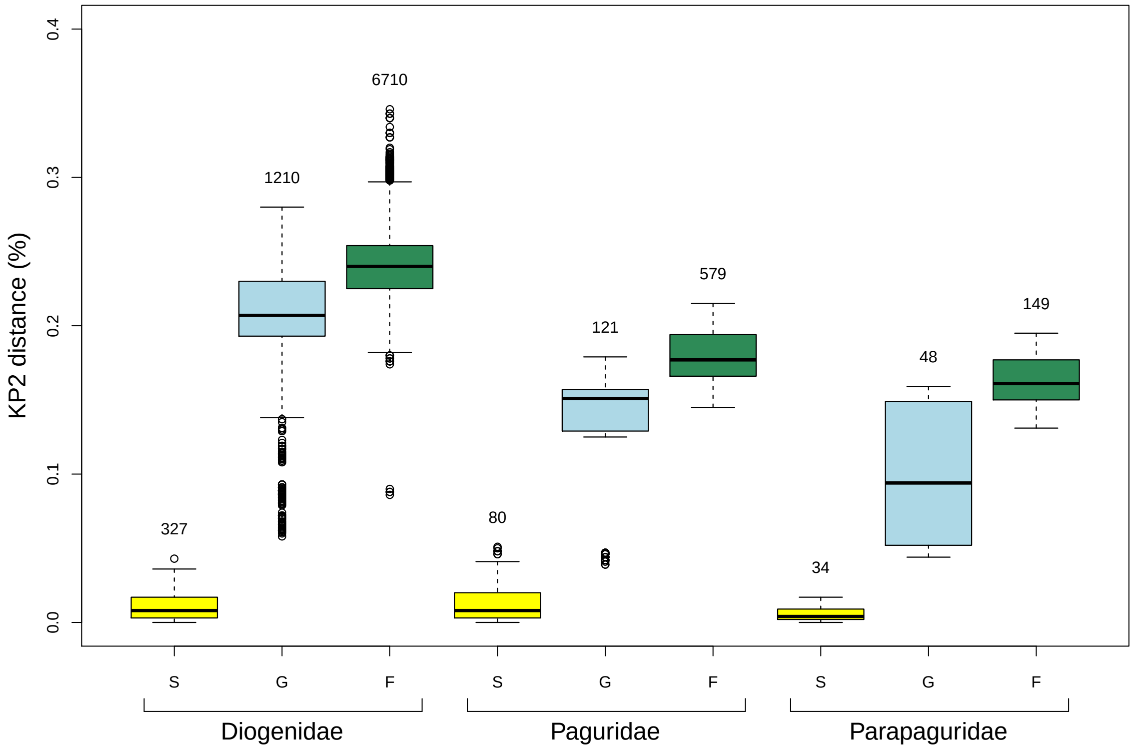

Figure 7.2: Boxplot distribution of hermit crab families intraspecific (S), intrageneric (G), and intrafamiliar (F) cytochrome *c* oxidase I (COI) Kimura 2-parameter (K2P) distances (%). Plot giving median as central bar, upper and lower quartiles as central box, and extreme values of the data as dots. Numbers above individual boxplots correlate to each groups total number of pairwise comparisons. Mean K2P distance (%) ± SE within taxa: Diogenidae S = 0.0110 ± 0.0005, G = 0.1982 ± 0.0015, F = 0.2417 ± 0.0003; Paguridae S = 0.0144 ± 0.0016, G = 0.1315 ± 0.0037, F = 0.1772 ± 0.0007; Parapaguridae S = 0.0056 ± 0.0009, G = 0.0974 ± 0.0065, F = 0.1620 ± 0.0016.

7.5 Discussion

7.5.1 Data scrutiny and study limitations

Currently, 72 nominal species of hermit crab are officially reported from South African mainland waters (see Chapter 8). Of these, 40 nominal taxa are represented in this dataset (56%), with sequences of 12 more putative species all collected from South African waters. Sequences are also included for *Dardanus woodmansoni* and two more un-identified species, *Diogenes* sp.1 and sp.2 from southern Mozambique neither of which are represented by a current South African record, as well as for one more hermit crab treated as a distinct taxon in this analysis, *Sympagurus dimorphus lineage 2* from Marion Island and New Zealand.

Despite the decision to keep some problematic sequences in the dataset, the overall quality of the sequence data can be considered high. With six sequences having more than two ambiguous bases, two sequences having stop codons potentially indicating numts, and 17 sequences being slightly shorter than the normal 658bp, about 90% of the barcodes in this dataset have the

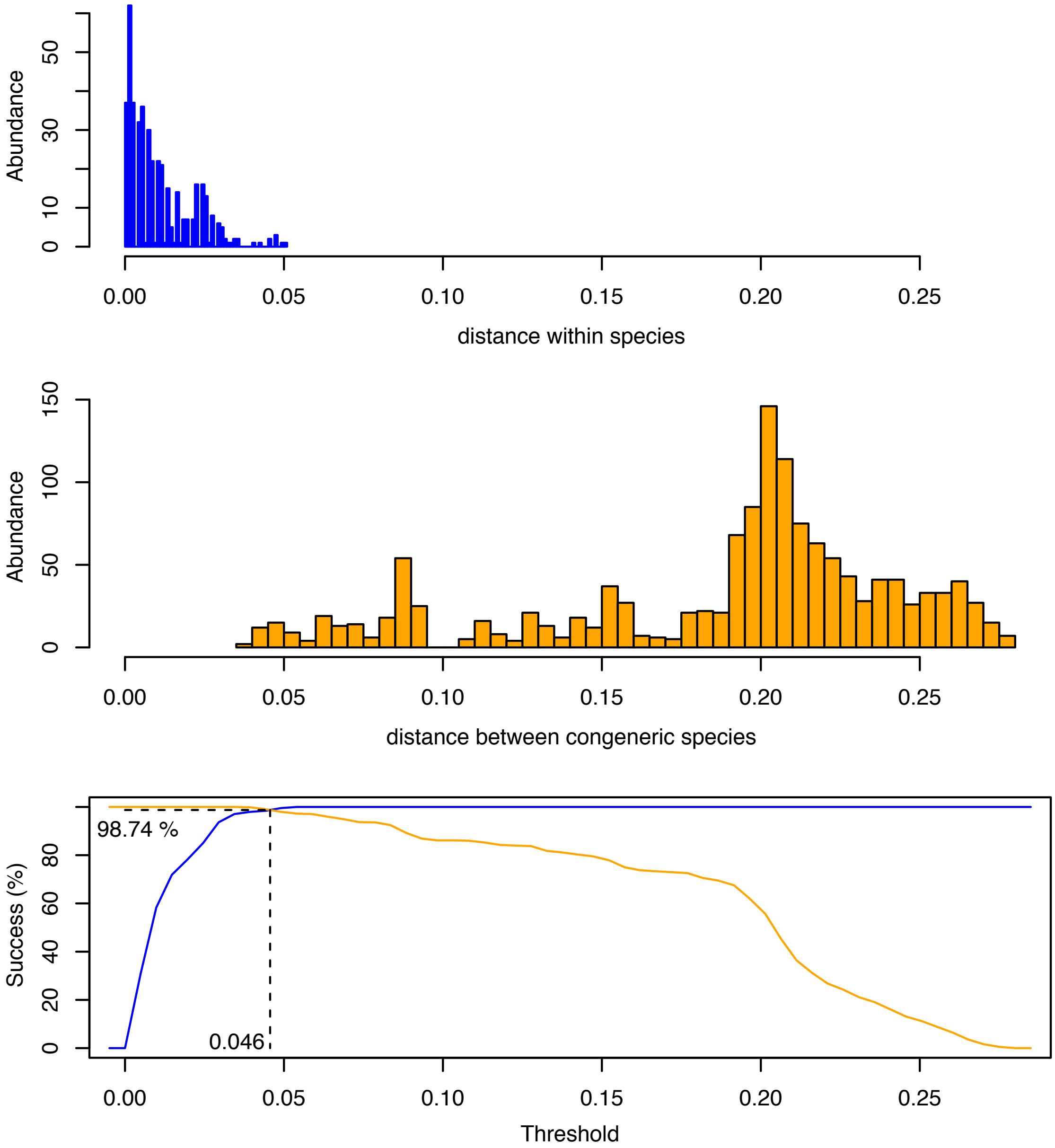

Figure 7.3: Overlap and threshold evaluation between conspecific (intra-species) and congeneric (inter-species but intra-genus) Kimura 2-parameter (K2P) cytochrome *c* oxidase I (COI) distances (%) of all hermit crabs in this study, using the assumption-free statistical approach by Lefébure et al. (2006). Lines in bottom graph show percentage of samples that are below (distribution of distances within species, blue) or above (distribution of distances between congeneric species, orange) the given range of thresholds. The percentage for each threshold value is thought to represent the chance of 'success' to discriminate samples from a distribution, where the best compromise, or 'threshold', is found where both success curves intersect.

Table 7.3: Hermit crab COI barcoding efficacy evaluation using the *threshOpt* function provided in the *spider* (Brown et al. 2012) package in *R* (*R* Core Team 2016). True and false positives as well as negatives tested for thresholds proposed in the literature given, and optimised for the current dataset.

	Threshold	**True neg**	**True pos**	**False neg**	**False pos**	**Cumulative error**
BOLD species identification	1.0%	16	158	0	20	20
Ratnasingham and Hebert 2013	2.0%	16	173	0	5	5
Hebert et al. 2003*	3.0%	16	175	0	3	3
10x intraspecific divergence (Hebert et al. 2004)	8.1%	15	140	39	0	39
Assumption-free statistical approach (Lefébure et al. 2006)**	4.6%	16	165	12	1	13
localMinima method (Brown et al. 2012)**	1.9%	16	173	0	5	5
threshold optimisation (Brown et al. 2012)**	3.7–3.9%	16	176	0	2	2

*Hebert et al.'s (2003) 3% coinciding with Meier et al.'s (2006) 95% rule.

**Values calculated for this dataset.

highest sequencing quality. However, future users of the provided data should consider that the sequences of lower quality might influence barcoding identifications. Because general aspects of homologous comparison are violated in COI-like genes (Buhay 2009), the two sequences of *Calcinus guamensis* consisting of potential numts will most likely lead to mis-identifications, even when compared to sequences of conspecific specimens.

The aim of this study was to generate a barcoding library for paguroids from South Africa with the highest possible species coverage possible. Therefore, the dataset is inevitably biased through unequal taxon sampling. Some taxa are well covered, as they are common and widespread, whereas 16 taxa are only represented by a single sequence, as only one or few individuals were available. Furthermore, and for obvious reasons, the dataset is limited in its geographic scale. While geographic coverage is generally better provided for taxa endemic to the South African region, which are most often found along the South Coast, almost all species from the subtropical East Coast north of Durban have widespread Indo-Pacific distributions. Therefore, future paguroid barcoding programmes in this ocean region should extend the geographical taxon coverage, ideally to the maximum true occurrence of each species. The current study is, however, valuable in that it provides records of those widespread taxa from their southwestern-most geographical distribution in South Africa.

7.5.2 Phylogenic considerations

While many phylogenetic aspects of the Paguroidea are moderately resolved at higher taxonomic levels, or within the Anomura (Mclaughlin 1983, Tudge 1997, McLaughlin et al. 2007a, Tsang et al. 2008, 2011, Bracken-Grissom et al. 2013), intrafamiliar relationships of hermit crabs are still poorly understood for most taxa. For example, the family Paguridae was identified as one of the most challenging groups within Anomura and its monophyly questioned (Bracken-Grissom et al. 2013). Although mitochondrial DNA is unfit to resolve evolutionary pathways (see Galtier et al. 2009) and phylogenies derived from COI in the Decapoda must be interpreted with caution (Chu et al. 2009) this barcoding study only provides a preliminary overview. However, given the lack of knowledge on intrafamiliar relationships in hermit crabs, the analysis given here highlights important taxonomic or evolutionary issues within/among the 20 represented genera. The arising phylogenetic uncertainties on generic and familiar levels stand in contrast to the monophyly recovered for the for 55 taxa (but see section on ambiguous species), which can be seen as a direct result of the high taxonomic efforts that went into the preparation of this dataset.

In the overview tree (Figure 7.1 A), species of the same or closely-related genera are given the same colour in order to indicate (non-) monophyletic taxa. Within the Paguridae, the para- or polyphyly of the genus *Pagurus* has been proposed before (McLaughlin 1974, Komai 1998, Bracken-Grissom et al. 2013), and is once more supported here. The weak support for topologies of the higher taxa within the Paguridae (Figure 7.1 A, D), may well be due to the limitations of using COI barcodes as a single marker. As one clear outcome, the sister-taxa relationship of *Pagurus emmersoni* to *P. liochele* seems to be certain and is consistent with their similar morphology (McLaughlin and Forest 1999). The close relationship of *P. cuanensis* with an unidentified pagurid, as well as a potentially a sister-taxa relationship between *Goreopagurus poorei* and *Nematopagurus spinulosensoris* is suggested, but the determination of the ancestral pathways within the Paguridae will require more detailed studies that increase resolution on a generic level. Recovering the family Parapaguridae as monophyletic is consistent with the findings of other molecular studies (Tsang et al. 2011, Bracken-Grissom et al. 2013), and the results further suggest that the monophyletic genus *Parapagurus* could be nested within the other genera presented. Being morphologically united by many absent characters, rather than autapomorphy (e. g. Lemaitre 1996), it would not be particularly surprising if the other two genera present in this dataset, *Paragiopagurus* and *Sympagurus*, would not be monophyletic, as shown by the data.

Based on nuclear protein coding genes (Tsang et al. 2011), or on mitochondrial and nuclear markers combined with morphological characters (Bracken-Grissom et al. 2013), non-monophyletic relationships have been discovered for the Diogenidae, similar to the results in this study (Figure 7.1 A–B). This indicates that COI barcodes may give a good phylogenetic overview for hermit crab relationships above species level. However, assuming monophyly of the genus, the position of *Clibanarius*, between the Paguridae and Parapaguridae, is probably incorrect. Previous studies with more molecular support found members of *Clibanarius* clustering well within the Diogenidae, usually close to *Calcinus* (Tsang et al. 2011, Bracken-Grissom et al. 2013). Respectively, the same authors also found *Coenobita* within *Calcinus* as sister taxon to *Clibanarius*, or found members of *Coenobita* clustering within *Calcinus* as a sister clade to *Petrochirus* and *Dardanus*. Nevertheless, Bracken-Grissom et al.'s (2013) study was limited to only two species of *Calcinus*. Based on broader species coverage of seven species of *Calcinus*, this present study extends the theory that Coenobitidae may not only be deeply nested within the Diogenidae, but that they could have even emerged from within the genus *Calcinus*. The similar situation of *Ciliopagurus* being nested within *Calcinus* in this analysis (Figure 7.1 A–B), however, is contrary to the results of Malay and Paulay (2010), who, based on exploratory phylogenetic analysis, chose *Ciliopagurus* as the closest outgroup taxa for the analysis of their extensive dataset of *Calcinus*.

Within the other diogenid genera, *Dardanus* is likely to be monophyletic, even if the support for incorporating *D. woodmansoni* was weak (16%, Figure 7.1 A, C). In fact, during exploratory tree-building analyses on partial or preliminary data, this species frequently jumped to different positions within the Diogenidae and away from *Dardanus*. However, in forming the basal taxon of *Dardanus* in the final analysis, *D. woodmansoni* could be closest to the ancestral form of this genus and this theory should be tested in the future. Taxonomically, the genera *Paguristes* and its allies *Areopaguristes* and *Pseudopaguristes* are among one of the most challenging hermit crab groups. The reason is to be found in high diversity that is often combined with the lack of species-delimiting morphological characters, as it can for example be observed in the specimens included in this study. In comparison to other clades in the Diogenidae such as *Calcinus*, *Dardanus* or *Diogenes*, branch lengths indicating genetic distances were much shorted in *Paguristes* (Figure 7.1 A), and intraspecific distances were among the lowest (<1% in *Paguristes*, Tables 7.1–7.2). This would suggest recent divergence and speciation at the species level. However, on the genera level, *Paguristes* was the only monophyletic genus with maximum bootstrap support (100%), and also the sister-taxa relationship to a well-supported clade formed by *Areopaguristes engyops* and *Pseudopaguristes* sp. had some moderate support (39%, Figure 7.1 A, C). The position of *Areopaguristes* cf. *jousseaumei*, which made this genus polyphyletic in this analysis, suggests that the taxonomic placement of *Areopaguristes* is probably incorrect and requires more detailed study. The proposition that *Paguristes* and *Areopaguristes* are more closely related to the Paguridae (Bracken-Grissom et al. 2013) was not apparent from the barcode phylogeny, again potentially because the COI data alone failed to detect deeper family divergences.

The genus *Diogenes* forming two separate and moderately well-supported clades (Figure 7.1 A–B) is of some interest. It had been proposed that *Diogenes* is monophyletic (Forest 1955), but no recent studies discuss phylogenetic relationships within this genus. Forest (1952) defined two separate *Diogenes* groups: group 1, the members of which have a spinous intercalary rostral process, and group 2 in which members have this process simple. Neither a member of group 1, nor a member of a third '*troglopagurus* group' with a reduced rostral process (Mclaughlin 2005), are represented in this study. All species of *Diogenes* in this study therefore belong to Forest's (1952) group 2. Later, this group 2 was split into further two subgroups, one of which, the '*edwardsii* group', has long antennal peduncles, while the other, the '*pallescens* group', has short antennal peduncles (Asakura and Tachikawa 2010). *Diogenes brevirostris*, *D. costatus*, and *Diogenes* n. sp., as well as probably *Diogenes* sp.1, sp.4 and sp.5 all belong to the *edwardsii* group, while *Diogenes* sp.2, sp.3, sp.6 probably belong to the *pallescens* group. However, *D. brevirostris*, *Diogenes* sp.3 and sp.4

fell into the first clade, while all others formed the quite distant second clade, indicating that the characters leading to the informal *edwardsii-pallescens* subdivision are unlikely based on mutual evolutionary pathways. It follows that *Diogenes* may not be monophyletic, although the two major subdivisions (group 1 and the *troglopagurus* group) of *Diogenes* not being reflected in the data. To get a better understanding and potentially resolve the ancestry of this genus, more detailed studies are needed.

7.5.3 Species determination and taxonomic ambiguities

A main bias in divergence assessment is incorrect or uncertain taxonomic classification (da Silva et al. 2011, Collins and Cruickshank 2012). Therefore, as part of a larger taxonomic study on the South African hermit crab fauna, great care went into the sorting of divergent organismal groups. This integrated approach, with the morphological examinations informed by the barcodes, led to the preliminary discovery of the many unnamed putative species in *Paguristes* and *Diogenes*, but also to the finding of the distinctive Marion Island *lineage 2* of *Sympagurus dimorphus*, all of which are candidate species to be described in the future, pending more detailed taxonomic work. The potential of barcoding to identify crustacean larval forms (Costa et al. 2007) also led to the validated identifications of four deep-water hermit crab glaucothoe larvae.

The decision to treat the Marion Island *lineage 2* of *S. dimorphus* as distinct was done with some hesitation. Currently, this taxon is thought to be monophyletic, with a widespread distribution in the southern hemisphere, but also with considerable morphological variation (Lemaitre 2004b). However, newly available colour information of specimens from the South African type locality compared to previous and unpublished photographs (see Landschoff and Lemaitre 2017b), already pointed towards the possibility of the presence of a cryptic species. With the additional sequences from New Zealand that clustered together with the Marion Island *lineage 2* (Figure 7.1 D), it seemed justified to consider the two lineages as separate for this study, even when the taxonomy remains to be resolved. This approach reduced intraspecific divergence rates in the overall analysis. At slightly below 1%, the overall K2P intraspecific distance observed was consistent with results of other barcoding studies within the Crustacea (Lefébure et al. 2006, Costa et al. 2007, Radulovici et al. 2009, da Silva et al. 2011, Puillandre et al. 2011, Robe et al. 2012, Raupach et al. 2015). In contrast, a few species with taxonomic ambiguities, in which the separation into further defined species entities was not justifiable based on the available information, explain the notably increased maximum intraspecific divergences of up to 5.1%.

In particular, three problematic species are represented in the dataset (*Goreopagurus poorei*, *Pagurus cuanensis*, and *Areopaguristes* cf. *jousseaumei*, see Table 7.1–7.2) that potentially contain additional cryptic taxa, but at this stage the available data are insufficient to make this determination. Recently, *G. poorei* was discovered along the southern South African shelf region, extending its distribution from Tasmania across the southern Indian Ocean (Landschoff and Lemaitre 2017a). Given such an extreme extension of the distribution, the authors were initially inclined to describe the South African specimens as a new species, but could find only marginal morphological differences to the type specimen series from the Tasman Sea, that did not justify splitting these taxa. The maximum COI genetic distance of 5.0% of the newly available barcode sequence from the type locality to the sequences of specimens from South Africa was high compared to the overall average of <1.0% in this dataset, and also other values from the literature (also see section 7.5.5). For example, the Marion Island *S. dimorphus lineage 2*, which was treated as distinct from the South African species in this analysis, was 4.4–5.6% distant to the South African specimens. This indicates that the two populations of *G. poorei* are most likely genetically distinct as well. However, at a maximum distance of 2.0%, the divergence rate within the South African specimens of *G. poorei* alone was also comparatively high (Figure 7.1 C). Zhang et al. (2010) found that an ideal barcoding sample size often greatly exceeds the usual numbers of 5–10 specimens. Thus more sequences of *G. poorei*, especially from Tasmania, should be compared to explain/contextualise the genetic variation. After all, the currently available morphological and genetic data are consistent in that they are both revealing a close relationship, but so far fail to draw a clear picture.

A similar problem occurred in *P. cuanensis*, as one sequence in the dataset analysed was at maximum 5.1% distant to the other three. However, whether this is due to a cryptic lineage needs to be validated by more data. Morphologically, no differences between those specimens of *P. cuanensis* were detectable that would fall outside acceptable intraspecific morphological variations, but the species does show intraspecific variation that has resulted in taxonomic issues before (McLaughlin and Forest 1999, also see Chapter 8). If moderately homogenous divergence rates are assumed for members of the Paguridae, and if *P. cuanensis* indeed shows intraspecific divergence rates up to about 5.1%, then based on 5.0% COI genetic divergence of a single sequence alone, there is little justification to assume that *G. poorei* from South Africa is distinct from the Tasmanian specimens and *vice versa*.

A third problematic species, *Areopaguristes* cf. *jousseaumei*, clustered apart from *Areopaguristes engyops*, such that at least one of these two taxa might be erroneously assigned to the genus. Moreover, one sequence within *A.* cf. *jousseaumei* was 4.3% distant to one of the other three sequences, suggesting there could also be another cryptic lineage present (Figure 7.1 A, C). Chapter 8 discusses the strong variations and taxonomic difficulties of this species, and both morphological and molecular tools consistently fall short in providing a reliable identification. This might stem from a number of speculative reasons. There could generally be a greater genetic diversity than in other species and, in fact, the maximum intraspecific distance of 4.3% in *A.* cf. *jousseaumei* is not too far away from the 3.5% in *Diogenes brevirostris* or *Anapagurus hendersoni*, which are clear monophyletic species entities, but have better and therefore more fully resolving taxon sampling in this dataset. Another reason could be related to sequence quality or pseudogene issues of the particular sequence, or the problem might even go back to a case of hybridisation. What is also of interest is that the different lineages are not only from the same location, but all specimens were collected during the same sampling event. If there is indeed another distinct evolutionary unit hidden in this taxon, the taxonomy can only be resolved by a combination of increased molecular effort and careful morphological examinations.

Leaving the so far unnamed putative species in *Diogenes* and *Paguristes* aside, what is noteworthy is that, out of four species (*S. dimorphus*, *G. poorei*, *P. cuanensis* and *A.* cf. *jousseaumei*) with taxonomic issues that have challenged classic morphological techniques (Dechancé 1963, McLaughlin and Forest 1999, Lemaitre 2004a, Landschoff and Lemaitre 2017a, also see Chapter 8), only the case of *S. dimorphus* seems resolvable by the molecular approach of this study.

7.5.4 Divergence rates in hermit crabs

As already discussed, the moderately low intraspecific divergence rates for this set of data find their extreme maxima in the presence of a few sequences that involve the problematic and unresolved cases. The overlap analysis (Figure 7.2) reveals that COI DNA sequences are highly efficient in discriminating between specific and generic divergences in hermit crabs, and this efficiency is even increased to zero overlap (equal to 100% success) when the few ambiguous sequences of the problematic species are removed. These findings are consistent for the overall patterns in the Crustacea (Lefébure et al. 2006), and specifically the Decapoda (da Silva et al. 2011). The overlap at the genus-family level, however, which is near complete for the Diogenidae and about half for the Paguridae and Parapaguridae (Figure 7.2), shows that COI divergences can provide broad patterns, but lack the resolution to be an accurate model of evolution in hermit crabs, particularly at higher taxonomic levels.

7.5.5 Threshold evaluation and barcoding efficacy

The thorough sorting and identification of species resulted in a dataset with high taxonomic accuracy to be applied *a priori*. This high resolution of morphological taxonomy positively influenced threshold and BG values, because these values could be determined for well-defined taxonomic groups. Thresholds and success rates were most impacted by the *a priori* decision to treat the two lineages of *S. dimorphus* as distinct taxa. That the BG was present when assessed for each single sequence, but absent for the genus *Pagurus* when presenting the BG based on averaging intra- and interspecific distances of each genus (Table 7.2), shows that the gap was small and caused by the single problematic sequence in *Pagurus*. While the other problematic sequences (see above) decreased the barcoding gaps, they did not close them in those taxa. This is also indicated by the persisting overlap on species-genera levels (Fig 7.2).

The optimal threshold range of 3.5–3.7% to separate paguroid species in this dataset was closest to the originally-proposed barcoding threshold of 3.0% (Hebert et al. 2003). Lefébure et al.'s (2006) assumption-free statistical approach had a high (98.74%) success rate for a 4.6% threshold (Figure 7.3). However, testing this threshold in the *spider* barcoding efficacy evaluations, it was less appropriate for this dataset (Table 7.3). The *spider* in-build *localMinima* function (Brown et al. 2012), suggesting a threshold of 1.9% that led to five misidentifications, was closer to the optimal test result of only two misidentifications. It is not surprising that the discussed taxonomically-ambiguous specimens were responsible for the two sequences that could not be matched to their *a priori* species identifications. It should be mentioned that removing the three ambiguous sequences would have resulted in an optimal threshold range of 2.7-3.7%, with a 100% success rate. However, the efficacy evaluations of nearly 99% success were already extremely high for the entire dataset, highlighting how effective barcoding can be in an integrated taxonomic framework.

7.5.6 Conclusions

The dataset analysed for the South African continental marine habitats is one of the most comprehensive barcoding libraries of hermit crabs for any bioregion. Testing this set of data for barcoding efficacy revealed that, in an integrated taxonomic framework, the technique reaches barcoding identification rates near 100% success. However, the path to an automated paguroid identification process through barcodes remains long and winding. Molecular barcoding alone is no substitute for morphological taxonomy. Speculations suggest that the true number of hermit crab species in South Africa may well exceed 100 (see Chapter 8). Barcoding massively helped to inform morphological identifications, including glaucothoe larval stages of two deep-water species and 12 putative species. The latter still require additional taxonomic attention, and so do the other three cryptic species lineages discovered. However, despite considerable species coverage of 55 taxa, the dataset remains only about 50% complete. This means that even with a near 100% identification success rate, only every second species of hermit crab from this region would be identifiable by matching its COI sequence to a taxon from this molecular library. Although this study has shown the benefits of barcoding for hermit crabs, including some insights into phylogenetic relationships within the three main paguroid families, the regional study design inevitably limits geographic and taxonomic coverage. It remains to be tested if the findings hold true when species coverage is extended to global species distributions.

CHAPTER 8

TAXONOMIC REVISIONS AND ADDITIONS TO THE HERMIT CRAB (CRUSTACEA: DECAPODA: PAGUROIDEA) FAUNA OF SOUTH AFRICA

8.1 Abstract

Hermit crabs, or paguroids, are an important invertebrate group in the marine benthic environment, but taxonomic knowledge on the hermit crabs of South Africa, a biogeographically important region, is scarce. The last monographic revision was that of K. H. Barnard in 1950, this listing 32 paguroids as occurring in South African waters. The manifold taxonomic changes in nomenclature, and a number of new descriptions of species and taxonomic additions to the regional fauna over the past 70 years demand a comprehensive update. The aim of this study is to summarise literature records, to examine and report existing specimens that have accumulated in the collections of the Iziko South African Museum over the past decades, and also to add new species records resulting from specifically paguroid-targeted sampling efforts over the past three years. Taxonomic accounts are given for 62 species of the now 72 officially reported species to occur in South African mainland waters. The total of 72 species is an expansion of 56% since Barnard, and of about 20% since a recent species list published by Emmerson in 2016. Inaccuracies resulting from ambiguous previous species lists are rectified where this was possible. In this study, 12 species are reported from South Africa for the first time, and *Calcinus elegans*, a remarkably-coloured reef hermit crab, was rediscovered to occur in KwaZulu-Natal, nearly 175 years after its first and only South African record by F. Krauss in 1843. Furthermore, colour photographs of 51 species (71% of the total fauna), many of which are the first colour documentation of the respective species, and barcode reference accession numbers for 40 species (56%) of the 72 overall paguroids are provided. This information is tabulated at the end of the study, and together with the accounts and figures stand as taxonomic reference, but can also be used as a preliminary guide to the regional fauna. However, the account given is estimated to still only consider perhaps 60–70% of the true faunal diversity. Hence the updated listing provides considerable progress, but is also only a first important step towards a fully illustrated taxonomic catalogue to be collated in future.

8.2 Introduction

In South Africa, work on the decapod crustacean fauna, that includes Paguroidea (*sensu* McLaughlin et al. 2007a) commonly known as hermit crabs, has a long tradition, dating back to taxonomic accounts resulting from the first sampling expeditions to the Cape during the mid and late 19th century (Krauss 1843, Stimpson 1858, Studer 1883, Henderson 1888). Subsequently, knowledge was gradually accumulated, predominantly in the form of contributions and catalogues on the Crustacea by Stebbing (1910, 1914, 1917b, 1920, 1924). Together with other scattered literature, this information was synthesised into a 'Descriptive Catalogue of South African Decapod Crustacea' (Barnard 1950) and this still remains the pivotal taxonomic publication on this group, nearly 70 years after its publication. By today's understanding of recognised taxa, Barnard's monumental work reported on 32 species of hermit crabs from the South African continental waters. Since then, the South African fauna, which occupies a unique biogeographical region, has attracted the interest of other international experts (e. g. Forest 1954, McLaughlin 1998, Lemaitre 1999; McLaughlin and Forest 1999), but such work has been inconsistent, often confined to individual groups, and has usually been based on limited material. A review of this South African taxonomic literature for the Paguridae was provided by Landschoff and Lemaitre (2017a), and for the Parapaguridae by Landschoff and Lemaitre (2017b). Kensley's (1981) biogeographic list is now out-dated, and Emmerson's (2016a–c) recent multi-volume guide and checklist on the Decapoda of the region contains many taxonomic inaccuracies, lacks species validations, and also does not meet national requirements, such as a treatment of species confined to South Africa Griffiths (2017). Therefore, for over 70 years, Barnard's (1950) catalogue has remained the only full taxonomic treatment of paguroids of the region, but it includes less than half of the currently known South African species and the majority of them have undergone taxonomic changes. New sampling that has specifically targeted hermit crabs, together with the accumulation of literature records and specimen depositions into the collections of the Iziko South African Museum, Cape Town over decades, therefore now demands a comprehensive update, documenting all known hermit crab species reported from South Africa. The aim of this study is to summarise the most recent available species information, to report on existing material, and to account for all new findings made. In doing this, Barnard's (1950) catalogue is taken as the general baseline and all new information, whether published or unpublished, that adds new species or revises the nomenclature of existing ones that originate after that date, is provided in the following account.

8.3 Methods

Over the period December 2014 to September 2017, samples were collected around the South African coast at various sites, during multiple occasions, and using various methods (hand, diving, dredging, trawling). Whenever possible, specimens were photographed alive, either in the wild prior to collection, or in a photographic tank soon after collection. Thereafter, they were anaesthetised in a 0.125 $\frac{ml}{l}$ clove-oil seawater solution before freezing, and then extracted from their shells using a table vice. Additionally, pictures showing live colouration of the whole animal were taken from different angles, and tissue for molecular barcoding was extracted from most samples prior to or after preservation in 96% ethanol. Sequences of the cytochrome *c* oxidase subunit I (COI) fragment were generated at the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, using a methodology described previously (Landschoff and Lemaitre 2017b), and were also barcoded at the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, Canada. Barcodes were uploaded to the SeaKeys (SEAKY) project on BOLD (www.boldsystems.org; Ratnasingham and Hebert 2007). When available, the database gene codes are included under each species, although a full report on the barcoding database and the analysis thereof is currently being prepared in a separate publication (see Chapter 7).

Several additional distribution records were derived from photographs taken by professional biologists or citizen scientists during shore sampling and diving events, or from pictures taken during scientific deep sea explorations using a remotely operated underwater vehicle (ROV). The latter were collected during cruises sponsored by the Department of Environmental Affairs (DEA) and the National Department of Science and Technology (DST), in particular on board the DST/South African National Research Foundation, Pretoria, South Africa (NRF)-African Coelacanth Ecosystem Programme (ACEP) 'Spatial Solutions' and the ACEP-Operation Phakisa 'Deep Secrets' cruises. Furthermore, museum collections were consulted for historic records and comparative material. The vast majority of the reported samples are housed at the Iziko South African Museum, Cape Town (SAMC), but some material was also examined at the United States National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM), the Lee Kong Chian Natural History Museum, Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC), and the Museum für Naturkunde Berlin, Germany (ZMB).

In the compilation of the revised species list (Table 8.1), species were grouped into five categories: 1. Species included in Barnard (1950) without taxonomic name changes, 2. Species listed in Barnard (1950), but that have since undergone taxonomic change, 3. Species that have been added to the local fauna since Barnard (1950) in a taxonomic study, 4. Species listed by Emmerson (2016c) as an addition to the local fauna, but without taxonomic validation, and 5. Species reported herein as new records for South Africa. Only species that have a South African mainland/continental distribution were considered. However, several Mozambican records were also included under the material examined sections when they were regarded as useful and/or extended the distributional information, and a few specimens from other localities were examined as comparative material.

The synonymy given for each species is restricted to the most recent literature, and the most applicable records from the region. Moreover, information given under each species consists of at least the sections *Remarks*, *Distribution* and *Habitat*, and also includes the sections *Material* *examined*, *Genetic data* and *Diagnosis* (full, or as reference only), depending on availability. However, the aim was to give all these sections for species of Category 4 and 5. *Colouration* was additionally reported for species of which live colour had been insufficiently recorded in previous literature. Species that have never before been listed to occur in South Africa are also highlighted as new records. The South African distribution is given in brackets under each *Distribution* section. Except for *Calcinus elegans*, which has not been reported in the region for more than a century, species falling into Category 1. were not given own species entries, but were still included in the summary (Table 8.1), and colour pictures were also provided for those species upon availability. The term endemic (to South Africa) is used in the knowledge that many species are only known from single or few sampling events and the true distribution may be found to extend beyond national boundaries in the future. Station coordinates are given using the Degrees Decimal Minutes system. For historic samples these were acquired from the recent georeferencing efforts by the data management team from the Iziko South African Museum, Cape Town. Because old samples usually carry descriptive station data only, the coordinates given can have uncertain degrees of accuracy. For all new samples collected during the study period, coordinate measurements were directly taken in the field, or looked up using geographical information systems immediately after sampling. The terminology used, in general, follows Tudge et al. (2012), but group-specific terminology was used for individual species, usually as applied in the most recent literature cited for each species. Measurements in mm of specimens listed in the material examined sections are for shield length (SL), taken from the tip of the rostrum to the midpoint of the posterior margin of the shield.

8.4 Systematic account

8.4.1 Family Coenobitidae Dana, 1851

8.4.1.1 Genus *Coenobita* Latreille, 1829

Coenobita perlatus H. Milne Edwards, 1837, new record

Figure 8.1 A–B

Coenobita perlata H. Milne Edwards, 1837: 242 (type locality: “la mer du Sud”, = Pacific Ocean). – Fize and Serène, 1955: 24, Fig 3C, 4A–C, Pl 1–2.

Coenobita perlatus. – Alcock, 1905: 19, Pl 14 Fig 2, 2a. – Dechancé, 1964: 29. – Reay and Haig, 1990: 581. – Hogarth et al., 1998: 153. – Poupin et al., 2013a: 25, Fig 12A–C. – Poupin et al., 2013c: 7, Fig 3A, C. – Poupin et al., 2013d: 10. (list). – Poupin, 2016: 50, Fig 3 (list).

Material examined. 7 May 2017, near Shaka’s Rock, north of Durban (KZN), S 29° 30.66’, E 31° 13.98’, supralittoral, one specimen (still alive and in the author’s terrarium).

Diagnosis. Adapted after Alcock (1905). Shield covered with tubercles, particularly near margins. Ocular peduncles reaching beyond middle of ultimate segments of antennular peduncles (also of fifth segement of antennal peduncle), dorsal surface granulose; ocular acicles narrow, sharply acute. Antennal acicles fused to second peduncular segments. Upper margins of both chelae with brush of setae; stridulatory organ on upper outer surface of palm of left chela composed of 1–2 series of oblique laminar tubercles. Left cheliped with outer surface of palm and fixed finger regularly covered by conspicuous, round or bluntly acute tubercles, with or without minute corneous tips. Lateral surfaces of dactyl of left third pereopod flattened and separated from dorsal surface by distinct crest; propodus laterally convex without or with very weak crest formed by large rounded tubercles. Coxae of male fifth pereopods asymmetrical, produced posteriorly as short (left) and long (right) sexual tubes.

Colouration. For specimen of intermediate size (small specimens more white, large specimens almost entirely red, see Poupin et al. 2013a). Shield orange to cream with orange-red or purple patches laterally in anterior half and posteriorly, and also with interrupted orange-red longitudinal line in anterior half. Ocular peduncles white, dorsal and ventral surfaces orange-red, and also with narrow subcorneal red band; corneas brown. Antennular and antennal peduncles and flagellae predominantly orange. Chelipeds and ambulatory legs with white to cream background colouration and extended patches of orange-red to purple on outer or lateral faces; inner or mesial faces predominantly white. Lateral faces of dactyls and propodi each with large red-purple patch in proximal half, carpi and meri with red-orange patches dorsoproximally.

Remarks. *Coenobita perlatus* is poorly studied, particularly populations in the Western Indian Ocean. The specimen collected here generally agrees with the reports by Fize and Serène (1955) from Vietnam, and, comparing the colouration, it is in close agreement with reports of *C. perlatus* from more tropical locations in the Western Indian Ocean (e. g. see Poupin et al. 2013a). Furthermore, the intermediate red-orange colouration suggests that this specimen is a young adult as these colour patterns are often observed in specimens of medium size (J. Poupin pers. comm.). From the colouration alone it is clear that this specimen is neither one of the other two terrestrial hermit crabs occurring in South Africa, *C. rugosus* or *C. violacens*. Both these species have a more cream-brownish or pink background colour, but no red patches like *C. perlatus*. Furthermore, *C. perlatus* cannot be confused with *C. violascens* as the latter lacks the stridulating organ on the upper outer surface of the left cheliped. Morphological characters distinguishing *C. perlatus* from *C. rugosus* include the presence (in *C. perlatus*) of markedly larger blunt or corneous-tipped tubercles on the outer surface of the chela of the left cheliped, and also on the lateral surface of the propodus of the third left pereopod. The latter is also more convex in *C. perlatus*, not clearly forming a ridge that deliminates the lateral from the dorsal surface as in *C. rugosus*.

This is the first record for South African waters and so far the southwesternmost report of *C. perlatus*. It is not unlikely that increasing air and water temperatures have started a southward migration of this tropical species and this possibility should be taken into consideration when further investigations are carried out. At present, the specimen reported here is still alive and held in the author's terrarium, but the first molt will be deposited as museum voucher.

Distribution. South Africa (KZN), Mozambique Channel, Juan de Nova Island, Tanzania, Madagascar, Mauritius, Seychelles, Maldives, Christmas Island.

Habitat. Supralittoral.

Coenobita violascens Heller, 1862

Figure 8.1 E–F

Coenobita violascens Heller, 1862: 524 (type locality: Nicobar Islands). – McLaughlin et al., 2007b: 17, 2 unnumbered Figs. – Nakasone, 1988: 172, Figs 7A–F, 9E. – McLaughlin et al., 2010: 16, note 8, Fig 3H. – Emmerson, 2016b: 107, unnumbered Fig; 2016c: 447 (list). – Rahayu et al., 2016: 471 (comparative material).

Coenobita cavipes. – Barnard, 1950: 470. – Kensley, 1981: 33 (list). – Bouchard et al., 2013: 12, Fig 9A–B. – Poupin et al., 2013a: 25. [not *Coenobita cavipes* Stimpson, 1858]

Coenobita rugosus. – Emmerson, 2016b: 100, unnumbered Fig [(Fig only) not *Coenobita rugosus* H. Milne Edwards, 1837]

Material examined. 24 Jan 1949, UCT E. S. sta RH. B. 54.C (Pelican Island, Richards Bay, KZN), S 28° 47.88’, E 32° 05.34’, 1 ♂ 5.3 mm (SAMC MB-A079329); 23 Apr 1952, UCT E. S. sta DBN 115J (Durban, KZN), S 29° 52.32’, E 31° 03.66’, 1 ovig. ♀ 19.5 mm (SAMC MB-A083785); 15 Jan 1986, Mkambati (E. C.), S 31° 19.38’, E 29° 57.96’, 1 ♂ 13.3 mm (SAMC MB-A045520), coll. W. Emmerson.

Other material. 11 Mar 2016, Inhaca Island near Marine Field Station (Mozambique), S 26° 02.34’, E 32° 54.12’, one specimen photographed and lost.

Diagnosis. See McLaughlin et al. (2007b).

Remarks. The lack of taxonomic knowledge on violet to bluish-purple species of *Coenobita* without a stridulating organ on the left upper palm has led to the situation that, in the Western Indian Ocean, such species have usually (and probably incorrectly) been identified as *C. cavipes* Stimpson, 1858. Supported by molecular data, Rahayu et al. (2016) examined the species pair of *C. violascens* and *C. cavipes*, described a third species to this group, *C. lila*, and also found that specimens from Madagascar and Mayotte (same specimens as in Bouchard et al. 2013) were actually *C. violascens* and not *C. cavipes*. The occurrence of the latter in the Western Indian Ocean is therefore doubtful and should be examined in future.

Coenobita violascens is distinguished from *C. cavipes* by a set of characters, including the shorter shield (1.4 times as long as broad vs. 1.7 times as broad), the smoother lower outer surface of the left palm, the absence of tiny corneous teeth on the ventral surface of the dactyl of the third right pereopod, and the telson that has the left posterior lobe distinctly longer than the right (see Rahayu et al., 2016). A re-examination of specimens from South Africa, including Barnard’s specimen from Durban (SAMC MB-A079329), revealed that they are *C. violascens*. With the verification of *C. violascens*, the new finding of *C. perlatus*, and the previous records of *C. rugosus*,

Figure 8.1: Paguroidea of South Africa, family Coenobitidae Dana, 1851 (A–C, F *in situ*): A–B *Coenobita perlatus* H. Milne Edwards, 1837, north of Durban **B–C** *Coenobita rugosus* H. Milne Edwards, 1837, Pumula, ♂ 8.8 mm (SAMC MB-A066713); **E–F** *Coenobita violascens* Heller, 1862, Inhaca Island (Mozambique), specimen lost.

three species of coenobits are now recorded from South Africa. Emmerson's (2016b) picture of *C. rugosus* is actually almost certainly of *C. violascens*, whereas Branch et al.'s (2010, 2016) picture of *'C. cavipes'* shows most likely a specimen of *C. rugosus*.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Tanzania, Madagascar, Nicobar Islands, Cebu Island, Philippine Islands, Taiwan, Japan.

Habitat. Supralittoral, coastal vegetation.

8.4.2 Family Pylochelidae Bate, 1888

8.4.2.1 Genus *Trizocheles* Forest, 1987b

***Trizocheles balssi* (Stebbing, 1914)**

Pomatocheles balssi Stebbing, 1914: 3, Pl 65 (type locality: Cove Rock, near East London, South Africa). – Barnard, 1950: 414.

Trizocheles balssi. – Forest, 1987b: 196 (in part), [not Figs 47c, 66a, 67a, b, 69a, b = *T. hoensonae*]. – Forest, 1987a: 315, Fig (in part). – McLaughlin and Lemaitre, 2009: 219, Fig 16.

Material examined. *Holotype:* No date, s. s. *Pieter Faure* sta 1106 (off Cove Rock, East London, E. C.), S 33° 13.74', E 28° 02.46', 146–240 m, ♂ 3.0 mm (SAMC MB-A001571).

Remarks. When McLaughlin and Lemaitre (2009) reclassified the Pylochelidae and examined and redescribed Stebbing's holotype of *Trizocheles balssi*, they found that Forest's report of the species from the Comoro Islands and La Réunion was in fact of a different species, *T. hoensonae* McLaughlin and Lemaitre, 2009. Therefore, *T. balssi* remains only known from the holotype. Komai (2013) erroneously listed another species, *T. mutus* Forest, 1987b, to occur in South African waters. However, that species was actually described from Java, collected during Dr. TH. Mortensen's 'Java – South Africa Expedition 1929–30'. Without checking the original reference to pick up the mistake, Emmerson (2016c) reiterated this wrong information in his checklist, where he also lists *T. balssi*. However, in his accompanying text descriptions (as *Pomatocheles balssi*) Emmerson (2016b) correctly states that, so far, only one species of this family is known from southern African waters.

Distribution. Endemic to South Africa (E. C.).

Habitat. Hollow pieces of coral, about 200 m depth.

8.4.3 Family Diogenidae Ortmann, 1892

8.4.3.1 Genus *Aniculus* Dana, 1852

***Aniculus maximus* Edmondson, 1952**

Figure 8.2 A

Aniculus maximus Edmondson, 1952: 79, Figs 7a–f, 8 (type locality: Honululu). – Forest, 1984: 61, Figs 14, 22, 59–61. – McLaughlin et al., 2007b: 105, 2 unnumbered Figs. – Poupin, 2009: 60, unnumbered Fig. – Poupin et al., 2013a: 26, Fig 13A. – Poupin et al., 2013b: 4 (list). – King and Fraser, 2014: 286, unnumbered Fig. – Branch et al., 2016: 116, Fig 49.4. – Emmerson, 2016c: 448 (list).

Material examined. 15 Dec 1984, Landers Reef off Park Rynie (KZN), S 30° 20.16', E 30° 47.82', 40 m, 1 ovig. ♀ 24.0 mm (SAMC MB-A079393); 18 Oct 1986, Sponge Reef (Sodwana Bay, KZN), S 27° 31.98', E 32° 40.98', 26 m, Scuba, 1 ♀ 24.1 mm (SAMC MB-A045491), coll. D. Hebert.

Photographic records. 4 Mar 2007, off Scottburgh (Park Rynie, KZN), S 30° 17.97', E 30° 49.11', 25 m, Scuba, one specimen not collected (photographed by V. Fraser); 17 Feb 2008, 9-Mile reef (Sodwana Bay, KZN), S 27° 24.81', E 32° 43.69', 18 m, Scuba, one specimen not collected (photographed by V. Fraser); 22 Jun 2012, 9-Mile reef (Sodwana Bay, KZN), S 27° 24.81',E 32° 43.69', 18 m, Scuba, two specimens fighting, not collected (photographed by V. Fraser).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. *Aniculus maximus* is one of three known species of *Aniculus* to occur in South African waters. Because previous authors overlooked literature records, this situation has led to some confusion. In his catalogue on the South African Crustacea, Barnard (1950) included two species of the genus, *Aniculus aniculus* (Fabricius, 1787), and *A. strigatus* (Herbst, 1804), of which the latter record is now accepted to be *Ciliopagurus tricolor* Forest, 1995. In the collections of the Iziko South African Museum there is only one specimen of *Aniculus sensu* Forest, 1984 dating back to Barnard's time, which is an ovigerous female specimen from Mauritius previously labelled as *A. aniculus*, but in fact the identity of this specimen is *Aniculus ursus* (Olivier, 1811). At Barnard's time, *A. maximus* had not yet been described. Most likely, Barnard therefore based his record of *A. aniculus* for the region not on an actual specimen, but solely on the previous report from Mozambique Island (Hilgendorf 1879, p. 824, as *Pagurus (Aniculus) aniculus*), while using the specimen from Mauritius as a reference. Kensley (1981) reiterated this information, and later, Forest (1984) corrected all records of *A. aniculus* from the Indian Ocean (including Barnard's) to *A. ursus* (also see remarks under that species). However, this name change was not picked up by later South African authors, so that Emmerson (2016c) listed *A. maximus* as a new record for Southern Africa (since Kensley 1981), while also retaining *A. aniculus* (Fabricius, 1787) as an occurrence record for the Western Indian Ocean (Mozambique). However, the true *A. aniculus* (Fabricius, 1787), as currently known, has a distribution confined to the central Pacific and does not occur in the region. Moreover, Emmerson (2016c) without comment did not provide validation for the identity of *A. maximus* such as a picture or a museum reference, but the two physical specimens reported here are with certainty the basis of his record.

The specimens agree with the diagnosis by McLaughlin et al. (2007b), even if some slight variations of the length relationships of the cephalic appendages were noticed. In the South African specimens the ocular peduncles are only about 0.8 the length of the shield, and the antennular peduncles do not reach the proximal margins of the corneas. In life, *A. maximus* is readily distinguished from *A. ursus* by the colouration (generally golden-orange to yellow vs. generally olive-green to blue with red and black). In preservative, the two species can be separated by the number of striae or grooves on the ventral surface of the coxae of the chelipeds. *Aniculus maximus* has a single, short transverse groove and *A. ursus* has two long ones. Because *A. maximus* can be identified from images (Poupin et al. 2013a), there is little doubt about the identity of the photographic records, which reveal that this species is not uncommon in South Africa.

Distribution. South Africa (KZN), Mozambique Channel, La Réunion, Seychelles, Taiwan, Japan.

Habitat. Rocky reefs, typically found under ledges or in caves, occupying large shells, 15–50 m depth.

Aniculus retipes **Lewinsohn, 1982a**

Figure 8.2 B–C

Aniculus retipes Lewinsohn, 1982a: 76, Figs 1–2 (type locality: Mersa Bareika, Red Sea). – Forest, 1984: 51, Figs 13, 20, 51–58. – Haig and Ball, 1988: 158. – Reay and Haig, 1990. – Rahayu, 2000: 378. – McLaughlin et al., 2007b: 101, 2 unnumbered Figs. – Poupin et al., 2013a: 26, Fig 13B. – Poupin et al., 2013d: 10 (list). – Emmerson, 2016c: 448 (list).

Material examined. Nov 1990, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', no depth, 1 ♀ 7.2 mm (SAMC MB-A045366), coll. W. Emmerson and G. Fotherby; 1989, Bazaruto (Mozambique), S 21° 31.90', E 35° 29.13', no depth, 1 ♂ 7.5 mm (SAMC MB-A045362), coll. W. Emmerson.

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Emmerson (2016c) listed *Aniculus retipes* as a new record to the region without comment or reference to a museum voucher, but his record is without doubt based on the specimens he collected himself, and which are officially reported here. The male specimen from Bazaruto, central Mozambique, is included here as it connects the recently reported South African record with the known East African distribution. The two specimens fully agree with the diagnosis by McLaughlin et al. (2007b), and this species, also much smaller in size and different in colouration, can easily be distinguished from *A. maximus* and *A. ursus* by the interrupted transversal striae on the propodi of the second and third pereopods. Both of the other species have uninterrupted striae.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Glorieuses Islands, Tanzania, Red Sea, Indonesia (Banda Sea), Vietnam, Taiwan, South China Sea, Japan.

Habitat. Shallow reefs, on coral or coral rubble, intertidal to 15 m. Specimens reported here without depth information, but probably from same habitat.

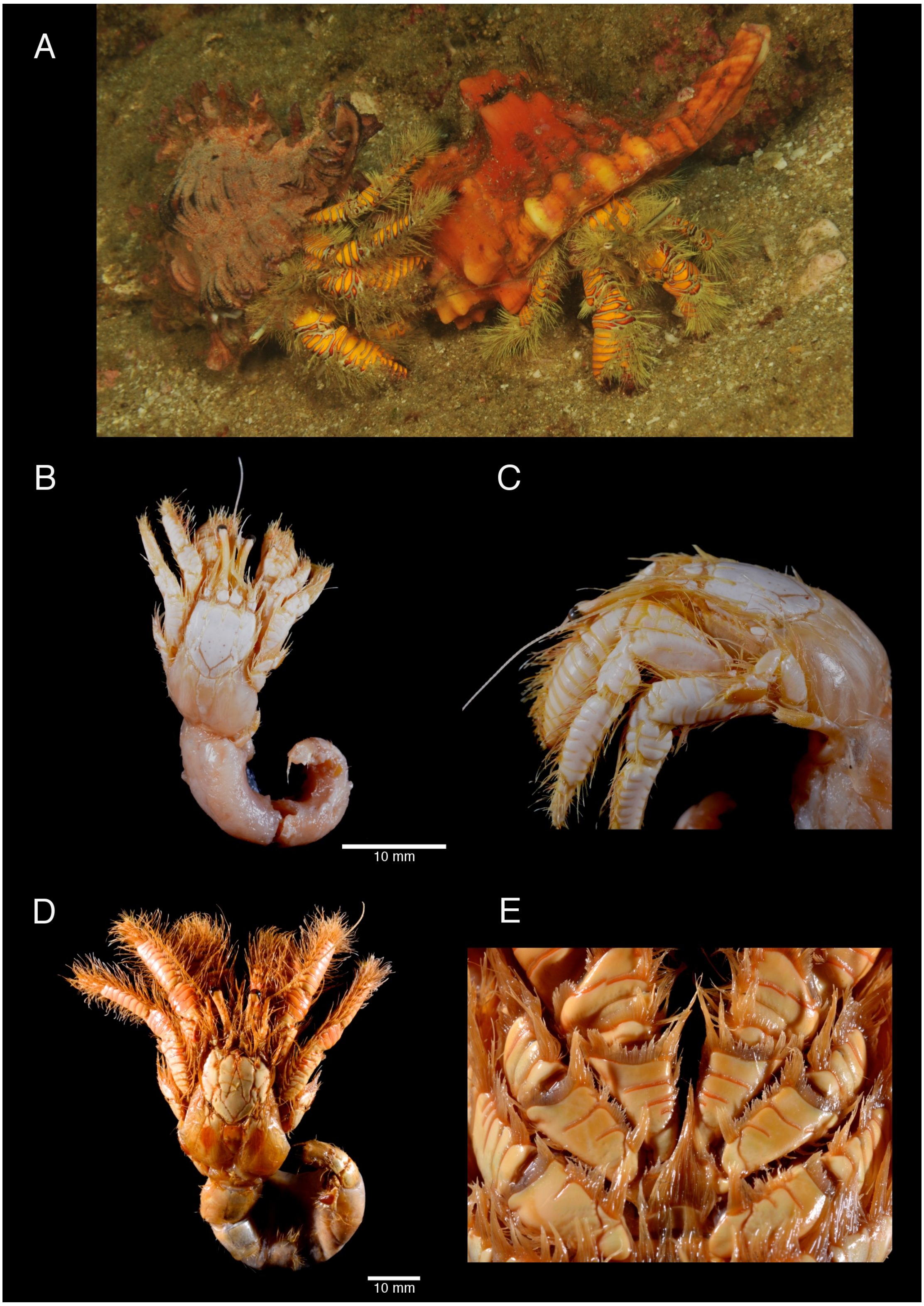

Figure 8.2: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A *in situ*, B–E in preservative): **A** *Aniculus maximus* Edmondson, 1952, Sodwana Bay, specimens not collected (photo V. Fraser) **B–C** *Aniculus retipes* Lewinsohn, 1982a, Sodwana Bay, ♀ 7.2 mm (SAMC MB-A045366), whole dorsal aspect (B), left lateral aspect (C) **D–E** *Aniculus ursus* (Olivier, 1811), ♂ 14.9 mm (SAMC MB-A045454), whole dorsal aspect (D), anterior ventral aspect with coxae of chelipeds and pereopods (E).

Aniculus ursus (Olivier, 1811), new record

Figure 8.2 D–E

Aniculus aniculus. – Barnard, 1950: 431. – Emmerson, 2016c: 447 (list). [all not *Aniculus aniculus* (Fabricius, 1787)]

Aniculus ursus Forest, 1984: 26, Figs. 1–7, 9, 17, 31, 36, 67, 69–73. – Reay and Haig, 1990. – McLaughlin et al., 2007b: 109, 2 unnumbered Figs. – Poupin, 2009: 60, unnumbered Fig. – Poupin et al., 2013a: 26, Fig 13C. – Poupin et al., 2013c: 7 (list), Fig 5D.

Material examined. 1935, Mauritius, no depth, 1 ovig. ♀ 19.2 mm (SAMC MB-A010926); 18 Aug 1989, Treasure Beach (Durban, KZN), S 29° 56.99', E 31° 00.00', no depth, 1 ♂ 14.9 mm (SAMC MB-A045454), coll. T. Stewart; 1989, Bazaruto (Mozambique), S 21° 31.92', E 35° 29.16', no depth, 1 ♂ 19.9 mm (SAMC MB-A045481), coll. W. Emmerson; 1935, Mauritius, no depth, 1 ovig. ♀ 19.2 mm (SAMC MB-A010926).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. For years this species has been subject to confusion in the local literature because previous authors overlooked the fact that Forest (1984) corrected Barnard's record of *A. aniculus* to *A. ursus* (also see remarks under *A. maximus*). Barnard (1950) only gave very little morphological information and a brief account on the colouration. Although slightly contradictory compared to the colour information from modern photographs, Forest (1984) changed the name, but it is unlikely that Forest examined the 1935's specimen from Mauritius in the collections of the formerly South African Museum. The other two specimens were only collected after Forest's revision of *Aniculus.* However, because Barnard gave the maximum carapace length (shield plus posterior carapace) as 40 mm, it seems clear that he indeed reported the intermediately-sized *A. ursus* and neither of the other two species.

The three specimens at the Iziko South African Museum (one from South Africa, one from Mozambique, one from Mauritius) agree well with the diagnosis by McLaughlin et al. (2007b). The only marginal difference observed is that the first proximal stria on the propodi of the pereopods are often interrupted. The male specimen from Bazaruto is damaged and in fact appears to be a moult, as the majority of the cephalic appendages are missing, but there is no doubt about the species identity. Because both Barnard and Emmerson listed *A. aniculus* (Fabricius, 1787) (actually *A. ursus*) only for Mozambique, this is the first validated record of *A. ursus* for South African waters.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, East coast of Africa, Madagascar, La Réunion, Mauritius, southern India, Cocos (Keeling) Islands, Australia, western Pacific, including Okinanwa and Taiwan to Fiji.

Habitat. Reef platforms and gullies, intertidal to 30 m depth.

8.4.3.2 Genus *Areopaguristes* Rahayu and McLaughlin, 2010

Areopaguristes engyops (Barnard, 1947)

Fig 8.3 A–B

Paguristes engyops Barnard, 1947: 375 (type locality: False Bay, Western Cape, South Africa). – Barnard, 1950: 421, Fig 78 h–i. – Forest, 1954: 204, Fig 25, 40, 51, 64. – Day et al., 1970: 56. – Kensley, 1974: 65 (list). – Kensley, 1981: 32 (list).

Stratiotes engyops. – Rahayu, 2005: 5.

Areopaguristes engyops. – McLaughlin et al., 2010: 18 (list). – Branch et al., 2016: 114, Fig 48.8. – Emmerson, 2016c: 448 (list).

Material examined. *Syntypes*: 1 Mar 1915, Buffels Bay (False Bay, W. C.), S 34° 19.20', E 18° 27.72', 3 ♂♂ 1.5–1.7 mm, 3 ovig. ♀♀ 1.4–1.9 mm, 1 ♀ 1.8 mm, 1 specimen (in shell) (SAMC MB-A003255). *Non-type material*: 24 Apr 1962, Schaapen Island (Langebaan, W. C.), S 33° 05.64', E 18° 01.38', 3 ♂♂ 3.6–3.9 mm (SAMC MB-A011079); 7 May 2016, Wooley's Pool (False Bay, W. C.), S 34° 07.98', E 18° 26.88', intertidal, 12 ♂♂ 1.3–2.0 mm, 11 ovig. ♀♀ 1.8–2.2 mm (SAMC MB-A066656), 1 ♂ 1.3 mm (SAMC MB-A066665), 1 ♀ 1.8 mm (SAMC MB-A066666), 1 ♂ 1.7 mm (SAMC MB-A066667), 1 ♀ 1.8 mm (SAMC MB-A066668), 1 ovig. ♀ 1.7 mm (SAMC MB-A066669); 14 Aug 2016, Wooley's Pool (False Bay, W. C.), S 34° 07.98', E 18° 26.88', intertidal, 1 ♂ 2.9 mm, 2 ovig. ♀♀ 1.8–1.9 mm, 1 brood. ♀ 1.8 mm (with 4 glaucothoe stages), 1 ♀ 1.9 mm (SAMC MB-A065650); 8 Aug 2017, Kommetjie (Cape Peninsula, W. C.), S 34° 08.34', E 18° 19.14', intertidal, 5 ♂♂ 1.4–2.8 mm, 1 ovig. ♀ 1.8 mm, 5 ♀♀ 1.4–2.5 mm (SAMC MB-A066657).

Genetic data. Wooley‘s Pool (False Bay), S 34° 07.98', E 18° 26.88', intertidal, two entire specimens used, BOLD: SEAKY232-15 (SAMC MB-A 065645), BOLD: SEAKY235-15 (SAMC MB-A065648).

Colouration. Shield and posterior carapace predominantly cream, with some faint orange. Branchiostegites cream, with some orange. Ocular peduncles cream to faintly blue or greenish; corneas brownish-red. Antennular peduncles bright blue, upper flagella faintly orange. Antennal peduncles cream, with some blue, fifth segments light orange, flagella bright orange. Chelipeds and ambulatory legs cream, usually each segment proximally with very faint orange ring or patch. Pleon light brown. Eggs orange.

Remarks. *Areopaguristes engyops* can be locally the most common hermit crab species in the Cape, as it occurs in the hundreds under boulders in the mid-intertidal zone. The colour of the cephalic appendages (orange antennal flagella and blue antennules) unmistakably separates it from co-occurring juvenile specimens of *Paguristes gamianus* (H. Milne Edwards, 1836), which have orange-red antennules. Colouration of *A. engyops* is herein reported for the first time. The syntypes are well-preserved, but many have lost their appendages. Moreover, they are considerably less setose, probably because previous workers removed parts of the setation.

Day et al. (1970) reported this species to occur in Lüderitz, Namibia, but this distribution has to be validated. *Areopaguristes engyops* broods its young, which are 'piggybacked' on the pleon of the brooding females. This fascinating behaviour deserves further study.

Distribution. ?Namibia, South Africa (W. C., from Paternoster, just north of Saldanha Bay, to Hermanus).

Habitat. Intertidal under rocks and boulders with rubble and coarse sand.

***Areopaguristes* cf. *jousseaumei* (Bouvier, 1892), new record**

Figure 8.3 C–D

Paguristes jousseaumei Bouvier, 1892: 50 (type locality: Red Sea). – Dechancé, 1963: 292, Figs 1, 4, 7, 10, 12.

?*Paguristes jousseaumei*. – Reay and Haig, 1990: 583.

?*Areopaguristes abbreviatus*. – Poupin et al., 2013a: 28, Fig 13 D–E. – Poupin et al., 2013d: 10 (list). – Poupin, 2016: 50 (list).

Material examined. 14 Oct 2015, off Pumula (KZN), S 30° 38.34', E 30° 32.94', 35 m, Scuba, 1 ♂ 3.7 mm (SAMC MB-A066412), 1 ♂ 3.4 mm (SAMC MB-A066413), 1 ♀ 2.9 mm (SAMC MB-A066414), 1 ♂ 3.0 mm (SAMC MB-A066415), 1 ♀ 2.6 mm (SAMC MB-A066416), 2 ovig. ♀♀ 2.1–2.3 mm (SAMC MB-A066677), 3 ♂♂ 1.6–2.7 mm, 2 ovig. ♀♀ 2.3–2.7 mm (SAMC MB-A066678), 2 ♂♂ 1.8–2.1 mm, 2 ♀♀ 2.3–2.7 mm (SAMC MB-A066675), 4 ♂♂ 2.3–3.3 mm, 2 ♀♀ 2.0–2.9 mm (SAMC MB-A066674); 2 Nov 2016, Taffy's Cracker Ground off Pumula (KZN), S 30° 39.24', E 30° 32.58', 36 m, Scuba, 2 ♂♂ 2.4–3.7 mm, 1 ♀ 2.0 mm (SAMC MB-A066686); 6 Nov 2016, Pumula 22 (KZN), S 30° 38.40', E 30° 34.20', 36 m, Scuba, 1 ♂ 2.2 mm, 1 ♀ 2.9 mm (SAMC MB-A066685); 11 Nov 2016, Sezela (KZN), S 30° 24.66, E 30° 44.46', 50 m, Scuba, 1 ♀ 2.5 mm (SAMC MB-A066721); 4 Dec 2016,"R"southwest of Port Shepstone (KZN), S 31° 02.28', E 30° 39.54', 70 m, Scuba, 1 ♂ 2.7 mm, 1 ♀ 2.5 mm (SAMC MB-A066676).

Genetic data. Off Pumula, S 30° 38.34', E 30° 32.94', 35 m, ♂ 3.4 mm, BOLD: SEAKY1151-16 (SAMC MB-A066413), ♀ 2.9 mm BOLD: SEAKY1152-16 (SAMC MB-A066414), ♂ 3.0 mm, BOLD: SEAKY1153-16 (SAMC MB-A066415), ♀ 2.6 mm, BOLD: SEAKY1154-16 (SAMC MB-A066416).

Diagnosis. Twelve pairs of biserial gills. Shield longer than broad, rostrum broadly triangular, reaching to or slightly overreaching bases of ocular acicles, terminating acutely; lateral projections about as long as rostrum, acutely triangular, each with terminal spine. Branchiostegites each with 1 or 2 minute spinules on distal margin. Ocular peduncles very swollen basally, distally slender and long, left marginally longer, about 0.6–0.7 length of shield; corneas small and rounded; ocular acicles distally elongated, subquadrate and approximate, terminal margins with 4 spines. Antennular peduncles exceeding corneal margins by 0.5–0.8 the length of ultimate segments, basal segments with small spine on lateral margin. Antennal peduncles overreaching

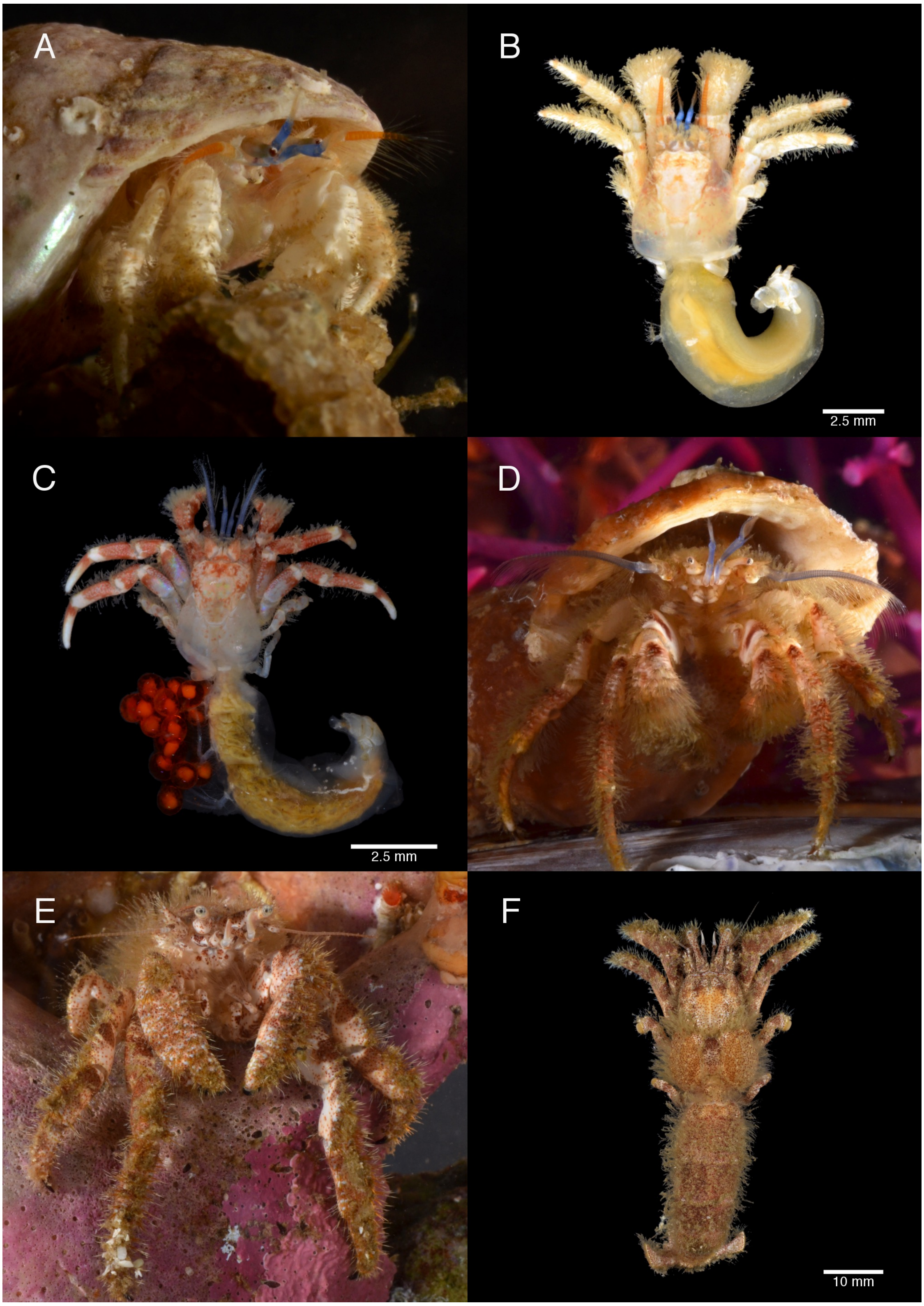

Figure 8.3: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A, D–E *in situ*): A–B *Areopaguristes engyops* (Barnard, 1947), False Bay, ♂ 2.0 mm (SAMC MB-A065650) (A), Kommetjie, ♂ 2.8 mm (SAMC MB-A066657) (B) **C–D** *Areopaguristes* cf. *jousseaumei* (Bouvier, 1892), Pumula, ovig. ♀ 2.1 mm (SAMC MB-A066677) (C), probably ♂ 2.6 mm (SAMC MB-A066678) (D); **E–F** *Cancellus macrothrix* Stebbing, 1924, False Bay, ♂/♀ 9.0 mm (SAMC MB-A066204).

bases of corneas; fifth and fourth segments unarmed; third segments ventrodistally with row of about 4 spinules on terminal margins; second segments with laterodistal angle produced and bearing 2 or 3 spines, mesiolateral angle with small spine; first segments with dorsolateral distal spine; antennal acicles with mesial margins somewhat sickle-shaped, each reaching to about 0.3 length of ultimate segment, terminating in strong bifid spine, mesial and lateral margins armed with 4 or 5 and 3 or 4 strong spines, respectively, concealed by dense long plumose setae; antennal flagella slightly longer than shield, proximal-most segments wider or about the same diameter as the corneas. Chelipeds subequal, left usually slightly larger, armature similar; dorsal surfaces of dactyls, chelae and carpi with variably plumose setae, usually short and stiff in proximal 0.2 and long and plumose distally; palms with row of 4 large corneous-tipped spines on dorsomesial margins; carpi with dorsomesial margins with 4 corneous-tipped spines, dorsal surfaces with row of tuberculate spines near dorsomesial margins, mesially weakly concave and smooth; meri with small dorsodistal spine and with 1 or 2 small subdistal spines or row of transversal subdistal spines, dorsal margins proximally without row of spines, ventromesial margin with row of about 6 strong, often corneous-tipped spines. Left second and third pereopods slightly longer than right, with rows of plumose setae on dorsal and ventral margins (ventral margins of dactyls hardly setose). Dactyls longer than propodi, dorsal margins with row of plumose setae, ventral margins usually with a single larger subdistal corneous spinule. Propodi of pereopods with (second) and without (third) row of corneous-tipped spines on dorsal margins. Carpi with 1–2 rows of prominent corneous-tipped spines (second) and row of small spines (third) on dorsal margins; lateral surfaces with longitudinal sulci near dorsal margins (usually with at least 1 prominent spine distally). Females with large, unpaired gonopore on coxa of third left pereopod, and also with variably pronounced, small brood pouch-like structure, consisting of row of moderately long to long plumose setae arising at posterior base of fourth pleopod, continuing onto central lateral surface, and usually leading into small triangular or oval flap with long setae on terminal margin. Right uropods very small, left markedly larger and longer. Telson with posterior lobes asymmetrical, left larger, separated by shallow median V-shaped cleft, terminal margins each with 4–6 (left) and 3 or 4 (right) spines.

Colouration. Shield cream to pinkish-white, with brown-pinkish patches in anterior half, usually with larger median patch, and also with one smaller patch proximal of the lateral projections. Ocular peduncles cream to pinkish-white proximally, in proximal half with weakly-defined diagonally-transversal brown-pinkish band or patch, and also with weak brown band distally; corneas black to golden; ocular acicles cream with darker pinkish-brown patch in proximal half. Antennular peduncles with basal segments cream; ultimate, penultimate segments and flagella transparent-light to darker blue, with weakly defined longitudinal blue stripes along ventromesial margins. Antennal peduncles cream to pinkish-white with brown-pinkish patches; fifth segments and flagella light blue, similar but generally slightly less intense as antennal peduncles; antennal acicle basally with brown-pinkish patch. Third maxilliped with each segment of endopod proximally with brown-pinkish band or patch. Chelipeds and pereopods cream to yellow-white with brownish patches, colouration markedly obscured by dense yellow-brown plumose setae. Chelipeds with brown bar or patch near proximal upper outer and inner margins of carpi; meri with similar central band. Pereopods similar, each with dactylus, propodus and carpus distally cream to white, centrally brownish-red to pinkish, and proximally with darker undefined band or patches. Pleon yellow. Uropods and telson cream-white. Eggs bright orange.

Remarks. Considerable uncertainties and taxonomic problems emerged with the attempt to assign the South African specimens. Two species of *Areopaguristes* Rahayu and McLaughlin, 2010, *A. abbreviatus* (Dechancé, 1963) and *A. micheleae* Rahayu, 2005 are reported from the vicinities of the Mozambique Channel and Madagascar, and a third South African endemic, *A. engyops* (Barnard, 1947), is found in the Cape. Because *A. engyops* inhabits intertidal habitats of much colder temperature, and *A. micheleae* occurs in deeper waters, when initially identifying the KwaZulu-Natal specimens in the field it was thought that *A. abbreviatus* had been discovered in South Africa. However, careful examination revealed that the South African specimens reported here, which look very similar to the reported *A. abbreviatus* from the Western Indian Ocean (Poupin et al. 2013a), are most certainly not *A. abbreviatus*. Instead, particularly in the dimensions of the cephalic appendages they agree with the drawings by Dechancé (1963) of *A. jousseaumei* (Bouvier, 1892), a poorly known species described from the Red Sea and previously assigned to *Paguristes* Dana, 1851. This species has tentatively been reported from Kenya (Reay and Haig 1990), and also from Somalia (Lewinsohn 1982b), but from much shallower depths (intertidal) than the South African specimens.

Following the revision and restriction of *Paguristes* by Rahayu (2005), gill condition is currently the main character to separate the two genera *Areopaguristes* (12 pairs of gills) and *Paguristes* (13 pairs of gills). Later, Rahayu (2007) revised *Paguristes abbreviatus* Dechancé, 1963, found it to have 12 pairs of gills, and transferred it to *Stratiotes* Thomson, 1899. Because *Stratiotes* Thomson, 1899 was subsequently discovered to be a junior homonym of *Stratiotes* Putzeys, 1846, (Coleoptera), the generic name was replaced by *Areopaguristes* Rahayu and McLaughlin, 2010. Up until now, *A. jousseaumei* had remained in *Paguristes*, simply because it has not been revised since Rahayu's (2005) restriction of *Paguristes* to species with 13 pairs of gills. Because no original material of *A. jousseaumei* was available for this study, uncertainty of the gill condition remains and requires to be confirmed pending a comparison and gill count in the type specimens residing in Paris. Nevertheless, the species is herein moved to *Areopaguristes* based on the close relationship (in particular the extended and elongated ocular peduncles) of the South African specimens with *A. abbreviatus* (and also *A. engyops*), and because the South African specimens have 12 pairs of gills.

The South African specimens agree with *A. jousseaumei*, and simultaneously disagree with *A. abbreviatus* in the following characters: the basally bulbous ocular peduncles; the long and slender ocular acicles; the long, considerably inwardly-curved antennal acicles armed with about 4 or 5 spinules on both the mesial and lateral margins; the antennal flagella that are longer than the shield; the chelipeds with the non-setose, unarmed, and weakly concave central area on the dorsal surface of the carpus. Another character, in which the South African specimens are different to *A. abbreviatus* is the armature of the merus of the chelipeds. Rather than having a row of spines on the dorsal margin, the South African specimens have a largely unarmed proximal dorsal margin. Contrastingly, they have more and stronger spines on the ventrolateral and ventromesial margins than *A. abbreviatus*. Furthermore, the third and second pereopods in *A. abbreviatus* have the ventral margins of the dactyls armed with numerous spinules, while the specimens here only have a single prominent subdistal spinule and are also different in the armature and setation of the other segments. None of the previous authors have described the meri of the chelipeds or pereopods for *P. jousseaumei* in detail and these characters should be studied in future when the type specimens can be examined.

Another character of interest is the small reported brood pouch in females of *A. abbreviatus*, that, according to Dechancé (1963) is lacking in the (probably damaged) female holotype (also see Rahayu 2007). The South African specimens have a very small pouch-like structure probably similar to *A. abbreviatus*, which according to Dechancé (1963) is not present in *P. jousseaumei*. To add even more confusion, the South African specimens can vary in the armature of the dorsolateral and lateral margin of the second segment of the antennal peduncle. Usually, they have a total of 2 spines like *P. jousseaumei*, but rarely they can have 1 or 2 additional lateral spines like *A. abbreviatus*. Extreme variation was observed in the setation. Some specimens are covered by densely plumose setae, while in others the distal plumose part of the setae can be almost entirely lacking, making the setae rather short and stiff. It seems that the extent of the setation is variable and hence not suitable for the separation of species. Using setation to deliminate species in this group of hermit crabs has led to considerable erroneous assumptions in the past (see Dechancé 1963). Moreover, preliminary genetic testing revealed that cryptic species might be hidden even within the South African population (see Chapter 7). To fully resolve the identity of the specimens reported here, *A. jousseaumei* and its allies probably will have to be revised, also using more data and more molecular markers. Nevertheless, this report constitutes the first record for South African waters.

Distribution. South Africa (KZN), ?Mozambique Channel, ?Glorieuses Islands, ?Kenya, Somalia, Red Sea.

Habitat. Intertidal to 70 m depth; in South Africa on rocky reefs, 35–70 m depth.

8.4.3.3 Genus *Calcinus* Dana, 1851

Calcinus elegans (H. Milne Edwards, 1836)

Figure 8.4 A–B

Pagurus elegans H. Milne Edwards, 1836: 278, Fig 2, Pl 13 (type locality: New Ireland, Papua New Guinea). – Krauss, 1843: 57.

Calcinus elegans. – Stebbing, 1910: 353. – Barnard, 1950: 438. – Dechancé, 1964: 29. – Kensley, 1981: 31 (list). – Lewinsohn, 1982b: 56. – Reay and Haig, 1990. – Gherardi and McLaughlin, 1994:

618. – McLaughlin et al., 2007b: 155, 2 unnumbered Figs. – Poupin, 2009: 64, unnumbered Fig. – Poupin et al., 2013d: 10. – Emmerson, 2016c: 448 (list). – Poupin, 2016: 50 (list).

Material examined. 21 Sep 2017, Isipingo (KZN), S 29° 59.88', E 30° 56.94', intertidal, 1 ♀ 9.2 mm (SAMC MB-A066661), coll. A. Botha and C. L. Griffiths.

Diagnosis. See McLaughlin et al. (2007b), and also Poupin (2003).

Remarks. Although *C. elegans* is neither a new record for South Africa nor has undergone taxonomic change since Barnard (1950), it is included here because finding a specimen in KwaZulu-Natal constitutes the first record of the species for South Africa in over 170 years. Krauss (1843) reported a single specimen from the coast of the former Natal giving a brief account on its colouration. His description fits moderately well to *C. elegans*, and seems certain based on the fact that he highlighted the row of red tufts of setae on the dactyls of the pereopods. However, his account is also contradictory in describing the antennular peduncles as blue (which are actually orange), and the chelipeds and ambulatory legs as whitish to blue with reddish brown transversal bands and a longitudinal stripe on the propodi (which are actually blue with brown bands and without a well defined longitudinal stripe). It is therefore most likely that Krauss prepared his description after preserving the sample in alcohol where the light blue colour fades quickly (pers. obs.).

It is unclear if Krauss' specimen still exists and its identity has never been verified. Another sample present in the collections of the Iziko South African Museum, SAMC MB-A043375, collected in 1917 in Durban, carried the label "?*Calcinus elegans*". However, this specimen was found to be *Clibanarius virescens* (Krauss, 1843) and it is unclear if any earlier carcinologist ever examined it. Hence although at least slightly doubtful, Barnard (1950) and all later authors accepted Krauss' record of *C. elegans* without questioning its identity. *Calcinus elegans* is uncommon, but widely distributed, and after 175 years can finally be confirmed to occur in South African waters.

Distribution. South Africa (KZN), Juan de Nova Island, Glorieuses Islands, Somalia, Tanzania, Madagascar, La Réunion, Mauritius, Seychelles, Chagos Islands, Western Australia, Taiwan, Japan, central Pacific.

Habitat. Exposed rocky shores, on algal ridges, coral or coral rubble of shallow reef edges, intertidal and subtidal to about 10 m depth.

***Calcinus guamensis* Wooster, 1984, new record**

Figure 8.4 C

Calcinus guamensis Wooster, 1984: 141, Fig 4 (type locality: Mariana Islands). – McLaughlin et al., 2007b: 174, 2 unnumbered Figs. – Poupin, 2009: 66, unnumbered Fig. – Poupin et al., 2013a: 54 (list). – Poupin et al., 2013c: 7 (list). – Poupin, 2016: 50 (list).

Material examined. 6 Dec 2012, Archers (3-Mile reef, Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 11 m, Scuba, 1 ♂ 2.5 mm (SAMC MB-A065984), 1 ♀ 2.1 mm (SAMC MB-A065985), 1 ♂ 1.4 mm

(SAMC MB-A065986), 1 ovig. ♀ 1.5 mm (SAMC MB-A065987), 1 ♂ 1.8 mm (SAMC MB-A065988), 1 ♂ 2.2 mm (SAMC MB-A066717).

Genetic data. Archers, 3-Mile reef, Sodwana Bay, S 27° 31.68', E 32° 41.22', 11 m, ♀ 2.1 mm, BOLD: SEAKY572-15 (SAMC MB-A065985), ♂ 1.8 mm, BOLD: SEAKY575-15 (SAMC MB-A065988).

Diagnosis. See McLaughlin et al. (2007b) and Poupin and Lemaitre (2003).

Remarks. The South African specimens agree well with previously reported morphology and colour pattern. This is the first record of *C. guamensis* in South African waters.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Juan de Nova Island, La Réunion, Cocos (Keeling) and Christmas Islands, northwestern Australia, Vietnam, Indonesia, Taiwan, southern Japan, Mariana and Hawaiian Islands.

Habitat. Coral reefs and rubble, often found in between branches of living coral, intertidal and subtidal to about 20 m depth.

Calcinus morgani Rahayu and Forest, 1999

Figure 8.4 E–F

Calcinus morgani Rahayu and Forest, 1999: 465, Figs 1B, 2C–D, 2G–H, 2J, 3 (type locality: Indonesia). – McLaughlin et al., 2007b: 159, 3 unnumbered Figs. – Poupin, 2009: 65, unnumbered Fig. – Poupin et al., 2013a: 30, Fig 15A–B. – Poupin et al., 2013b: 4 (list). – Poupin et al., 2013c: 7 (list), Fig 4A. – Poupin et al., 2013d: 10 (list). – Asakura, 2002: 43, Figs 1D, 9–11, 21E–I. – Emmerson, 2016b: 119, 2 unnumbered Figs. – Emmerson, 2016c: 448 (list). – Poupin, 2016: 50 (list).

Calcinus gaimardii. – Barnard, 1947: 376. – Barnard, 1950: 439. – Day, 1974: 107. – Kensley, 1981: 31. – Emmerson, 2016c: 448 (list). [all not *Calcinus gaimardii* H. Milne Edwards, 1848]

Calcinus gaimardi. – Dechancé, 1964: 30. [not *Calcinus gaimardii* H. Milne Edwards, 1848]

Calcinus areolatus Rahayu and Forest, 1999: 465, Fig 1B, 2C, D, G, H, 3. [junior synonym, see Komai (2004)]

Material examined. 1939, Umpangazi (KZN), S 28° 07.56', E 32° 33.72', 1 ♂ 6.2 mm (SAMC MB-A010728); Jul 1968, Jangamo (Mozambique), S 24° 06.46', E 35° 30.07', 1 ♂ 8.4 mm, 1 ♀ 5.1 mm (SAMC MB-A013519); no date, Bazaruto (Mozambique), S 21° 33.76', E 35° 27.69', 2 ♂♂ 2.8–4.1 mm, 1 ♀ 4.1 mm (SAMC MB-A045459), coll. W. Emmerson; Nov 1989, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', 2 ♂♂ 5.1–5.6 mm, 2 ♀♀ 4.3–4.7 mm (SAMC MB-A045332), coll. W. Emmerson and G. Fotherby; Nov 1990, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', 1 ♂ 8.5 mm (SAMC MB-A045390), coll. W. Emmerson and G. Fotherby; 27 Mar 1990, Treasure Beach (Durban), S 29° 56.88', E 30° 59.88', 1 ♂ 7.3 mm (SAMC MB-A045455), coll. T. Stewart; 5 Dec 2014, Jesser Point (Sodwana Bay, KZN), S 27° 32.40', E 32° 40.86', intertidal, 1 ♂ 2.1 mm (SAMC MB-A065928), 1 ♀ 2.7 mm (SAMC MB-A065929), 1 ♀ 2.5 mm (SAMC MB-A065930), 1 ♂

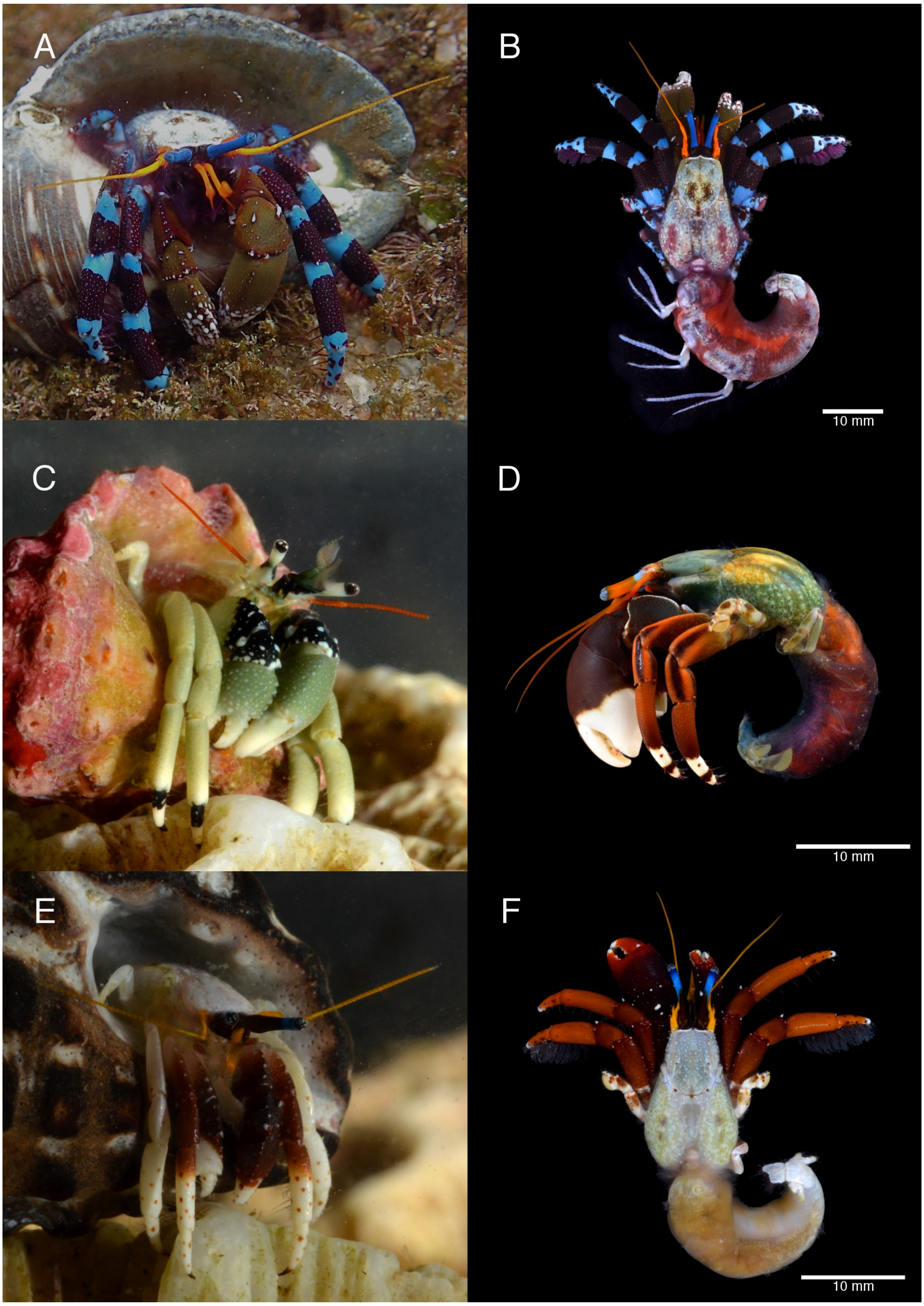

Figure 8.4: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A, C, E *in situ*): A–B *Calcinus elegans* Dana, 1851, Isipingo, ♀ 9.2 mm (SAMC MB-A066661) (A, photo C. L. Griffiths) **C** *Calcinus guamensis* Wooster, 1984, Sodwana Bay, ♂ 2.5 mm (SAMC MB-A065984) **D** *Calcinus laevimanus* Randall (1840), Pumula, ♂ 6.7 mm (SAMC MB-A066395) **E–F** *Calcinus morgani* Rahayu and Forest, 1999, Sodwana Bay, ♀ 2.2 mm (SAMC MB-A065997)(E), Inhaca Island (Mozambique), ♂ 6.2 mm (specimen lost)(F).

5.2 mm (SAMC MB-A065931), 1 ♂ 6.9 mm (SAMC MB-A065932); 6 Dec 2012, Archers (3-Mile reef, Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 11 m, Scuba, 1 juv. ♂ 1.4 mm (SAMC MB-A065993), 1 damaged juv. (SAMC MB-A065995), 1 ♀ 2.7 mm (SAMC MB-A065996), 1 ♀ 2.2 mm (SAMC MB-A065997), 1 ♂ 2.1 mm (SAMC MB-A066037); 21 Sep 2017, Isipingo (KZN), S 29° 59.88', E 30° 56.94', intertidal, 1 juv. ♂ 1.5 mm (SAMC MB-A066660), coll. A. Botha and C. L. Griffiths.

Other material. 10 Mar 2016, Inhaca Island (Mozambique), S 25° 58.20', E 32° 59.58', intertidal, 1 ♂ 6.2 mm (specimen lost).

Genetic data. Jesser Point, Sodwana Bay, S 27° 32.40', E 32° 40.86', intertidal, ♂ 2.1 mm, BOLD: SEAKY515-15 (SAMC MB-A065928), ♀ 2.7 mm, BOLD: SEAKY516-15 (SAMC MB-A065929), ♀ 2.5 mm, BOLD: SEAKY517-15 (SAMC MB-A065930), ♂ 5.2 mm, BOLD: SEAKY518-15 (SAMC MB-A065931), ♂ 6.9 mm, BOLD: SEAKY519-15 (SAMC MB-A065932). Archers, 3-Mile reef, Sodwana Bay, S 27° 31.68', E 32° 41.22', 11 m, juv. 1.4 mm, BOLD: SEAKY580-15 (SAMC MB-A065993), damaged juv., BOLD: SEAKY582-15 (SAMC MB-A065995), ♀ 2.7 mm, BOLD: SEAKY583-15 (SAMC MB-A065996), ♀ 2.2 mm, BOLD: SEAKY584-15 (SAMC MB-A065997).

Diagnosis. See McLaughlin et al. (2007b) and Poupin and Lemaitre (2003).

Remarks. South African specimens, for the first time reported by Barnard (1950) (as *Calcinus gaimardii*), have long been identified as *C. morgani*, e. g. Rahayu and Forest (1999). Moreover, the identity was confirmed by colour images provided by Emmerson (2016b), and is now documented for the new material, revealing the typical colour patterns of *C. morgani*: mainly the greyish shield, with darker anterolateral patches extending onto the anterior sections of the branchiostegites; ocular peduncles each with a dark subdistal ring (also see Poupin et al. 2013a). In addition, the colour patterns of juvenile or subadult specimens (Figure 8.4 E–F) match the colour photograph in McLaughlin et al. (2007b), and the identity of South African specimens is also supported by molecular data (unpubl. data).

Some of the samples identified as *C. gaimardii* at the Iziko South African Museum carry labels 'verified' by P. McLaughlin, so that Emmerson (2016c) included both *C. morgani* and *C. gaimardii* in his species list for Southern Africa. However, Emmerson did not provide any validation for his record and probably also missed out on the fact that McLaughlin visited Cape Town before Rahayu and Forest (1999) separated the two species. *Calcinus gaimardii* appears to have a restricted western Pacific distribution (Malay and Paulay 2010), and based on the current knowledge, there is no reason to assume that both species occur in South Africa.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Juan de Nova Island, Glorieuses Islands, Somalia, Madagascar, La Réunion, Australia, Indonesia, Malaysia, Vietnam, Taiwan, southern Japan, New-Guinea, Vanuatu, Marianas, French Polynesia.

Habitat. Coral, and rocky reef substrate, intertidal and subtidal to about 15 m.

Calcinus pulcher Forest, 1958 *sensu lato*, new record

Figure 8.5 A

Calcinus pulcher Forest, 1958: 287, Figs 4, 12, 13, 16 (type locality: Vietnam). – Asakura and Nomura, 2001: 95, Figs 1–3, 8A–F. – McLaughlin et al., 2007b: 178, 2 unnumbered Figs. – Poupin, 2009: 66, unnumbered Fig. – Poupin et al., 2013b: 4 (list). – Poupin et al., 2013c: 7 (list). – Poupin et al., 2013d: 10 (list). – Poupin, 2016: 50 (list), Fig 5B.

Calcinus aff. *pulcher* Malay and Paulay, 2010: Fig 13. – Poupin et al., 2013a: 31, Fig 15D.

Material examined. 6 Dec 2012, Archers (3-Mile reef, Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 11 m, Scuba, 1 ♀ 1.5 mm (SAMC MB-A065992), 1 ♀ 2.3 mm (SAMC MB-A065994); 8 Dec 2014, Sodwana Bay (KZN), S 27° 30.72', E 32° 41.10', 20 m, Scuba, 1 ♀ 1.9 mm (SAMC MB-A066036).

Genetic data. Archers, 3-Mile reef, Sodwana Bay, S 27° 31.68', E 32° 41.22', 11 m, ♀ 1.5 mm, BOLD: SEAKY579-15 (SAMC MB-A065992), ♀ 2.3 mm, BOLD: SEAKY581-15 (SAMC MB-A065994), Sodwana Bay, S 27° 30.72', E 32° 41.10', 20 m, ♀ 1.9 mm, BOLD: SEAKY623-15 (SAMC MB-A066036).

Diagnosis. See McLaughlin et al. (2007b), and also Poupin (2003).

Remarks. The South African specimens principally agree with the diagnosis by McLaughlin et al. (2007b), and also with the redescription by Asakura and Nomura (2001). However, at least the largest female reported here (2.3 mm) bears considerably strong spines on the upper margin and upper outer surface of the palm and carpus of the left cheliped, described to only have low protuberances and spines on the distal margin, respectively (Asakura and Nomura, 2001), or to be tuberculate or with a row of spines (McLaughlin et al. 2007b). Furthermore, all South African specimens have an asymmetrical telson with a larger left posterior lobe that is slightly more asymmetrical, as figured in Asakura and Nomura (2001), whereas the telson is depicted symmetrically in McLaughlin et al. (2007b). The South African specimens also have small tubercles or spines on the ventral margin of the meri of the second pereopods, not mentioned before. In their genetic study on peripatric speciation in *Calcinus*, Malay and Paulay (2010) found that specimens from the Mascarene Islands in the south-western Indian Ocean, and specimens collected in the western Pacific, represent distinct evolutionary significant units. Although their colour pictures of members of the two different groups show remarkably similar colour patterns, specimens from the Pacific have a broad rose to maroon band on the carpi of the second pereopods (also see Asakura and Nomura 2001, McLaughlin et al. 2007b), which is lacking in specimens from the Mascarene Islands (Malay and Paulay 2010), from the Mayotte region (Poupin et al. 2013a), and also in the specimens from South Africa (Figure 8.5 A). Genetically, the South African specimens are conspecific with Malay and Paulay's specimens from Mascarenes (unpubl. data). However, the three specimens reported here are small, all female, and also moderately damaged after shell extractions, so that further collecting and study will be necessary to clarify the status of *C. pulcher* in the western Indian Ocean. Nevertheless, this study constitutes the first report of this species from South Africa.

Distribution. South Africa (KZN), Mozambique Channel, Juan de Nova Island, Glorieuses Islands, Mascarene Islands, Andaman Sea off Phuket, Thailand, Cocos (Keeling) Islands, northwestern Australia, Indonesia, Vietnam, Taiwan, southern Japan.

Habitat. On coral and coral rubble, subtidal to about 30 m.

Calcinus rosaceus **Heller, 1861**

Figure 8.5 B–D

Calcinus rosaceus Heller, 1861: 23 (type locality: Red Sea). – Asakura and Tachikawa, 2003: 729. – Poupin, 2009: 67, unnumbered Fig. – Poupin et al., 2013a: 32, Fig 16 A–D. – Poupin et al., 2013b: 4 (list). – Poupin et al., 2013c: 7 (list), Fig 4D. – Poupin et al., 2013d: 10 (list). – Poupin, 2016: 50 (list).

?*Calcinus haigae*. – Gherardi and McLaughlin, 1994: 619. – McLaughlin and Hogarth, 1998: 5. – Hogarth et al., 1998: 155.

Calcinus haigae. – Emmerson, 2016c: 448 (list). [not *Calcinus haigae* Wooster, 1984]

Material examined. Nov 1990, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', no depth, 2 ♂♂ 3.1–3.4 mm (SAMC MB-A045446), 1 ♂ (tiny ♀ gonopores) 5.2 mm (SAMC MB-A045447), coll. W. Emmerson and G. Fotherby; no date, Bazaruto (Mozambique), S 21° 31.92', E 35° 29.16', no depth, 2 ♀♀ 2.4–3.6 mm (SAMC MB-A045445); 6 Dec 2014, Leadsman Shoal (Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 18 m, Scuba, 1 ♂ 3.1 mm (SAMC MB-A065963), 1 ovig. ♀ 4.3 mm (SAMC MB-A065964), 1 ♂ 4.3 mm (SAMC MB-A065965), 1 ♀ 2.8 mm (SAMC MB-A065966), 1 ♂ 3.9 mm (SAMC MB-A066485); 6 Dec 2014, Archers (3-Mile reef, Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 11 m, Scuba, 1 ♂ 4.1 mm (SAMC MB-A065981), 1 damaged juv. (SAMC MB-A065990), 1 ♂ 3.6 mm (SAMC MB-A066714).

Genetic data. Leadsman Shoal, Sodwana Bay, S 27° 31.68', E 32° 41.22', 18 m, ♂ 3.1 mm, BOLD: SEAKY550-15 (SAMC MB-A065963), ovig. ♀ 4.3 mm, BOLD: SEAKY551-15 (SAMC MB-A065964), ♂ 4.3 mm, BOLD: SEAKY552-15 (SAMC MB-A065965), ♀ 2.6 mm, BOLD: SEAKY553-15 (SAMC MB-A065966). Archers, 3-Mile reef, Sodwana Bay, S 27° 31.68', E 32° 41.22', 11 m, ♂ 4.1 mm, BOLD: SEAKY568-15 (SAMC MB-A065981), damaged juv., BOLD: SEAKY577-15 (SAMC MB-A065990).

Diagnosis. Extended from Poupin (2003). Shield longer than broad; rostrum broadly triangular, acute. Ocular peduncles long, considerably overreaching antennular and antennal peduncles; ocular acicles usually with two terminal spines. Upper margin of right chela tuberculated or spinous. Outer face of left palm regularly convex. Dactyls of third pereopods subequal or slightly shorter than propodi; no brush of setae on ventral margins of dactyls and propodi; ventral margins of dactyls with less than 10 spines; dorsolateral margins of propodi rounded. Telson with posterior lobes asymmetrical, left larger; terminal margins of left lobe with several spines not exceeding onto lateral margin, right lobe with several spines.

Colouration. Shield brown-purple mottled white-cream, markedly paler in posterior half, anterolateral areas slightly darker in colour, but without well-defined patch, rostrum and surface posterior of lateral projections with small white-cream patches. Posterior carapace and pleon pink-purple, mottled white-cream. Ocular peduncles brown-purple to pink, distally sometimes orange, with narrow white ring close to cornea; ocular acicles brown-purple, white-cream at base. Antennular peduncles dark brown-purple, distal half of ultimate segments bright blue; flagella brown-grey. Antennal peduncles brown-purple with white-cream spots; fifth segments distally transparent; antennal acicles distally white-cream. Exopods of first and second maxillipeds blue. Chelipeds brown-purple, dactyls marginally less intense in colour, distally white-cream and with few small orange-yellow dots, flagella transparent. Ambulatory legs purple-pink with similar colour tone to dactyls of chelipeds, sprinkled with small orange to yellow dots most prominent on the dactyls. Juveniles markedly different in colouration, particularly distal parts of chelipeds and ambulatory legs, which are yellow and uniformly covered with orange-yellow dots.

Remarks. *Calcinus rosaceus* is closely allied to *C. haigae* Wooster, 1984, from which it appears to be morphologically indistinguishable (Asakura and Tachikawa 2003). The only reliable character separating the two species so far is living coloration, which is here for the first time reported in detail and for South African specimens. The two species differ predominantly by the colour of the shield (purple-brown with darker anterolateral patches in *C. haigae*, vs. dark purple-brown in anterior half, paler in posterior half, and also without clearly separated anterolateral darker patches in *C. rosaceus*), by the more uniformly coloured chelipeds of *C. rosaceus* (dactyls and fixed fingers of *C. haigae* are less colour-intense in relation to the remaining parts of the cheliped), and by the spots on the dactyls and distal parts of the propodi of the pereopods (broad and orange-red to pinkish in *C. haigae*, vs. small and orange-yellow in *C. rosaceus*). Because the small orange-yellow spots on the pereopods of *C. rosaceus* have not been reported before, and probably also because they are fading more quickly in alcohol than the broader spots of *C. haigae*, it has so far been incorrectly assumed that *C. rosaceus* has no such spots. This assumption might be the cause of considerable confusion between the two species and it is very possible that *C. haigae* does not occur in the Indian Ocean (also see Asakura and Nomura 2001; Poupin et al. 2013a).

Nevertheless, the matter might be more complicated, as Malay and Paulay (2010) found *C. rosaceus* to be one of the few species of *Calcinus* that falls into a genetically unresolved species complex. Based on a preliminary genetic analysis, the South African specimens are conspecific with Malay and Paulay's specimens from the Gulf of Oman, and also with the H310 specimen from Mascarenes (unpubl. data).

Emmerson (2016c) did not give any information on his reported *C. haigae* and the previously collected specimens (in three samples – two Sodwana Bay, one Bazaruto) that are deposited at the Iziko South African Museum have lost all colour. Although the presence of *C. haigae* in South Africa cannot be ruled out entirely, Emmerson's records of *C. haigae* are very likely to be *C. rosaceus*, and are herein regarded as misidentifications. Hence, this study represents the first validated record of *C. rosaceus* from South Africa.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Juan de Nova Island, Glorieuses Islands, Red Sea, La Réunion, Mauritius.

Habitat. Intertidal rocky shores, in South Africa subtidal on coral reef.

Calcinus vachoni **Forest, 1958** ***sensu lato*****, new record**

Figure 8.5 E–F

Calcinus vachoni Forest, 1958: 285, Figs 2, 3, 9, 10, 15, 19 (type locality: Vietnam). – Gherardi and McLaughlin, 1994: 624. – McLaughlin et al., 2007b: 170, 2 unnumbered Figs. – Poupin, 2009: 66, unnumbered Fig. – Poupin et al., 2013b: 4 (list). – Poupin et al., 2013c: 7 (list). – Poupin et al., 2013d: 10 (list).

Calcinus aff. *vachoni* Malay and Paulay, 2010: Fig 6. – Poupin et al., 2013a: 33, Fig 15F.

?*Calcinus* cf. *vachoni* McLaughlin and Hogarth, 1998: 9.

Material examined. 6 Dec 2014, Archers (3-Mile reef, Sodwana Bay, KZN), S 27° 31.68’, E 32° 41.22’, 11 m, Scuba, 1 ovig. ♀ 1.5 mm (SAMC MB-A065989), 1 ♀ 1.7 mm (SAMC MB-A065991), 1 ovig. ♀ 1.3 mm (SAMC MB-A066068); 15 Oct 2015, Pumula (KZN), S 30° 38.28’, E 30° 32.22’, intertidal, 1 ♀ 2.3 mm (SAMC MB-A066397), 1 ♀ 2.9 mm (SAMC MB-A066398), 1 ♀ 3.1 mm (SAMC MB-A066399), 2 ♂♂ 2.1–2.4 mm (SAMC MB-A066486); 15 Oct 2015, Port Shepstone (KZN), S 30° 44.82’, E 30° 27.42’, intertidal, 1 ♀ 2.9 mm (SAMC MB-A066419), 1 ♀ 3.0 mm (SAMC MB-A066420), 1 ♀ 3.1 mm (SAMC MB-A066487).

Genetic data. Archers, 3-Mile reef, Sodwana Bay, S 27° 31.68’, E 32° 41.22’, 11 m, ovig. ♀ 1.5 mm, BOLD: SEAKY576-15 (SAMC MB-A065989), ovig. ♀ 1.3 mm, BOLD: SEAKY655-15 (SAMC MB-A066068). Pumula, S 30° 38.28’, E 30° 32.22’, intertidal, ♀ 2.3 mm, BOLD: SEAKY1135-16 (SAMC MB-A066397), ♀ 2.9 mm, BOLD: SEAKY1136-16, (SAMC MB-A066398), ♀ 3.1 mm, BOLD: SEAKY1137-16 (SAMC MB-A066399). Port Shepstone, S 30° 44.82’, E 30° 27.42’, intertidal, ♀ 2.9 mm, BOLD: SEAKY1157-16 (SAMC MB-A066419), ♀ 3.0 mm, BOLD: SEAKY1158-16 (SAMC MB-A066420).

Diagnosis. See McLaughlin et al. (2007b), and also Poupin (2003).

Remarks. Malay and Paulay (2010) found that specimens from the Western Indian Ocean are genetically different from specimens from the Central Indo-Pacific, with a third distinct group from the Cooks Islands. The South African specimens reported here agree with the currently available diagnoses and keys, and large specimens have the same colour patterns (ocular peduncles cream to greenish grey, without black patches) as the specimen from Mascarenes. However, small South African specimens have dark patches on the proximal ocular peduncles, predominantly on the mesioventral surfaces (Figure 8.5 E–F), which have also been reported from Mayotte specimens (Poupin et al. 2013a). Based on preliminary genetic findings, the South African specimens are conspecific with the ones from Mascarenes (unpubl. data), suggesting that this lineage is the one that

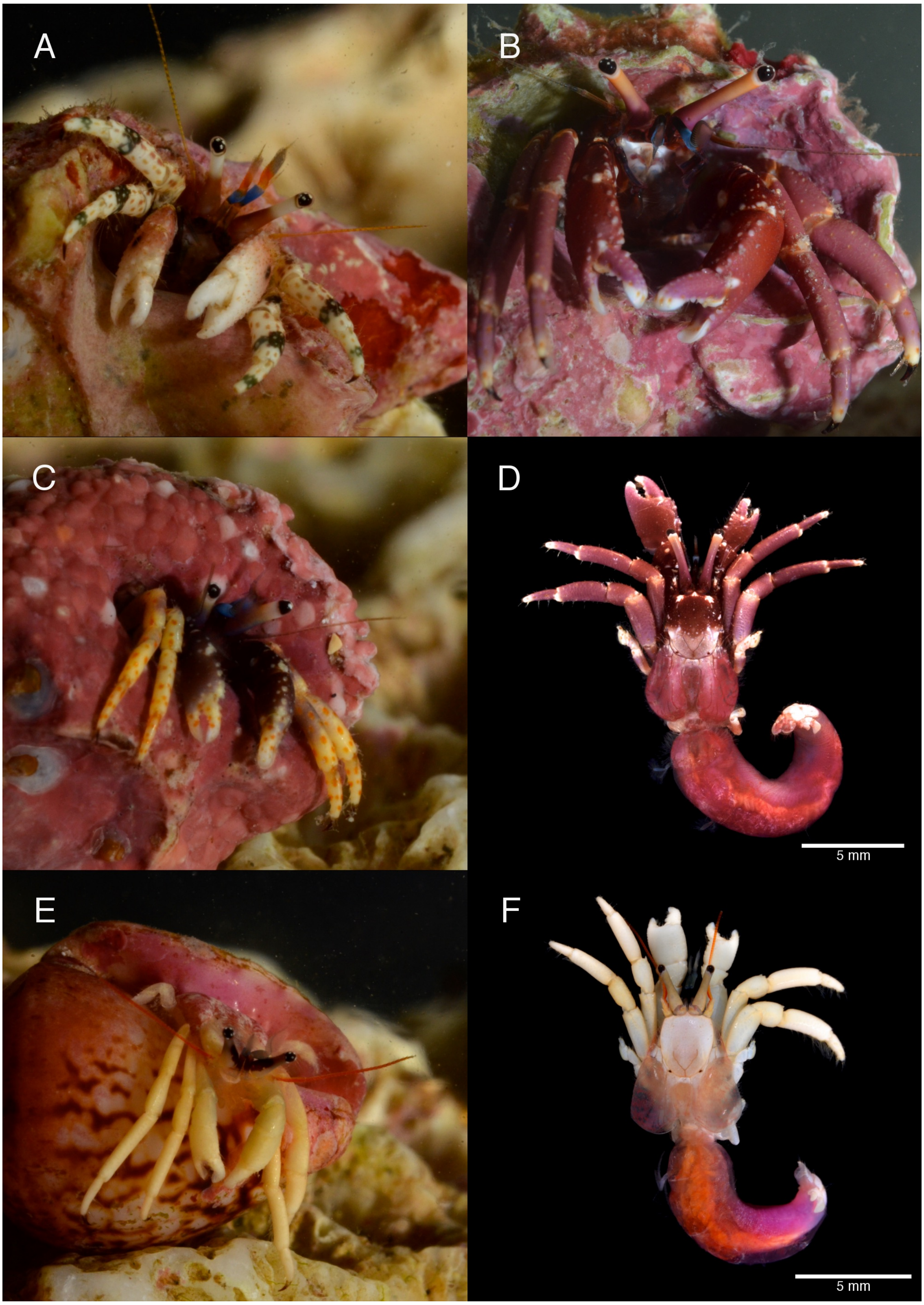

Figure 8.5: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A–C, E *in situ*): **A** *Calcinus pulcher* Forest, 1958, Sodwana Bay, ♀ 2.3 mm (SAMC MB-A066994) **B–D** *Calcinus rosaceus* Heller, 1861, Sodwana Bay, ovig. ♀ 4.3 mm (SAMC MB-A065964)(B), juv. (SAMC MB-A065990)(C), ♂ 3.8 mm (SAMC MB-A066714) (D) **E–F** *Calcinus vachoni* Forest, 1958, Sowana Bay, ♀ 1.7 mm (SAMC MB-A065991)(E), Pumula, ♀ 2.3 mm (SAMC MB-A066397)(F).

is present in the Western Indian Ocean. More detailed study is necessary to find suitable characters that can be used to separate this candidate species from the other two. Nevertheless, this is the first report of the species from South Africa.

Distribution. South Africa (KZN), Mozambique Channel, Glorieuses Islands, La Réunion, Mauritius, Northern Western Australia, Vietnam, Taiwan, southern Japan, French Polynesia.

Habitat. Coral, coral rubble and rocky reefs; intertidal or shallow subtidal to 20 m.

8.4.3.4 Genus *Ciliopagurus* Forest, 1995

Ciliopagurus shebae **(Lewinsohn, 1969), new record**

Figure 8.6 D

Trizopagurus shebae Lewinsohn, 1969: 55, Fig 8 (type locality: Gulf of Aquaba, Red Sea).

Ciliopagurus shebae. – Forest, 1995: 69, Fig 12e, 15a, 16, 33a, 37f, 41c–d. – McLaughlin and Hogarth, 1998: 9. – Kato and Okuno, 2001: 75, unnumbered Fig. – Okuno and Arima, 2006: 32, Fig 2H. – Okuno et al., 2006: 149, Fig 2, Pl 2B. – Arima, 2014: 5 unnumbered Figs.

Material examined. 24 Jan 2015, Southport (KZN), S, 30° 40.14', E 30° 32.82', 52 m, Scuba, 1 ♂ 9.6 mm (SAMC MB-A066672); 23 Sep 2016, Pumula 22 (KZN), S 30° 38.40', E 30° 34.20', 40–65 m, Scuba, 1 ♂ 8.2 mm (SAMC MB-A066670); 20 Jan 2017, Pumula 22 (KZN), S 30° 38.40', E 30° 34.20', 40–65 m, 1 ovig. ♀ 6.6 mm (SAMC MB-A06671); 10 Apr 2017, Sezela (KZN), S 30° 24.66', E 30° 44.46', 50–55 m, 1 ♂ 7.5 mm (SAMC MB-A0666706).

Genetic data. Pumula, S 30° 38.40', E 30° 34.20', 40–65 m, ♀ 6.6 mm, BOLD: SEAKY1426-17 (SAMC MB-A06671).

Diagnosis. Ocular peduncles 0.8–0.9 length of shield. Distal segment of antennular peduncle 0.3 length of shield. Ocular acicles acutely triangular, elongated and pointed towards mesial, bearing 1 or 2 (very rarely 3) terminal spines. Chelipeds subequal, one or the other slightly larger (usually left); outer face of palm of chela with 4 somewhat straight and parallel to slightly undulating striae interspersed by narrow and frequently interrupted or uninterrupted streaks; striae smooth or proximally with minute spinules, near dorsal margin with larger, flattened to drop-shaped spinules leading into stridulating organ. Left chela 1.1–1.3 length of shield and 0.55–0.65 as high as long; finger about 0.5 length of chela; main stridulating area on inner margin of distal palm with row of 15 parallel corneous crests (the 4 outermost less developed, spine-like), proximally on inner margin of finger usually with 2 main short and parallel upper crests and 2 lower crests. Dactyls of third pereopods 1.3–1.5 length of propodi. Posterior lobes of telson subequal, left slightly larger and deeply divided by V-shaped cleft, terminal margins broadly rounded and usually without spines.

Colouration. Shield greyish-white faintly orange and sparsely sprinkled with minute orange dots, proximal and proximolateral margins orange. Posterior carapace greyish-white to brown, sprinkled with small orange dots. Cephalic appendages uniformly bright-orange to orange, antennal flagella less intense and transparent, corneas greenish-brown. Chelipeds and first and second pereopods bright-orange, all segments except dactyls with transversal white rings sometimes flanked by two orange-red rings. Fingers of chelipeds and dactyls, as well as distal part of propodi of walking legs light orange, propodi and carpi proximally with broader white ring or narrow band (most pronounced in walking legs). Fourth and fifth pereopods orange with white spots. Pleon bright-orange to orange-brown with yellowish transversal lines on the pleomers, and sometimes also with irregular lines on dorsal and lateral surfaces. Pleopods yellow-orange. Uropods and telson cream-white with orange patches. Eggs orange-red.

Remarks. *Ciliopagurus shebae* is superficially very similar to *C. tricolor* Forest, 1995, see next species. The South African specimens of *C. shebae* agree with Forest's (1995) redescription and the additional identification characters provided by Poupin and Malay (2009). This species appears to be the deep-water form of a species-pair with *C. tricolor*, and it can be separated from the latter by the ocular acicles (elongated and mesially pointed vs. truncated, and with 1 or 2 vs. 2–5 spines), and furthermore by morphometric differences: longer ocular peduncles (ratio to shield length about 0.8 vs. 0.7), longer chelae than the shield (vs. shorter chelae than the shield), and longer dactyls of the third pereopod (ratio to propodi >1.3 vs. <1.2). Moreover, *C. shebae*, that also grows to a larger size, has four complete transversal striae on the outer face of the palm, while *C. tricolor* only has three. Despite the fact that the two species have basically identical colour patterns (Poupin and Malay 2009), some colour differences are noticeable that can aid identification. These are the colour of the dactyls of the chelipeds and walking legs that are more orange in *C. shebae* (vs. yellow in *C. tricolor*), but more importantly the broader white proximal rings or bands on the propodi and carpi most pronounced on the walking legs. Overall, the white rings of *C. shebae* are also of less equal width compared to *C. tricolor*, which has rings of equal width.

Ciliopagurus shebae occurs in greater depths (20–130 m, in South Africa 40–65 m) than *C. tricolor* (mostly shallow waters). However, in South Africa *C. tricolor* is now recorded from 34 m (see remarks under that species), so depth distribution alone might prove unsuitable for identification. This is the first report of *C. shebae* from South African waters.

Distribution. South Africa (KZN), Red Sea, Madagascar, La Réunion, Seychelles, Japan.

Habitat. Rocky substrates from 20–130 m, in South Africa only known from 40–65 m depth, inhabiting shells with narrow apertures, such as *Conus* spp.

***Ciliopagurus tricolor* Forest, 1995**

Figure 8.6 E–F

Ciliopagurus tricolor Forest, 1995: 54, Figs 8b, 10b, 12b, 31c, 37e, 40b, 41a–b (type locality: Madagascar, Toliara). – Poupin, 2009: 61, unnumbered Fig. – Poupin and Malay, 2009: 216, Fig 1B, 3B, 4B, 6–9. – Poupin et al., 2013a: 33, Fig 3D, 17A. – Poupin et al., 2013b: 4 (list). – Poupin et al.,

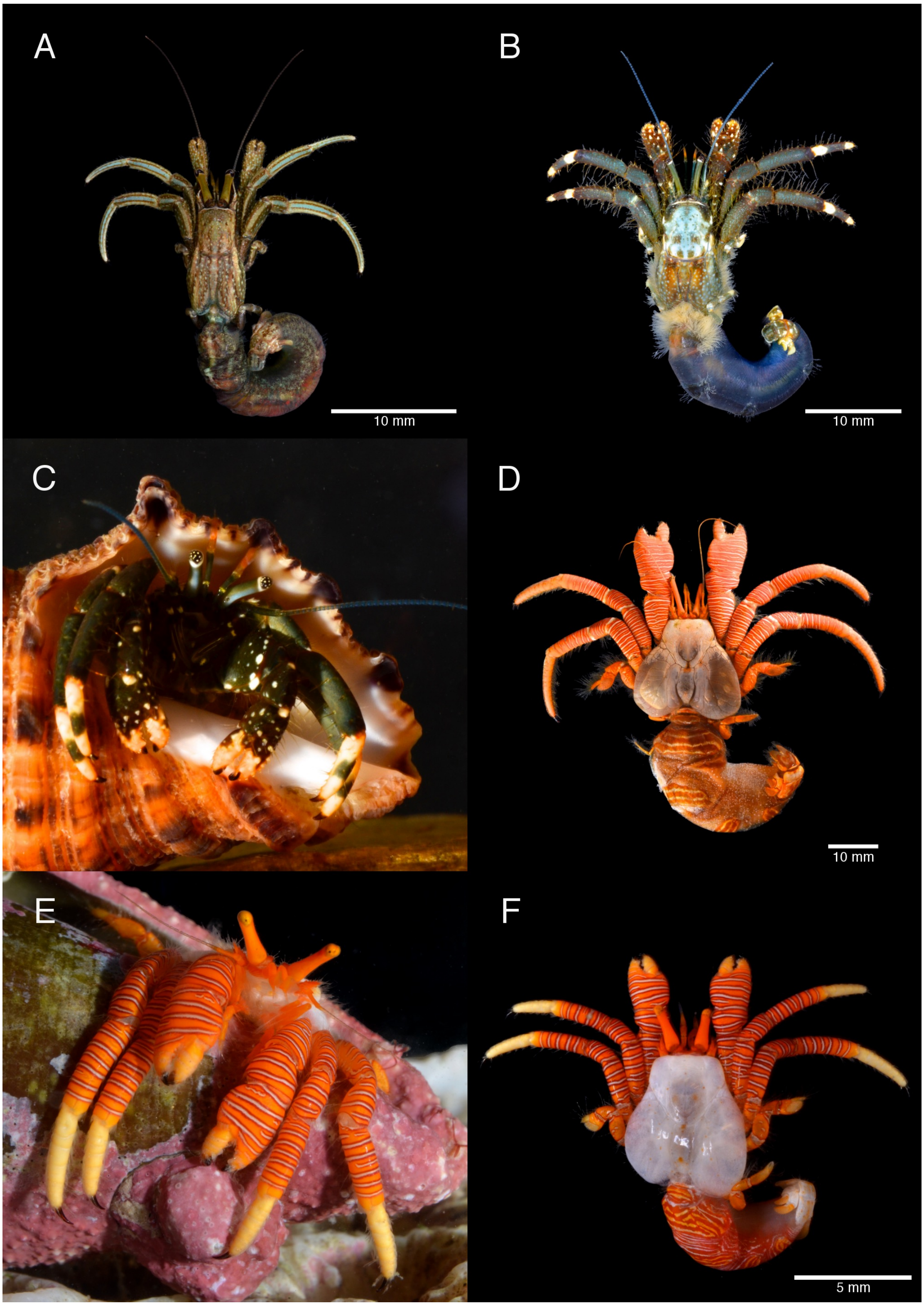

Figure 8.6: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (C, E *in situ*): A *Clibanarius longitarsus* (De Haan, 1849), Inhaca Island (Mozambique), specimen lost (SAMC MB-A066474) **B–C** *Clibanarius virescens* Krauss, 1843, Gonubie, ♂ 6.1 mm (SAMC MB-A066123)(B), Durban, ♂ 3.9 mm (SAMC MB-A066122)(C) **D** *Ciliopagurus shebae* (Lewinsohn, 1969), Southport, ♂ 9.6 mm (SAMC MB-A066672) **E–F** *Ciliopagurus tricolor* Forest, 1995, Sodwana Bay, ♂ 3.2 mm (SAMC MB-A066034)(D), ♀ 2.5 mm (SAMC MB-A066716).

2013c: 7 (list), Fig 5E. – Poupin et al., 2013d: 10 (list). – Emmerson 2016b: 123, unnumbered Fig. – Emmerson, 2016c: 448 (list). – Poupin, 2016: 50 (list).

Pagurus (s. s.) *strigatus.* – Hilgendorf, 1879: 820, Fig 8, Pl 2. [not *C. strigatus* (Herbst, 1804)]

Aniculus strigatus. – Barnard, 1950: 431, Fig 80a. [not *C. strigatus* (Herbst, 1804)]

Ciliopagurus strigatus. – King and Fraser, 2014: 288, unnumbered Fig. – Emmerson, 2016c: 448 (list). [not *C. strigatus* (Herbst, 1804)]

Material examined. 1934, Inhaca Island (Mozambique), 1 ♂ 6.6 mm (dry) (SAMC MB-A008208); Nov 1989, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', 10 m, 1 ♂ 5.3 mm (SAMC MB-A045343); 6 Dec 2015, Archers (Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 11 m, Scuba, 1 ♂ 2.1 mm (SAMC MB-A065982), 1 ♀ 2.9 mm (SAMC MB-A065983), 1 ♀ 2.5 mm (SAMC MB-A066716); 8 Dec 2015, Sodwana Bay (KZN), S 27° 30.72', E 32° 41.10', 20 m, Scuba, 1 ♂ 3.2 mm (SAMC MB-A066034); 24 Sep 2016, Tracker Ground (off Pumula, KZN), S 30° 39.12', E 30° 32.82', 34 m, Scuba, 1 ♂ 5.9 mm (SAMC MB-A066673).

Genetic data. Archers, 3-Mile reef, Sodwana Bay, S 27° 31.68', E 32° 41.22', 11 m, ♂ 2.1 mm, BOLD: SEAKY569-15 (SAMC MB-A065982), ♀ 2.9 mm, BOLD: SEAKY570-15 (SAMC MB-A065983). Sodwana Bay, S 27° 30.72', E 32° 41.10', 20 m, ♂ 3.2 mm, BOLD: SEAKY621-15 (SAMC MB-A066034).

Diagnosis. See Poupin and Malay (2009).

Remarks. Emmerson (2016b,c) accepted Barnard's (1950) record (as *Aniculus strigatus*) of *Ciliopagurus strigatus* (Herbst, 1804) and, in addition, listed *C. tricolor* as a new species record to southern Africa (from Sodwana Bay, South Africa). Although it cannot be excluded that *C. strigatus* occurs in South African waters, all specimens from the east coast of Africa are *C. tricolor* and not *C. strigatus*, the latter having a more widespread Indo-Pacific distribution with La Réunion and Mauritius as the southeastern boundary (Poupin and Malay 2009). It is therefore unlikely that Barnard's specimen from Inhaca (Mozambique) is *A. strigatus.* Although this specimen has lost all colour, there is no justified reason to retain this record. Another closely-related species, *C. shebae*, occurs at greater depths (for distinguishing characters see remarks section of that species). It is particularly noticeable that the Pumula specimen of *C. tricolor* was collected at 34 m, considerably extending the depth range of *C. tricolor*, which now potentially overlaps with that of *C. shebae.*

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Juan de Nova Island, Glorieuses Islands, Tanzania, Somalia, Madagascar, La Réunion, ?Chagos Islands.

Habitat. Rocky or coral reefs, intertidal to 34 m depth, but usually not deeper than 10 m; in shells with a narrow aperture, such as *Conus* spp.

8.4.3.5 Genus *Dardanus* Paul'son, 1875

Dardanus arrosor (Herbst, 1796)

Figure 8.7 A–B

Cancer arrosor Herbst, 1796: 170, Pl 43 Fig 1.

Pagurus arrosor. – Barnard, 1950: 123, Fig 79a–b.

Dardanus arrosor. – Kensley, 1981: 32 (list). – McLaughlin et al., 2007b: 76, 3 unnumbered Figs. – Branch et al., 2010: 116, Fig 49.2. – Emmerson, 2016b: 138, unnumbered Fig. – Emmerson, 2016c: 448 (list).

Material examined. 10 Jun 1898, s. s. *Pieter Faure* sta 60 (Cape St. Blaize, W. C.), S 34° 19.20', E 22° 00.12', 11 m, 1 ♀ 15.5 mm (dry) (SAMC MB-A001469); 15 Jun 1898, s. s. *Pieter Faure* sta 73C (Mossel Bay, W. C.), S 34° 04.98', E 22° 13.98', no depth, shrimp trawl, 1 ♂ 15.3 mm, 1 ♀ 11.3 mm (SAMC MB-A001467); 20 Jun 1898, s. s. *Pieter Faure* sta 75B (off Cape St. Blaize, W. C.), S 34° 13.74', E 22° 14.16', 80 m, 2 ♂♂ 14.2–15.7 mm (SAMC MB-A001468); 22 Jul 1898, s. s. *Pieter Faure* sta 239 (off Great Fish Point Lighthouse, E. C.), S 33° 31.50', E 27° 08.28', 80 m, large dredge, 1 ♂ 15.3 mm (dry) (SAMC MB-A001461), s. s. *Pieter Faure* sta 246A–C (off Cape St. Blaize, W. C.), S 34° 13.74', E 22° 14.16', 81 m, shrimp trawl, 1 ♂ 17.8 mm (dry) (SAMC MB-A001465), 1 ♀ 4.5 mm (dry) (SAMC MB-A001484); 30 Sep 1898, s. s. *Pieter Faure* sta 358 (Buffels Bay, False Bay, W. C.), S 34° 19.02', E 18° 28.02', no depth, trawl, 1 ♂ 16.7 mm (SAMC MB-A001473); 19 Nov 1898, s. s. *Pieter Faure* sta 674 (near Kowie, E. C.), S 33° 45.00', E 26° 44.22', 76 m, trawl, 2 ♂♂ 19.8–22.1 mm (SAMC MB-A001567); 21 Dec 1898, s. s. *Pieter Faure* sta 757 5 (E. C.), S 33° 13.32', E 27° 39.42', 68 m, trawl, 1 dry specimen in bad condition (SAMC MB-A001472); 12 Jan 1899, s. s. *Pieter Faure* sta 860 (East of Cape Morgan, E. C.), S 32° 45.42', E 28° 26.10', 66 m, dredge, 1 ovig. ♀ 15.0 mm (dry) (SAMC MB-A001481); 22 Mar 1899, s. s. *Pieter Faure* sta 1125 (off Bird Island, Port Elizabeth, E. C.), S 33° 52.56', E 26° 18.60', 36 m, 6 ♂♂ 8.4–12.8 mm, 4 ♀♀ 7.2–12.2 mm (SAMC MB-001477); 2 Apr 1899, s. s. *Pieter Faure* sta 1144 (Mossel Bay, W. C.), S 34° 12.00', E 22° 15.00', 66 m, trawl, 2 ♂♂ 16.9–19.2 mm, 1 ♀ 12.7 mm (SAMC MB-A001474); 22 Oct 1900, s. s. *Pieter Faure* sta 10465 (Cape St. Blaize, W. C.), S 34° 23.52', E 22° 09.00', 77 m, 1 dry specimen (SAMC MB-A003266); 7 Mar 1901, s. s. *Pieter Faure* sta 12227 (off Scottburgh Lighthouse, KZN), S 30° 10.32', E 30° 50.16', 168 m, dredge, 1 ♀ 5.4 mm (dry) (SAMC MB-A001485); 14 Mar 1901, s. s. *Pieter Faure* sta 12355 (off Umhlangakulu River, KZN), S 30° 47.22', E 30° 34.86', 91 m, dredge, 1 juv. specimen (in shell, dry) (SAMC MB-A001483); 15 Mar 1901, s. s. *Pieter Faure* sta 12425 (off Port Shepstone, KZN), S 30° 45.96', E 30° 29.70', 44 m, dredge, 2 ♀♀ 7.4–12.0 mm (dry) (SAMC MB-A001471); 17 Jul 1901, s. s. *Pieter Faure* sta 13095 (off Cove Rock, East London, E. C.), S 33° 06.48', E 27° 47.28', 46 m, shrimp trawl, 1 glaucothoe (SAMC MB-A003271); 25 Jul 1901, s. s. *Pieter Faure* sta 13126 (off Cape Morgan, E. C.), S 32° 49.98', E 28° 18.30', 86 m, dredge, 1 ♂ 8.6 mm (dry) (SAMC MB-A001482); 17 Dec 1903, s. s. *Pieter Faure* sta 18330-3 (off Cape St. Blaize, W. C.), S 34° 12.36', E 22° 17.28', 55 m, trawl, 2 ♂♂ 18.1–20.0 mm, 1 ovig. ♀ 1.4 mm, 2 (in shell) (SAMC MB-A001463); 29 Jan 1904, s. s. *Pieter*

Faure sta 18420 (Flesh Point, W. C.), S 34° 22.98’, E 22° 01.02’, 60 m, trawl, 1 ♂ 21.0 mm (SAMC MB-A10716); 29 Mar 1904, s. s. *Pieter Faure* sta 18454-6 (off Bird Island Lighthouse, Port Elizabeth, E. C.), S 33° 55.68’, E 26° 23.28’, 73 m, trawl, 2 ♂♂ 12.3–14.5 mm (SAMC MB-A001462); 29 Mar 1904, s. s. *Pieter Faure* sta 18464-5 (off Nanquas Peak, E. C.), S 33° 51.24’, E 26° 28.74’, 90 m, trawl, 3 ♂♂ 10.2–16.8 mm, 1 ♀ 10.9 mm (SAMC MB-A001480); 6 Apr 1904, False Bay (W. C.), S 04° 10.98’, E 18° 37.02’, no depth, 1 glaucothoe (in shell) (SAMC MB-A004350); 2 Jul 1904, s. s. *Pieter Faure* sta 18538 (off Nanquas Peak, E. C.), S 33° 52.38’, E 26° 27.30’, 90 m, trawl, 1 ♂ 9.0 mm, 5 ♀♀ 11.8–14.2 mm (SAMC MB-A001479); no date, East London E. C., S 33° 00.00’, E 27° 57.00’, no depth, 1 ♂ 20.6 mm (SAMC MB-A010974), coll. Walker; no date, Durban (KZN), S 30° 00.00’, E 30° 57.00’, no depth, crayfish trawl, 1 ♂ 14.7 mm (SAMC MB-A11003); no date, Agulhas Bank, S 35° 00.00’, E 20° 00.00’, no depth, 1 ♂ 15.1 mm (SAMC MB-A011044); 9 Nov 1947, UCT E. S. sta TRA23 (off Arniston, W. C.), S 34° 49.02’, E 20° 21.52’, 91 m, trawl, 2 ♂♂ 17.2–18.4 mm (SAMC MB-A019469); 7 Jan 1948, UCT E. S. sta AFR864 F (off Gansbaai, W. C.), S 34° 35.40’, E 19° 14.70’, 66 m, dredge, 5 ♂♂ 11.7–29.7 mm, 3 ovig. ♀♀ 11.1–14.0 mm, 4 ♀♀ 3.4–13.6 mm (SAMC MB-A043459); 15 Dec 1957, UCT E. S. sta TB241 (Table Bay, W. C.), S 33° 48.60’, E 18° 24.60’, 15 m, dredge, 2 ♂♂ 16.2–16.5 mm (SAMC MB-A043451); 23 May 1958, UCT E. S. sta SCD27 A (Port Elizabeth, E. C.), S 33° 46.98’, E 26° 04.02’, 26 m, 4 ♂♂ 5.6–9.8 mm, 1 ♀ 15.6 mm, 1 juv. 3.4 mm (SAMC MB-A043458); 15 Aug 1958, UCT E. S. sta SCD62 N (E. C.), S 32° 17.70’, E 28° 54.48’, 46 m, 2 ♀ 7.0–8.8 mm (SAMC MB-A043454); 13 Jul 1959, UCT E. S. NAD26 S (Durban, KZN), S 29° 53.52’, E 31° 06.48’, 71 m, dredge, 1 ♂ 8.0 mm, 1 ovig. ♀ 9.1 mm, 1 ♀ 4.0 mm (SAMC MB-A043452); 11 Feb 1962, UCT E. S. sta SCD337 H (off Plettenberg Bay, W. C.), S 34° 01.56’, E 23° 28.08’, 41 m, dredge, 1 ovig. ♀ 14.0 mm (SAMC MB-A043457); 8 Dec 1962, UCT E. S. sta SCD389 W (off Plettenberg Bay, W. C.), S 34° 04.38’, E 23° 25.62’, 42 m, 1 ♀ 13.4 mm (SAMC MB-A043453); 12 Feb 1963, Mossel Bay (W. C.), S 34° 04.98’, E 22° 13.98’, no depth, 2 ♂♂ 19.2–21.3 mm (SAMC MB-A011817); 6 Jun 1963, Muizenberg (False Bay, W. C.), S 34° 06.60’, E 18° 28.38’, no depth, 1 ♂ 11.9 mm (dry) (SAMC MB-A012012); 24 May 1964, Bloubergstrand (W. C.), S 33° 46.98’, E 18° 27.00’, wash-up, 1 ♀ 13.2 mm (SAMC MB-A012081); 4 Nov 1964, Bokkom Bay (Bloubergstrand, W. C.), S 33° 48.24’, E 18° 27.66’, no depth, 1 ♂ 18.7 mm (SAMC MB-A012122); 26 May 1978, R. V. *Meiring Naudé* sta SM163 (off East London, E. C.), S 33° 04.60’, E 28° 06.60’, 90 m, heavy dredge, 1 juv. specimen (in shell) (SAMC MB-A043461); 29 May 1978, R. V. *Meiring Naudé* sta SM180 (E. C.), S 33° 29.40’, E 27° 21.18’, 80 m, heavy dredge, 1 ♂ 6.8 mm, 1 ♀ 5.6 mm (SAMC MB-A043428); 31 May 1978, R. V. *Meiring Naudé* sta SM185 (E. C.), S 33° 39.30’, E 27° 11.58’, 90 m, heavy dredge, 1 ♂ 6.1 mm (SAMC MB-A043412); 27 Jun 1979, R. V. *Meiring Naudé* sta SM250 (E. C.), S 31° 59.28’, E 29° 22.50’, 175 m, heavy dredge, 3 juv. specimens (in shell) (SAMC MB-A043462); 10 Oct 1984, off Danger Point (Gansbaai, W. C.), S 34° 39.18’, E 19° 17.28’, 36 m, Scuba, 1 specimen (in shell) (SAMC MB-A019140); 1985, East London Harbour (E. C.), S 33° 01.68’, E 27° 54.72’, no depth, 3 ♂♂ 8.4–11.4 mm, 3 ♀♀ 7.7–10.9 mm (SAMC MB-A045502); 18 May 1988, R. V. *Africana* South Coast Survey sta A7146-063-035-1071 (off Jeffrey’s Bay, E. C.), S 34° 02.22’, E 25° 04.50’, 35 m, trawl, 1 ♂ 23.2 mm (SAMC MB-A043460); 28 Dec 1993, off Hawsten (W. C.), S 34° 25.62’, E 19° 04.80’, 10 m, crayfish trap, 1 ♂ 20.0 mm (SAMC MB-A043395); 10 Jun 1994, R. V. *Algoa* Scad Survey sta C00808-014-006-2193 (off Xai-Xai, Mozambique), S 25°

13.98’, E 33° 54.60’, 174 m, trawl, 1 specimen (in shell) (SAMC MB-A041690); 12 Jun 1994, R. V. *Algoa* Scad Survey sta C00813-014-011-3115 (Mozambique), S 23° 28.02’, E 35° 43.02’, 185 m, trawl, 1 ♂ 16.7 mm (SAMC MB-A041689); 13 Oct 1994, R. V. *Africana* South Coast Survey sta A16663-125-081-3685 (off Cannon Rocks, E. C.), S 33° 59.52’, E 26° 30.42’, 105 m, trawl 1 ♂ 19.4 mm (SAMC MB-A03372); 14 Oct 1994, R. V. *Africana* South Coast Survey sta A16676-125-087-2330 (off Kasouga, E. C.), S 33° 44.88’, E 26° 48.12’, 72 m, trawl, 1 ♂ 16.0 mm (SAMC MB-A03371); 12 Apr 2015, South Coast Survey sta D0491 (Agulhas Bank), S 35° 54.30’, E 20° 45.78’, 135 m, trawl, 1 ♂ 13.6 mm (SAMC MB-A066125); 1 May 2015, South Coast Survey sta D00563-076-3690 (Agulhas Bank), S 33° 55.32’, E 26° 35.64’, 101 m, trawl, 1 ♂ 17.4 mm (SAMC MB-A066844); 8 May 2015, South Coast Survey sta D00589-102-3421 (Agulhas Bank), S 34° 40.86’, E 22° 31.20’, 106 m, trawl, 1 ♀ 12.4 mm (SAMC MB-A066824), 1 ♀ 9.2 mm (SAMC MB-A066825); 19 May 2015, South Coast Survey sta D00583-096-3487 (Agulhas Bank), S 34° 35.58’, E 23° 19.74’, 112 m, trawl, 1 ♀ 9.5 mm (SAMC MB-A066842); 15 May 2016, South Coast Survey sta D00796-3677 (off Port Elizabeth, E. C.), S 34° 08.64’, E 26° 18.48’, 113 m, trawl, 1 ♂ 13.1 mm (SAMC MB-A066498).

Other material. 23 Sep 2016, South Coast Survey sta A32811-064-82427 (Agulhas Bank), S 33° 55.56’, E 26° 29.70’, 99 m, trawl, 1 ♂ 32.2 mm (in spiny lobster ‘crayfish’ trap caught in trawl net, photographed and released).

Genetic data. Sta D00589-102-3421, S 34° 40.86’, E 22° 31.20’, 106 m, ♀ 12.4 mm, BOLD: SEAKY873–15 (SAMC MB-A066824), ♀ 9.2 mm, BOLD: SEAKY959-15 (SAMC MB-A066825). Sta D00583-096-3487, S 34° 35.58’, E 23° 19.74’, 112 m, ♀ 9.5 mm, BOLD: SEAKY958-15 (SAMC MB-A066842). Sta D00563-076-3690, S 33° 55.32’, E 26° 35.64’, 101 m, ♂ 17.4 mm, BOLD: SEAKY877-15 (SAMC MB-A066844).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. A widespread species that is also common and widely distributed in South African waters, easily identified by the scute-like tuberculate or granular ridges on the chelipeds. One of the most-sampled hermit crabs of the region as reflected by the extensive collections at the Iziko South African Museum. Preliminary genetic testing suggests that *D. arrosor* is a species complex and that South African specimens belong to a Indo-Pacific group, and are different from specimens in the Atlantic (unpubl. data).

Distribution. East Atlantic, Mediterranean Sea, South Africa (False Bay to KZN), Red Sea, Philippine Islands, Taiwan, East China Sea, Korea Straight, Australia, Japan, New Zealand.

Habitat. Most often found on sandy substrates from 15–337 m depth, specimens in South Africa (particularly large ones) mostly carry large and elongated anemones.

Dardanus brachyops **Forest, 1962, new record**

Figure 8.7 C–D

Dardanus brachyops Forest, 1962: 365, Figs 1–3 (type locality: Hawaii). – Dechancé, 1964: 33. – Poupin, 1996a: 18, Pl 8d. – Poupin, 1996b: 17. – Asakura et al., 2003: 190, Figs 1–10. – Poupin et al., 2013a: 54 (list).

Material examined. 11 Nov 2016, Sezela (KZN), S 30° 24.66', E 30° 44.46', 50 m, Scuba, 1 ♂ 16.5 mm (SAMC MB-A066724).

Other material. 8 Jun 2014, R. Y. *Angra Pequena* sta New S4 off Kingsburgh (KZN), S 30° 07.42', E 30° 56.43', 66 m, ROV, one specimen not collected (photographed during ACEP Spatial Solutions Project cruise); 29 Jan 2016, off Umzumbe (KZN), S 30° 37.07', E 30° 37.11', 40 m, Scuba, one specimen not collected (photographed by V. Fraser).

Diagnosis. Adapted after Asakura et al. (2003). Shield about as broad as long, lateral projections bluntly large and produced. Ocular peduncles 0.4–0.6 length of shield, centrally weakly constricted; corneas dilated. Ocular acicles broad, each with 3–5 strong spines. Antennular peduncles long and slender, 1.6–1.8 length of ocular peduncles. Antennal peduncles reaching or slightly overreaching distal margins of corneas. Antennal acicles each with 4 or 5 spines on dorsomesial margins, dorsolateral margins with 1 or 2 subdistal spines. Left cheliped stout and considerably larger than moderately slender right, merus with 4 or 5 large spines on distal half of ventromesial margin, and 3 or 4 stronger spines on proximal half. Both chelipeds with outer faces of chela and carpus covered with corneous-tipped spines and tufts of long, stiff setae. Left second pereopod slightly shorter than third. Left third pereopod with distal 0.2–0.4 of spines corneous; dactyl with median longitudinal sulcus dorsally and ventrally with rows of spines, ventral margin with row of tooth-like protuberances and tufts of setae. Females with thin, very large, triangular fleshy-membranous plates between the fourth and fifth pleopods. Telson strongly asymmetrical with shallow median cleft; terminal margins with 4–6 corneous-tipped spines (left) and 5–7 corneous spines (right).

Colouration. See Asakura et al. (2003).

Remarks. The male South African specimen agrees well with previous descriptions and reports, although slight differences are that the shield is marginally longer than broad, the ocular peduncles are slightly longer than previously reported (0.6 length of shield), the antennal peduncles reach to the distal margin of the corneas, and the telson is armed with a slightly different number of spines (6 on each lobe). Given that few specimens of *Dardanus brachyops* have been collected, all these deviations can well be regarded as being within the natural variation of the species. The photographic records without physical specimens are included here because the colour information leaves little to no doubt about their identifications. Furthermore, they reveal information on the habitat and show that the species is not uncommon. This is the first record of the species from South African waters. Recently, *D. brachyops* has also been found at La Réunion (Legall and Poupin 2017), showing that this species is widespread and probably not uncommon.

Distribution. South Africa (KZN), Madagascar, La Réunion, Japan, Hawaii, French Polynesia.

Habitat. Fine and coarse sand on soft sediments; 33–300 m depth.

Dardanus crassimanus (H. Milne Edwards, 1836)

Figure 8.7 C–F

Pagurus crassimanus H. Milne Edwards, 1836: 277 (type locality: “la mer du Sud”, = Pacific Ocean).

Pagurus setifer. – Barnard, 1950: 426 (in part), Fig 79d.

Dardanus setifer. – Kensley, 1981: 32 (list, in part).

Dardanus crassimanus. – Buitendijk, 1937: 55. – McLaughlin et al., 2007b: 98, 2 unnumbered Figs. – Emmerson, 2016b: 143, unnumbered Fig. – Emmerson, 2016c: 448 (list).

Material examined. 15 Mar 1901, s. s. *Pieter Faure* sta 12428 (off Port Shepstone, KZN), S 30° 45.96’, E 30° 29.70’, 44 m, dredge, 1 ♂ 4.7 mm (SAMC MB-A001456); 15 May 1948, sta AFR 1028.U (KZN), S 28° 34.02’, E 32° 25.08’, no depth, dredge, 2 ♂♂ 2.1–3.8 mm (SAMC MB-A079342); 20 Jan 1954, UCT E. S. sta MOR 45 (Linga-Linga, Morrumbene, Mozambique), S 23° 42.54’, E 35° 21.24’, 7.5 m, dredge, 1 ♀ 7.4 mm (SAMC MB-A066662); Dec 1968, Tugela River mouth (KZN), S 29° 13.38’, E 31° 30.48’, no depth, 1 ♂ 14.8 mm (SAMC MB-A079387); 15 Dec 1984, Landers Reef (off Park Rynie, KZN), S 30° 20.16’, E 30° 47.82’, 40 m, 1 ♂ 11.8 mm (SAMC MB-A079392); 3 Oct 1986, Vetch’s Pier (Durban, KZN), S 29° 52.02’, E 31° 03.00’, no depth, 1 ♂ 17.9 mm (SAMC MB-A045507), coll. W. Emmerson; 18 Aug 1989, Treasure Beach (Durban, KZN), S 29° 57.00’, E 31° 00.00’, no depth, 1 ♂ 9.7 mm (SAMC MB-A045449), coll. T. Stewart; 16 Aug 2004, R. V. *Algoa* 130 (Pebane, Mozambique), S 17° 19.62’, E 38° 37.62’, 48 m, 1 ♀ 7.7 mm (SAMC MB-A079325); 8 Dec 2014, Sodwana Bay (KZN), S 27° 30.72’, E 32° 41.10’, 25 m, Scuba, 1 ♀ 4.0 mm (SAMC MB-A066033); 13 Oct 2015, off Pumula (KZN), S 30° 38.34’, E 30° 32.94’, 20 m, Scuba, 1 ♀ 6.7 mm (SAMC MB-A066421), 1 ♂ 3.7 mm (SAMC MB-A066422), 1 juv. ♂ 1.7 mm (SAMC MB-A066423), 1 ovig. ♀ 5.7 mm (SAMC MB-A066424), 1 ♂ 4.3 mm (SAMC MB-A066425), 7 ♂♂ 3.3–13.1 mm, 5 ♀♀ 4.1–10.3 mm (SAMC MB-A066488); 15 Oct 2015, off Hibberdene (KZN), S 30° 34.68’, E 30° 34.86’, 20 m, Scuba, 1 juv. ♂ 1.9 mm (SAMC MB-A066489); 15 Feb 2016, outside Taffy’s Cracker Ground off Pumula (KZN), S 30° 39.24’, E 30° 32.58’, 36 m, Scuba, 10 ♂♂ 4.0–7.1 mm, 2 ovig. ♀♀ 5.3–6.0 mm (SAMC MB-A066633); 10 Sep 2016, Pumula 36 (KZN), S 30° 38.40’, E 30° 34.20’, 36 m, Scuba, 3 ♀♀ 4.5–6.7 mm (SAMC MB-A066632); 17 Sep 2016, Pumula 22 (KZN), S 30° 38.40’, E 30° 34.20’, 42 m, Scuba, 1 ♀ 5.1 mm (SAMC MB-A066631); 24 Sep 2016, Taffy’s Cracker Ground off Pumula (KZN), S 30° 39.24’, E 30° 32.58’, 34 m, Scuba, 2 ♀♀ 5.8–5.9 mm (SAMC MB-A066634); 11 Nov 2016, Sezela 711 (KZN), S 30° 24.66’, E 30° 44.46’, 50 m, Scuba, 1 ♀ 3.7 mm (SAMC MB-A066722); 14 Dec 2016,“R”southwest of Port Shepstone (KZN), S 31° 02.28’, E 30° 39.54’, 70 m, Scuba, 2 ♂♂ 2.2–4.0 mm (SAMC MB-A066679).

Comparative material. *Dardanus setifer*: no date, Inhaca Island (Mozambique), no depth, 1 ♂ 9.6 mm (SAMC MB-A012038); 20 Jan 1954, UCT E. S. sta MOR 45 (Linga-Linga, Morrumbene, Mozambique), S 23° 42.54’, E 35° 21.24’, 7.5 m, dredge, 1 ♂ 10.4 mm (SAMC-A019462). *Indeterminate*: 20 Jan 1954, UCT E. S. sta MOR 45 (Linga-Linga, Morrumbene, Mozambique), S 23° 42.54’, E 35° 21.24’, 7.5 m, dredge, 1 ♂ 9.4 mm (SAMC MB-A066663), missing left cheliped.

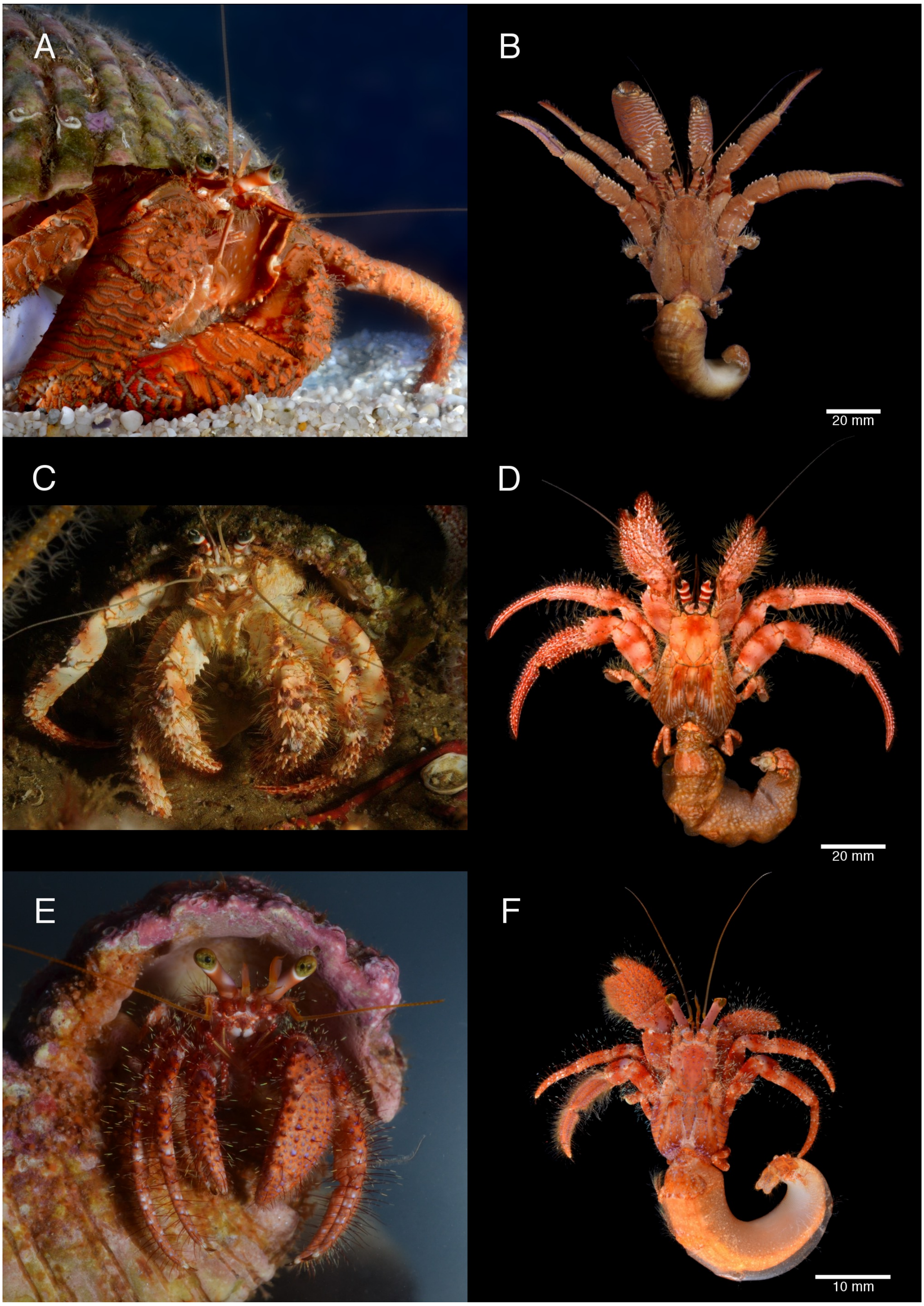

Figure 8.7: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A, C, E *in situ*): A–B *Dardanus arrosor* (Herbst, 1796), Agulhas Bank, ♂ 32.2 mm (released) (A), ♂ 17.4 mm (SAMC MB-A066844) (B) **C–D** *Dardanus brachyops* Forest, 1962, off Umzumbe, specimen not collected (photo V. Fraser) (C), Sezela, ♂ 16.5 mm (SAMC MB-A066724) (D) **E–F** *Dardanus crassimanus* (H. Milne Edwards, 1836), Sowana Bay, ♀ 4.0 mm (SAMC MB-A066033) (E), off Pumula, ♀ 6.7 mm (SAMC MB-A066421) (F).

Genetic data. Sodwana Bay, S 27° 30.72', E 32° 41.10', 25 m, ♀ 4.0 mm, BOLD: SEAKY620-15 (SAMC MB-A066033). Off Pumula, S 30° 38.34', E 30° 32.94', 20 m, ♀ 6.7 mm, BOLD: SEAKY1159-16 (SAMC MB-A066421), ♂ 3.7 mm, BOLD: SEAKY1160-16 (SAMC MB-A066422), juv. ♂ 1.7 mm, BOLD: SEAKY1161-16 (SAMC MB-A066423), ovig. ♀ 5.7 mm, BOLD: SEAKY1162-16 (SAMC MB-A066424), ♂ 4.3 mm, BOLD: SEAKY1163-16 (SAMC MB-A066425). Sezela 711, S 30° 24.66', E 30° 44.46', 50 m, 1 ♀ 3.7 mm, BOLD: SEAKY1427-17 (SAMC MB-A066722).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Specimens reported here generally agree with the diagnosis by McLaughlin et al. (2007b), but examination of a considerable sample size revealed that they vary in the length of the antennular peduncles. These can be from substantially longer to slightly shorter than the ocular peduncles, but are always well exceeding the proximal margins of the corneas. *Dardanus crassimanus* is therefore best identified by the characteristically shaped and tesselated lateral face of the two distalmost segments of the third left pereopod, in which especially the propodus has a strongly elevated, elongated ridge. In all but one (♀ 3.7 mm, MB-A066722, 50 m) South African specimens this surface is almost entirely smooth and predominantly without any spines, spinules or setae. The small female from slightly deeper waters, however, differs by having short stiff setae covering the ridge, and the transversal palisades on the ventral surface each have a distal row of short setae. Although this specimen was also found to be less purple in colour, it is otherwise conspecific in colouration and morphology with the other specimens, which is also supported genetically (Chapter 7). *Dardanus crassimanus* is closely allied to the poorly known species *D. setifer* (H. Milne Edwards, 1836), and this has caused confusion with regards to the South African distribution of both these species. Based on the synonymy for *D. setifer* given by McLaughlin and Hogarth (1998), Emmerson (2016b,c) correctly changed Barnard's (1950) record of *D. setifer* to *D. crassimanus*. Indeed, there is no doubt that Barnard's figure and text describe *D. crassimanus*. However, Emmerson missed out on the fact that McLaughlin and Hogarth had actually retained the South African distribution record of *D. setifer*, and he (Emmerson) also did not examine Barnard's specimens. Re-examination of the material housed at the Iziko South African Museum revealed that the majority of the material and all specimens from within the national boundaries of South Africa are *D. crassimanus*. However, two specimens from Mozambique (and potentially a third specimen that lost the left cheliped, initially from the same sample as SAMC MB-A019462) were found to be *D. setifer*, as they have the outer surface of the left chela covered by short corneous spinules circumscribed by short and thin setae, instead of long spinules with bristles, as in *D. crassimanus*. Moreover, the lateral face of the propodus of the third left pereopod is differently shaped in those specimens of *D. setifer*, with a less prominent ridge and also covered by small corneous spinules. Because *D. setifer* occurs in Mozambique, Emmerson should have retained the record for the Southern African region. Two more similar species, *D. scutellatus* (H. Milne Edwards, 1848) and *D. woodmasoni* (Alcock, 1905), also occur in Mozambique (pers. photographic records) and have not yet been recorded from South African waters. Great care should be applied in the identification of future samples.

Dardanus crassimanus is one of the most common hermit crabs on the deeper rocky reefs between Port Shepstone and Durban, but has probably so far remained unnoticed because of the inaccessibility of these diving locations.

Distribution. South Africa (KZN), East coast of Africa including Mozambique, Mauritius, Australia, Hong-Kong, Philippine Islands, Japan, Taiwan.

Habitat. Sandy and muddy substrates, in South Africa often in proximity to subtidal rocky reefs and down to 70 m.

Dardanus deformis **(H. Milne Edwards, 1836)**

Figure 8.8 A–B

Pagurus deformis H. Milne Edwards, 1836: 272, Pl 13 Fig 4 (type locality: Mauritius and Seychelles). – Barnard, 1950: 428.

Dardanus deformis. – Kensley, 1981: 32 (list). – McLaughlin et al., 2007b: 79, 2 unnumbered Figs. – McLaughlin and Hogarth, 1998: 11, Pl 1 Fig E–F. – Poupin, 2009: 59, unnumbered Fig. – Poupin et al., 2013a: 38, Fig 20 A–B. – Poupin et al., 2013c: 7 (list). – Poupin et al., 2013d: 10 (list). – Emmerson, 2016c: 448 (list).

Material examined. 8 Jan 1951, Durban (KZN), S 29° 52.68', E 31° 03.72', no depth, 1 ♂ 9.9 mm, 1 ♀ 6.4 mm (SAMC MB-A019629); Jun 1971, Inhaca Island, 1 ♀ 14.0 mm (SAMC MB-A079384); Oct 1986, Preslies Bay (E. C.), S 31° 53.16', E 29° 15.78', no depth, 1 ♀ 11.7 mm (SAMC MB-A045514).

Other material. 8 Mar 2016, Inhaca Island, S 26° 03.72', E 32° 57.06', intertidal, 2 specimens lost (SAMC MB-A066470, MB-A066471), both with photographic record, the former also with molecular barcode; 19 Jan 2010, Pomene Estuary (Mozambique), S 22° 54.44', E 35° 33.28', 3–5 m, one specimen not collected (photographed by V. Fraser); 20 Jan 2010, Pomene Estuary (Mozambique), S 22° 54.44', E 35° 33.28', 3–5 m, one specimen not collected (photographed by V. Fraser).

Genetic data. Inhaca Island, S 26° 03.72', E 32° 57.06', intertidal, specimen lost, BOLD: SEAKY1199-17 (SAMC MB-A066470).

Diagnosis. See McLaughlin et al. (2007b), and also remarks in Lewinsohn (1982b).

Remarks. The reported specimens agree well with the diagnosis in McLaughlin et al. (2007b), and can be distinguished from the closely related *D. pedunculatus* (Herbst, 1804) by the dorsal crest on the dactyl of the left pereopod (absent in *D. pedunculatus*), less tubercles on the outer face of the left chela, and the strongly cristate outer upper (dorsolateral) margin of the propodus of the third left pereopod (more rounded in *D. pedunculatus*). Males of *D. deformis* also have female-like gonopores on the coxae of the third pereopods which are absent in males of *D. pedunculatus.* The two species are also fundamentally different in colour as *D. deformis* is creamish brown and *D. pedunculatus* has a purple-cream left cheliped.

Slight variations observed in the specimens herein can be found in the margins of the dactylus and propodus of the third left walking leg. Particularly the ventrolateral margin of the dactyl is rather smooth, while the dorsolateral and especially ventrolateral margin of the propodus vary in the extend of the crest, and the ventrolateral margin is smooth instead of crenulate. The female specimen from Preslies Bay (SAMC MB-A045514) furthermore has some deformation growth patterns where especially the dorsal and ventral margins of the propodus of the third left pereopod have several irregular indentations.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Glorieuses Islands, Tanzania, Kenya, Somalia, Red Sea, La Réunion, Mauritius, Seychelles, Maldives, Australia, Taiwan, Philippine Islands, Mariana, Fiji, Cook Islands, Hawaii, French Polynesia.

Habitat. On sandy substrates, commonly associated with anemones, intertidal and sublittoral zones.

Dardanus gemmatus **(H. Milne Edwards, 1848)**

Figure 8.8 C

Pagurus gemmatus H. Milne Edwards, 1848: 60 (type locality: Marquesas Islands, French Polynesia).

Dardanus gemmatus. – McLaughlin et al., 2007b: 81, 2 unnumbered Figs. – Poupin, 2009: 59, unnumbered Fig. – Poupin et al., 2013a: 39, Fig 20C. – Poupin et al., 2013c: 7 (list). – Poupin et al., 2013d: 10 (list). – Emmerson, 2016c: 448 (list).

Material examined. Jul 1987, Umtata River mouth (KZN), S 31° 57.24', E 29° 11.28', no depth, 1 ♂ 9.6 mm (SAMC MB-A045516), coll. M. Schramm; Nov 1990, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', no depth, 1 ♂ 7.9 mm (SAMC MB-A045314), 1 ♀ 12.0 mm (SAMC MB-A045467), coll. W. Emmerson and G. Fotherby.

Comparative material. no date, "South Seas", no depth, 1 ovig. ♀ 15.3 mm, (SAMC MB-A043385), Godeffroy collection 3461; 8 Aug 1901, Hailua (Hawaiian Islands), no depth, 1 ♂ 20.9 mm (USNM 57912); 8 May 1902, Honululu Reef (Hawaiian Islands), no depth, 1 ♂ 10.0 mm (USNM 78454).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Except for their two reddish rings on the ocular peduncles (or thin white band on a red-maroon ocular peduncle) the preserved South African samples have lost their colour information. Morphologically they generally agree for example with the diagnosis given by McLaughlin et al. (2007b), or the report by Poupin (1994). However, it is noteworthy that when visiting Cape Town, P. McLaughlin tentatively identified the three specimens from South Africa as '*Dardanus* cf. *gemmatus*'. Despite her hesitation to make a clear determination, Emmerson (2016c) without comment reported (with no reference to museum vouchers, but most likely based on these samples)

D. gemmatus from South Africa. Since he collected at least two of the three specimens he probably had made an identification (also on colour) before McLaughlin saw them. Re-examining the specimens it is difficult to be sure about McLaughlin's exact source of uncertainty as she never published these findings. What seems most likely is that she observed the specimens not having the entire left chela covered by tubercles, as the outer face is ventroproximally somewhat smooth, bearing very few tubercles. Moreover, the dorsal half of the outer face of the left palm is not evenly convex, but has two moderately prominent longitudinal grooves. Maybe even more importantly, the propodus of the left third pereopod is laterally somewhat convex and has no clearly delimited dorsolateral angular margin.

During the course of this study three additional specimens of *D. gemmatus*, two from Hawaii (housed at USNM), and one from the "South Seas" (referring broadly to the Southern Pacific, housed at SAMC), were examined. Of these, the two larger specimens both have more pronounced tubercles on the palm, and also more clearly defined dorsolateral margins on the propodus of the third left pereopod. However, it appears that almost all characters are more clearly defined in these larger specimens, for example also the serrations on the margins of the dactylus and propodus of the third left pereopod. All three additional specimens also have the longitudinal grooves on the upper outer palm, even if these may be slightly deeper in the South African specimens. The small male specimen housed at the Smithsonian Institution also shows a tendency for less strongly developed tubercles on the anterioventral face of the palm, but has lost or damaged left appendages, so that the shape of the left pereopods was not compared amongst specimens of similar size. Because the South African specimens are rather small and the armature of the left chela and shape of the left pereopod appear to be subject to ontogenetic changes, the observed differences are herein treated as intraspecific variation. However, if these characters are found to be significant in future, they should be examined in more detailed studies with molecular support.

Distribution. Western Indian Ocean to French Polynesia, including South Africa (KZN), Mozambique Channel, Glorieuses Islands, La Réunion, Japan, Taiwan, Hawaii.

Habitat. Outer edges of reefs, usually in association with anemones, 10–50 m.

***Dardanus guttatus* (Olivier, 1811)**

Figure 8.8 D

Pagurus guttatus Olivier, 1811: 640 (type locality: Mauritius). – Barnard, 1950: 428.

Dardanus guttatus. – Kensley, 1981: 32 (list). – McLaughlin and Hogarth, 1998: Pl 2 Fig E–F. – McLaughlin et al., 2007b: 89, 2 unnumbered Figs. – Poupin, 2009: 58, unnumbered Fig. – Poupin et al., 2013a: 39, Fig 3B, 20D. – Poupin et al., 2013b: 4 (list). – Poupin et al., 2013c: 8. – Poupin, 2016: 50 (list). – Emmerson, 2016b: 144, unnumbered Fig. – Emmerson, 2016c: 448 (list).

Material examined. 23 Jun 1989, Treasure Beach (Durban, KZN), S 29° 57.00', E 31° 00.00', no depth, 1 ♂ 10.5 mm (SAMC MB-A045450), coll. T. Stewart.

Other material. 14 Sep 2013, Pomene Estuary (Mozambique), S 22° 54.44', E 35° 33.28', 3–5 m, one specimen not collected (photographed by V. Fraser).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Widespread, but in South Africa only known from a few records. Barnard's specimen (Fishery Survey 1948), and also another catalogue record from Durban in 1952 (SAMC MB-A019467), were not present in the collections of the Iziko South African Museum. The species is easily recognised by the broad light blue patches on the carpi of the chelipeds and first and second pereopods.

Distribution. South Africa (KZN), Mozambique, Mozambique Channel, Tanzania, Kenya, Somalia, Madagascar, La Réunion, Seychelles, Chagos, Indonesia, South China Sea, Taiwan, Mariana, New Guinea, Australia, New Caledonia, Wallis and Futuna, Samoa, Cook Islands, French Polynesia.

Habitat. Intertidal down to about 20 m.

Dardanus jacquesi **Asakura and Hirayama, 2002, new record**

Figure 8.8 E

Dardanus jacquesi Asakura and Hirayama, 2002: 214, Figs 1–6 (type locality: Okinawa, Japan). – Arima, 2014: 75, 2 unnumbered Figs.

Dardanus dearmatus. – McLaughlin and Hogarth, 1998: 10, Pl 1, Figs A–B. [not *Dardanus dearmatus* (Henderson, 1888)]

Material examined. 10 Apr 2017, Sezela (KZN), S 30° 24.66', E 30° 44.46', 50–55 m, Scuba, 1 ♀ 6.0 mm (SAMC MB-A066710).

Genetic data. Sezela, S 30° 24.66', E 30° 44.46', 50–55 m, ♀ 6.0 mm, BOLD: SEAKY1428-17 (SAMC MB-A066710).

Diagnosis. Adapted after Asakura and Hirayama (2002). Shield slightly broader than long. Ocular peduncles slightly shorter than extended antennular peduncles, weakly inflated distally; corneas 0.3 of peduncular length, dilated. Ocular acicles broad, each with 4 or 5 strong spines. Antennal peduncles 0.65–0.85 length of ocular peduncles; antennal acicle strong and slightly curved towards ventral, terminating in strong spine and with several spines on dorsolateral and dorsomesial margin. Left cheliped larger and longer than right, very stout; outer surface of chela strongly convex, evenly covered with small tubercles and without any setation. Left third pereopod with dactyl laterally with longitudinal sulcus, dorsal margin with corneous-tipped spines on proximal 0.7–0.8; propodus 2.55–2.90 longer than high, with numerous tubercles in dorsal 0.7, ventral margin with subquadrate protuberances. Females with thin, large, elongated triangular plate ventrally between the fourth and fifth pleopods. Telson asymmetrical with shallow median cleft, margins of posterior lobes continuously armed with corneous spines and variously-sized setae.

Colouration. Shield cream to orange with darker patches and mottled white dots. Posterior carapace similar, laterally darker and with pinkish patch. Branchiostegites cream to white with irregular but somewhat longitudinal red stripe medially. Ocular peduncles cream to white with broad orange-red median band that is dorsally divided, appearing like two individual bands in dorsal view, dorsodistally with small orange-red patch near the corneal margins; corneas black; ocular acicles cream with mesial red patch at base. Antennulae and antennae predominantly cream to white. Chelipeds and ambulatory legs with cream to white background. Left cheliped with dactyl pinkish distally and at upper base, with small orange spot on upper outer and also on inner surface proximally; fixed finger distally pinkish; palm with outer and inner surface cream with tiny orange dots, upper inner surface with orange-red patches, orange on upper margin; carpus and merus more orange with irregular orange-red spots or patches, lines or stripes. Right cheliped similar to left one, but fingertips not pinkish; dactyl with orange dots and with pinkish patch at upper base; palm and fixed finger with slightly larger dots than on left, upper margins orange, upper surface pinkish; merus with orange-red narrow transversal band in distal half. Second and third pereopods very similar to each other, with red-orange bands generally uncontinuous ventrally; dactyls pinkish with faint orange tips and at base and also with small orange dots; propodi with central orange-red to purple broad bands (pinkish and more faint on third left), also with small orange dots; carpi with central orange-red broad band and some small orange dots; meri with one broader orange-red band in proximal half, a narrower one in distal half, and a narrow 90°-shaped line distally. Fourth and fifth pereopods each with a broad orange-red central band on the propodus, carpus and merus. Pleon orange. Pleopods and triangular plate cream to white. Uropods cream with some faint orange-red patches. Telson cream with tiny orange dots.

Remarks. Initially, the assignment of this single female specimen to this species was done with some hesitation. Although in the majority of characters it agrees with the description of *D. jacquesi* by Asakura and Hirayama (2002), some differences are noticeable. The antennal peduncles are slightly longer, reaching to about the middle of the corneas, and the spinulation on the antennal acicles is different in having 4 spines on the dorsomesial margins. Furthermore, the left cheliped, although still very stout, does not seem to be as stout as previously described. With regard to these characters alone, the South African specimen appears much closer to the allied and equally poorly known sister species *Dardanus dearmatus* (Henderson, 1888). To add some confusion, Asakura and Hirayama (2002) reported two thin plates (one suboval between the third and fourth pleopods, and one elongated triangular one between the fourth and the fifth pleopods) in *D. jacquesi*, and a single large suboval plate between the fourth and fifth pleopods in *D. dearmatus*. The female South African specimen has only one such plate, like *D. dearmatus*, but it agrees in form and shape with the larger triangular one in *D. jacquesi*. All other identification characters are in strong agreement with *D. jacquesi*, such as the dimensions of the left third pereopod, and also the colouration. One noticeable character that had not been reported before is the several long, corneous setae on the exopod of the fourth left pleopod, which are present in the female specimen from South Africa.

Both *D. jacquesi* and *D. dearmatus* are poorly known and because the South African specimen agrees well with the majority of the description of *D. jacquesi*, the differences reported here are regarded as variation. However, this specimen can be placed intermediate to both species, so that additional sampling with detailed species comparison and genetic testing may reveal synonymy. Should colour information in life come available for *D. dearmatus*, these can be compared to the detailed colour information provided here. Another character that should be examined is the tuberculation of the left cheliped. While in *D. jacquesi* the palm is tuberculate, the palm in *D. dearmatus* can be entirely smooth (D. L. Rahayu, pers. comm.). Moreover, Asakura et al. (2003) discussed the significance of the fleshy membranous protuberance on the pleon of some species of *Dardanus*, also present in females of both *D. dearmatus* and *D. jacquesi*. The significance of this structure still requires investigations. In the collections of the Iziko South African Museum there is another specimen of *Dardanus* (SAMC MB-A13462) from Silhouette (Seychelles) that has an elongated, triangular plate ventrally between the fourth and fifth pleopods, similar to the specimen of *D. jacquesi* recorded here. The Seychelles specimen is a male of a different species, and its identity remains uncertain, as the specimen has lost all appendages. Nevertheless, the report here of *D. jacquesi* represents the first record of this species in South Africa waters.

Distribution. South Africa (KZN), Seychelles, Okinawa Islands (Japan).

Habitat. In the Seychelles found in proximity to calcareous sand with rhodoliths, stones and soft corals; from 40–73 m depth.

***Dardanus lagopodes* (Forskål, 1775)**

Figure 8.8 F, Figure 8.9 A

Cancer lagopodes Forskål, 1775: 93 (type locality: Red Sea).

Pagurus euopsis. – Barnard, 1950: 427.

Dardanus euopsis. – Kensley, 1981: 32 (list).

Dardanus lagopodes. – Lewinsohn, 1969: 32, Pl 2. – McLaughlin and Dworschak, 2001: 150. – McLaughlin et al., 2007b: 91 (in part), 2 unnumbered Figs. – Poupin, 2009: 58, unnumbered Fig. – Poupin et al., 2013a: 39 (in part), Fig 21B. – Emmerson, 2016b: 148, unnumbered Fig. – Emmerson, 2016c: 448 (list).

?*Dardanus lagopodes*. – Poupin et al., 2013d: 10 (list). – Poupin, 2016: 50 (list). – Poupin et al., 2013c: 8 (list).

Material examined. Jun 1988, Bazaruto (Mozambique), no depth, 2 ♂♂ 11.3–12.7 mm, 1 ♂ (in shell) 11.5 mm (SAMC MB-A045493); Jul 1988, Sodwana Bay (KZN), S 27° 31.98’, E 32° 40.98’, no depth, 1 ovig. ♀ 6.7 mm (SAMC MB-A045330), coll. W. Emmerson and G. Fotherby; 18 Aug 1989,

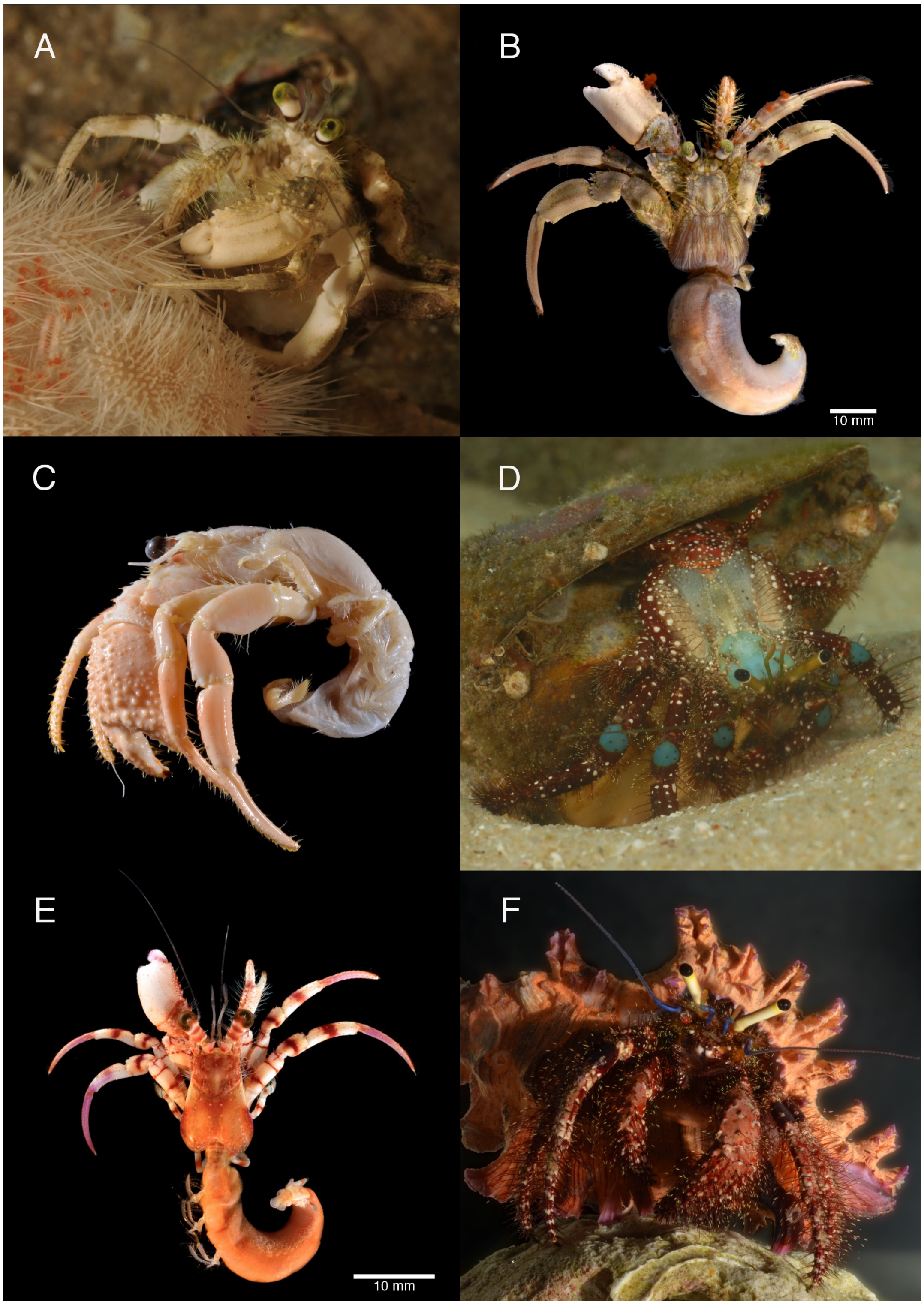

Figure 8.8: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A, D, F *in situ*, C in preservative): A–B *Dardanus deformis* (H. Milne Edwards, 1836), Pomene (Mozambique), specimen not collected (photo V. Fraser)(A), Inhaca Island (Mozambique), specimen lost (SAMC MB-A066470)(B) **C** *Dardanus gemmatus* (H. Milne Edwards, 1848), Sodwana Bay, ♀ 12.0 mm (SAMC MB-A045467) **D** *Dardanus guttatus* (Olivier, 1811), Pomene (Mozambique), specimen not collected (photo V. Fraser) **E** *Dardanus jacquesi* Asakura and Hirayama, 2002, Sezela, ♀ 6.0 mm (SAMC MB-A066710) **F** *Dardanus lagopodes* (Forskål, 1775), Sodwana Bay, ♀ 8.4 mm (SAMC MB-A065968).

Treasure Beach (Durban, KZN), S 29° 57.00', E 31° 00.00', subtidal (in small gully), 1 ♀ 9.4 mm (SAMC MB-A045451), coll. T. Stewart; Nov 1989, Sodwana Bay (KZN), S 27° 31.98', E 32° 40.98', no depth, 2 ♂♂ 6.1–6.6 mm, 1 ♀ 7.4 mm (SAMC MB-A045359), coll. W. Emmerson and G. Fotherby; 6 Dec 2014, Leadsman Shoal (Sodwana Bay, KZN), S 27° 31.68', E 32° 41.22', 18 m, Scuba, 1 ♂ 9.3 mm (SAMC MB-A065967), Archers (Sodwana Bay, KZN), S 27° 30.72', E 32° 41.10', 11 m, Scuba, 1 ♀ 8.4 mm (SAMC MB-A065968), 1 ♂ 13.3 mm (SAMC MB-A065969), 1 ♂ 14.4 mm (SAMC MB-A065970); 15 Oct 2015, off Hibberdene (KZN), S 30° 34.92', E 30° 34.86', 20 m, Scuba, 1 juv. ♂ 2.8 mm, 1 juv. ♀ 2.7 mm (SAMC MB-A066664).

Genetic data. Leadsman Shoal (Sodwana Bay), S 27° 31.68', E 32° 41.22', 18 m, ♂ 9.3 mm, BOLD: SEAKY554-15 (SAMC MB-A065967). Archers (Sodwana Bay), S 27° 30.72', E 32° 41.10', 11 m, ♀ 8.4 mm, BOLD: SEAKY555-15 (SAMC MB-A065968), ♂ 13.3 mm, BOLD: SEAKY556-15 (SAMC MB-A065969), ♂ 14.4 mm, BOLD: SEAKY557-15 (SAMC MB-A065970).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Adding to the considerable taxonomic confusion regarding specimens of *Dardanus lagopodes sensu lato* with differently coloured bands (red vs. dark) on the carpi of the chelipeds and walking legs (see detailed remarks under *D. umbella*), even the identity of this 'true' *D. lagopodes* with dark bands is somewhat questionable when examining colour photographs in life. For a long time known as *Dardanus euopsis* (Dana 1852), Forest (1953) provided a full synonymy for this species and accordingly changed the name to *D. sanguinolentus* (Quoy and Gaimard, 1824). Later, when comparing fresh material from the first 'Israel South Red Sea Expedition, 1962' collected by L. B. Holthuis, Lewinsohn (1969) synonymised both these names with *D. lagopodes* (Forskål, 1775), which had priority to all later-dated descriptions. It is noticeable that Lewinsohn wrote he had both the red and the dark colour form in his material, an observation that was probably based on field notes – unfortunately the darker black colour turns red in preservative (pers. obs.). Forskål's original description (as *Cancer*) remarks on the "Antennae flavae" (yellow antennae, likely referring to both the antennules and antennae) as well as mentioning the colour to be "cinereo-fuscus" (grey-brown). By this description, the *D. lagopodes* with the dark bands is the true one, as modern pictures taken of *D. lagopodes* from the Red Sea (e. g. Wikipedia contributors 2017) reveal that indeed the antennules and antennae are yellow (actually probably of both the red and the dark form). However, specimens from South Africa with dark bands have dark to bright-blue antennules and antennae (Figure 8.8 F), even if the antennae of juvenile specimens can be yellowish or orange (Figure 8.9 A). Morphologically the specimens reported on here agree, for example, with the diagnosis by McLaughlin et al. (2007b).

Accounting for modern taxonomic knowledge on the significance of colour pattern in hermit crabs, it seems unlikely that the same species (*D. lagopodes* with dark bands) has such differently-coloured antennas (yellow vs. blue). It is therefore very possible, yet speculative, that the true *D. lagopodes* (with dark bands) is actually restricted to the Red Sea (and has yellow antennae) and that other specimens of the dark form reported from the Indo-West Pacific (with blue antennae)

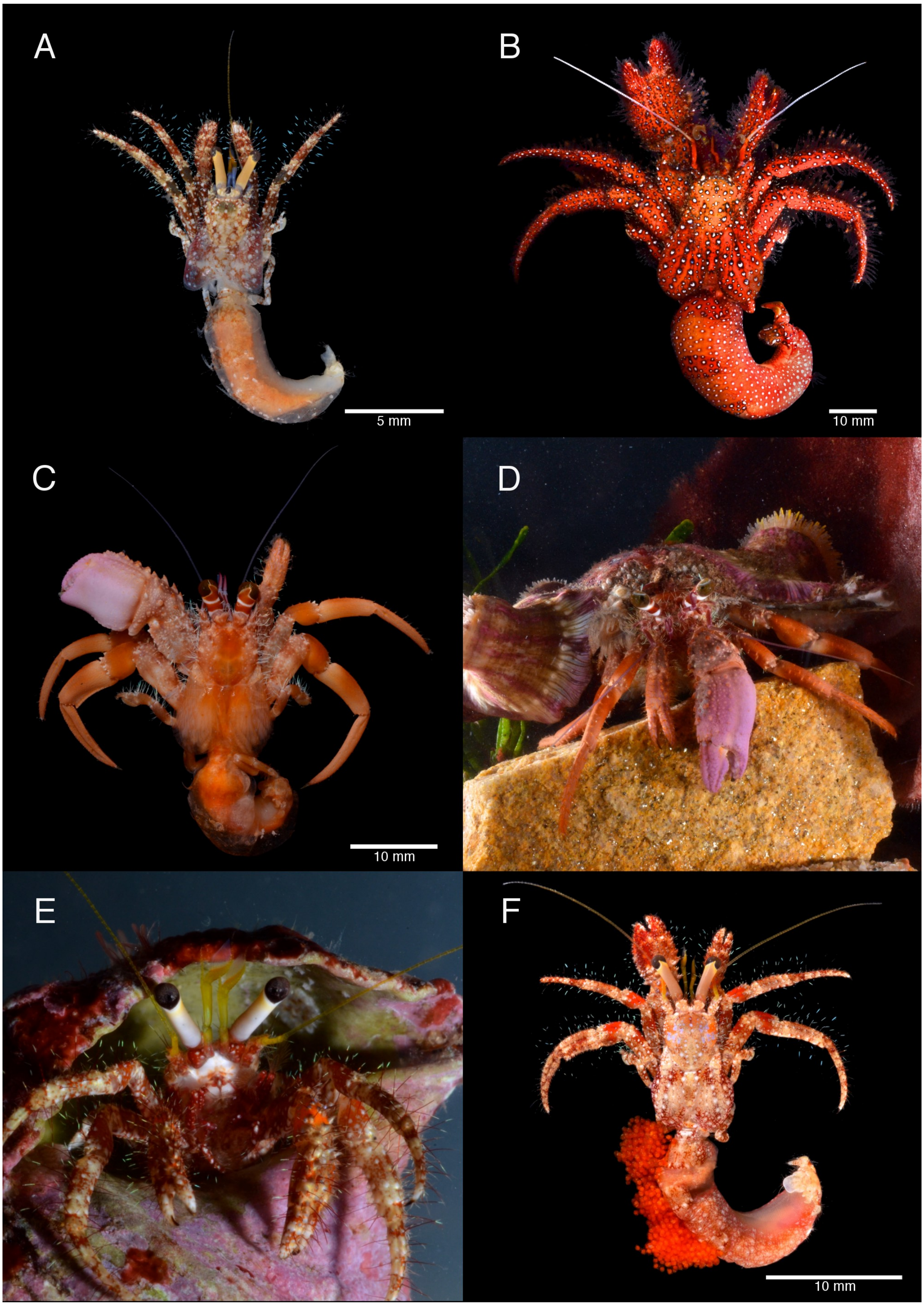

Figure 8.9: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (D–E *in situ*): A *Dardanus lagopodes* (Forskål, 1775), off Hibberdene, juv. ♂ 2.8 mm (SAMC MB-A066664) **B** *Dardanus megistos* (Herbst, 1804), Inhaca Island (Mozambique), ♀ 11.9 mm (SAMC MB-A066479) **C–D** *Dardanus pedunculatus* (Herbst, 1804), off Pumula, ♂ 6.2 mm (SAMC MB-A066418)(C), ♀ 11.5 mm (SAMC MB-66428)(D) **E–F** *Dardanus* cf. *umbella* Asakura, 2006a, Sodwana Bay, ♂ 2.9 mm (SAMC MB-A066035)(E), ovig. ♀ 4.8 mm (SAMC MB-A066715)(F).

belong to one or more different species. More detailed studies that include molecular tools are needed to resolve this conundrum.

Distribution. East coast of Africa including South Africa (KZN), Red Sea, Madagascar, Seychelles, Mauritius, southern India, Malaysia, Philippine Islands, Taiwan, Japan, New Guinea, Australia, Samoa, French Polynesia.

Habitat. Intertidal to shallow reefs.

Dardanus megistos **(Herbst, 1804)**

Figure 8.9 B

Cancer megistos Herbst, 1804: 23, Pl 61 Fig 1 (type locality: East India).

Pagurus megistos. – Stebbing, 1910: 350; Barnard, 1950: 425, Fig 79c.

Dardanus megistos. – McLaughlin et al., 2007b: 94, 2 unnumbered Figs. – Kensley, 1981: 32 (list). – Poupin, 2009: 58, unnumbered Fig. – Branch et al., 2010: 116, Fig 49.1. – Poupin et al., 2013a: 41, Fig 21D. – Poupin et al., 2013c: 8 (list). – Emmerson, 2016b: 152, unnumbered Fig. – Emmerson, 2016c: 448 (list). – Poupin, 2016: 50 (list).

Material examined. 1935, Mauritius, 1 ♂ 23.1 mm (SAMC MB-A010925); 23 Jul 1953, between wracks at Linga-Linga (Morrumbene, Mozambique), S 23° 43.56', E 35° 22.98', 1 ♀ 14.7 mm (SAMC MB-A019464); no date, "South Seas", 2 ♂♂ 13.7–13.8 mm, 1 ♀ 14.8 mm (SAMC MB-A043387); Jun 1971, Inhaca Island (Mozambique), 1 ♀ 15.1 mm, 1 specimen (in shell) (SAMC MB-A09391); 21 May 1973, Vilankulo (Mozambique), 1 ♀ 11.9 mm (SAMC MB-A079386); 20 May 1987, Bassas D'India, 1 ♂ 18.5 mm (SAMC MB-A045501); Jun 1988, Bazaruto (Mozambique), S 21° 31.90', E 35° 29.13', 1 ♀ 17.8 mm (SAMC MB-A045480); 16 Mar 2016, Inhaca Island (Mozambique), S 26° 02.46', E 32° 53.88', intertidal, 1 ♀ 11.9 mm (SAMC MB-A066479).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. This remarkably coloured and widely distributed species is common in the Western Indian Ocean, but it has not recently been recorded from within South Africa. The only historical national record is a specimen from Durban Bay (see Stebbing 1908, Barnard 1950), and it remains unknown if this specimen still exists. It was not present in the collections of the Durban National Science Museum (N. Govender, pers. comm.). However, the Mozambican occurrence close to the South African border leaves little doubt that Stebbing's and consecutively Barnard's record is correct.

Distribution. East coast of Africa including South Africa (KZN), Red Sea, throughout Indo-Pacific to Liu-Kiu Islands, Australia, South China Sea, Taiwan, French Polynesia, Hawaii.

Habitat. On sand and mud, including seagrass beds, often on outer edges of reef, intertidal to 50 m depth.

Dardanus pedunculatus (Herbst, 1804)

Figure 8.9 C–D

Cancer pedunculatus Herbst, 1804: 25, Pl 61 Fig 2 (type locality: East India).

Pagurus pedunculatus. – Barnard, 1950: 429, Figure 79a.

Pagurus asper. – Barnard, 1950: 430.

Dardanus pedunculatus. – Kensley, 1981: 32. – Lewinsohn, 1982b: 43. – McLaughlin et al., 2007b: 83, 2 unnumbered Figs. – Branch et al., 2010: 116, Fig 49.4. – Poupin et al., 2013a: 41, Fig 21E. – Poupin et al., 2013b: 4 (list), Fig 2 topright. – Poupin et al., 2013c: 8. – King and Fraser, 2014: 288, unnumbered Fig. – Emmerson, 2016c: 448 (list).

Dardanus tinctor Emmerson, 2016b: 155, 2 unnumbered Figs. [not *Dardanus tinctor.* – (Forskål, 1775)]

?*Dardanus tinctor.* – Kazmi et al., 2007: 96, Fig 1c–f.

Material examined. 1920, Durban (KZN), S 29° 52.68', E 31° 03.72', no depth, 2 ♂♂ 11.6–18.7 mm (dry) (SAMC MB-A006087); 15 Oct 2015, off Pumula (KZN), S 30° 38.34', E 30° 32.94', 20 m, Scuba, 1 ♀ 5.3 mm (SAMC MB-A066417), 1 ♂ 6.2 mm (SAMC MB-A066418), 1 juv. ♂ 2.6 mm (SAMC MB-A066426), 1 ♀ 7.5 mm (SAMC MB-A066427), 1 ♀ 11.5 mm (SAMC MB-A066428); 15 Feb 2016, outside Taffy's Cracker Ground off Pumula (KZN), S 30° 39.24', E 30° 32.58', 36 m, Scuba, 1 juv. ♂ 5.8 mm, 1 ♀ 9.6 mm (both infested by rhizocephalan barnacles) (SAMC MB-A066696); 21 Aug 2016, UMNT off Port Shepstone (KZN), S 30° 44.46', E 30° 33.66', 46 m, 1 ♂ 8.3 mm (SAMC MB-066696).

Genetic data. Off Pumula, S 30° 38.34', E 30° 32.94', 20 m, ♀ 5.3 mm, BOLD: SEAKY1155-16 (SAMC MB-A066417), ♂ 6.2 mm, BOLD: SEAKY1156-16 (SAMC MB-A066418), juv. ♂ 2.6 mm, BOLD: SEAKY1164-16 (SAMC MB-A066426), ♀ 11.5 mm, BOLD: SEAKY1166-16 (SAMC MB-A066428).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Emmerson (2016b,c) was confused by this species, writing an entire entry on *Dardanus tinctor* (Forskål, 1775), but then instead listing *D. pedunculatus* in his accompanying checklist. His misleading report finds its roots in Lewinsohn's (1969) speculation that Barnard's (1950) specimens might have been *D. tinctor*, an unverified assumption later shared by McLaughlin and Dworschak (2001), as well as by Kazmi et al. (2007). A re-examination of museum specimens that are likely the basis of Barnard's record, as well as the collection and identification of new material, revealed that the South African specimens are more likely *D. pedunculatus*, and not *D. tinctor*.

According to Lewinsohn (1969), the tubercles on the dorsal half of the outer surface of the palm of the left cheliped are evenly distributed in *D. tinctor*, whereas they are 'irregular' in *D. pedunculatus*, referring to the fact that they are arranged in rows interspersed by two longitudinal furrows. The South African specimens have pronounced furrows, but the tuberculation is variable. Smaller specimens usually have few tubercles, and large specimens have more tubercles, which are then regularly spaced, but of irregular size. With this variation some specimens also agree quite well with the text and illustration of *D. tinctor* by Kazmi et al. (2007). The authors must have based their identification predominantly on the shape of the propodus of the left third pereopod, which in *D. tinctor* has a longitudinal serrated keel on the upper outer surface. This keel is lacking in *D. pedunculatus* and the upper outer surface (in McLaughlin et al. (2007b) referred to as the dorsolateral margin) is rounded or acute. This margin was found to be variable in the South African specimens, from usually rounded in smaller specimens to strongly acute in some larger specimens. It can furthermore bear small and low tubercles that together could potentially be interpreted as a 'keel'. These tubercles were also illustrated by Barnard (1950, Fig 79a), however, in the specimens examined they are nothing like the strongly produced and serrated keel in *D. tinctor* from the Red Sea (Lewinsohn 1969). In combination with the rounded, non-crested dorsal margin, which only bears a few spinulose tubercles and setae, the specimens herein are identified as *D. pedunculatus*. Another character in which the specimens vary slightly is that the antennal peduncles only reach the distal margins of the corneas, whereas McLaughlin et al. (2007b) state that they are overreaching. Nevertheless, the finding that some South African specimens have keel-like tubercles questions the identity of the report of *D. tinctor* by Kazmi et al. (2007), in which the illustration shows only a small keel (but slightly larger than in the South African specimens).

The species pair of *D. tinctor* and *D. pedunculatus* is very closely related and with the South African specimens showing intermediate characters, both species should be taxonomically revised. Such a study may also shed light on the currently dubious distribution of the two species in the Western Indian Ocean. Another related species, *D. deformis*, can more easily be identified by a dorsal crest on the dactyl of the left cheliped (also see remarks under this species). In South Africa, *D. pedunculatus* is common in KwaZulu-Natal and associated with mutualistic anemones. Several specimens were also found to be heavily infested by an unknown species of rhizocephalan barnacle.

Distribution. Probably from South Africa (KZN) to Somalia, Mozambique Channel, Madagascar, La Réunion, Seychelles, Australia, Indonesia, Taiwan, Philippines, Japan, New Caledonia, Cook Islands, French Polynesia, Hawaii.

Habitat. Sandy substrates and on subtidal rocky reefs, associated with anemones, from 10–100 m depths.

***Dardanus* cf. *umbella* Asakura, 2006a, new record**

Figure 8.9 E–F

Dardanus umbella Asakura, 2006a: 27, Figs 16–20, 32 (type locality: Yap Island, Micronesia).

?*Dardanus lagopodes*. – McLaughlin et al., 2007b: 91, unnumbered Fig (in part). – Arima, 2014: 71, 6 unnumbered Figs. – Poupin, 2009: 59, unnumbered Fig. – Poupin et al., 2013a: 39 (in part), Figs 3C, 21A, B.

?*Dardanus sanguinolentus*. – Dechancé, 1964: 34. – Forest, 1956: 49.

Material examined. 6 Dec 2014, Archers (Sodwana Bay, KZN), S 27° 30.72', E 32° 41.10', 11 m, Scuba, 1 ♂ 2.9 mm (SAMC MB-A066035), 1 ovig. ♀ 4.8 mm (SAMC MB-A066715).

Genetic data. Archers (Sodwana Bay), S 27° 30.72', E 32° 41.10', 11 m, ♂ 2.9 mm, BOLD: SEAKY622-15 (SAMC MB-A066035), ovig. ♀ 4.8 mm, BOLD: SEAKY1441-17 (SAMC MB-A066715).

Diagnosis. Carapace not obviously depressed, shield about as long, or longer, than broad. Ocular peduncles longer than antennular peduncles, distally inflated; corneas about 0.25 of peduncular length. Left cheliped broader and slightly longer than right; palm and fixed finger armed with often corneous-tipped spines, lower half of outer face weakly concave and with numerous minute setae reminiscent of umbrella-like ribs; lower face with 1–3 irregular rows of prominent corneous-tipped spines. Dactyl of left third pereopod about 1.3–1.5 length of propodus, lateral face with shallow to moderately deep longitudinal median or dorsal groove, ventrally usually with scattered corneous spines. Propodus broad, dorsal margin with row of furrows creating lobes, dorsolateral face of each lobe usually with long corneous spines; lateral face in dorsal half with very deep longitudinal concavity, ventral half with 2–4 rows of protuberances, each bearing 1–3 spiniform setae or long corneous spines, and also minute setae reminiscent of umbrella-like ribs. Females with thin, large, plate ventrally between the fourth and fifth pleopods consisting of a long and broad rounded main flap, and also of a small notch on the distal margin of the flap. Telson asymmetrical with shallow median cleft, posterior lobes without or with up to 3–5 corneous-tipped calcareous spines on terminal margin, and with various numbers of long corneous spines lateroventrally near terminal margin.

Colouration. Shield beige-orange, mottled brown-maroon, with white-cream spots anteriorly and posteriorly, and bright blue-purple spots centrolaterally, near anterior margin with narrow maroon lines, lateral areas orange. Posterior carapace similar, but with larger white spots and also with irregular maroon patches and pattern. Branchiostegites maroon with white spots. Ocular peduncles dorsally beige-red to grey with subcorneal orange-yellow ring, ventrally entirely white except for pale subcorneal ring; ocular acicles beige-orange, terminal margins maroon. Antennular peduncles yellow, maroon at base, upper flagellum with some orange. Antennal peduncles beige-orange with maroon and white dots, distally from midlength of fourth segment onwards yellow. Chelipeds and ambulatory legs with beige-orange background colouration, with band and patches of maroon-red and also with irregular white spots, covered in moderately long, maroon setae with white tips in about distal 0.2. Outer face of left chela predominantly maroon to orange. Carpi of chelipeds dorsally with large orange patch and also with bright blue-purple spots or patches. Second and third pereopod with bright red band on carpi, and with slightly darker band on distal meri. Pleon orange, mottled cream. Uropods and telson predominantly light orange. Eggs orange-red.

Remarks. Tentatively assigned to *Dardanus umbella* the identity of the two South African specimens needs further clarification upon the availability of more and comparative material. Both specimens have the characteristic umbrella-like setae, even if they are very scarce in the small male individual. The specimens also agree in the armature of the lower margin of the left chela and many other characters, such as the characteristic shape of the thin plate ventrally between the fourth and fifth pleopods in the female specimen. However, the uncertainty of the identity derives from a number of differences from the description and illustrations by Asakura (2006a). These include, but are not limited to, the shape of the shield in having a convex anterior margin, differently-shaped ocular acicles, which have the terminal margin laterally convex, the left chela and third left dactyl and propodus with varying degree of armature, and the telson with several calcified corneous-tipped spines on the terminal margin and no or fewer long, corneous spines ventrolaterally. Nevertheless, intraspecifically the two South African specimens vary greatly in these characters, for example in the armature of the left cheliped (almost no spines in the juvenile male vs. rows of corneous-tipped spines in the ovigerous female). As Asakura (2006a) described the species based on only two specimens, the observed differences may well be intraspecific variation. The resulting problem raises a general question if new hermit crab taxa should be described based on very limited and old museum material for which neither colour information in life, nor genetic information, is available.

Furthermore, several uncertainties arise from the literature regarding species of *Dardanus* that have red bands on the carpi of the walking legs. In the Western Indian Ocean (e. g. Poupin et al. 2013a) as well as in the Indo-West Pacific (e. g. McLaughlin et al. 2007b) many reports of *D. lagopodes* (Forskål, 1775) *sensu lato* combine two colour forms under this same name: one with bluish-black or dark bands, and one with reddish bands, on the chelipeds and walking legs. For some time it has been suspected that the red form is a different species to the dark-banded form (e. g. McLaughlin et al. 2007b), and *D. lagopodes* is herein reported as the bluish-black form (see species entry and remarks under this name).

To complicate the matter further, when Asakura (2006a) defined the *Dardanus sanguinocarpus* Degener, 1925 species complex, he described three additional new species (one of these being *D. umbella*) and defined the group predominantly by the shape of the left chela of the cheliped, having the lower outer half concave (convex in *D. lagopodes*). Although present, this concavity is not very pronounced in the two South African specimens of *D. umbella*, and with regard to all other defining characters (combination of dimensions and armature of the cephalic appendages, chelipeds, pereopods and telson) a close relationship to *D. lagopodes* exists (particularly when considering the colouration patterns). Unfortunately, Asakura did not compare any of his new species to *D. lagopodes*, nor did he include the latter in his proposition of the *sanguinocarpus* species complex.

Concluding the newly available information, it is very possible that *D. umbella* has been frequently overlooked and is rather common, potentially across the Indo-Pacific, but that many other records of this species in the literature are hidden under the name *D. lagopodes*. Existing museum specimens of doubtful records should be examined and checked for the umbrella-like setae.

Distribution. South Africa (KZN), Mozambique Channel, ?Madagascar, La Réunion, Cocos (Keeling) Islands, Taiwan, Japan.

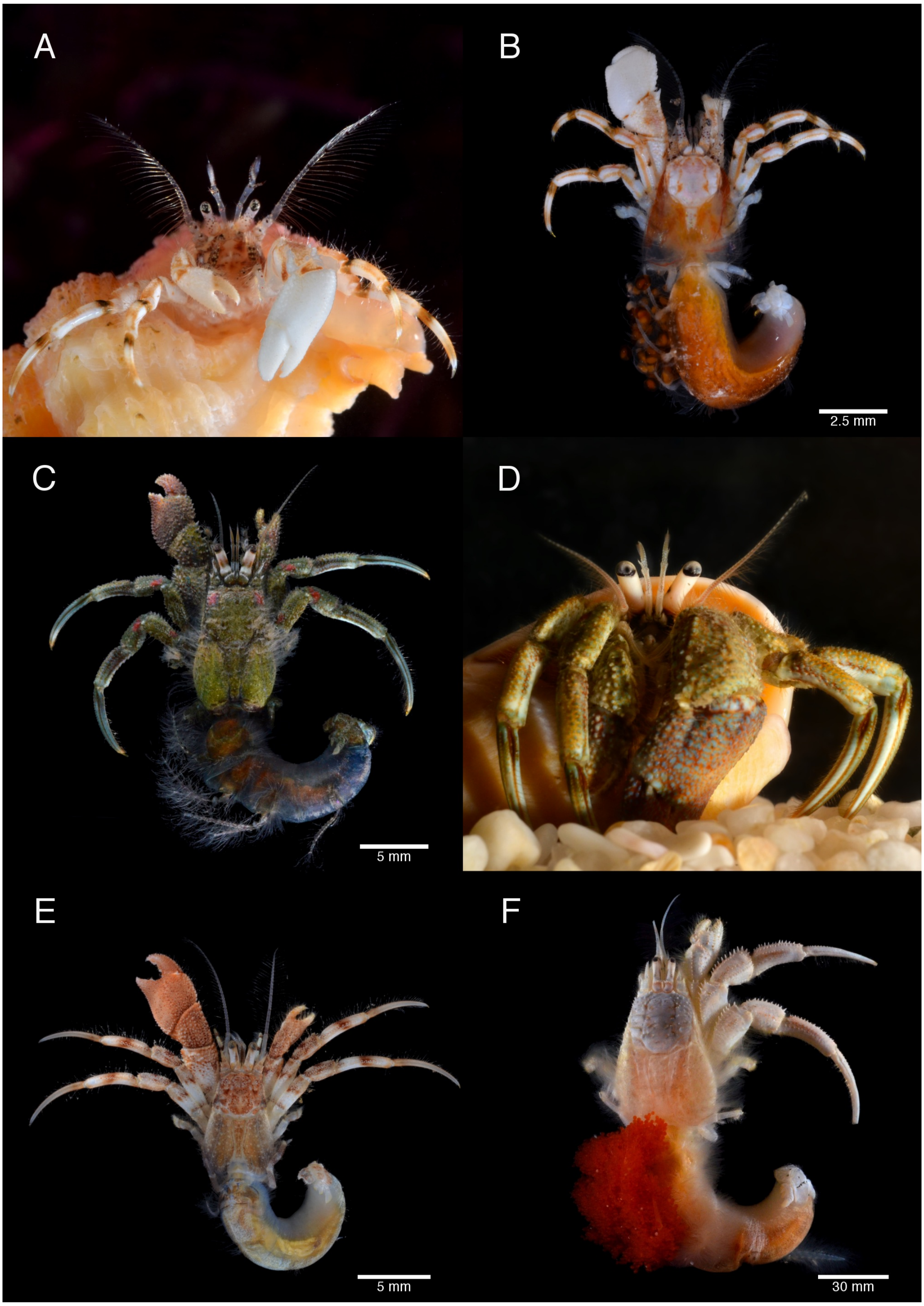

Figure 8.10: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (A, D *in situ*): A–B *Diogenes* n. sp. Landschoff and Rahayu, in press, Pumula, holotype, ovig. ♀ 2.0 mm (SAMC MB-A066353) **C–D** *Diogenes brevirostris* Stimpson, 1858, Jongensfontain, ♀ 4.9 mm (SAMC MB-A066521)(C), Langebaan, ♂ 3.7 mm (SAMC MB-A066762)(D) **E** *Diogenes costatus* Henderson, 1893, Agulhas Bank, ♂ 3.4 mm (SAMC MB-A066757) **F** *Diogenes extricatus* Stebbing, 1910, Fish Hoek, ovig. ♀ 8.5 mm (damaged) (SAMC MB-A066741).

Habitat. In South Africa associated with coral reefs, subtidal to 11 m depth.

8.4.3.6 Genus *Diogenes* Dana, 1851

Diogenes n. sp. Landschoff and Rahayu, in press

Figure 8.10 A–B

Material examined and genetic data. See Chapter 3.

Remarks. Currently being described from KwaZulu-Natal, this small *Diogenes* is readily identified by its unusual colouration, a bright-white left chela and longitudinal orange stripes on the pereopods. Because the taxonomic status of the other South African species of *Diogenes* has not changed since Barnard (1950), they are not included in this report. Kensley's (1969) mentioning of *D. custos* from Durban was not listed by Kensley's biogeographic study (1981), and this particular South African record could not be verified for now. However, this does not rule out the possibility that *D. custos* does occur in South Africa. A revision of the local members of the genus, with the likely description of several new species that are suspected to be present, is needed, but lies beyond the scope of this study.

Distribution. Only known from the type locality and potentially endemic to South Africa (KZN).

Habitat. Rocky reef, collected at 20 m depth.

8.4.3.7 Genus *Paguristes* Dana, 1851

Paguristes agulhasensis Forest, 1954

Paguristes agulhasensis Forest, 1954: 205, Figs 26, 37, 53, 67 (type locality: Agulhas Bank, South Africa). – Kensley, 1981: 32 (list). – Emmerson, 2016c: 448 (list).

Material examined. *Holotype:* no date, s. s. *Pieter Faure* (Agulhas Bank), 55 m, 1 ♂ 3.0 mm (SAMC 008497).

Remarks. Forest (1954) described this species from a single, small male specimen collected on the Agulhas Bank. In his 'material examined' section he stated that the length of the carapace of the specimen was 5.5 mm. The shield length of the specimen was re-measured and is in fact 3.0 mm. The holotype is in a moderate condition, as two of the ambulatory legs are not present with the sample.

Species of *Paguristes sensu lato* are difficult to identify and in the course of this study several specimens were collected from the Agulhas Bank that are heterospecific to Forest's taxon and could not be identified to species level (see Chapter 7). The group is in need for a local revision and several species have to be described as new to science. Within the limited taxonomic knowledge, *Paguristes agulhasensis* is similar to *P. macrotrichus* Forest, 1954 from the deeper waters of KwaZulu-Natal, and can be distinguished from the latter by the armature and length relationships of the cephalic appendages. For example, *P. agulhasensis* has shorter antennular peduncles not overreaching the ocular peduncles, and the antennal acicles are only armed each with a single proximal spine on the mesial margin, instead of several such spines.

Distribution. Known only from the type locality, South Africa (Agulhas Bank).

Habitat. Unknown, collected at 55 m depth.

Paguristes barnardi **Forest, 1954**

Figure 8.11 A, C

Paguristes barnardi Forest, 1954: 208, Figs 39, 54, 66, Pl 4 (type locality: South Coast of South Africa). – Day, 1974: 106, unnumbered Fig. – Kensley, 1981: 32 (list). – Emmerson, 2016c: 449 (list).

Paguristes rosaceus Barnard, 1947: 375.

Material examined. *Syntypes:* 29 Sep 1939, UCT E. S. sta AG 4D (Cape Agulhas), 3 ♂♂ 5.2–7.7 mm (SAMC 012779); 23 Nov 1939, UCT E. S. sta AR 2 K (Arniston), 2 ♂♂ 4.6–4.7 mm, 1 ovig. ♀ 4.1 mm (SAMC MB-A012780). *Non-type material:* 20 Jul 2015, Buffels Bay (W. C.), S 34° 05.40', E 22° 58.68', intertidal, 1 ♂ 6.9 mm (SAMC MB-A066247), 1 ovig. ♀ 4.9 mm (SAMC MB-A066248), 1 ovig. ♀ 4.1 mm (SAMC MB-A066249), 1 ovig. ♀ 4.7 mm (SAMC MB-A066250), 1 ovig. ♀ 4.3 mm (SAMC MB-A066251); 7 Apr 2016, Gonubie (East London, E. C.), S 32° 56.58', E 28° 02.10', intertidal, 2 ♂♂ 2.1–2.3 mm, 1 ♀ 3.3 mm (SAMC MB-A066780); 8 Apr 2016, Aquarium Rocks (East London, E. C.), S 33° 01.02', E 27° 55.32', intertidal, 8 ♂♂ 2.9–4.8 mm (SAMC MB-A066635), 11 ♀♀ 2.5–4.0 mm (SAMC MB-A066636); 3 juv. 1.9–2.1 mm (SAMC MB-A066637), 1 ♂ 5.3 mm (SAMC MB-A066638), 1 ♂ 5.5 mm (SAMC MB-A066639), 1 ♂ 5.3 mm (SAMC MB-A066640), 1 brood. ♀ 3.8 mm (SAMC MB-A066641), 1 ovig. ♀ 3.7 mm (SAMC MB-A066642), 1 ♂ 5.0 mm (SAMC MB-A066643); 18 Feb 2017, Jongensfontain (W. C.), S 34° 25.62', E 21° 20.64', intertidal, 1 ♂ 5.3 mm (SAMC MB-A066522), 1 ♂ 6.4 mm (SAMC MB-A066523).

Genetic data. Buffels Bay, S 34° 05.40', E 22° 58.68', intertidal, ♂ 6.9 mm, BOLD: SEAKY864-15 (SAMC MB-A066247), ♀ 4.9 mm, BOLD: SEAKY865-15 (SAMC MB-A066248), ovig. ♀ 4.1 mm, BOLD: SEAKY866-15 (SAMC MB-A066249), ovig. ♀ 4.7 mm, BOLD: SEAKY867-15 (SAMC MB-A066250), ovig. ♀ 4.3 mm, BOLD: SEAKY868-15 (SAMC MB-A066251); Jongensfontain S 34° 25.62', E 21° 20.64', intertidal, ♂ 5.3 mm, BOLD: SEAKY1382-17 (SAMC MB-A066522), ♂ 6.4 mm, BOLD: SEAKY1383-17 (SAMC MB-A066523).

Colouration. Shield rose, with orange-red patches and dots. Posterior carapace translucent to cream, with orange-red dots. Ocular peduncles predominantly red, proximally and distally with thin cream band; corneas golden green; ocular acicles cream, with orange-red patches. Antennular peduncles red, each segment proximally and distally with some cream; flagella red. Antennal peduncles similar to antennular peduncles; second segments cream with large orange-red patch, with 1 or 2 white dots; flagella red, each article with narrow white ring distally. Chelipeds and ambulatory legs orange to rose. Pleon cream to orange. Uropods and telson cream with some rose. Eggs orange.

Remarks. *Paguristes barnardi* is common in the intertidal zones along the South Coast, where it theoretically occurs sympatrically with the more westerly distributed species *P. gamianus* H. Milne Edwards, 1836. The two species are superficially similar, but can be distinguished by the armature of the dactyl of the second left pereopod. *Paguristes barnardi* has a row of long corneous spines on the ventral margin and the dorsal margin unarmed, whereas *P. gamianus* has much shorter corneous spines, and also the dorsal margin armed with strong, corneous-tipped spines. Moreover, the smaller *P. barnardi* has a rose-pink or orange colouration, while *P. gamianus* is more purple. This difference in colouration is obvious when the specimens are observed next to each other (Figure 8.11 C). However, the image in Figure 8.11 was taken in an aquarium and it remains unclear if the two species co-occur in the wild. Kensley (1981) listed *P. barnardi* to occur in False Bay, but the southwestern extend of the distribution remains to be confirmed. Both species brood their young in specialised brood pouches, a behaviour that is basically unstudied in hermit crabs and which merits future research. *Paguristes barnardi* being only known from the intertidal zone might be due to a lack of sampling. Colouration is reported for the first time.

Distribution. Endemic to South Africa (South Coast, from Kleinmond to East London).

Habitat. Intertidal under rocks and boulders.

***Paguristes macrotrichus* Forest, 1954**

Paguristes macrotrichus Forest, 1954: 211, Figs 27, 41 (type locality: off KZN, South Africa). – Kensley, 1981: 33 (list). – Emmerson, 2016c: 449 (list).

Material examined. *Holotype:* no date, s. s. *Pieter Faure* sta 12346 (off Umhlangakulu River, KZN), S 30° 47.22', E 30° 34.86', 90 m, 1 ♀ 3.8 mm (SAMC 000851).

Remarks. Forest (1954) described *Paguristes macrotrichus*, like *P. agulhasensis*, from a single small specimen (here a female), and as a result it is now difficult to account for variation occurring in this species. Several specimens collected from KwaZulu-Natal during the course of this study (not reported on here, see Chapter 7), are similar to Forest's taxon, but probably not conspecific. Although the holotype is undated, its voucher number is the earliest number of any hermit crab in the collection of the Iziko South African Museum, and given its age the specimen is in a reasonable condition. Present in the sample is also an additional smaller left cheliped that is probably conspecific. Along with all South African members of the group, *P. macrotrichus* has to be taxonomically revised and additional candidate species from KwaZulu-Natal need to be described.

Distribution. Known only from the type locality in South Africa (KZN).

Habitat. Dredged from soft sediments, from 90–100 m depth.

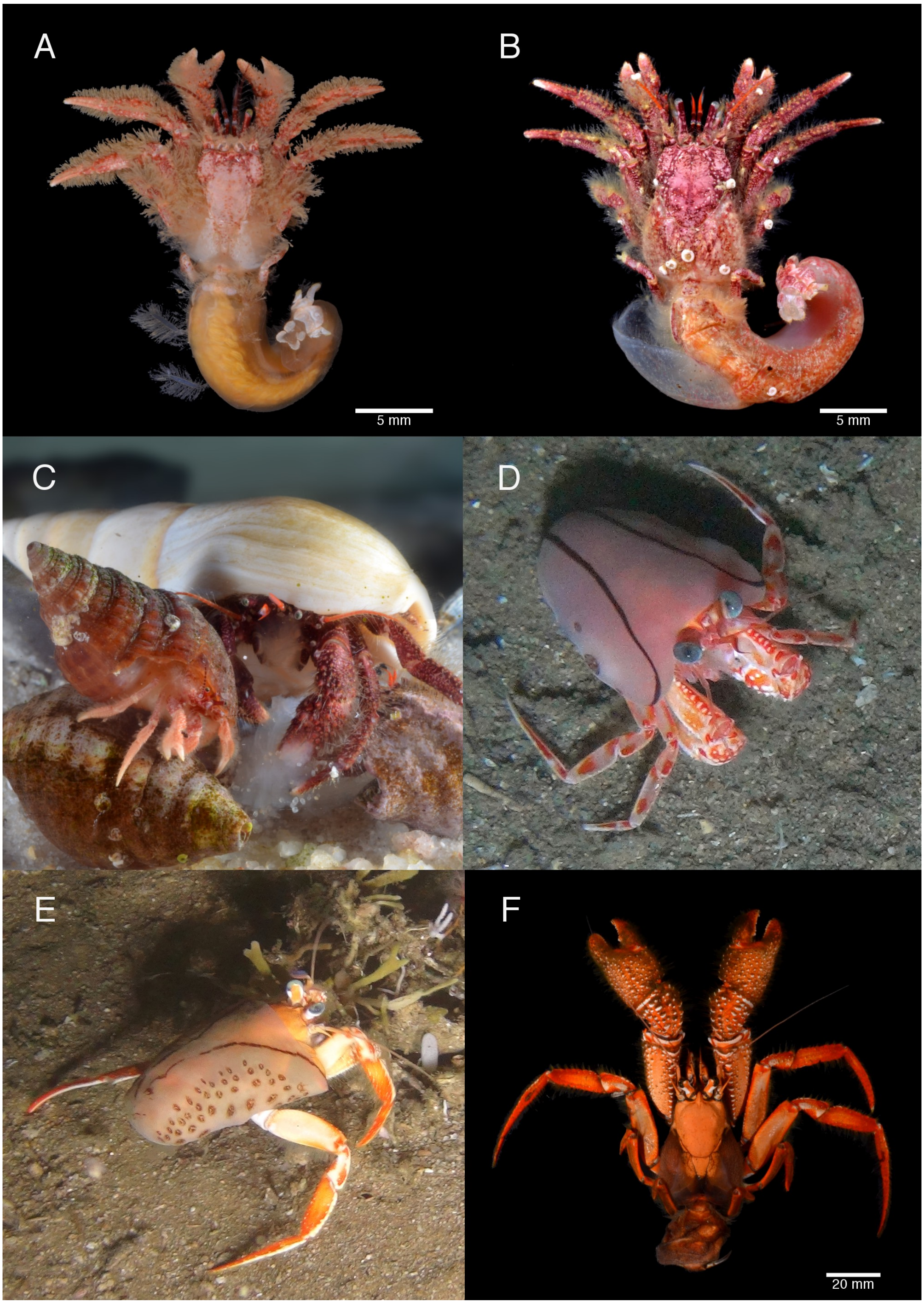

Figure 8.11: Paguroidea of South Africa, family Diogenidae Ortmann, 1892 (C–E *in situ*): A *Paguristes barnardi* Forest, 1954, East London, ♂ 5.1 mm (SAMC MB-A066640) **B** *Paguristes gamianus* H. Milne Edwards, 1836, False Bay, ♀ 8.1 mm (SAMC MB-A066480) **C** *P. barnardi* (left, East London) and *P. gamianus* (right, False Bay) in photographic tank, specimens lost **D** *Paguropsis* sp. Lemaitre et al., in prep., off Durban, specimen not collected (photo ACEP Spatial Solutions) **E–F** *Paguropsis typica* (Henderson, 1888), Aliwal, specimen not collected (photo ACEP Spatial Solutions)(E), Coffee Bay, ♂ 24.1 mm (SAMC MB-A066723)(F).

8.4.3.8 Genus *Paguropsis* Henderson, 1888

Paguropsis typica Henderson, 1888

Figure 8.11 E–F

Paguropsis typica. – Kensley, 1981: 33 (list). – Barnard, 1962: 240.

Material examined. 23 Apr 1958, UCT E. S. sta NAD 11H (off Durban, KZN), S 29° 46.02', E 31° 16.98', 110–130 m, dredge, 1 ♂ 15.0 mm (SAMC MB-A019489); 12 Dec 1994, R. V. *Algoa* Mozambique Scad Survey SFRI sta C00815-014-012-2144 (Mozambique), S 23° 07.98', E 35° 42.00', 180 m, trawl, 1 ♂ 16.8 mm (SAMC MB-A041691); 18 Feb 2010, Oceanographic Research Institute (ORI) 68 sta ACEP 1-4 (off Durban, KZN), S 29° 58.56', E 31° 04.98', 119 m, trawl, 1 ovig. ♀ 14.4 mm (ZRC 2013.0535); 21 Feb 2010, ORI 17 sta ACEP 4-1 (off Durban, KZN), S 29° 06.60', E 32° 07.32', 128 m, trawl, 1 ♂ 14.2 mm (ZRC 2013.0537); 10 Sep 2016, Coffee Bay (E. C.), S 31° 59.34', E 29° 09.96', 100 m, dredge, 1 ♂ 24.1 mm (SAMC MB-A066723).

Other material. 5 Jun 2017, R. Y. *Angra Pequena* sta R50 Aliwal outer reef (KZN), S 30° 12.36', E 30° 59.16', 106–149 m, ROV, one specimen not collected (photographed during DST/NRF ACEP Spatial Solutions cruise).

Genetic data. Off Durban, S 29° 58.56', E 31° 04.98', 119 m, ovig. ♀ 14.4 mm BOLD: SEAKY1179-17 (ZRC 2013.0535), S 29° 06.60', E 32° 07.32', 128 m, ♂ 14.2 mm, BOLD: SEAKY1178-17 (ZRC 2013.0537).

Remarks. *Paguropsis* is currently monotypic as it officially only contains this single taxon. However, McLaughlin et al. (2010) reported that *P. andersoni* (Alcock, 1905) from the Indian Ocean was found not to be a synonym of *P. typica* and that Alcock's taxon should be reinstated. The genus is currently being taxonomically revised and the South African specimens probably belong to a different species than *P. typica* (R. Lemaitre, pers. comm.). Therefore, the assignment to the name *P. typica* in this report is to be regarded preliminary. A diagnosis is not given to not cause additional confusion prior to the revision being officially published, and the synonymy and distribution given is limited to the South African data. However, this large species of *Paguropsis* can be safely identified by the longitudinal and weakly calcified depressions on the proximal half of lateral face of the dactyls of the third pereopods.

Distribution. South Africa (off the coasts of northern E. C. and KZN).

Habitat. Inhabiting a cloak or blanket for pleonal protection formed by living anemones, on soft sediments, from 100–180 m depth.

***Paguropsis* sp. Lemaitre et al., in prep**

Figure 8.11 D

Material examined. None.

Other material. 23 Jun 2016, R. Y. *Angra Pequena* sta R45 Echinoderm Extravaganza (off Durban, KZN), S 29° 52.80', E 31° 11.76', 177–215 m, ROV, one specimen not collected (photographed during ACEP Spatial Solutions Project cruise).

Diagnosis. Not given due to lack of physical material to examine, but a description will soon be provided by Lemaitre et al. (in prep).

Remarks. As for the other *Paguropsis* in this report, because no specimens was collected the taxonomic status of this species is equally preliminary. As the species is only being described in a global revision of the genus, this record is not treated here as an official first new record. However, it is included in this report for completeness, because of the significance of the finding, and because the distinct orange-red patches on the pereopods clearly identify it (R. Lemaitre, pers. comm.). The unique colouration will make it easily recognisable should it be found again, even when due to the lack of physical material a diagnosis cannot be given here.

Distribution. South Africa (KZN).

Habitat. Inhabiting a cloak or blanket for pleonal protection formed by living anemones, soft sediments, at depths of 215 m.

8.4.4 Family Paguridae Latreille, 1802

8.4.4.1 Genus *Goreopagurus* McLaughlin, 1988a

***Goreopagurus poorei* Lemaitre and McLaughlin, 2003**

Figure 8.12 C–D

Goreopagurus poorei Lemaitre and McLaughlin, 2003: 222, Figs 1–3. – McLaughlin et al., 2010: 29. Landschoff and Lemaitre, 2017a: 272, Figs 1–4.

Material examined and genetic data. See Landschoff and Lemaitre (2017a), Chapter 5.

Remarks. Recently discovered along the edge of the southeastern South African shelf (Landschoff and Lemaitre 2017a), the record extended the distribution and taxonomic knowledge on this species. However, preliminary genetic results have shown that the South African specimens are quite different to specimens from Tasmania. More sampling and genetic data might reveal that South African specimens are indeed of a different species (see Chapter 7).

Distribution. Western Tasman Sea and Australia, South Africa (Agulhas Shelf).

Habitat. Probably soft sediments, from 334–1300 m depth.

8.4.4.2 Genus *Manucomplanus* McLaughlin, 1981

Manucomplanus ungulatus (Studer, 1883)

Eupagurus ungulatus Studer, 1883: 26, Pl 2, Fig 13a–c (type locality: entrance to Table Bay, Cape Town). – Balss, 1912: 106 (footnote).

Pylopagurus ungulatus. – Barnard, 1950: 454. – Kensley, 1981: 33 (list).

Manucomplanus ungulatus. – Lemaitre and McLaughlin, 1996: 113, Figs 11, 12a–d. – Emmerson, 2016c: 449 (list).

Material examined. *Holotype:* No date, entrance to Table Bay, Cape of Good Hope, 91 m, 1 ♀ 2.8 mm (ZMB 5682).

Diagnosis. See Lemaitre and McLaughlin (1996).

Remarks. A single specimen collected during the '*Gazelle* Expedition' from Table Bay formed the basis of Studer's (1883) description. Apart from two additional specimens from South Africa, all housed at the collections of the Museum für Naturkunde Berlin, Germany, the species has not been found again from the type locality, but is common in the eastern United States. Lemaitre and McLaughlin (1996) re-examined the holotype and found no specific differences to the specimens from the western Atlantic, which was confirmed in the present study. However, they also remarked on the broad range of morphological variations, potentially masking differences that are sufficient to separate the group into two species. Fresh material from South Africa with colour information and from which molecular barcodes could be derived might well reveal that the American specimens are a separate species.

Distribution. Eastern United States from North Carolina to Florida into the Gulf of Mexico, West Africa, South Africa (W. C.).

Habitat. Frequently in shells overgrown by horned bryozoans and sometimes by sponges, 20–298 m depth, type collected from 91 m.

8.4.4.3 Genus *Nematopagurus* A. Milne-Edwards and Bouvier, 1892

Nematopagurus crosnieri McLaughlin, 1998

? Figure 8.12 E

Nematopagurus crosnieri McLaughlin, 1998: 318, Fig 1 (type locality: Madagascar).

Nematopagurus squamichelis. – Kensley, 1969: 163, Fig 6a–d. – Kensley, 1981: 33 (list). – Emmerson, 2016c: 449 (list). [all not *Nematopagurus squamichelis* Alcock, 1905]

Material examined. *Paratypes:* 18 Aug 1964, UCT E. S. sta ABD 8 V (off Inharrime Mozambique), S 24° 40.02', E 35° 28.02', 347 m, Agassiz trawl, 2 ♂♂ 4.0–4.5 mm, 1 ♀ 3.0 mm (SAMC MB-A019479).

Other material. Photographic record of ?*Nematopagurus crosnieri.* 17 Jun 2017, R. Y. *Angra Pequena* sta lR59 off Isipingo (Durban, KZN), S 30° 02.66', E 31° 03.43', 226–238 m, ROV, one specimen not collected (photographed during ACEP Spatial Solutions Project cruise).

Diagnosis. See short description by McLaughlin (2004).

Remarks. This species (as *N. squamichelis*) was reported as occurring off KwaZulu-Natal ("off Natal") by Kensley (1981), and this record has been reiterated as a South African occurrence by most subsequent authors. However, the station at which Kensley's specimens were collected actually lies within Mozambican territories (even if close to the South African border), so that the South African record is technically invalid. Nevertheless, the species is herein retained in the national species list, based on the tentatively identified photograph taken off Durban at 226–238 m depth (Figure 8.12 E). Apart from this photographic record *N. crosnieri* remains only known from the type material, another reason why the picture is cautiously included here.

Although main taxonomic characters defining the genus of *Nematopagurus* (e. g. pleopod condition, sexual tubes) cannot be assessed from photographs taken in the wild from specimens still within their shells, based on the shape and dimensions of the subequal chelipeds and long ambulatory legs, it seems certain that Figure 8.12 E shows one of three species of *Nematopagurus* that share the characters of striaform scutes on the dorsal surfaces of the chelipeds. These species are *N. crosnieri*, *N. scutellichelis* Alcock, 1905, and *N. scutelliformis* McLaughlin, 1997. However, colouration in life is unknown for all of these candidate species, so cannot be used to inform the identification. Although the angle and resolution of the photograph does not allow for an accurate identification between the three species, some speculation may be possible. *N. scutelliformis* is set apart from *N. crosnieri* by the spines on the dorsomesial margins of the palm and dorsolateral margins of the palm and fixed finger of the chelipeds, which are absent in *N. crosnieri.* Although the chelae of the specimen in the picture are bend over, slightly twisted and also weakly out of focus, no such spines are visible. Furthermore, *N. scutelliformis* has so far only been reported from the Philippines, Indonesia and New Caledonia, so that the presence of this species in South Africa is unlikely. The second possible candidate, *N. scutellichelis*, is set apart from *N. crosnieri* by the presence of a dorsal row of carpal spines on the ambulatory legs, while *N. crosnieri* only has a single dorsodistal spine. Seeing such small spines in a picture is usually not possible, but the angle at which the specimen was photographed exposes the dorsal surface of the carpi of the second pereopods, which indicates that only one distal spine is present. Moreover, the westernmost distribution of *N. scutellichelis* are the Maldives, while *N. crosnieri* is known to occur in the vicinity of the station where the photo was taken. In addition, *N. crosnieri* is also the largest of the three species and the photograph, taken by a ROV camera with limited macro functions, is clearly of a specimen of moderate size. In the light of the combination of all the listed arguments, it seems most likely that the specimen in the picture is a large specimen of *N. crosnieri.* However, as it is also always possible that Figure 8.12 E might show an undescribed species, this record should be handled with care and must be confirmed by more sampling, in which the colouration for each species is documented. Should this information come available, then the colour picture provided here should be of sufficient quality to make a final determination.

By retaining *N. crosnieri* in the South African species list, six species within this genus now occur within the national borders, opposed to only two listed in the recently published decapod checklist by Emmerson (2016c), who overlooked most literature records.

Distribution. ?South Africa (KZN), Mozambique Channel, Madagascar.

Habitat. Shell substrate, from 347–410 m depth, possibly shallower from 226 m.

Nematopagurus diadema Lewinsohn, 1969

Nematopagurus diadema Lewinsohn, 1969: 74, Fig 13 (type locality: Red Sea). – McLaughlin, 1998: 325, Fig 3. – McLaughlin, 2004: 185, Fig 12. – Poupin et al., 2013a: 54 (list).

Specimen update. 7 Jun 1987, R. V. *Meiring Naudé* sta ZA 13 (off Kosi River mouth, KZN), S 26° 54.60', E 32° 56.59', 75 m, 1 ♂ 1.9 mm (USNM 1292120).

Diagnosis. See short description by McLaughlin (2004).

Remarks. Since Lewinsohn's (1969) description from the Red Sea and McLaughlin's (1998) report of a single ovigerous female specimen (apparently actually a male, see below) from off Sodwana Bay (KZN), the distribution of *N. diadema* has been extended to now cover a vast range across the Indo-Pacific (McLaughlin 2004). However, with few individual records the species remains rare, particularly in the Western Indian Ocean, and has so far not been rediscovered in South African waters. *Nematopagurus diadema* is readily identified by the large, rounded or pear-shaped tubercles on the dorsal surface of the chelae.

McLaughlin (1998) specifically mentioned that only one individual specimen (an ovigerous female 3.5 mm) from South Africa was present in her study, which she listed as part of her personal collection, without an identification number. In an attempt to locate this specimen, a single male specimen from KwaZulu-Natal (1.9 mm, USNM 1292120) was found in the collections of the United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., which had been willed and donated to the museum after McLaughlin's death (R. Lemaitre, pers. comm.). It seems certain that this is the specimen referred to in McLaughlin's record, but that she confounded the sample label in the material examined section with the holotypic specimen of *N. kosiensis*, which she listed with the identical locality and specimen data (including a misspelling of "Sodesawa Bay" instead of "Sodwana Bay"). Furthermore, using the provided scale bar, the illustrated shield of the specimen measures about 1.8 mm (McLaughlin 1998, Fig 3, also in the legend incorrectly as ovig. ♀ 3.5 mm SL). This concurs with the measurement of the actual specimen size of 1.9 mm measured by R. Lemaitre. Consequently, the specimen information is updated here, based on the original label that is present with the specimen at the Smithsonian Institution. The true locality is 40 nautical miles north of the type locality of *N. kosiensis* and still lies within the South African border.

Distribution. South Africa (KZN), Mozambique Channel, Red Sea, South China Sea, Indonesia, New Caledonia, Vanuatu, Fiji.

Habitat. Unknown, but reported from several species of gastropod shell, from 62–295 m depth.

***Nematopagurus gardineri* Alcock, 1905**

Nematopagurus gardineri Alcock, 1905: 834, Pl 68, Fig 3 (type locality: Maldives). – McLaughlin, 2004: 212, Fig 23. – Poupin et al., 2013a: 54 (list).

Nematopagurus holthuisi McLaughlin and Hogarth, 1998: 25, Figs 19–26 (type locality: Seychelles). – McLaughlin and Hogarth, 1998: 326, Fig 4.

Not *Nematopagurus gardineri*. – Kensley, 1969: 163, Fig 6e–h. – Kensley, 1981: 33 (list). – Emmerson, 2016c: 449. [all *Nematopagurus meiringae* McLaughlin, 1998]

Diagnosis. See redescription by McLaughlin (2004).

Remarks. The South African record for this species is taxonomically confusing. Kensley (1969) reported *Nematopagurus gardineri* Alcock, 1905 from KwaZulu-Natal, but his single male specimen was later transferred to the new species *N. meiringae* McLaughlin, 1998. However, in the same publication, McLaughlin and Hogarth (1998) also reported *N. holthuisi* from South Africa, which, in 2004, the same author subsequently synonymised with Alcock's *N. gardineri*. Therefore, *N. gardineri* does occur in South Africa, although both Kensley's (1969, 1981) and Emmerson's (2016c) records of *N. gardineri* were actually of *N. meiringae*. A set and combination of characters distinguish this species from *N. meiringae*, which both have a median longitudinal row of spines on the dorsal surface of each chela that extends onto the fixed finger and hence are easily confused (see McLaughlin 1998, 2004).

Distribution. South Africa (KZN), Mozambique Channel, Seychelles, Maldives, Cocos (Keeling) Islands, Japan, New Caledonia.

Habitat. Muddy sand, seagrass beds, variety of substrates, from 18–99 m depth.

***Nematopagurus kosiensis* McLaughlin, 1998**

Nematopagurus kosiensis McLaughlin, 1998: 329, Fig 5 (type locality: off Gobey's Point, Sodwana Bay, KZN, South Africa). – McLaughlin, 2004: 196, Fig 17. – McLaughlin et al., 2007b: 232, 2 unnumbered Figs.

Diagnosis. See McLaughlin et al. (2007b).

Remarks. *Nematopagurus kosiensis* was described from a single ovigerous female specimen collected in KwaZulu-Natal. Since then it has not been rediscovered in South African waters, but has been found to be widespread in the Indo-Pacific. Amongst the known South African species of *Nematopagurus, N. kosiensis* can be identified by the median longitudinal row of spines on the dorsal surface of each chela not extending onto the fixed finger (as in *N. gardineri* or *N. meiringae*).

Distribution. South Africa (KZN), Philippines, Taiwan, Ogasawara Islands, New Caledonia, Tuamotu Archipelago, Hawaii.

Habitat. Collected from sandstone rubble with glass sponges in South Africa, from 82–490 m depth.

Nematopagurus meiringae McLaughlin, 1998

Nematopagurus meiringae McLaughlin, 1998: 332, Fig 6. – McLaughlin, 2004: 218, Fig 25. – McLaughlin et al., 2007b: 236, unnumbered Fig.

Nematopagurus gardineri.– Kensley, 1969: 163, Fig 6e–h. – Kensley, 1981: 33 (list). – Emmerson, 2016c: 449 (list). [all not *Nematopagurus gardineri* Alcock, 1905]

Material examined. *Paratype:* 9 Sep 1964, UCT E. S. sta NAD 45 P (off KwaDukuza, KZN), S 29° 34.98', E 31° 42.00', 138 m, Agassiz trawl, 1 ♂ 2.4 mm (SAMC MB-A019478).

Diagnosis. See McLaughlin et al. (2007b).

Remarks. Since its description from only two specimens from South Africa, *N. meiringae* has not been found there again, but is now known to be widespread across the Indo-Pacific. Amongst the known South African species *N. meiringae* is most similar to *N. gardineri* Alcock, 1905, but has shorter and more broadly dilated corneas. A detailed character comparison is provided by McLaughlin (1998).

Distribution. South Africa (KZN), Western Australia, East and South China Sea, Indonesia, Philippine Islands, Taiwan, Japan, New Caledonia.

Habitat. Sand and rubble substrate, from 12–461 m depth.

Nematopagurus spinulosensoris McLaughlin and Brock, 1974

Figure 8.12 F

Nematopagurus spinulosensoris McLaughlin and Brock, 1974: 246, Figs 1–3 (type locality: Hawaii). – McLaughlin, 1998: 335, Fig 7. – McLaughlin, 2004: 201, Fig 19. – McLaughlin et al., 2007b: 226, unnumbered Fig. – Poupin et al. 2013a: 54 (list).

Material examined. 15 Sep 2016, Coffee Bay (E. C.), S 31° 59.34', E 29° 09.96', 100 m, dredge, 2 ♀♀ 6.5–8.5 mm (SAMC MB-A066683); 20 Nov 2016; Coffee Bay (E. C.), S 31° 59.34', E 29° 09.96', 94 m, dredge, 1 ♀ 7.2 mm (SAMC MB-A066704); 15 Jan 2017, Pumula 22 (KZN), S 30° 38.40', E 30° 34.20', 40–65 m, Scuba, 1 ♂ 5.7 mm (SAMC MB-A066712).

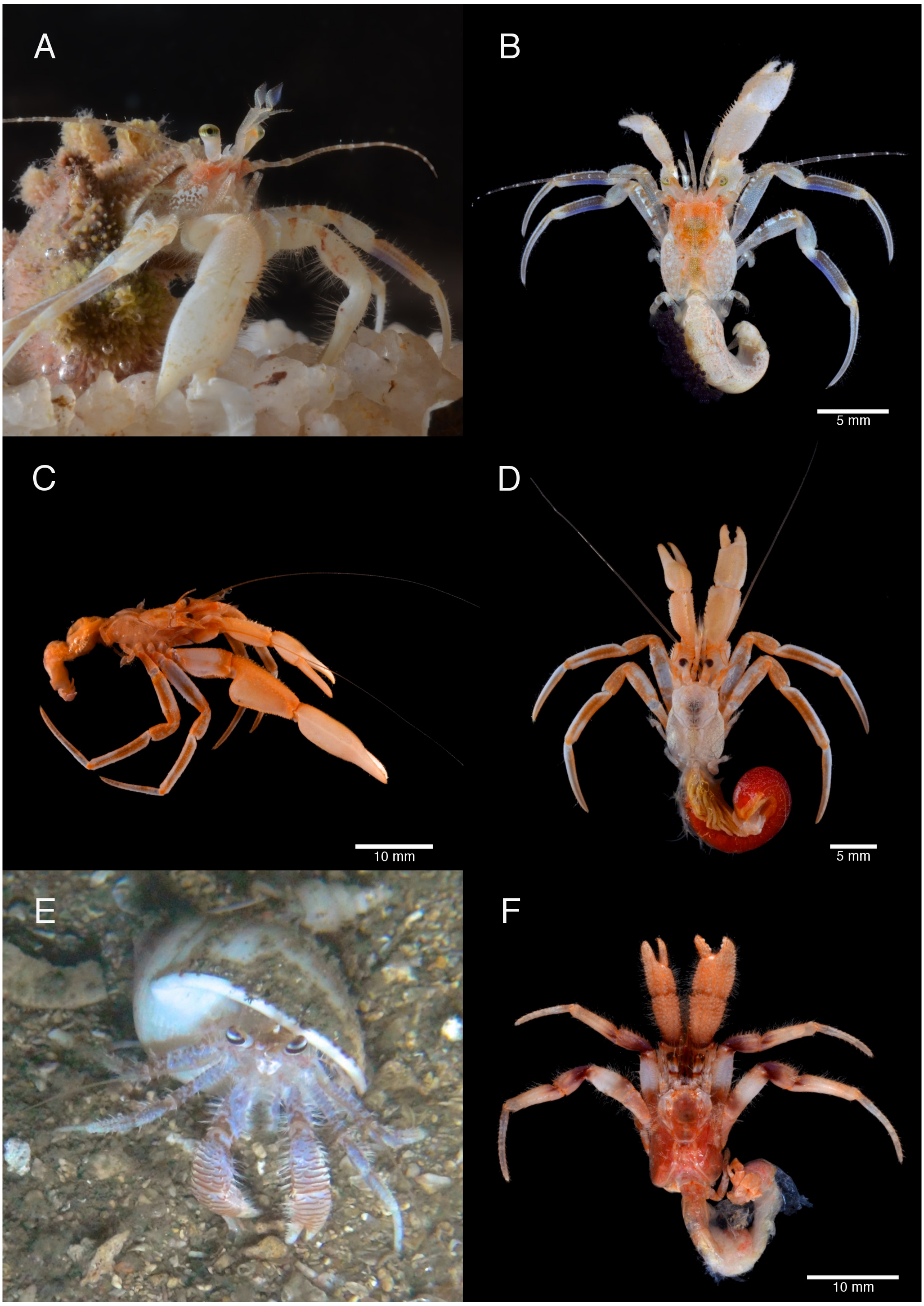

Figure 8.12: Paguroidea of South Africa, family Paguridae Latreille, 1802 (A, E *in situ*): A–B *Anapagurus hendersoni* Barnard, 1947, False Bay, ovig. ♀ 3.6 mm (SAMC MB-A066215) **C–D** *Goreopagurus poorei* Lemaitre and McLaughlin, 2003, Agulhas Shelf, ♂ 4.5 mm (USNM 1292090)(C), ♀ 4.5 mm (USNM 1292089)(D) **E** ?*Nematopagurus crosnieri* McLaughlin, 1998, off Durban, specimen not collected, (photo ACEP Spatial Solutions) **F** *Nematopagurus spinulosensoris* McLaughlin and Brock, 1974, Pumula, ♂ 5.9 mm (SAMC MB-A066712).

Genetic data. Coffee Bay, S 31° 59.34', E 29° 09.96', 94 m, ♀ 7.2 mm, BOLD: SEAKY1437-17 (SAMC MB-A066704); Pumula, S 30° 38.40', E 30° 34.20', 40–65 m, ♂ 5.7 mm, BOLD: SEAKY1435-17 (SAMC MB-A066712).

Diagnosis. See short description by McLaughlin (2004).

Colouration. (South African specimens) Shield orange-brown medially, lighter in colour or cream to white anterolaterally, anterior carapace orange, both with white setae with median broad orange bands. Ocular peduncles cream-white and each with orange-brown dorsodistal patch, and also with median, slightly oblique, red transversal band. Corneas black to golden-brown. Ocular acicles white with some orange around margins, tips of terminal spines orange. Antennular peduncles with basal segments translucent, penultimate and ultimate segments red, flagella orange. Antennal peduncles cream to white with orange patches or bands, spines and spinules usually with orange tip, antennal acicles with broad orange-red band in distal half, flagella orange with white bands. Chelipeds with outer surfaces of chelae and carpus uniformly light orange, spines salmon to cream with orange tips, covered by white setae with median broad orange bands; ventroproximal margins of palms laterally with small red dot; carpi with proximal red to maroon large patches on both lateral and mesial angle; meri more cream-white with some orange, latero- and mesiodistally with orange-red patch. Ambulatory legs similar in colouration, cream to salmon with some orange and red-purple patches; propodi (less prominent) and carpi (prominent) proximally with deep red-purple patches both laterally and mesially; meri with median broad white band, distally with purple to orange patches. Pleon orange-brown. Uropods salmon to orange, terminal margin of telson with narrow cream band.

Remarks. *Nematopagurus spinulosensoris sensu* McLaughlin, 2004 exhibits a range of morphological variations. The four specimens reported here fit into these variations and have a slightly longer than broad shield. The broadly rounded rostrum, which has a very broad, bulbous, but low elevated ridge on the dorsal surface, reaches the level of the lateral projections. The ocular peduncles are 0.6 the length of the shield, the antennular peduncles overreach the distal margins of the corneas by about 0.5–0.6 the length of the ultimate segment, and the antennal peduncles slightly overreach the distal margin of the corneas. Hence the morphometric measurements of the shield and cephalic appendages are often at one extreme range of the species (see McLaughlin 2004). Furthermore, the South African specimens have the dorsomesial margin of the palm of the right cheliped covered with the same spines (modified with a sensory organ) as on the dorsal surface, but the meri have a row of unmodified, moderately strong spines proximally on the lateral dorsal surface. It is also noticeable that the dorsal surfaces of the palm and carpus (also and particularly of the left cheliped) have considerably more modified spines than currently reported. The spines on the dorsal margins of the carpi of the second and third pereopods appear particularly strong and numerous.

Different colouration patterns have been reported for *N. spinulosensoris* before (McLaughlin et al. 2007b), which also differ from the colouration of the South African specimens, reported here in detail. The specimens are generally more colourful and, for example, have differently coloured antennae indicating that *N. spinulosensoris* is potentially a species complex and requires taxonomic resolution.

Distribution. South Africa (E. C. to KZN), Mozambique Channel, Seychelles, Maldives, Western Australia, Indonesia, East China Sea, Taiwan, Japan, Vanuatu, New Caledonia, Hawaii, French Polynesia.

Habitat. Coral rubble, from 110–540 m depth, possibly down to 950 m, in South Africa found in shallower waters from 40–65 m to 140 m depth.

8.4.4.4 Genus *Pagurus* Fabricius, 1775

Pagurus cavicarpus (Paul'son, 1875)

Eupagurus cavicarpus Paul'son, 1875: 91, Pl 12, Fig 3–3a (type locality: Red Sea).

Pagurus cavicarpus. – McLaughlin and Forest, 1999: 301, Fig 1A–C, E–I, K. – Emmerson, 2016c: 449 (list).

Diagnosis. See McLaughlin and Forest (1999).

Remarks. Although numerous records indicate that *Pagurus cavicarpus* is common in the deeper waters of northern KZN, no new material has come available since McLaughlin and Forest (1999), and colouration in life remains unknown. The species can be identified by the stout ocular peduncles and by usually having a prominent foramen on the ventral surface of the carpus of the right cheliped.

Distribution. South Africa (northern KZN), Red Sea, South Arabian coast, Indian Ocean between Maldives and Cape Comorin.

Habitat. Unknown, from 38–1507 m depth, in South Africa recorded only from shallower depths from 38–60 m.

Pagurus cuanensis Bell, 1846

Figure 8.13 A–B

Pagurus cuanensis Bell, 1846: 178, unnumbered Fig (type locality: Ireland). – Kensley, 1981: 33 (list). – McLaughlin and Forest, 1999: 309, Fig 2A–L. – Emmerson, 2016c: 449 (list).

Eupagurus placens. – Barnard, 1950: 462, Fig 85e.

Pagurus placens. – Kensley, 1981: 33 (list).

Material examined. 28 Apr 2015, South Coast Survey sta D00550-063-3520 (off Plettenberg Bay, W. C.), S 34° 15.84', E 23° 41.40', 103 m, trawl, 1 ♂ 7.7 mm (SAMC MB-A066822); 5 May 2015, Roman Rock (Simonstown, False Bay, W. C.), S 34° 10.80', E 18° 27.48', 20 m, Scuba, 1 ♂ 5.4 mm

(SAMC MB-A066190), 1 ♂ 4.1 mm (SAMC MB-A066191), South Coast Survey sta D00577-090-1058 (off Ersterivierstrand, W. C.), S 34° 10.62’, E 24° 15.24’, 88 m, trawl, 1 ♂ 9.6 mm (SAMC MB-A066843); 7 May 2015, South Coast Survey sta D00584 (off Knysna, W. C.), S 34° 34.56’, E 23° 06.06’, 111 m, trawl, 1 ♂ 6.6 mm (SAMC MB-A066837); 8 May 2015, South Coast Survey sta D00589-102-3421 (Agulhas Bank), S 34° 40.86’, E 22° 31.32’, 106 m, trawl, 1 ♂ 9.1 mm (SAMC MB-A066827), 1 ♀ 8.1 mm (SAMC MB-A066515); 10 May 2015, South Coast Survey sta D00594-107-3402 (Agulhas Bank), S 34° 43.62’, E 22° 22.80’, 105 m, trawl, 1 ♂ 7.9 mm (SAMC MB-A066834); 13 May 2015, Roman Rock (Simonstown, False Bay, W. C.), S 34° 10.80’, E 18° 27.48’, 20 m, Scuba, 1 ovig. ♀ 6.6 mm (SAMC MB-A066192), 1 ♀ 3.9 mm (SAMC MB-A066193); 10 May 2016, South Coast Survey sta D00778-049-2206, S 34° 41.22’, E 22° 00.18’, 91 m, trawl, 1 ♂ 7.5 mm (SAMC MB-A066516), 1 ♂ 9.2 mm (SAMC MB-A066517); 28 May 2016, South Coast Survey sta D00849-117-2050 (Agulhas Bank), S 34° 58.74’, E 20° 47.76’, 93 m, trawl, 1 ♂ 7.1 mm (SAMC MB-A066654); 1 Aug 2016, UMNT west off Port Shepstone (KZN), S 30° 44.46’, E 30° 33.66’, 46 m, Scuba, 1 ovig. ♀ 3.8 mm (SAMC MB-A066709); 16 Aug 2016,“R”southwest off Port Shepstone (KZN), S 31° 02.28’, E 30° 39.54’, 53 m, Scuba, 1 ovig. ♀ 4.1 mm (SAMC MB-A066705); 9 Sep 2016, Long Beach Simonstown (False Bay, W. C.), S 34° 11.22’, E 18° 25.62’, 4 m, Scuba, 1 ovig. ♀ 4.9 mm (SAMC MB-A066655); 14 Dec 2016,“R”southwest off Port Shepstone (KZN), S 31° 02.28’, E 30° 39.54’, 70 m, Scuba, 2 ♂♂ 1.6–3.6 mm (SAMC MB-A066681); 10 Apr 2017, Sezela (KZN), S 30° 24.66’, E 30° 44.46’, 50–55 m, 1 ♀ 2.7 mm (SAMC MB-A066708).

Genetic data. False Bay, S 34° 10.80’, E 18° 27.48’, 20 m, ovig. ♀ 6.6 mm, BOLD: SEAKY931-15 (SAMC MB-A066192); South Coast, S 34° 40.86’, E 22° 31.32’, 106 m, ♀ 8.1 mm, BOLD: SEAKY1376-17 (SAMC MB-A066515); Port Shepstone, S 31° 02.28’, E 30° 39.54’, 53 m, ovig. ♀ 4.1 mm, BOLD: SEAKY1444-17 (SAMC MB-A066705), S 30° 44.46’, E 30° 33.66’, 46 m, ovig. ♀ 3.8 mm, BOLD: SEAKY1443-17 (SAMC MB-A066709).

Diagnosis. See McLaughlin and Forest (1999).

Colouration. Shield red-brown to rose, mottled white and also with few small red dots. Posterior carapace similar, with two red to brown patches medially and cream patches anterolaterally. Ocular peduncles dull orange to yellow, with white patches or transversal band near base; corneas black to cyan blue; ocular acicles red-brown to rose, distally white. Antennular peduncles dull orange to yellow, basal segments white; penultimate segments proximally with faint white band; ultimate segments with brightly white-blue distal band; upper flagella translucent; lower flagella light orange. Antennal peduncles red-brown to rose with white patches and sprinkles; antennal flagella cream and each with a mesial and a lateral longitudinal stripe and also with a brightly white-blue bands about every fourth article. Chelipeds and ambulatory legs cream to orange-brown or rose with red and white patches, usually largely obscured by thick yellow-brown setae. Pleon orange to cherry red, mottled white and also with white dots. Uropods and telson similar in colour. Eggs maroon-red.

Remarks. This species is common and frequently found during shallow water dives and also during trawl and dredge surveys along the shallower waters of the southeastern continental shelf.

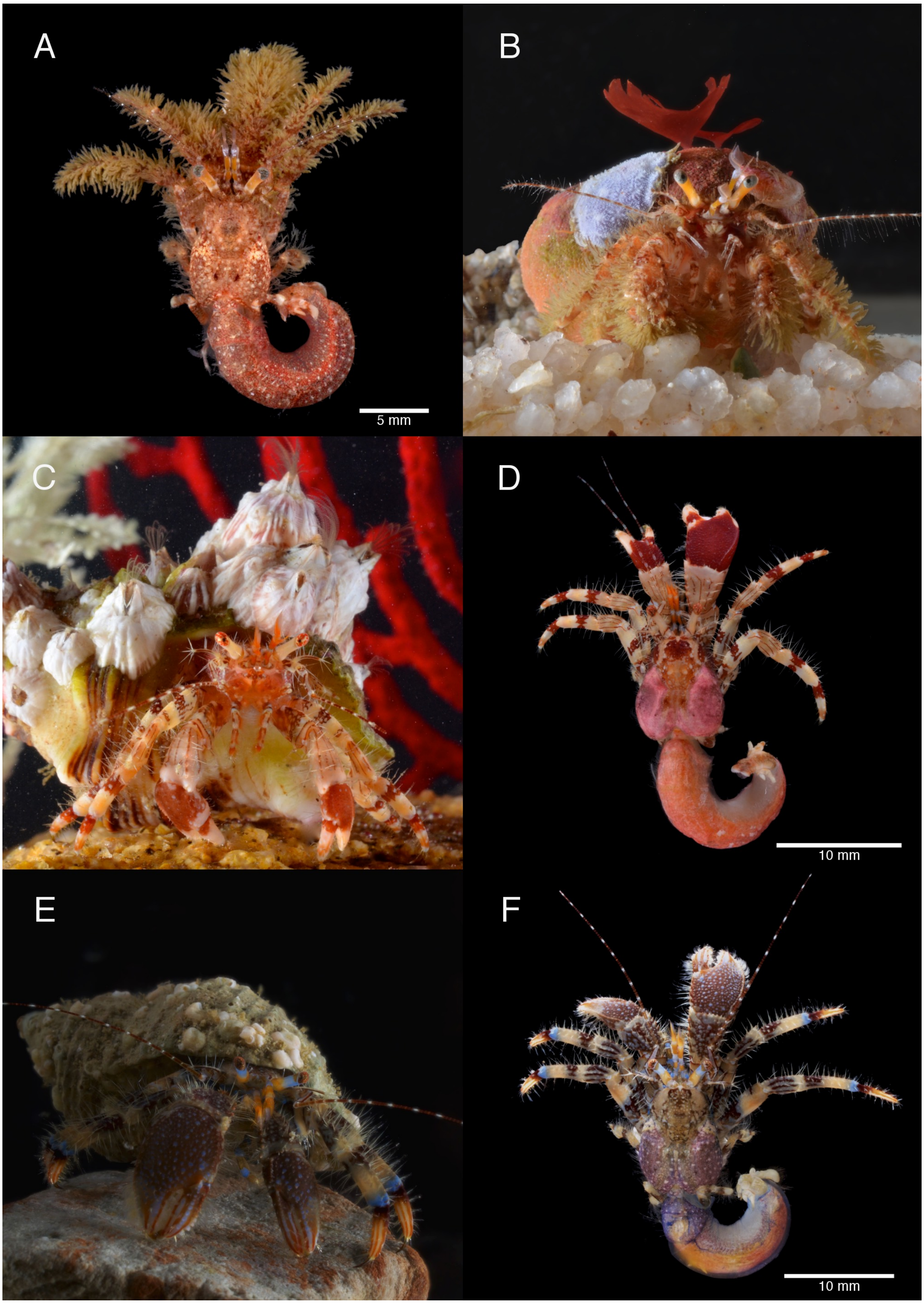

Figure 8.13: Paguroidea of South Africa, family Paguridae Latreille, 1802 (B–C, E *in situ*): A–B *Pagurus cuanensis* Bell, 1846, False Bay, ♀ 5.4 mm (SAMC MB-A066190) **C–D** *Pagurus emmersoni* McLaughlin and Forest, 1999, off Pumula, ovig. ♀ 3.7 mm (SAMC MB-A066649)(C), ♂ 4.6 mm (SAMC MB-A066401)(D) **E–F** *Pagurus liochele* (Barnard, 1947), Buffels Bay, ♂ 5.5 mm (SAMC MB-A066246).

Nevertheless, this report represents the first photograph of a live specimen from South Africa, so colouration of local specimens is documented for the first time. Specimens reported here from KwaZulu-Natal have an overall more slender appearance and are less densely setose (but they were also smaller than the specimens from False Bay and the South Coast). Moreover, they often reside on one extreme end of variation in that they generally have slightly more, and also more pronounced (longer and more slender) spines. For example, some specimens have 5 or 6 rows of spines on the dorsal surface of the palm, numerous small spines on the dorsal surface of the carpus of the right cheliped, generally longer spines on the ventrolateral and ventromesial margins of the meri of the cheliped, and up to 5 spines on the distal margin of the sternite of the third pereopods. One small specimen (♂ 1.6 mm, SAMC MB-A066681) also has an unusual, hook-like spine distally on the mesial surface of the ischium of the left cheliped. Preliminary and unpublished genetic data suggests that there might be more cryptic species hidden under this taxon (see Chapter 7).

Distribution. North Atlantic from Norway and Sweden to France, Mediterranean, Central and South Atlantic from Spain to São Tomé and Príncipe, southern Africa from Angola to South Africa (Vema Seamount, False Bay to KZN).

Habitat. In sponge-covered shells or rarely overgrown by compound ascidians, from intertidal to 250 m depths, South African specimens often in heavily overgrown shells, from shallow subtidal (False Bay) to 130 m depth (Agulhas Shelf and KZN).

Pagurus emmersoni McLaughlin and Forest, 1999

Figure 8.13 C–D

Pagurus emmersoni McLaughlin and Forest, 1999: 313, Fig 3A–F (type locality: Tugela River mouth, KZN, South Africa). – Emmerson, 2016c: 449 (list).

Material examined. 13 Oct 2015, off Pumula (KZN), S 30° 38.52', E 30° 32.40', 20 m, Scuba, 1 ♀ 3.1 mm (SAMC MB-A066400), 1 ♂ 4.6 mm (SAMC MB-A066401), 1 ♂ 5.0 mm (SAMC MB-A066402), 1 ♂ 4.4 mm (SAMC MB-A066403), 1 ♂ 6.5 mm (SAMC MB-A066404), 1 ♂ 3.7 mm (SAMC MB-A066650), 2 ♂♂ 2.9–6.4 mm, 2 ♀♀ 2.5–4.2 mm (SAMC MB-A066653); 14 Oct 2015, off Pumula (KZN), S 30° 38.34', E 30° 32.94', 35 m, Scuba, 1 ♂ 5.2 mm (SAMC MB-A066652); 15 Oct 2015, off Hibberdene (KZN), S 30° 34.68', E 30° 34.86', 20 m, Scuba, 1 ♀ 3.7 mm (SAMC MB-A066649); 15 Feb 2016, outside Taffy's Cracker Ground off Pumula (KZN), S 30° 39.24', E 30° 32.58', 36 m, Scuba, 1 ♂ 4.9 mm, 1 ovig. ♀ 5.5 mm (SAMC MB-A066645); 21 Aug 2016, UMNT off Port Shepstone (KZN), S 30° 44.46', E 30° 33.66', 46 m, Scuba, 1 ♂ 4.0 mm, 1 ovig. ♀ (in shell) 5.5 mm (SAMC MB-A066646); 23 Sep 2016, Pumula 22 (KZN), S 30° 38.40', E 30° 34.20', 40–65 m, Scuba, 1 ♂ 7.3 mm, 1 ♀ 4.7 mm (SAMC MB-A066648); 24 Sep 2016, Taffy's Cracker Ground (off Pumula, KZN), S 30° 39.24', E 30° 32.58', 34 m, Scuba, 1 ♂ 7.5 mm (SAMC MB-A066647); 14 Dec 2016,"R"southwest off Port Shepstone (KZN), S 31° 02.28', E 30° 39.54', 70 m, Scuba, 1 ♂ 2.4 mm (SAMC MB-A066680).

Genetic data. Off Pumula, S 30° 38.52’, E 30° 32.40’, 20 m, ♀ 3.1 mm, BOLD: SEAKY1138-16 (SAMC MB-A066400), ♂ 4.6 mm, BOLD: SEAKY1139-16 (SAMC MB-A066401), ♂ 5.0 mm, BOLD: SEAKY1140-16 (SAMC MB-A066402), ♂ 4.4 mm, BOLD: SEAKY1141-16 (SAMC MB-A066403), ♂ 6.5 mm, BOLD: SEAKY1142-16 (SAMC MB-A066404).

Diagnosis. See McLaughlin and Forest (1999).

Colouration. Shield cream to orange and brown, in anterior half centrally and laterally with large dark-brown or maroon areas, rostrum cream, and also with two broad longitudinal patches at the level of the lateral projections running parallel to the lateral margins, posterior half dull orange with cream and white spots. Posterior carapace with calcified parts dull orange mottled cream, laterally pink, branchiostegites light brown. Ocular peduncles cream with narrow, weakly oblique band near base and also with narrow subcorneal band; corneas orange-red with gold; ocular acicles brown at base and cream in distal half. Antennular peduncles with basal segments brownish proximally and white-blue distally; penultimate segments orange; ultimate segments orange with proximal white-blue bands; flagella bright orange. Antennal peduncles cream, with reddish maroon patches and stripes; fifth segments with lateral and mesial longitudinal maroon stripes; fourth segments with several thin stripes; third segments proximally with irregular maroon patch; second and first segments brown-maroon with patches of cream; antennal acicles mesially and laterally with thin longitudinal maroon stripe; flagella with alternating maroon (3–5 articles long) and white (2–3 article long) bands. Chelipeds with dorsal surface of chelae deep maroon and with white patch mesiodistally; finger and fixed finger usually white in distal half and with longitudinal red-orange stripe; carpi with numerous nearly parallel thin longitudinal reddish lines; meri with similar lines and patterns, but usually with one transversal thin line in distal half, and with maroon patches proximally. Ambulatory legs cream with orange to maroon bands and thin lines, dactyls with broad orange band distally and broad red-maroon band proximally; propodi with red-maroon band in proximal half; carpi with numerous parallel longitudinal reddish lines; meri distally with 1 or 2 similar lines and with reddish-brown dorsal patches and lines (sometimes forming interrupted band) near midlength and also with small patch each dorsodistally and dorsoproximally; ischia with dark patches. Pleon orange-pink to brownish. Uropods and telson cream to orange brown.

Remarks. The specimens reported here are the first records since the relatively recent description of *Pagurus emmersoni*, which was based on only three specimens. The species now appears to be common on subtidal reefs on the coast of KwaZulu-Natal, but its occurrence on the South Coast is still restricted to an individual specimen record off Danger Point. *Pagurus emmersoni* forms a closely-related species pair with *P. liochele* (Barnard, 1947), and this relationship has strong molecular support (see Chapter 7). *Pagurus emmersoni* is distinguished by the less developed ventromesial angles of the carpus and merus of the right cheliped that form wing-like projections in *P. liochele*, and also by very different colour patterns. Colouration in life is here described for the first time. It should be noted that the intensity of the colour, particularly of the chelipeds, can vary considerably and in some specimens the chelipeds are not dark maroon, but rather light-red or orange, or even entirely cream. Furthermore, the depth range is extended to 70 m.

Distribution. Potentially endemic to South Africa (South Coast to KZN).

Habitat. Subtidal reefs, from 12–70 m depths.

Pagurus liochele (Barnard, 1947)

Figure 8.13 E–F

Pylopagurus liochele Barnard, 1947: 376 (type locality: off Cape Seal and Algoa Bay, South Africa). – Barnard, 1950: 455, Fig 84a–f. – Kensley, 1974: 66; 1981: 33 (list).

'Incertae sedis'. – Barnard, 1950: 456.

Pagurus barnardi Forest, 1966: 153. – Forest and Ngoc-Ho, 1992: 224.

Pagurus liochele. – McLaughlin, 1988b: 6, Figs 1–2. – McLaughlin and Forest, 1999: 319, Fig 4A–J. – Branch et al., 2010: 116, Fig 49.5.

Material examined. 30 Apr 2015, South Coast Survey sta D0056-073-1089 (Algoa Bay, Port Elizabeth, E. C.), S 33° 50.10', E 25° 57.00', 50 m, trawl, 1 ovig. ♀ 5.7 mm (SAMC MB-A066845), 1 ♂ 7.1 mm (SAMC MB-A066846); 20 Jul 2015, Buffels Bay, S 34° 05.40', E 22° 58.68', intertidal, 1 ♂ 5.5 mm (SAMC MB-A066246); 17 May 2016, South Coast Survey sta D00805 (Jeffrey's Bay, E. C.), S 33° 59.64', E 25° 13.26', 35 m, 1 specimen in sponge-covered shell (SAMC MB-A066494), 1 ovig. ♀ 6.7 mm (SAMC MB-A066495), 1 ovig. ♀ 5.1 mm (SAMC MB-A066496), 1 ovig. ♀ 6.4 mm (SAMC MB-A066497); 14 Jun 2017, False Bay (W. C.), S 34° 06.42', E 18° 31.08', 19 m, dredge, 1 ovig. ♀ 5.0 mm (SAMC MB-A066644), coll. L. de Vos.

Genetic data. Buffels Bay, S 34° 05.40', E 22° 58.68', intertidal, ♂ 5.5 mm, BOLD: SEAKY863-15 (SAMC MB-A066246). Sta D00805, S 33° 59.64', E 25° 13.26', 35 m, ovig. ♀ 6.7 mm, BOLD: SEAKY1209-17 (SAMC MB-A066495). Sta D0056-073-1089, S 33° 50.10', E 25° 57.00', 50 m, ovig. ♀ 5.7 mm, BOLD: SEAKY878-15 (SAMC MB-A066845), ♂ 7.1 mm, BOLD: SEAKY879-15 (SAMC MB-A066846).

Diagnosis. See McLaughlin and Forest (1999).

Colouration. Shield beige-brown with a central brown patch anteriorly and also with low light blue tubercles, laterally sometimes with larger white-blue patches. Posterior carapace purple to pink with cream or white-blue dots. Branchiostegites cream with light or cobalt blue dots. Ocular peduncles beige-orange in proximal half, light to cobalt blue in distal half and with dorsodistal brown-orange patch, corneas golden-red. Ocular acicles cream to transparent or dull orange (at base) and white-blue along distal margins. Antennular peduncles with basal segments dull brown at base, light to cobalt blue in about distal half, statocyst lobes cobalt blue; penultimate segments orange and distally with cobalt blue bands; ultimate segments orange and proximally with broad cobalt blue bands; antennal flagella bright orange. Antennal peduncles cream to beige with darker areas, patches and lines; fifth segments with mesial and lateral longitudinal red-brown line; fourth segments also with lateral line, but with mesial longitudinal red-brown patch; third, second and first segments with darker brown or orange areas and with white-blue dots; antennal acicles laterally with weak longitudinal orange line and also with weakly-defined orange-brown band subdistally; antennal flagella red with blue-white band about every fifth article. Third maxillipeds with bright cobalt blue patches dorsodistally on dactyls, propodi and carpi. Chelipeds similar to each other, dactyls brownish proximally turning bright orange towards distal, with two longitudinal while-blue stripes on outer surface armed with low white-blue tubercles; fixed fingers bright orange distally with broad longitudinal white stripe covered by low light to cobalt blue tubercles; outer surface of palm purple-brown with light to cobalt blue tubercles; carpi similar, but also with larger creamish patches; meri subdistally with broad cream band fringed by distal and proximal narrow brown-red bands, near midline with large cobalt blue half-moon-shaped patch each on dorsal, lateral and mesial surface fringed by narrow brown line. Ambulatory legs similar to each other, dactyls proximally brown-red, turning bright orange towards distal, dorsally with one, laterally with two longitudinal white stripes; propodi cream with cobalt blue distal band, proximally with brown-red patches or stripes intermitted by light blue stripes continued and more regular on carpi; meri predominantly cream in distal half, proximally with irregular, large brown-red patch on light blue background. Pleon purple to pink-orange with whitish dots. Uropods and telson predominantly cream or light brown with some light blue. Eggs deep purple to maroon.

Remarks. This attractive pagurid is common on the South Coast and frequently seen during dives in False Bay, but currently no distribution records are available from the southern West Coast that would link the southern population with the single record from the Orange River mouth near the Namibian border. Equally, no records are available from the Eastern Cape Province to link the few records from KwaZulu-Natal. This leads to the assumption that the main population may occur in the southern region, and also that it does not regularly overlap to the east with *P. emmersoni*. However, the latter point has to be confirmed by more sampling efforts. In life, *P. liochele* is readily identified by colour, for example by the cobalt blue tubercles covering the chelipeds, or the cobalt blue distal ring on the propodi of the walking legs. Colouration, previously only partially known from Barnard's (1950) account of his *incertae sedis* specimens, is herein updated in detail. Specimens from deeper water (South Coast Surveys) are usually less intense in colour.

Distribution. Potentially endemic to South Africa (from Orange River mouth to Transkei).

Habitat. On fine mud and sand, often associated with gorgonians (then shells often overgrown by bryozoans), on sandy substrates commonly found in shells covered by mutualistic sponge *Suberites* sp., from intertidal to 110 m depth.

***Pagurus prideaux* Leach, 1815**

Figure 8.14 A–B

Pagurus prideaux Leach, 1815: Pl 26, Figs 5–6 (type locality: Great Britain). – McLaughlin and

Forest, 1999: 324, Fig 5A–F. – Emmerson, 2016c: 449 (list).

Eupagurus tristanensis. – Stebbing, 1910: 356. [not *Eupagurus tristanensis* Henderson, 1888]

Eupagurus spinulentus. – Stebbing, 1920: 260. – Barnard, 1950: 460, Fig 85a–d. – Emmerson, 2016c: 449 (list). [not *Eupagurus spinulentus* Henderson, 1888]

Material examined. 20 Nov 2016, Coffee Bay (E. C.), S 31° 59.34', E 29° 09.96', 94 m, dredge, 1 ♂ 7.0 mm (SAMC MB-A066527); 14 Dec 2016,“R”southwest of Port Shepstone (KZN), S 31° 02.28', E 30° 39.54', 70 m, Scuba, 1 ovig. ♀ 4.8 mm (SAMC MB-A066691).

Diagnosis. See McLaughlin and Forest (1999).

Colouration. Shield brown-orange mottled white or with whitish patches, few tiny red dots. Posterior carapace similar, uncalcified areas mostly transparent. Ocular peduncles brown-orange, distally weakly reddish and also with very weak cream band near medial constriction; corneas brownish-green to black; ocular acicles orange with cream on terminal margins. Antennular and antennal peduncles cream to yellow-orange. Chelipeds and ambulatory legs predominantly orange and irregularly sprinkled with tiny red dots. Chelipeds with tips of fingers cream, and with proximal half of dorsal surface of chelae bluish to violet, medially interrupted by orange ridge. Propodi, carpi and meri of ambulatory legs very weakly banded or with whitish patch laterally near midlength of segment, most pronounced in propodi, which are more strongly pigmented distally. Pleon cream to orange with white dots. Uropods orange. Telson cream. Eggs light yellow to orange.

Remarks. Elements of uncertainty about Henderson's *Pagurus spinulentus* in South African waters were clarified with McLaughlin and Forest's (1999) finding that the specimens from the south-eastern coast actually represent *P. prideaux* Leach, 1815. At the time, *P. spinulentus* (Henderson, 1888) was poorly known, but has recently been rediscovered and its distribution appears to be restricted to the Philippines, which is also the type locality (Komai and Rahayu 2014). However, Emmerson (2016c) erroneously retained Henderson's taxon in his species list, although the species is not known to occur in South Africa. Amongst the other local species in the genus, *P. prideaux* is identified by the combination of the chelipeds covered with small granules and the long dactyls of the ambulatory legs, which are 1.5 times longer than the propodi. Males of this species exhibit the peculiarly of not having any pleopods. Detailed colouration is given for South African specimens for the first time.

Distribution. Eastern Atlantic from Norway to Cape Verde, Mediterranean Sea, South Africa (Mossel Bay to KZN), Red Sea.

Habitat. Usually found with associated anemones of *Adamsia* sp., but the identity of South African anemones requires clarification, from 20–400 m depth.

Pagurus sp. McLaughlin and Forest, 1999

Pagurus sp. McLaughlin and Forest, 1999: 328, Fig 6A–H. – Emmerson 2016c: 449 (list).

Diagnosis. See description by McLaughlin and Forest (1999).

Remarks. Included here for completeness, McLaughlin and Forest (1999) described a juvenile male specimen of an unidentified species with spines on the dorsal surface of the chelae that is, amongst other characters, distinguished from *P. cuanensis* by not having a dorsal row of spines on the propodus of the second left pereopod.

Distribution. Only known from South Africa (off Park Rynie, KZN).

Habitat. Unknown, collected at 140 m depth.

***Pagurus* n. sp. Landschoff and Komai, in prep.**

Figure 8.14 C–D

Material examined and genetic data. See Chapter 4.

Remarks. Recently described from Hibberdene and Pumula (KZN).

Distribution. Known only from and potentially endemic to KZN, South Africa.

Habitat. Rocky subtidal reefs, at 6–20 m depth.

8.4.4.5 Genus *Propagurus* McLaughlin and de Saint Laurent, 1998

***Propagurus deprofundis* (Stebbing, 1924)**

Figure 8.14 E

Eupagurus deprofundis Stebbing, 1924: 243, Pl 70 (type locality: off Cape Morgan, Eastern Cape, South Africa). – Barnard, 1950: 164.

Pagurus deprofundus. – Kensley, 1981: 33 (list, misspelling).

Propagurus deprofundis. – McLaughlin and de Saint Laurent, 1998: 170, Figs 2D–E, 4B, 7B, 8A–D, 9, 11C–D. – McLaughlin and Forest, 1999: Fig 7A–K. – Emmerson, 2016c: 449 (list).

Material examined. 26 May 1975, R. V. *Meiring Naudé* sta SM 22 (off KZN), S 27° 45.00', E 32° 43.98', 492–700 m, trawl, 1 ovig. ♀ 8.5 mm (SAMC MB-A015340), in carcinoecium of colonial zoanthid; 27 May 1975, R. V. *Meiring Naudé* sta SM 31 (off KZN), S 28° 04.50', E 32° 42.78', 740 m, dredge, 1 ♀ 3.1 mm (SAMC MB-A043422); 20 May 1976, R. V. *Meiring Naudé* sta SM 66 (off KZN), S 27° 16.98', E 32° 54.00', 720–780 m, trawl, 1 ♂ 9.3 mm (SAMC MB-A015339), in carcinoecium of colonial zoanthid; 25 Jun 1979, R. V. *Meiring Naudé* sta SM 233 (off KZN), S 32° 15.18', E 29° 09.78', 540–580 m, trawl, 1 ovig. ♀ 6.7 mm (SAMC MB-A043423); 2 Sep 2006, ORICru15-10/06 sta B.1.2, (off Durban, KZN), S 29° 55.44', E 31° 29.94', 450 m, trawl, 1 ♂ 9.3 mm (ZRC 2013.0546); 18 Mar 2010, ORI/ACEP 48 sta ACEP 1-1 (off Durban, KZN), S 30° 05.22', E 31° 22.86', 449 m, trawl, 1 ♂ 12.6 mm (ZRC 2013.0539); 18 Aug 2010, sta ACEP 3-6 (off Tugela River mouth, KZN), S 29°

29.10’, E 31° 54.36’, 569 m, trawl, 1 ovig. ♀ 9.5 mm (ZRC 2013.0541); 10 May 2015, South Coast Survey sta D00540-6542 (Agulhas Shelf), S 35° 21.30’, E 22° 49.98’, 585 m, trawl, ♀ 7.0 mm (SAMC MB-A066835); 22 May 2015, South Coast Survey sta D00825 (Agulhas Shelf), S 35° 22.26’, E 22° 47.22’, 583 m, trawl, 1 ♀ 8.6 mm (SAMC MB-A066500), South Coast Survey sta D00825 (Agulhas Shelf), S 35° 21.54’, E 22° 42.84’, 563 m, trawl, 1 ♂ 8.0 mm (SAMC MB-A066501), 1 ♀ 5.7 mm (SAMC MB-A066502).

Genetic data. Sta ACEP 1-1, S 30° 05.22’, E 31° 22.86’, 449 m, ♂ 12.6 mm, BOLD: SEAKY1177-17 (ZRC 2013.0539). Sta ACEP 3-6, S 29° 29.10’, E 31° 54.36’, 569 m, ovig. 9.5 mm, BOLD: SEAKY1176-17 (ZRC 2013.0541). Sta D00825, S 35° 22.26’, E 22° 47.22’, 583 m, ♀ 8.6 mm, BOLD: SEAKY1338-17 (SAMC MB-A066500). Sta D00825, S 35° 21.54’, E 22° 42.84’, 563 m, ♀ 5.7 mm, BOLD: SEAKY1340-17 (SAMC MB-A066502). Sta D00540-6542, S 35° 21.30’, E 22° 49.98’, 585 m, ♀ 7.0 mm, BOLD: SEAKY1423-17 (SAMC MB-A066835).

Diagnosis. See McLaughlin and Forest (1999).

Colouration. Shield with cream background colouration and varying amount of orange, anteriorly with large darker oval patch. Posterior carapace with calcified parts cream. Ocular peduncles orange, dorsodistally with lighter patches; corneas black; ocular acicles orange and usually with white distal margins. Antennular and antennal peduncles orange with some cream areas; fifth segments of antennal peduncles cream with lateral and mesial longitudinal stripes. Chelipeds and ambulatory legs orange with varying degree of cream (irregular and undefined dots on legs), tips of spines often cream; meri distally with very narrow white ring laterally and mesially widened into small patches, and laterally usually also with elongated whitish patch. Fourth and fifth pereopods cream with some orange. Pleon brown-yellow to purple-orange. Uropods and telson cream with some weak orange.

Remarks. *Propagurus deprofundis* is unmistakably identified by the longitudinal keel on the mesial surface of the propodi of the second pereopods. The specimens reported here are the first record from the type locality since its original description from off Cape Morgan, 457–585 m. The rediscovery, and finding the species repeatedly off KwaZulu-Natal, also shows that *P. deprofundis* is not uncommon and probably present along the entire southern and eastern South African shelf region. The slightly larger Durban specimens were sent to Singapore and are now housed at the Lee Kong Chian Natural History Museum. They had initially been identified as *P.* cf. *deprofundis* by D. L. Rahayu, but a re-examination revealed that they are conspecific with the new material collected along the South Coast, which is also supported by molecular data (Chapter 7). Moreover, the very widespread distribution is confirmed by preliminary genetic tests, suggesting that the South African specimens may be conspecific with specimens from New Zealand (unpubl. data). It is also noticeable that the two specimens from northern KwaZulu-Natal are housed in carcinoecia formed by colonial zoanthids, as usually the case among parapagurid hermit crabs. Colouration in life is reported for the first time for specimens from the type locality, and the South African depth range is extended.

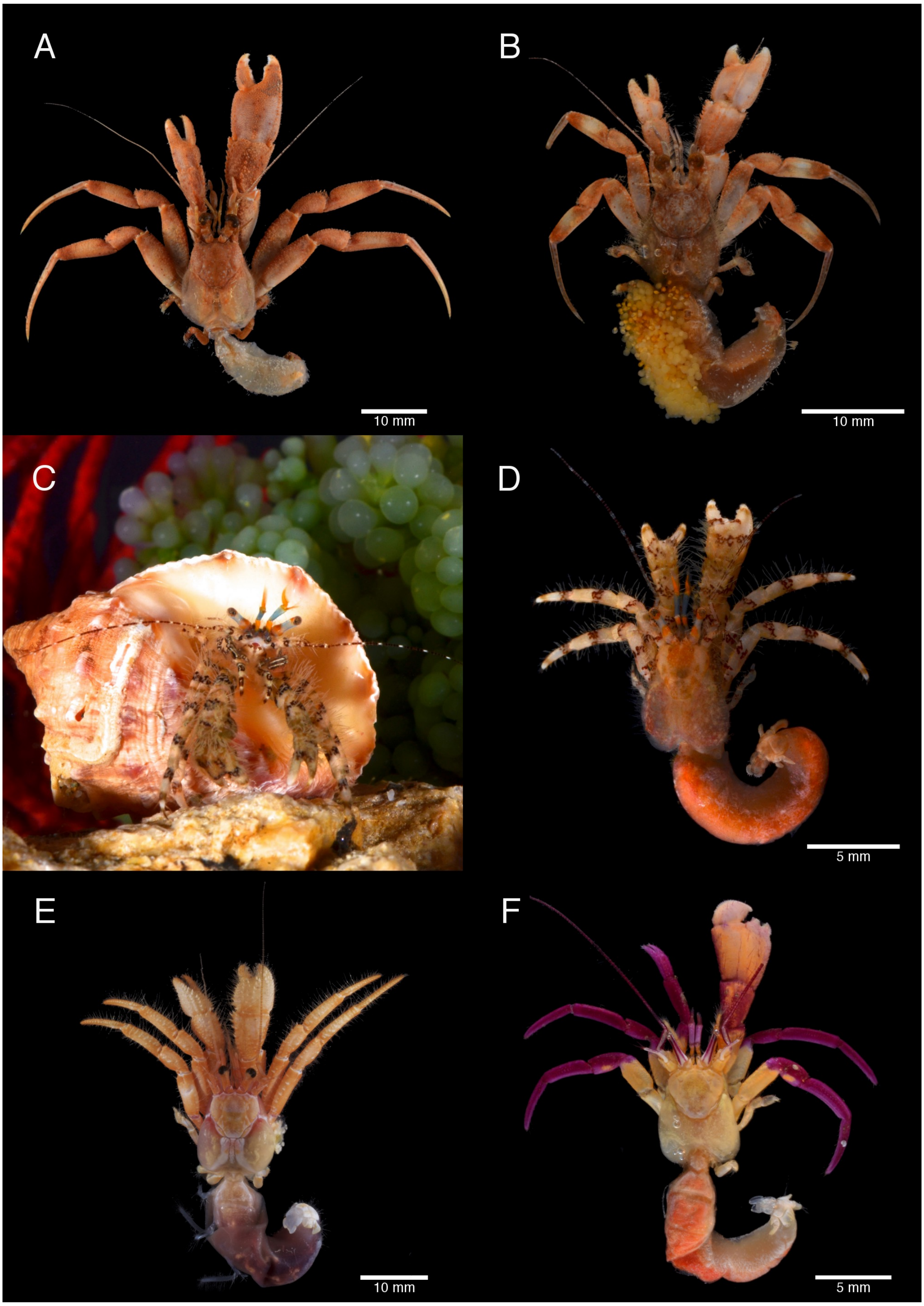

Figure 8.14: Paguroidea of South Africa, family Paguridae Latreille, 1802 (C *in situ*): A–B *Pagurus prideaux* Leach, 1815, Coffee Bay, ♂ 7.0 mm (SAMC MB-A066527)(A), off Port Shepstone, ovig. ♀ 4.8 mm (SAMC MB-A066691)(B) **C–D** *Pagurus* n. sp. Landschoff and Komai, in prep., off Pumula, paratype, ♀ 2.4 mm (SAMC MB-A066407)(C), holotype, ♂ 2.7 mm (D) (SAMC MB-A066790) **E** *Propagurus deprofundis* (Stebbing, 1924), Agulhas Shelf, ♀ 7.0 mm (SAMC MB-A066835) **F** *Pylopaguropsis keijii* McLaughlin and Haig, 1989, Pumula, ♂ 3.5 mm (SAMC MB-A066711).

Distribution. South Africa (southern and eastern shelf region), Philippines, southern Australia, New Zealand, Hawaii.

Habitat. Probably on soft sediments, in shells and carcinoecia formed by zoanthids, in South Africa from 449–780 m depth, elsewhere shells sometimes with attached anemone and from 200–915 m depth.

8.4.4.6 Genus *Pylopaguropsis* Alcock, 1905

Pylopaguropsis keijii McLaughlin and Haig, 1989 new record

Figure 8.14 F

Pylopaguropsis keijii McLaughlin and Haig, 1989: 150, Figs 2i, 3d, 5d, 7e, 9d, 11d, 13d (type locality: Hawaii). – Hogarth et al., 1998: 168. – Asakura, 2000: 84, Figs 6, 7, 19B, 19C. – Poupin et al., 2013b: 4 (list). – Poupin et al., 2013a: 47, Fig 26A–C.

Pylogapuropsis lemaitrei. – Poupin, 2009: 62, unnumbered Fig. [not *Pylopaguropsis lemaitrei*]

Material examined. 20 Sep 2016, Pumula (KZN), S 30° 38.34', E 30° 32.94', 40 m, Scuba, 1 ♂ 3.5 mm (SAMC MB-A066711).

Diagnosis. See Asakura (2000).

Colouration. See Asakura (2000).

Remarks. Apart from a few varying characters, the single male specimen reported here agrees well with the description by McLaughlin and Haig (1989), the diagnosis by Asakura (2000), and also matches the reported colouration. Notably though, this specimen has two instead of a single spine on the dorsomesial distal angle of the second segment of the antennal acicles, and only three (right lobe) and four (left lobe) moderately strong spines on the terminal margins of the posterior lobe of the telson, but these differences are treated as intraspecific variation. Although the specimen bears a strong deformation on the fixed finger of the right cheliped (see Figure 8.14), it can be relatively safely identified and is the first record of *Pylopaguropsis keijii* in South Africa. *Pylopaguropsis keijii* can be distinguished from the so far only other recorded regional species, *P. zebra* (Henderson, 1893), by the basally swollen ocular peduncles and by the lack of a median ridge on the lateral surface of the propodus of the third right pereopod. Furthermore, colouration is distinctive, as *P. keijii* has no stripes on the pereopods. Moreover, this species occurs in shallower waters than *P. zebra.*

Distribution. South Africa (KZN), Tanzania (Zanzibar), La Réunion, Maldives, Guam, Yap (West Caroline) Islands, Japan, Hawaiian Islands.

Habitat. Reported from 2.5–79 m depth, in South Africa only collected at 40 m depth.

Pylopaguropsis zebra (Henderson, 1893)

Eupagurus zebra Henderson, 1893: 425 (? in part), Pl 39, Figs 12–15 (type locality: Holothuria Bank, Northwest Australia). – Balss, 1912: 106. – Forest, 1955: 107.

Eupagurus zebra. – Stebbing, 1920: 259. – Barnard, 1950:459. [not *P. zebra* (Henderson, 1893)]

Pagurus zebra. – Kensley, 1981: 33 (list). [not *P. zebra* (Henderson, 1893)]

Pylopaguropsis zebra. – McLaughlin and Haig, 1989: 143, Figs 3b, 5b, 7b, 9b, 11b, 13b. – McLaughlin et al., 2007b: 193, 2 unnumbered Figs.

Pylopaguropsis zebra. – Emmerson 2016c: 449 (list). [not *P. zebra* (Henderson, 1893)]

Diagnosis. See McLaughlin et al. (2007b).

Remarks. McLaughlin and Haig (1989) came to the conclusion that Stebbing's (1920) and consequently Barnard's (1950) specimens must be considered *incertae sedis.* They based their arguments on both Stebbing's hesitation to attribute his specimens to Henderson's taxon, as well as on his remark on the slender pereopods, a terminology they deemed unsuitable to describe the pereopods of *P. zebra.* The only other species of the genus now reported from South Africa, *P. keijii*, has even stronger and therefore less slender pereopods. Also because Stebbing mentioned the "beautiful stripes of colour on those limbs", which *P. keijii* does not have, it is clear that neither Stebbing nor Barnard had this species. Otherwise, both of their non-illustrated accounts are insufficient to identify their specimens, which McLaughlin and Haig (1989) failed to locate. Despite extensive searches in the collections of the Iziko South African Museum, Stebbing's specimens, which were referred to by Barnard as 'returned to the South African Museum', still remained undetected. At this stage they must be regarded as lost and thus cannot be re-examined. Therefore, the only verified report from South Africa goes back to Balss (1912), and after this record, *P. zebra* has not been found again from within the national borders. Both Kensley (1981) and Emmerson (2016c) only referred to Barnard's unverifiable specimens.

Distribution. South Africa (Agulhas Bank), Sri Lanka, northern Australia, Korea Strait, East China Sea, Taiwan, Southern Japan.

Habitat. Unknown, from 50–180 m depth.

8.4.5 Family Parapaguridae Smith, 1882

8.4.5.1 Genus *Oncopagurus* Lemaitre, 1996

Oncopagurus africanus (de Saint Laurent, 1972)

Parapagurus africanus de Saint Laurent, 1972: 109, Figs 3, 15 (type locality: Angola).

Sympagurus africanus. – Lemaitre, 1990: 229, Figs 6–7.

Oncopagurus africanus. – Lemaitre, 2014: 214, Figs 1A–I, 51. – Emmerson, 2016c: 449 (list).

Material examined. 30 Jun 1964, Division of Sea Fisheries sta K 220 (SE off Bluff, Durban, KZN), S 29°56', E 31°12.50', 366 m, 1 ♂ 4.7 mm (SAMC MB-A012715).

Diagnosis. See Lemaitre (1990, 2014).

Remarks. *Oncopagurus africanus* remains known from only a few specimens, and in South Africa from a single male specimen that is also the basis of Lemaitre's reports. Colouration for this species is unknown, but the South African specimen had initially been mis-identified, carrying a label reading *'Eupagurus zebra'*, which might be an indication that *O. africanus* could have some form of longitudinal stripes. The genus *Oncopagurus* is readily identified by the presence of a strongly upwardly-curved epistomial spine (see Lemaitre 1989, Fig 1A, Lemaitre 2014, e. g. Fig 2C). In South Africa, *O. africanus* is currently the only known occurring member of the genus.

Distribution. Congo, Angola, South Africa (off Durban, KwaZulu Natal).

Habitat. Gastropod shells often with anthozoan polyps, from 235–366 m depth.

8.4.5.2 Genus *Paragiopagurus* Lemaitre, 1996

Paragiopagurus atkinsonae Landschoff and Lemaitre, 2017b

Figure 8.15 A–B

Paragiopagurus atkinsonae Landschoff and Lemaitre, 2017b: 25, Figs 2–6, 9.

Material examined and genetic data. See Landschoff and Lemaitre (2017b).

Remarks. Recently described from the West Coast of South Africa, which constituted as the first record of this genus from South African waters.

Distribution. Potentially endemic to South Africa (restricted to a small area on the West Coast).

Habitat. Occupying carcinoecia formed by colonies of *Epizoanthus* sp., from 199–277 m depth.

8.4.5.3 Genus *Parapagurus* Smith, 1879

Parapagurus andreui Macpherson, 1984

Figure 8.15 C

Parapagurus andreui Macpherson, 1984: 81, Figs 24–27 (type locality: Valdivia Bank). – Lemaitre, 1986: 526; 1989: 11; 1990: 221, Fig 1; 1999: Figs 8–9, 47, 49. – Emmerson, 2016c: 449 (list).

Material examined. 7 Feb 2015, SEAFO2015 sta 12 (Valdivia Seamount, Namibia), S 24° 49.02', E 06° 24.66', 887 m, 1 ♂ 16.0 mm (SAMC MB-A066725); 6 Feb 2017, West Coast Survey AFR291 sta A33168-109-6090 (South Africa), S 31° 18.24', E 15° 38.04', 731 m, trawl, 1 ♂ 15.2 mm (SAMC MB-A066788).

Genetic data. Valdivia Bank, Namibia, sta 12, S 24° 49.02’, E 6° 24.66’, 887 m, ♂ 16.0 mm, BOLD: SEAKY1437-17 (SAMC MB-A066725). West Coast, South Africa, sta A33168-109-6090, S 31° 18.24’, E 15° 38.04’, 731 m, ♂ 15.2 mm, BOLD: SEAKY1438-17 (SAMC MB-A066788).

Diagnosis. See Lemaitre (1999).

Remarks. Although *Parapagurus andreui* has been reported from South Africa before (off Durban, KZN), this is the first record from the West Coast. The species appears to have a disrupted distribution, as it occurs both in the southeastern Atlantic and also in the Western Indian Ocean. However, it remains unreported from the South Coast of South Africa, so that the connectivity of the Atlantic and Indian Ocean populations is somewhat speculative.

Parapagurus andreui is morphologically very similar to *P. latimanus* Henderson, 1888, and can be distinguished from the latter by a combination of the unarmed antennal acicles, the conical scales of the propodal rasp on the fourth pereopod, and the long (>4 times as long as broad) propodi of the ambulatory legs (see Lemaitre 1999). However, *P. latimanus* does not occur in South African waters. Although there can be little doubt about the identity of the two specimens reported here (especially with the proximity to the type locality), they both have 1 or 2 minute spinules or tubercles proximally on the mesial margin of the antennal acicles. Moreover, the differentiation between conical and lanceolate scales (Lemaitre 1999, Fig 2c–d) is not always clear and the specimens were found to have both types of scales. Maybe most importantly, the propodi of the second pereopods were only found to be more than 4 times longer than broad on the right, and 3.5–3.9 times longer than broad on the left side. This means that when using Lemaitre’s (1999) key, both specimens could equally key out as *P. latimanus*, when only the left legs would be measured.

Distribution. Southern Angola, Namibia (including Valdivia Bank), South Africa (West Coast, KZN), Mozambique Channel, Madagascar, La Réunion.

Habitat. In carcinoecia formed by anthozoan polyps of *Epizoanthus* sp., from 406–2970 m depth.

***Parapagurus richeri* Lemaitre, 1999**

Parapagurus richeri Lemaitre, 1999: 334, Fig 19–23, 47–48 (type locality: New Caledonia). – McLaughlin et al., 2007b: 332, 4 unnumbered Figs.

Diagnosis. See McLaughlin et al. (2007b).

Remarks. *Parapagurus richeri* is a common deep-water species in the Indo-West Pacific and has its westernmost distributional range in the deep sea off KwaZulu-Natal. Here, it co-occurs with *P. stenorhinus* Lemaitre, 1999, from which it is distinguished by a suite of characters, for example by the presence of 1–3 distinct spines on the mesial margin of the antennal acicles (as opposed to 5–8), or by the rasp of the left uropodal exopod, which is moderately broad (as opposed to narrow). Emmerson (2016c) missed this species when compiling his species list.

Distribution. South Africa (KZN), Philippine Islands, Indonesia, South China Sea, Taiwan, Australia, New Zealand, Vanuatu.

Habitat. Gastropod shells often covered by anthozoan polyps, occasionally in scaphopods, from 311–4470 m depth.

***Parapagurus stenorhinus* Lemaitre, 1999**

Parapagurus stenorhinus Lemaitre, 1999: 352, Figs 32–35, 47, 49 (type locality: Madagascar and Western Indian Ocean).

Remarks. Only known from a few samples, the distribution of *Parapagurus stenorhinus* overlaps in the Western Indian Ocean with *P. richeri.* However, *P. stenorhinus* is characterised by a narrow rasp of the left uropodal exopod, from which the species name is derived. In South Africa it has not been found again since its original description. Emmerson (2016c) missed this species when compiling his species list.

Distribution. Indian Ocean including South Africa (off KZN), Kenya, Madagascar, Shri Lanka.

Habitat. Housed in both gastropod and scaphopod shells, from 2400–4930 m depth.

8.4.5.4 Genus *Strobopagurus* Lemaitre, 1989

***Strobopagurus sibogae* (de Saint Laurent, 1972)**

Parapagurus sibogae de Saint Laurent, 1972: 116, Figs 10, 23 (type locality: Indonesia).

Parapagurus kilburni Kensley, 1973: 285, Figs 1–2; 1974: 66; 1981: 33 (list). – Lemaitre, 1989: 36; Lemaitre, 1996: 167.

Strobopagurus sibogae. – Lemaitre, 1989: 36; Lemaitre, 2004a: 369, Figs 1F, 3E–H, 4J–K, 5H–I, 8E. – McLaughlin et al., 2007b: 288, 2 unnumbered Figs. – Poupin et al., 2013a: 48. – Emmerson, 2016c: 449 (list).

Material examined. *Paratypes* of *Parapagurus kilburni*: Aug 1972, off Durban (KZN), 270 m, 2 ♂♂ 6.2–7.0 mm (SAMC MB-A013186), coll. R. N. Kilburn.

Diagnosis. See Lemaitre (2004a), and also McLaughlin et al. (2007b).

Remarks. Kensley (1973), being unaware of de Saint Laurent's (1972) publication, described *Strobopagurus kilburni* (as *Parapagurus kilburni*) from off Durban. Later, Lemaitre (2004a) found his species to be a junior synonym to *S. sibogae.* Members of this distinct parapagurid genus are diagnosed by the broad shield (considerably broader than long), the straight dactyls of the ambulatory legs, and the strongly dilated corneas. Furthermore, *S. sibogae* is distinguished by the spinose dorsomesial and dorsolateral margins of the right chela. It has not been found again in South African waters since Kensley's description. Of Kensley's specimens, three (the holotype

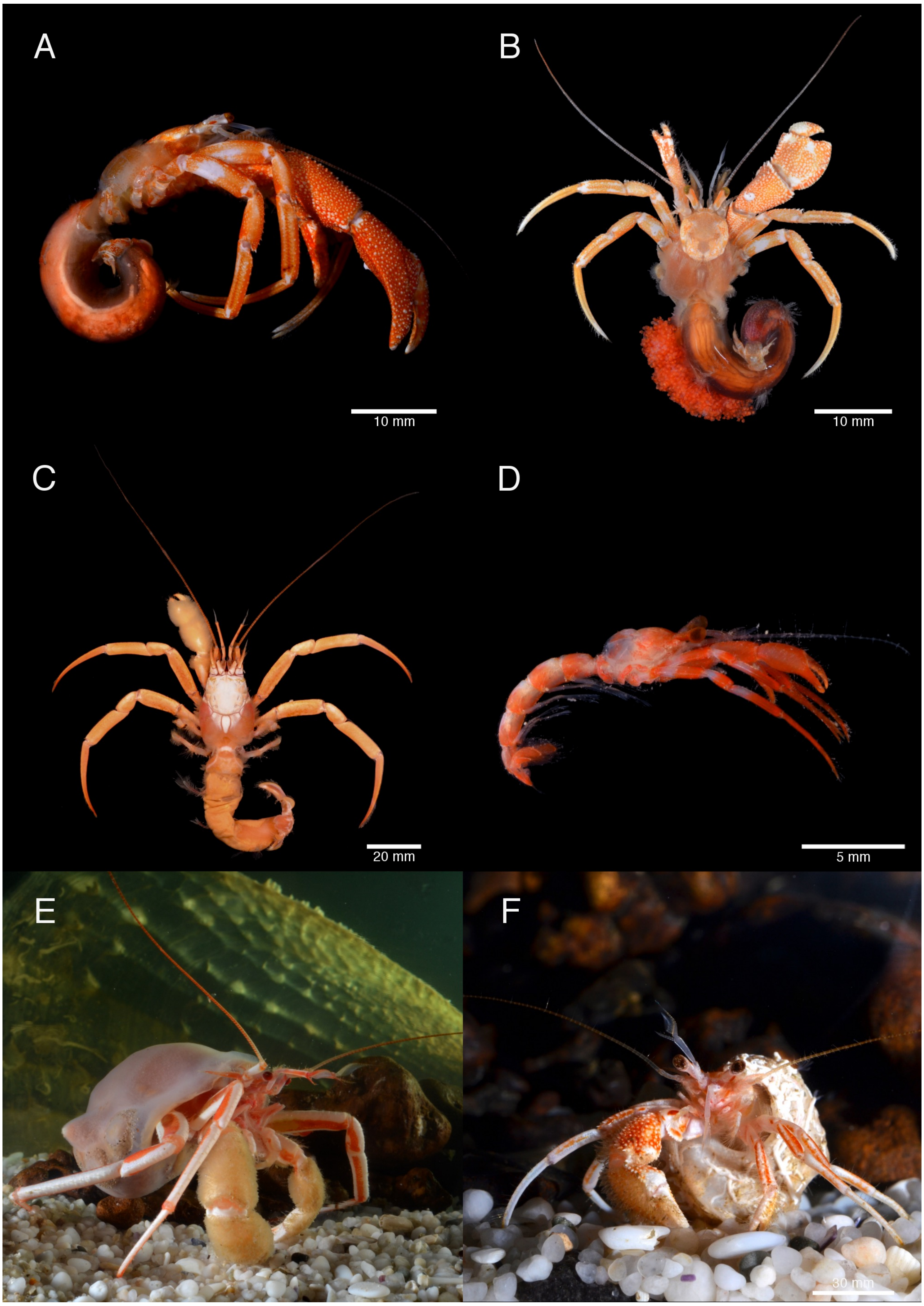

Figure 8.15: Paguroidea of South Africa, family Parapaguridae Smith, 1882 (E–F *in situ*): A–B *Paragiopagurus atkinsonae* Landschoff and Lemaitre, 2017b, West Coast, holotype, ♂ 7.0 mm (USNM 1292083)(A), paratype, ovig. ♀ 6.4 mm (SAMC MB-A066809)(B) **C** *Parapagurus andreui* Macpherson, 1984, West Coast, ♂ 15.2 mm (SAMC MB-A066788) **D–E** *Parapagurus bouvieri* Stebbing, 1910, Agulhas Shelf, glaucothoe (SAMC MB-A066785)(D), Agulhas Bank, ♂ 10.6 mm (SAMC MB-A066794)(E) **F** *Sympagurus dimorphus* (Studer, 1883), Agulhas Bank, specimen lost.

and 2 of the 4 paratypes) were lost during the process of returning the material to Cape Town (R. Lemaitre, pers. comm.).

Distribution. South Africa (KZN), Mozambique Channel, Madagascar, Philippines, Indonesia, Solomon Islands, China Sea, Taiwan, Japan, New Caledonia.

Habitat. Unknown, from 40–980 m depth.

8.4.5.5 Genus *Sympagurus* Smith, 1883

Sympagurus dimorphus (Studer, 1883)

Figure 8.15 F

Eurpagurus dimorphus Studer, 1883: 24, Figs 11–12 (type locality: Cape of Good Hope, South Africa).

Parapagurus dimorphus. – Barnard, 1950: 452, Fig 83c, d. – Kensley 1981: 33.

Sympagurus dimorphus. – Lemaitre, 1989: 71, Figs 26–28, 40E–H; Lemaitre, 2004b: 103, Figs 1c$_{1,2}$, 11, 34, 35a. – Emmerson, 2016c: 450 (list). – Landschoff and Lemaitre, 2017b: 34, Figs 7A–B, 8.

Material examined and genetic data. See Landschoff and Lemaitre (2017b).

Additional data. Cape Canyon Survey: 10 Mar 2016, CCSD006-INV-144 (West Coast), S 33° 21.48', E 17° 40.26', 350 m, dredge, 1 glaucothoe, BOLD: SEAKY1367-17 (SAMC MB-A066742); 18 Mar 2016, CCSD014-INV-457 (West Coast), S 33° 11.22', E 17° 51.60', 358 m, dredge, 1 glaucothoe, BOLD: SEAKY1368-17 (SAMC MB-A066743); CCSD014-INV-436 (West Coast), S 33° 11.22', E 17° 51.60', 358 m, dredge, 1 glaucothoe, BOLD: SEAKY1369-17 (SAMC MB-A066744).

Diagnosis. See description by Lemaitre (2004b).

Remarks. Recently, Landschoff and Lemaitre (2017b) reported colouration for specimens from South Africa. Based on this updated taxonomic information, and also on preliminary molecular tests, it appears that this widespread deep-water hermit crab consists of a species complex. A different genetic lineage may occur around the Prince Edward and Marion Islands that is closer to specimens from New Zealand than to the ones on the South African mainland (see Chapter 7).

Distribution. All around the southern hemisphere from S 22°–57°, South Africa (West and South Coast).

Habitat. Found in gastropod shells (usually South Coast) or in carcinoecia formed by zoanthid polyps (predominantly of West Coast), from 91–1995 m depth.

Sympagurus dofleini (Balss, 1912), new record

Parapagurus dofleini Balss, 1912: 96, Fig 4b (type locality: Japan).

Sympagurus dofleini. – Lemaitre, 2004b: 128, Figs 1i$_{1,2}$, 26c–d, 27, 34. – Poupin et al., 2013b: 4 (list), Fig 3 mid-right. – Poupin et al., 2013a: 49, Fig 27D. – Poupin et al., 2013d: 10 (list). – Emmerson, 2016c: 450 (list).

Material examined. 25 Feb 2006, sta B.8.2 off Durban (KZN), S 29° 50.52', E 31° 36.72', 365–475 m, 1 ♂ 15.0 mm (ZRC 2013.0543); 20 Mar 2010, sta ACEP 3-5 off Durban (KZN), S 29° 29.10', E 31° 54.36', 563 m, 2 ♂♂ 10.8–16.8 mm (ZRC 2013.0548).

Genetic data. Sta ACEP 3-5, S 29° 29.10', E 31° 54.36', 563 m, ♂ 16.8 mm SEAKY1173-17 (ZRC 2013.0548), ♂ 10.8 mm, BOLD: SEAKY1175-17 (ZRC 2013.0548).

Diagnosis. Adapted after Lemaitre (2004b). Gills with lamellae at most distally divided. Shield broader, or about as broad, as long; dorsal surface usually with irregular weakly-calcified areas; rostrum broadly triangular, with low dorsal ridge. Ocular peduncles usually less than half the length of shield, corneas weakly dilated; ocular acicles terminating in strong spine (rarely bifid on 1 side). Antennular and antennal peduncles both overreaching distal corneal margins; antennal acicles reaching to or exceeding distal margin of cornea, mesial margin setose and armed with 7–18 small spines. Epistomial spine short and straight. Chelipeds both covered in dense plumose setae obscuring surfaces of propodi and carpi; palm of right cheliped with dorsomesial and dorsolateral margins well defined by irregular rows of spines, dorsal surface unarmed, carpus with numerous small tubercles or spines on dorsal surface; chela of left cheliped unarmed. Ambulatory legs with dactyls about 1.3 times (pereopod 2) and 1.4–1.7 times (pereopod 3) as long as propodi, each with irregular row of 20–45 small corneous spines on ventromesial margin, carpi each with small dorsodistal spine. Fourth pereopods with propodal rasp consisting of 3 or 4 rows of conical scales. Telson with posterior margin separated into 2 lobes by rounded, deep (U-shaped) cleft; lobes armed distally with numerous weak corneous spines.

Colouration. From pictures in Poupin et al. (2013a), and in Poupin et al. (2013b). Shield yellow to orange, anterior margin lighter in colour or cream. Ocular peduncles white with lateral longitudinal orange stripe. Corneas black. Antennular and antennal peduncles yellow or cream to orange. Chelipeds and ambulatory legs yellow or cream to orange; fingertips and tips of dactyls orange. Ambulatory legs with dactyls paler or entirely cream, propodi and meri with longitudinal, faint cream to white stripes near dorsal and ventral margins. Meri and distal areas of ischia cream to white.

Remarks. The three South African male specimens were identified in collaboration with R. Lemaitre (Smithsonian Institution), yet show some variation to the description in Lemaitre (2004b), to which the diagnosis above has been adapted. Characters in which the specimens from South Africa deviate are mainly the dimensions of the shield and cephalic appendages. The two smaller specimens have the shield marginally longer than broad and the smallest specimen has ocular peduncles with the same length as the shield. Furthermore, in all specimens the antennal acicles overreach the distal corneal margins by about a third of their length, and they are also armed with only 7–9 spines. With regards to the ambulatory legs, the dactyls of the second pereopods are only 1.4–1.5 the length of the propodi. The chelae of the right chelipeds range from 1.7 times as long as broad in the smallest, to 3.0 times as long as broad in the largest specimen. In addition to the chelae and propodi, the meri of both chelipeds are covered with dense plumose setae except in the proximal third. The dactyls of the ambulatory legs have deep to moderately deep longitudinal sulci in the proximal half, which are more pronounced mesially, and also have diagonally transversal rows of stiff setae in the distal third dorsomesially. The anterior lobe of the sternite of the third pereopods is armed with 1 or 2 moderately prominent spines. The specimens from South Africa reported here also show a markedly denser coverage of setae on the chelipeds than the specimens reported by Poupin et al. (2013a), and by Poupin et al. (2013b) from the Mayotte region and La Réunion. Because these authors provided important colour photographs in life, but did not report on the colouration, and because the previously described colouration of this species has been limited to a low-resolution and slightly distorted picture (see Lemaitre 1994: 419, Fig 28d), the colouration is added here, based on the pictures from Mayotte and La Réunion. This colour varies slightly compared to the report by Lemaitre from French Polynesia, and specimens from the Western Indian Ocean might contain more orange and also have orange-tipped dactyls. No colour pictures of the South African specimens were taken prior to preservation, but there is little doubt that they are conspecific. This is the first record of the species for South Africa.

Distribution. South Africa (KZN), Tanzania (Zanzibar), Mozambique Channel, Glorieuses Islands, Madagascar, La Réunion, Australia, Indonesia (Borneo), Mariana Islands (Guam), Japan, New Caledonia, Wallis and Futuna, Tonga, Samoa, Hawaiian Islands, French Polynesia, Nazca, and Sala y Gomez ridges.

Habitat. Occupying pseudo-shells or carcinoecia produced by anemones; commonly found living symbiotically with the anemone *Stylobates aeneus* Dall that produces a flexible, golden-shiny carcinoecia housing, which has been confused to be (and falsely described as!) a species of gastropod (see Lemaitre 2004b). From 183–950 m depth.

Sympagurus trispinosus (Balss, 1911)

Parapagurus arcuatus var. *trispinosa* Balss, 1911: 3 (type locality: Zanzibar, Tanzania).

Sympagurus trispinosus. – Lemaitre, 1989: 3; 2004b: 139, Figs $1l_{1,2}$, 33–34. – McLaughlin et al., 2007b: 305, 2 unnumbered Figs. – Emmerson, 2016c: 450 (list).

Material examined. 22 May 1976, R. V. *Meiring Naudé* sta SM 83 (off KZN), S 28° 00.00', E 32° 46.00', 600–810 m, beam trawl, 5 ♂♂ 4.5–13.3 mm, 4 ovig. ♀♀ 8.8–11.4 mm, 1 ♀ 5.7 mm (SAMC MB-A015337).

Diagnosis. See Lemaitre (1994), and also McLaughlin et al. (2007b).

Remarks. This widespread species is reported from South Africa only from a single sampling event during the cruises of the R. V. *Meiring Naudé*. The specimens were identified by R. Lemaitre and returned to the Iziko South African Museum. Like most parapagurids, *S. trispinosus* is identified by a combination of characters and among the South African species it is superficially similar to the previous *S. dofleini*, but has bifid or multifid ocular acicles.

Distribution. South Africa (KZN), Tanzania (Zanzibar), Madagascar, La Réunion, South China Sea, Philippines, Indonesia, Australia, Vanuatu, New Caledonia, French Polynesia.

Habitat. In symbiotic relationship with the anemone *Stylobates cancrisocia* Carlgren, reported from 350–1500 m depth.

8.5 Discussion

Following the present study, 72 paguroid hermit crabs from five families are now included in the national species list (Table 8.1). In this list, Krauss' (1843) record of *Clibanarius clibanarius* (Herbst, 1791, as reiterated by all later authors, is considered to represent *C. longitarsus* (De Haan, 1849), and the former taxon is therefore excluded. Furthermore, three more species from the literature and first listed to occur in South Africa by Kensley (1981), *Clibanarius padavensis* De Man, 1888, *C. striolatus* Dana, 1852, and *Diogenes custos* (Fabricius, 1798), require further species validations and are not included here either. Barnard's (1950) record of *Diogenes senex* Heller, 1865 is preliminarily retained, but should be investigated further. As stated by Landschoff and Rahayu (in press), also see Chapter 3, the regional fauna of *Diogenes* is in need of a more extensive taxonomic revision that lies beyond the scope of this study, and it seems very likely that any such study will reveal additional cryptic species within this genus. The presence of several genetically distinct candidate species has already been noted (see Chapter 7). Lastly, Forest's (1954) report of an undescribed species of *Paguristes* from Table Bay is regarded to represent *P. gamianus* H. Milne Edwards, 1836 pending a more detailed description of *P. gamianus* that accounts for better information on intraspecific variation. Like the members of *Diogenes*, the local species of *Paguristes* require more detailed taxonomic attention and the targeted collecting efforts of this study have revealed the presence of several species of this group, which were unidentifiable to species level and which are not covered in this report (but again see Chapter 7). Hence these findings are likely to represent several species new to science that await detailed formal description in the near future.

Since Barnard's (1950) ground-breaking catalogue that listed 32 nominal hermit crab species from South African continental territories, the number of reported taxa has more than doubled. At the time of Emmerson's (2016a, b, c) multi-volume guide, 56 valid species were recorded with a South African distribution, although not all of these were reflected or correctly attributed in his fauna list. Since then, two more hermit crabs, *Paragiopagurus atkinsonae* and *Goreopagurus poorei* have been added (Landschoff and Lemaitre 2017b,a). Finally, another two new species descriptions, *Pagurus* n. sp. and of *Diogenes* n. sp., are currently underway (Landschoff and Rahayu in press, Landschoff et al. in prep., or see Chapters 3–4), bringing the number of paguroids known prior to this study up to 60. By adding 12 more species as new records, this report therefore brings the South African national hermit crab fauna to 72, an expansion of 20% (Figure 8.16).

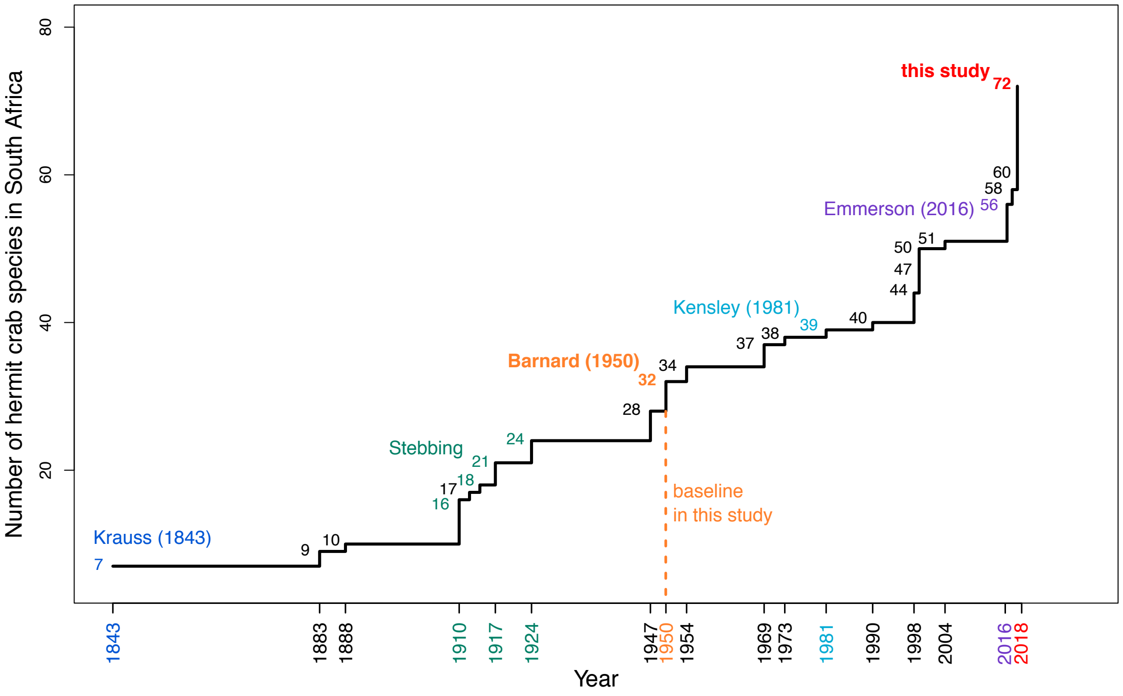

Figure 8.16: Accumulation curve of hermit crabs added to the South African fauna list over time, as new descriptions to science or as new records. Barnard (1950), taken as a baseline in this study, is indicated by the orange-dotted line. In total, 12 species are added to the national fauna, accounting for 17% of all national species.

Overall, this study provides taxonomic accounts for 62 of the total of 72 species. Of these 62 nominal taxa, *Calcinus elegans* (H. Milne Edwards, 1836) is the only species that was listed in Barnard (1950) under its currently accepted name, so that actually no update would have been necessary. However, the discovery of this characteristic hermit crab, nearly 175 years after its first and only South African record (Krauss, 1843), deserved specific mention. In addition to the 12 species that are new national records, the other species included 23 taxa with updated names, 22 taxa that have been added by various taxonomic studies over the past 70 years, and four taxa that were listed by Emmerson as new records for South Africa, but without providing any supporting evidence or locality data (see Table 8.1). A large number of inaccuracies or taxonomic problems emerging from Emmerson's list were addressed and corrected whenever possible.

Despite the considerable progress reported on here, many South African hermit crabs still remain to be revised and described. Hence, this study must be regarded as preliminary and can be estimated to probably only consider 60–70% of the true faunal diversity. It is therefore only the first, but important, step towards a fully illustrated taxonomic catalogue that needs to be collated in future. In the meantime, however, the provided taxonomic accounts, in combination with the list, and also with colour pictures of 51 out of 72 species, can serve as reference, or within their limitations, even be utilised as a temporary identification guide to the local fauna.

Table 8.1: List of hermit crab species known from South Africa, comprising 72 nominal species. C = category, 1: in Barnard (1950) and without taxonomic name change, 2: in Barnard (1950) but has undergone taxonomic change, 3: added to the local fauna since Barnard (1950) in a taxonomic study (species lists by Kensley (1981) and Emmerson (2016c) excluded), 4: listed in Emmerson (2016c) as an addition to the local fauna without taxonomic validation, 5: new addition to the local fauna; BC = barcode available, CP = colour pictures available: Y = Yes. Endemicity given based on available information.

Genus	species	C	SA distribution	SA depth	BC	CP
Family *Coenobitidae*						
Coenobita	*perlatus* H. Milne Edwards, 1837	**5**	North of Durban	supralittoral		Y
	rugosus H. Milne Edwards, 1837	1	KZN	supralittoral	Y	Y
	violascens Heller, 1862	2	Mkambati, KZN	supralittoral		Y
Familiy *Pylochelidae*						
Trizocheles	*balssi* (Stebbing, 1914)	2	endemic, East London	142–240 m		
Family *Diogenidae*						
Aniculus	*maximus* Edmondson, 1952	4	KZN	18–40 m		Y
	retipes Lewinsohn, 1982a	4	Sodwana Bay	shallow reefs		
	ursus (Olivier, 1811)	**5**	Durban	shallow reefs		
Areopaguristes	*engyops* (Barnard, 1947)	2	?endemic, Paternoster to Hermanus	intertidal	Y	Y
	cf. *jousseaumei* (Bouvier, 1892)	**5**	KZN	35–70 m	Y	Y
Calcinus	*elegans* Dana, 1851	1	KZN	intertidal		Y
	guamensis Wooster, 1984	**5**	Sodwana Bay	11 m	Y	Y
	laevimanus (Randall, 1840)	1	KZN	intertidal	Y	Y
	morgani Rahayu and Forest, 1999	2	KZN	intertidal to 11 m	Y	Y
	pulcher Forest, 1958 *sensu lato*	**5**	Sodwana Bay	11–20 m	Y	Y
	rosaceus Heller, 1861	4	Sodwana Bay	11–18 m	Y	Y
	vachoni Forest, 1958 *sensu lato*	**5**	KZN	intertidal to 11 m	Y	Y
Cancellus	*macrothrix* Stebbing, 1924	1	endemic, False Bay to East London	5–25 m	Y	
Clibanarius	*longitarsus* (De Haan, 1849)	1	KZN	intertidal	Y	Y
	virescens Krauss, 1843	1	East London to KZN	intertidal	Y	Y
Ciliopagurus	*shebae* (Lewinsohn, 1969)	**5**	KZN	40–65 m	Y	Y
	tricolor Forest, 1995	2	KZN	11–34 m	Y	Y
Dardanus	*arrosor* (Herbst, 1796)	2	False Bay to KZN	10–337 m	Y	Y
	brachyops Forest, 1962	**5**	KZN	40–66 m		Y

	crassimanus (H. Milne Edwards, 1836)	2	KZN	20–70 m	Y	Y
	deformis (H. Milne Edwards, 1836)	2	EC, KZN	shallow subtidal	Y	Y
	gemmatus (H. Milne Edwards, 1836)	4	KZN	unknown		
	guttatus (Olivier, 1811)	2	Durban	shallow subtidal		Y
	jacquesi Asakura and Hirayama, 2002	**5**	Sezela	50–55 m	Y	Y
	lagopodes (Forskål, 1775)	2	KZN	shallow subtidal to 20 m	Y	Y
	megistos (Herbst, 1804)	2	Durban	shallow subtidal		Y
	pedunculatus (Herbst, 1804)	2	KZN	20–46 m	Y	Y
	cf. *umbella* Asakura, 2006a	**5**	Sodwana Bay	11 m	Y	Y
Diogenes	n. sp.	3	endemic, Pumula	20 m	Y	Y
	brevirostris Stimpson, 1858	1	endemic, Langebaan to Port Alfred	intertidal	Y	Y
	costatus Henderson, 1893	1	False Bay to KZN	19.5–98 m	Y	Y
	extricatus Stebbing, 1910	1	endemic, False Bay to Port Alfred	13–46 m		Y
	senex Heller, 1865	1	Durban	unknown		
Paguristes	*agulhasensis* Forest, 1954	2	endemic, Agulhas Bank	55 m		
	barnardi Forest, 1954	2	endemic, Kleinmond to East London	intertidal	Y	Y
	gamianus H. Milne Edwards, 1836	1	endemic, Hondeklip Bay to Plettenberg Bay	intertidal to 24 m	Y	Y
	macrotrichus Forest, 1954	2	endemic, KZN	90 m		
Paguropsis	*typica* (Henderson, 1888)	3	Coffee Bay, KZN	100–130 m	Y	Y
	sp. Lemaitre et al., in prep.	3	off Durban	215 m		Y
Family *Paguridae*						
Anapagurus	*hendersoni* Barnard, 1947	2	endemic, West Coast to KZN	9–226 m	Y	Y
Goreopagurus	*poorei* Lemaitre and McLaughlin, 2003	3	Agulhas Shelf	334–622 m	Y	Y
Manucomplanus	*ungulatus* (Studer, 1883)	2	Table Bay	91 m		
Nematopagurus	*crosnieri* McLaughlin and Hogarth, 1998	3	northern KZN	347 m		?
	diadema Lewinsohn, 1969	3	off Kosi River mouth	75		

	gardineri Alcock, 1905	3	off Kosi River mouth	48 m		
	kosiensis McLaughlin and Hogarth, 1998	3	Sodwana Bay	120–150 m		
	meiringae McLaughlin and Hogarth, 1998	3	Transkei, KZN	96–138m		
	spinulosensoris McLaughlin and Brock, 1974	3	Coffee Bay, KZN	40–140 m	Y	Y
Pagurus	*cavicarpus* (Paul'son, 1875)	3	northern KZN	38–60 m		
	cuanensis Bell, 1846	2	Vema Seamount, False Bay to KZN	subtidal to 250 m	Y	Y
	emmersoni McLaughlin and Forest, 1999	3	endemic, Gansbaai to KZN	12–70 m	Y	Y
	liochele (Barnard, 1947)	2	endemic, Orange River mouth to Transkei	intertidal to 110 m	Y	Y
	prideaux Leach, 1815	2	Mossel Bay to KZN	38–183 m		Y
	sp. McLaughlin and Forest, 1999	3	endemic, off Park Rynie	140 m		
	n. sp. Landschoff and Komai, in prep.	3	endemic, KZN	6–20 m	Y	Y
Propagurus	*deprofundis* (Stebbing, 1924)	2	southern and eastern shelf	449–780 m	Y	Y
Pylopaguropsis	*keijii* McLaughlin and Haig, 1989	**5**	Pumula	40 m		Y
	zebra (Henderson, 1893)	3	Agulhas Bank	102 m		
Family *Parapaguridae*						
Oncopagurus	*africanus* (de Saint Laurent, 1972)	3	off Durban	336 m		
Paragiopagurus	*atkinsonae* Landschoff and Lemaitre, 2017b	3	endemic, West Coast	199–277 m	Y	Y
Parapagurus	*andreui* Macpherson, 1984	3	West Coast, off KZN	731–2720 m	Y	Y
	bouvieri Stebbing, 1910	2	West Coast to KZN	369–812 m	Y	Y
	richeri Lemaitre, 1999	3	off KZN	2765–4470m		
	stenorhinus Lemaitre, 1999	3	off Durban	3530 m		
Strobopagurus	*sibogae* (de Saint Laurent, 1972)	3	off Durban	270 m		
Sympagurus	*dimorphus* (Studer, 1883)	2	West Coast to East London	170–585 m	Y	Y
	dofleini (Balss, 1912)	**5**	off Durban	365–563 m	Y	Y
	trispinosus (Balss, 1911)	3	off KZN	600–810 m		

CHAPTER 9

SYNTHESIS

The overall objective of this thesis was to add to, revise, and provide an updated taxonomic listing of the Paguroidea of South Africa. The general framework for this study was set out in Chapter 1, by introducing the taxonomic group of hermit crabs, pointing out some of the intriguing biology of hermit crabs, discussing their importance in the marine benthos, and by listing the global paguroid diversity in order to compare it with the representation of species, genera and families in South African waters.

For years, uncertainty had remained on the identities of the parapagurid hermit crabs in the bycatch of the governmental fishery survey programmes on the western and southern shelf region of South Africa, and the presence of a different new species was speculated upon. Chapter 2 provided detailed taxonomic data for the three most common and occasionally highly abundant deep-water hermit crabs recorded in the demersal research surveys, with the description of one of these, *Paragiopagurus atkinsonae* n. sp., as new to science. The new species was named after Lara Atkinson, who oversees the marine offshore benthic invertebrate monitoring. It is here fully described and illustrated, and compared in detail to the morphologically most similar *P. ventilatus*, a species associated with hydrothermal vents. However, *P. ventilatus* does not occur in South African waters, and to aid in future field identifications and to facilitate accurate data gathering during the offshore monitoring programme, a comparison of *P. atkinsonae* n. sp. with the superficially similar *Sympagurus dimorphus* was provided, along with descriptions of colouration and photographs of live specimens of all three regional parapagurid species (*P. atkinsonae* n. sp., *S. dimorphus*, and *Parapagurus bouvieri*) commonly caught in the trawl surveys. Information on the taxonomy of these species is now summarised, as well as knowledge of their distribution in the demersal research survey regions of South Africa. Chapter 2 therefore lays the taxonomic foundation for future studies on the hermit crab assemblages on the South African West and South Coast offshore regions, and indeed many biological aspects of parapagurids caught in the surveys remain to be explored. Due to their remarkable abundance or even dominance in the research catches, Landschoff and Lemaitre (2017b) surmised that they must play an important ecological role in the offshore ecosystems (see Figure 2.1). The western and southern shelf regions are the fishing grounds predominantly for South African hake (*Merluccius* spp.), one of South Africa's most important fisheries. Therefore, understanding the part these organisms play in the functioning of the ecosystem, and monitoring their populations, is important, especially in the light of the implementation of an Ecosystem Approach to Fisheries. A recent Masters project at the University of Cape Town quantified distributional abundance and population structures of *S. dimorphus* and *P. bouvieri* on the West and South Coasts of South Africa, summarising nearly 3 decades of offshore invertebrate research catch data. These analyses revealed that *S. dimorphus* occurred at higher sampling mass than *P. bouvieri*, and that both species have their preferred depth ranges (200–299 m vs. 400–499 m respectively), however, there was no signal of long-term trends in catch numbers (Wright 2017). In an additional Honours project, the two species also showed different niche separation in symbiont associations, highlighting a potential evolutionary continuum from a partially facultative to a fully obligate use of zoanthid carcinoecia shells (Botha 2016). However, so far these findings are preliminary in that especially the long-term dataset did not account for the presence of *P. atkinsonae* n. sp. on the West Coast, which was probably lumped together with *S. dimorphus* in the historic data collection. Further research that will explore ecological aspects and the dominant role of parapagurids in the offshore invertebrate communities of South Africa should better quantify the abundance of *P. atkinsonae* n. sp. and study its distribution to see how the new species biologically interacts with the other two co-occurring parapagurids. The current data suggest that *P. atkinsonae* n. sp. may be restricted to a small area on the West Coast. This is intriguing and should be clarified, particularly considering the ongoing debate over the establishment of an offshore marine protected area network in this region through the Operation Phakisa Oceans Economy (Sink 2016). Anthropogenic environmental impacts on this small area where *P. atkinsonae* n. sp. occurs could have severe impacts on its population. If *P. atkinsonae* really has such a restricted distribution, another question is what makes this area unique and also whether additional species, other than hermit crabs, might be endemic to the same or similar area.

In Chapter 3 a small and uniquely coloured species of *Diogenes* from subtidal rocky reefs off Pumula, southern KwaZulu-Natal, was fully described and illustrated and compared to morphologically similar species, in particular *D. holthuisi* and *D. dorotheae*. The new species was shown to be markedly different from all other South African species in this genus, yet the knowledge on the regional species in *Diogenes* is very poor and requires major taxonomic attention (see section on research gaps on *Diogenes* below).

Despite the fact that among all South African hermit crabs the genus *Pagurus* is known the best, the discovery of a common but unidentifiable species of *Pagurus* was taken up in Chapter 4. This chapter described *Pagurus* n. sp. as new to science. The species was shown to be closely related to two Indo-Pacific species, *P. boriaustraliensis* and *P. pitagsaleei*, but is morphologically and genetically compared and shown to be distinct from both. It also differs markedly in colouration and with the colour images provided in Chapter 4, the new species can easily be identified in the field. For the first time in crustacean taxonomy, *Pagurus* n. sp. was described by using μCT imaging techniques for a suite of calcified body parts. The use of this technique and the resulting 3D applications were discussed, highlighting that μCT could well become an important item in the toolbox of crustacean taxonomists. However, many questions remain to be answered. The potential to visualise taxonomic characters through μCT scanning is density-dependent and soft structures are usually not depicted, or only with difficulties, even when staining agents are used. Thus hermit crabs, with their many soft structures, are only partially suitable for this approach. Yet in this study they formed a challenging model for giving the technique a practical 'reality check'. If hermit crabs can be scanned and if these scans can be used to inform taxonomy, then μCT has the potential to be a valuable tool for taxonomic studies of a good number of groups in the Crustacea. Overlaying the μCT images with manually drawn soft tissue characters was a novel aspect that resulted in promising and detailed illustrations. Producing these illustration was relatively quick, drawing simple setae into already existing complex 3D structures that normally take long to draw manually. This approach should be extended further, as it could streamline the time-consuming production of high-quality taxonomic illustrations in a semi-automated way.

Chapter 5 reports on a remarkable range extension of the deep sea species *Goreopagurus poorei* that deserved the treatment in a separate chapter. This genus had only been known from the western coasts of the Americas and from the western Pacific. Hence the finding of *G. poorei* in South African waters constituted not only a considerable range extension for the species, but also formed the missing link between the two former ranges and revealed that the genus is globally more widespread than previously thought. Colouration in life was reported for the first time for the species, along with additional morphological information. At the time when the manuscript of Chapter 5 was prepared for publication, the COI barcodes of South African specimens could not be compared to genetic data from the Tasman Sea, because no fresh material was available from the type locality. Later, in Chapter 7 and towards the end period of this thesis, a single such barcode was obtained, pointing towards the possibility that *G. poorei* from South African waters might be of a different species (specimens are genetically about 5% K2P distant). However, the genetic variation within the South African population was found to be moderately high (about 2% K2P distant), so that more specimens from Tasmania or the South Pacific should be sequenced, and more genetic markers might have to be explored, before *Goreopagurus* from South Africa could potentially be described as a new species. Compared to the specimens from the Tasmanian type locality, the South African individuals showed some marginal morphological variation in having slightly different armature on the dactyls of the ambulatory legs. This variation is reported in Chapter 5 and is so far treated to be of an intraspecific nature. Overall, both the morphology (Chapter 5) and the genetics (Chapter 7) were consistent in revealing a close relationship that did not justify splitting the species, and more data will be needed to find a clear answer.

Chapter 6 is a datanote prepared along with the production of the μCT images, videos and interactive figure of the previous Chapters 2–4. Because it was initially speculated that the South African individual of *G. poorei* might be of a different and new species, the largest male was scanned in case the newly found specimens needed to be described as new to science, in which case this individual would probably have been selected as the holotype. However, when the careful examination of the collected individuals proved that they were morphologically conspecific with *G. poorei* from Tasmania, which had been sufficiently illustrated before, the scan images were not used in the reporting of the species range extension (Chapter 5). Nevertheless, the raw data are now made available for this rare deep sea hermit crab, and they might prove particularly useful in the future, should more data reveal that the South African lineage is indeed distinct. Scans were also produced for the rare species *Cancellus macrothrix*, pending a detailed species revision.

In total, there are now seven μCT scans of five species available, and three of these scans are of holotypes from species described in this thesis. The quality and limitations of the scan data were discussed in detail, pointing towards many unresolved questions with regards to the usage of this technique for taxonomy. The limitation of μCT in detecting soft tissue structures are the main and reoccurring problem, but on the other hand this characteristic of μCT data also showed the benefits of producing detailed surface scans of calcified structures, without having to remove the setation. Thus the μCT did not damage the specimens scanned in this thesis, and 3D scanning (μCT or magnetic resonance imaging) is currently the best method to achieve this. Furthermore, Chapter 6 was also written in the context of the benefits to disseminate the μCT data as cybertypes (*sensu* Faulwetter et al. 2014), as all the virtual representations of the types in this thesis could generally act as a virtual type series. Faulwetter et al. (2014) based a hypothetical definition of a cybertype on three criteria: 1. Identical accuracy and reliability in morphological anatomy, as provided by the physical type material, 2. Linkability to the original type material, and 3. Accessibility of the data through a reliable internet source. With the publishing of the 3D data, all of the candidate cybertypes in this thesis meet Criterion 2. and 3., but all of them fall short of Criterion 1., as they failed to provide the same information as the physical specimen (e. g. not showing soft tissue structures). However, Criterion 1. can be criticised for always remaining hypothetical in any way, because no virtual dataset will ever be a true 1:1 representation of a physical specimen, since it comprises digital data compared to organic matter. The argument as to whether the scans discern all “taxonomically important characters of the organism in question” (Faulwetter et al. 2014) is also invalid, because future studies might need to consult taxonomic characters in the physical specimen that are not, or will not be, visible in the 3D scans. In short, the term ‘cybertype’ is not clearly defined and probably never will be, but it is an intriguing concept that should be explored further. This study has shown that μCT data can add valid information to taxonomic studies. The dissemination of the data is also advocated. Because a set of data can, at least theoretically, be scrutinised more easily than physical type specimens, for example also during a reviewing process, the availability of the volumetric data can make taxonomy more transparent. Moreover, images derived from μCT scans may generally be less subjective to the skills of the artist than manually-drawn illustrations. One major obstacle to be solved though is the lack of a global initiative for a volumetric data archive, as for example exists for genetic data (Faulwetter et al. 2014). In this study, the GigaScience Database was used to make the data available, but ideally there should be one dedicated place where taxonomists can find virtual specimens more easily. Data derived from μCT would probably become available much more rapidly and be more accessible once such a global database existed. After all, μCT for taxonomy is still in its infancy, but as shown in this thesis it is also an attractive tool to advertise a perishing discipline, so that producing and making scanning data available could help in multiple aspects.

In contrast to the lack of a dedicated μCT repository for volumetric data, global databases are rapidly available for depositing genetic sequences and specimen information, and Chapter 7 was designed around the global barcoding life initiative BOLD that has an extensive data repository. In fact, the main goal of Chapter 7 was to provide a comprehensive barcoding library for South African hermit crabs, which was achieved by generating 194 COI sequences for 43 nominal and 12 additional putative species. A near 100% success in COI barcode identifications revealed very high barcoding efficacy in this integrative taxonomic approach. Only three problematic cases were observed and will require more molecular work. Because morphology and molecular identifications were reciprocally informed, the Chapters 7 and 8 validated each other and made the findings of each chapter more accurate. Therefore, the biggest value of this set of barcode data is that it informed and supported the morphological taxonomy in Chapter 8. The phylogenetic considerations in Chapter 7 have to be regarded preliminary, for the above-mentioned reason that COI are better not used alone for firm conclusions on relationships above species level. However, some interesting patterns, such as the two different clades in *Diogenes*, should be investigated further. Despite considerable sampling and sequencing efforts, with the generated knowledge on the South African hermit crab fauna, the barcoding dataset was estimated to only contain about half the species of the region and needs to be progressively enhanced in the future. Another value of generating barcode sequences from South Africa is that many species have widespread distributions. Particularly species from the eastern coast of South Africa usually occur across much of the Indo-Pacific, and for these species South Africa is the southwestern-most geographical distribution. To test barcoding efficacy across the entire geographical range of these species, the dataset therefore also needs to be extended on a more global scale, and the South African records generated and provided here will be valuable data points in any such study.

As it investigates the South African hermit crab fauna as a whole, Chapter 8 is the main taxonomic component of this thesis. With the finalisation of this chapter the main objective of the study was accomplished as taxonomic knowledge on the faunal diversity is now thoroughly updated and summarised. This chapter increased the number of officially reported species to a total of 72, an expansion of 56% since Barnard (1950), and about 20% since the recent species list by Emmerson (2016c). For these 72 species, colour images are provided for 51 taxa (71%), and barcodes are available for 40 of these (56%), so that the overall product can act as an ample taxonomic reference for the identification of South African paguroids. Taxonomic accounts are given, in short or in detail depending on the available knowledge of the respective taxon, for 62 of the 72 taxa. However, the remaining 10 species have not undergone any name changes since Barnard (1950) and were therefore left unmentioned for the time being. Chapter 8 also only accounted for species with a certain degree of clarity over the identification, i. e. species from new collections that could not be assigned to an available taxon name are not represented. The genetics in Chapter 7 had shown that about 10 more putative species occur in South Africa, and those were only the ones for which barcode data were available. Over the later period of this project, a handfull more unidentifiable species were also collected that could not be sequenced, so that the number of all putative species collected during this project is about 15. All these 15 taxa are likely to be new to science and are pending an official description. This could not be achieved in the time of this study. Only a few or even single specimens were collected for many of these, so it will often be necessary to collect more material prior to attempting detailed taxonomic work. However, the unidentifiable and putative new species have all been photographed in detail and are deposited at the Iziko South African Museum until time and sufficient material allows for their description. The estimation that the fauna covered in Chapter 8 is probably only 60–70% complete was made based on the many unnamed species remaining in the collections, and because so many of the sampling events yielded new or unknown taxa, instead of re-finding the ones that have already been sampled. It is very likely that over 100 species occur in South African waters.

In the process of compiling the taxonomic accounts of Chapter 8, and also with the newly generated knowledge of Chapter 7, it became apparent that many species or entire genera in the Diogenidae need thorough taxonomic revisions that lay far beyond the scope of this project. However, this study laid the foundation for this future work, pointing towards many unanswered questions. Below is a summary of species or entire genera of South African hermit crabs for which questions remained or were raised and for which the taxonomy will have to be clarified.

Areopaguristes, *Paguristes* and *Pseudopaguristes*

These three genera remain problematic on both a global and regional scale. Each genus in this group is defined primarily on the number of gills. However, ongoing phylogenetic molecular work indicates that gill condition is not necessarily a character leading to monophyletic classification among the three current genera (C. Craig, University of Louisiana at Lafayette, pers. comm.). In South Africa, and despite Forest's (1954) fairly detailed accounts, none of the occurring species in this group is described adequately, based on the criteria of modern taxonomic knowledge and terminology. In this study it was also not possible to match new material to Forest's (1954) species descriptions of *P. agulhasensis* or *P. macrotrichus*, both of which are based on only the holotypic specimens, which are both small and potentially juveniles. Therefore, all the described species will have to be redescribed before new species can be described as new, and this task would have been too extensive to be achieve in this thesis. The same applies to the species *Areopaguristes abbreviatus* (Dechancé, 1964) and *Paguristes jousseaumei* Bouvier, 1892, of which both descriptions need to be updated. However, the genetics in Chapter 7 drew a fairly clear picture on species entities and generic relationships, so that any revision can take the barcoding results as a valuable starting point. For South African specimens alone, *Paguristes* was shown to be monophyletic and at least four additional species will have to be described in this genus. Although *Areopaguristes engyops* and *Pseudopaguristes* sp. formed a well-supported clade in Chapter 7, *A. engyops* was left in *Areopaguristes* for reasons of name stability until the taxonomy is clarified (*A. engyops* was found to have 12 pairs of gills, but the vestigial arthrobranchs at the bases of chelipeds and maxillipeds 3 are very small). Similarly, the case of *A.* cf. *jousseaumei* is difficult and needs to be resolved through a more detailed taxonomic revision, ideally supported by more molecular work with more genetic markers. With the knowledge accumulated during this thesis, a concluding working hypothesis for such a South African revision would suggest that: 1. *Paguristes* is monophyletic with at least four undescribed candidate species; 2. *A. engyops* needs to be transferred to the genus *Pseudopaguristes* in which at least one new species needs to be described; and 3. Specimens of *A.* cf. *jousseaumei* consist of 1–2 species that might either be new, or belong to one/both of the species *A. abbreviatus*, and *A. jousseaumei*.

Calcinus

Malay and Paulay (2010) found genetic evidence for the presence of distinct evolutionary significant units (ESUs) in both the species *C. pulcher* and *C. vachoni*, but since their study there has been no attempt to delimit these species taxonomically. Both of the different ESUs show some slightly different colour patterns, and both putative species are now recorded from South African waters (Chapter 7 and 8). In Chapter 8 they are denoted as *sensu lato*, as the taxonomy remains to be refined.

Cancellus

The only known member of *Cancellus* in South Africa is an endemic species and, prior to the collections made during this study, *C. macrothrix* had not been found for over a century. The species is also of interest because it is the only species of the genus to inhabit gastropod shells, as all other members occupy pieces of wood or sponges. New material now demands some taxonomic updates, but these should be covered by a thorough study. Due to time constraints, such a revision was not included in this thesis, but it is currently being prepared in collaboration with R. Lemaitre, for which the scans from Chapter 6 will be valuable.

Clibanarius

Some degrees of uncertainty remain over the South African records of *Clibanarius*. While *C. virescens* is very common and thus moderately well-known, none of the other species was found in South African waters during this study. What is clear is that *C. longitarsus* occurs in northern KwaZulu-Natal and new specimens of this species were collected at Inhaca Island, Mozambique, and are included in Chapter 7. But the presence of *C. padavensis* and *C. striolatus*, as listed by Kensley (1981), require confirmation and further sampling efforts. Thus due to remaining uncertainties and no new material, these records were not included in Chapter 8. It would probably be advisable to revise the records from South Africa with specimens and records from Mozambique and the Mozambique Channel in a separate report on the genus.

Dardanus

A number of uncertainties about South African identities in the genus *Dardanus* persisted or became apparent, and these are mostly a result of imperfect taxonomic resolution of the genus globally. Chapter 7 revealed that the genus is probably monophyletic, and the weak support for *D. woodmansoni* within *Dardanus* was considered a combination of the species probably standing at the base of the genus and the low resolution due to COI being the only marker. Nevertheless, the COI-based phylogeny presented in Chapter 7 is the most comprehensive one currently available for *Dardanus*, another indication that *Dardanus* should be revised at a global level.

On a species level, some updates were provided for *D. arrosor*, a species that was shown to be common on the southeastern shelf region. Exploratory COI comparisons to specimen data derived from BOLD from the Atlantic and Pacific regions showed that the South African specimens cluster with the Pacific clade, and that the Atlantic clade could be a distinct lineage (unpubl. data not shown in this thesis). This possibility should be examined further. The South African records of *D. gemmatus* in Chapter 8 should also be verified, especially when fresh material becomes available. *Dardanus jacquesi* was reported for the first time in South African waters, and based on the new report in Chapter 8 it seems likely that *D. jacquesi* is a synonym for *D. dearmatus*, but a final decision should only be made based on more material. *Dardanus lagopodes* is another interesting case, as this species has a long history of taxonomic misunderstandings, and some of the problems with South African relevance were highlighted in Chapter 8. During the final process of writing this thesis and after finalising Chapter 8, an article was published on the diogenid hermit crabs of the Philippines by Malay et al. (2018), markedly improving the knowledge on this species. Thereby, *D. lagopodes sensu stricto* in this thesis and in Malay et al. (2018) is the "blue knee" form, whereas *D. sanguinolentus* is the "red knee" form in Malay et al. (2018). However, in Chapter 8 *D.* cf. *umbella* was reported from South Africa for the first time, and this species also has the same red patches on the carpi of the ambulatory legs as *D. sanguinolentus*, and seems to be conspecific with Malay et al.'s (2018) specimens of *D. sanguinolentus*. This theory was supported by exploratory COI comparisons from Chapter 7 with the sequences from Malay et al.'s (2018), and also to sequences kindly provided by G. Paulay (unpubl. data not shown in this thesis). Furthermore, according to M. Malay (pers. comm.) *D. sanguinolentus* can indeed bear the minute umbrella-like spines that are the diagnostic feature of *D. umbella*, so that future studies are likely to show that the latter taxon is actually a synonym of *D. sanguinolentus*. However, this confusion will need to be addressed in more detail and merits a comprehensive study to finally understand the taxonomy of this group of *Dardanus*. Lastly, another species that has caused taxonomic issues in the past, *D. pedunculatus*, was included in Chapter 8 and the incorrect assumption by Emmerson (2016b) that this species might not be *D. pedunculatus* but could actually be *D. tinctor*, was rectified. However, the distribution of this species pair is probably sympatric, or erroneously reported along the eastern coasts of Africa. More sampling will be necessary to better understand this sister-species relationship and each species' distribution. In conclusion, a global revision of

Dardanus is high on the wish list, as the many taxonomic problems of South African species cannot be resolved locally. It is surprising how so many issues have remained unaddressed in such a common and conspicuous genus. The provided updates on the South African representatives of the genus, along with the colour photographs and the barcodes, will hopefully initiate and facilitate future taxonomic studies on this group.

Diogenes

The case of the genus *Diogenes* in South Africa is similar to that of *Paguristes sensu lato*, in the sense that the group has never been revised, but that many species occur in the region, and this became particularly apparent through the barcoding in Chapter 7. *Diogenes brevirostris* and *D. costatus* are relatively well known from Barnard's (1950) account, but all South African species remain to be revised. Especially *D. extricatus* was insufficiently described and poorly illustrated by Stebbing (1910). The identity of Barnard's (1950) *D. senex* is also unclear and it is quite possible that Barnard had one of the many undescribed putative species collected during this study. This needs to be investigated in detail. Kensley's (1969) listing of *D. custos* should also be followed up on and is a dubious case, because the author excluded his own record in his later zoogeographical analysis (Kensley 1981), where he only listed *D. custos* to occur in Mozambique. Because the nomenclature of the known species has not changed, and to avoid duplication in a later taxonomic revision of South African species of *Diogenes*, these species were not taken up in Chapter 8. The elaborate task of revising the entire group would have been too extensive to be included here and such an attempt should be a project on its own. However, with the new species description in Chapter 3, the available barcodes of nine species (two from Mozambique, Chapter 7), and available colour photographs of all the newly available specimens, a future taxonomic revision of the South African members of *Diogenes* is now feasible.

Paguropsis

This study has shown that two species of *Paguropsis* occur in the Indian-Ocean part of South African waters, but the genus is currently undergoing a global revision by Lemaitre et al. (in prep). Therefore, the taxon name used in Chapter 8, *Paguropsis typica*, is preliminary, as the South African record actually represents a different species. The second species is a species that is currently being described as new, but this information will be soon available, leaving no doubt about the identities of the South African specimens. The taxonomic accounts for the two species will be updated for the publication of Chapter 8.

Sympagurus

In Chapter 7 specimens of *Sympagurus dimorphus* were genetically compared from the West and South Coasts of South Africa to specimens from Marion Island and New Zealand. It was found that the Marion Island and New Zealand specimens were distant enough to justify preliminarily treating them as different species entities for the purpose of the barcoding analysis. Whether they are really distinct, however, needs to be confirmed by more detailed taxonomic studies and molecular work. Should the Marion Island/New Zealand lineage indeed be found to be a separate species, then it has to be described as new, and *S. dimorphus sensu stricto* would only occur on the shelf region of South Africa's West and South Coasts and in Namibia.

The objectives of this thesis were to sample as many hermit crabs from South African waters as possible and examine museum vouchers to: 1. Describe as many new species or add as many new records of species to the fauna list as possible; 2. Explore the use of μCT as a tool for hermit crab taxonomy; 3. Generate a barcoding library for the local fauna; and 4. Compile an updated listing that summarises all available old and new information and which acts as a taxonomic reference and preliminary listing of, and guide to, the hermit crab fauna of South Africa. These objectives have now been achieved by the seven free-standing Chapters 2–8. One species each is described as new to science from the three largest hermit crab families and μCT images informed these descriptions, showing that the technique could become a valuable tool for crustacean taxonomy. A barcoding reference library is now generated for South African hermit crabs, and finally all information on the local fauna is revised, giving 62 species accounts and adding 12 hermit crabs (in addition to the three newly described species) to the local fauna as new records. This study has also shown that the biodiversity of South African hermit crabs had been greatly underestimated and the rate at which new species have been discovered over the period of this project could not have been anticipated before. Therefore, not all of this diversity could be addressed during this project and this thesis lays the foundational knowledge to also explore this diversity further. With a greatly extended and updated collection at the Iziko South African Museum, a molecular reference library, and with the updated taxonomy of the last seven decades, future work can now attempt the goal of compiling a complete, fully illustrated catalogue on the South African Paguroidea.

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