

A Guide to,  
and Checklist for,  
the Decapoda of  
Namibia, South Africa  
and Mozambique  
(Volume 1)



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By

W. D. Emmerson

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This book is dedicated to the carcinologists of the past, present and future, especially the late Dr Burke Hill who, through an honours project at Rhodes University, Grahamstown, piqued my interest and steered me along a lifelong career involving decapods.



*Uca (Paraleptuca) chlorophthalmus*, female.



Cape Crayfish, "Kreef" (*Jasus lalandii*) by Vladimir Tretchikoff, 1958–1959 by kind permission Dr Graeme Read.

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# INTRODUCTION

Barnard's (1950) descriptive catalogue still stands as the best text for decapods from southern Africa. He used the 15° S latitude for both the west (Moçâmedes) and east coasts (Mozambique Island) to define his biogeographic limits. Kensley (1981a) listed 707 decapod species for southern Africa, from the Kunene River (on the border between Namibia and Angola) on the west coast, to Vilanculos (Mozambique) on the east coast. Offshore, Kensley did not place a strict limit, as not much is known beyond the 200m isobaths (Fig. 2-1), which roughly coincide with the continental shelf. He thus included the offshore seamounts Tripp and Vema off the west coast, as well as Walters Shoal off the east coast. This limit is fine for benthic decapods, but for oceanic pelagic decapods, especially shrimp, which live in moving gyres of water influenced by currents such as the Benguela and Agulhas (Fig. 2-1), and which also migrate diurnally, such limits become blurred. This work therefore includes the geographic areas of Namibia, South Africa and Mozambique, with its offshore seamounts and shoals (including Valdivia Bank), and includes studies on fresh water species, published work from deeper offshore sites (Burukovsky & Romensky, 1982; Macpherson, 1983, 1984, 1988a, 1990b, 1991; Crosnier, 1985; Vereshchaka, 2000, 2009; Burukovsky, 2011) and published work from Tristan da Cunha and the Prince Edward group, mainly Marion Island (Pollock, 1991; Branch et al., 1991; Pakhomov et al., 1991).

In recent years decapod research has grown exponentially worldwide, with a number of important works being published such as Ng et al's (2008) "Systema Brachyurorum", a checklist of extant brachyuran crabs of the world, which was followed by world checklists of other groups including the Lithodidae, Lomisoidea and Paguroidea (McLaughlin et al., 2010), Porcellanidae (Osawa & McLaughlin, 2010), Hippoidea (Boyko & McLaughlin (2010) and marine lobsters (Chan, 2010). De Grave et al. (2009) also published their classification of living and fossil genera of Decapod Crustaceans, followed by "Carideorum Catalogus: the Recent Species of Dendrobranchiate, Stenopodidean, Procarididean and Caridean shrimps" (De Grave & Fransen, 2011). More recently the treatises on the systematics and classification of the Brachyura and Brachyuran phylogeny (Davie et al., 2015a, 2015b) stand out. The body of work done by



Stebbing, Barnard and Kensley, to name but a few, thus badly needed to be updated and revised. In this work, the tally of decapods in Namibian, South African and Mozambican waters has been taken to over 1000 species as taxa have been revised, new species discovered and new families found for this area.

Southern Africa lies like a wedge between the older, warm, species-rich Indo-Pacific Ocean and the younger, colder Atlantic, which only formed with the break-up of Gondwana, beginning around 130 Mya during the Early Cretaceous and resulting in open marine conditions around 110 Mya. The east coast is washed by the South Equatorial Current which flows south to become the warm Mozambique Current and supports biomes such as coral reefs, seagrass beds and mangroves, which in turn offer numerous niches to decapod and other tropical and subtropical species (Kensley, 1981; Branch & Branch, 1983), some of which are commercially important such as *Fenneropenaeus indicus* (Forbes & Benfield, 1985; de Freitas, 1989; Demetriades & Forbes, 1993; Fennessy, 1997; Fennessy & Groeneveld, 1997). The Atlantic west coast, on the other hand, is washed by the Benguela Current which wells up cold, nutrient-rich water from the Southern Ocean, and has few species, such as *Jasus lalandii*, which are numerous enough to support commercial fisheries (Pollock, 1982, 1986, 1989; Pollock et al., 2008; Fig. 2-1).

The understanding of the biodiversity of decapods occurring in our rivers, lakes, estuaries, shores, reefs, shelves, slopes, seamounts and oceans is now urgent; one needs to know what species are present so that they and their environment can be conserved, particularly at a time when biodiversity is being lost due to habitat destruction and global warming. This biogeographic region not only covers typical Atlantic and Indo-West Pacific species, both benthic and pelagic, but also southern species such as certain dromiid crabs, which are endemic to southern African waters due to “cool water stenothermic radiation” (Kensley, 1981a), and which seem to have an ancient origin (McLay, 1993).

The number of decapods worldwide was estimated at 1000 genera and 8321 species by Chace (1951), while Martin & Davis (2006) estimated 7905 species. Ng et al. (2008) found the figure to be 6793, while De Grave et al. (2009) raised the estimate to 2725 genera and 14,756 species, with the Brachyura accounting for nearly half with 6835 species. This figure for the Brachyura has now been updated to over 7250 species (Davie et al., 2015a). In addition, the number of fossil species has also been estimated at 3300 (De Grave et al., 2009). Important new ecosystems such as hydrothermal vents, seeps, submerged anchialine larval tubes, freshwater cave systems and disappearing ice shelves have been found to harbour not

only new species, genera and families, but even new crab superfamilies such as Bythograeoidea from hydrothermal vents (Ng et al., 2008). Similarly, new troglobitic and anchialine shrimps in their own order Procarididea (suborder Pleocyemata) have been discovered living in caves and submerged larva tubes on isolated islands such as Ascension Island (*Procaris ascensionis*; Chace & Manning, 1972), Christmas Island (*Procaris noelensis*) and Hawai'i (*Vetericaris chaceorum*; Kensley & Williams, 1986). De Grave & Fransen (2011) observed that Schweitzer et al. (2010) placed the genus *Udora* in the Procarididae, which, if correct, extends the fossil record of this group back to the Mid-Jurassic around 180 Mya, which is equivalent to the finding of a living coelacanth. Similarly, the relatively recent discovery of the living fossils *Neoglyphea inopinata* from the Philippines and *Laurentaeglyphea neocaledonica* from the Coral Sea—the only living members of the Glyptheoidea, in which two of the three families are exclusively extinct—has similarly been a revelation (Forest et al., 1976; Holthuis, 1991; Richer de Forges et al., 2013). The glypheids were known from the Mesozoic but were thought to have been extinct since the Eocene, 50 Mya, before being rediscovered and called “phoenix lobster” and “Jurassic shrimp” respectively. Glypheids were originally placed in the “Palinura” (Holthuis, 1991), but more detailed studies on *N. inopinata* revealed they were closer to the Astacidae, with *L. neocaledonica* even closer to the glypheids, like “missing links” (Forest, 2006; Richer de Forges et al., 2013).

Decapods are the culmination of Crustacean evolution, spanning nearly 600 million years, during which time they have survived geological extinction events and have adaptively radiated out into a wide variety of superfamilies, families, genera and species (De Grave et al., 2009; Schweitzer et al., 2010; Schweitzer & Feldmann, 2015; Table 2-1), many of which have southern African representatives, occupying a wide variety of niches from freshwater lakes and streams to ocean abysses.

Many decapods are commercially important worldwide and support a seafood industry worth billions of dollars each year. In southern African waters, penaeids such as *Fenneropenaeus indicus* and *Penaeus monodon* (de Freitas, 1980; Demetriades & Forbes, 1993), palinurids such as *Jasus lalandii* and *Panulirus homarus*, nephropids such as *Metanephrops mozambicus*, and geryonids such as *Chaceon maritae* and *C. macphersoni* support fisheries and fetch high prices in upmarket restaurants (Fennessy & Groeneveld, 1997). Other decapods, such as the cleaner shrimps *Lysmata amboinensis* and *Stenopus hispidus* and the peppermint shrimp *Rhynchocinetes durbanensis*, are important in the aquarium business (Calado et al., 2003). Decapods such as the *Jasus lalandii*, *Scylla serrata*,

*Portunus segnis*, *Neosarmatium africanum* and *Ocyropode* species also support an artisanal fisheries, which sustainably support coastal human communities from the Cape to Mozambique and beyond (de Boer & Prins, 2002; Pedersen et al., 2003).

Decapods also form highly evolved relationships with other groups, together with which they have co-evolved. Examples of such relationships are legion. *Trapezia* species live as obligate symbionts with scleractinian corals; cryptochirids such as *Hapalocarcinus marsupialis* and *Cryptochirus coralliodytes* become entombed in coral; hermit crabs such as *Dardanus arrosor* carry the anemone *Calliactis* on their shells as protection against octopus predation (Balasch & Cuadras, 1976); majoids such as *Acanthonyx* camouflage themselves with sponges and other organisms to be cryptic (Branch & Branch, 1983); pontoniids such as *Conchodytes tridacnae* are only found living in the mantle of the giant clam *Tridacna* (Humann & Deloach, 2010); shrimp such as *Stenopus hispidus* and *Lysmata amboinensis* clean fish (Debelius, 2001); the commensal shrimp *Anchistus custos* and the pea crab *Pinnotheres* are found living inside the shells of both the mussels *Pinna* and *Atrina* (Kalk, 1995); various species of alpheid shrimp share burrows with gobies (Karplus et al., 1974); the sand prawn *Callichirus kraussi* shares its burrow with the shrimp *Betaeus juncundus*; and the hexapodid crab *Spiroplax spiralis* and dorippid crabs carry sponges or shells for protection (Holthuis & Manning, 1990). Sometimes the decapod is the “host”, as with the stone crab *Lithodes ferox*, whose gills are often “infected” with the eggs of the liparid fish *Careproctus griseldeia* (Melville-Smith & Louw, 1987).

Often the relationships are fairly complex, like the one between the spiny lobster *Panulirus homarus*, the octopus and the moray eel. The spiny lobsters often share holes with the eels, which in turn protect the lobsters. One of the octopus’ favourite food items is spiny lobster, but when one enters a hole in search of them, the lobsters stridulate and warn the eels, who then attack the octopus (Berry, 1971a). The inter-relationship between the pistol shrimp *Alpheus lottini*, various species of *Trapezia* and hawkfish is equally complex. Before a shrimp can share a coral head with the crab, it first has to “appease” the more aggressive crab, which defends the head fiercely (Vannini, 1985). Another coral resident, the hawkfish sits atop the coral head and aggressively defends its territory, but will not consume the *Alpheus* or *Trapezia*, feeding in mid-water on small fish and other shrimps instead, thus giving the coral head added protection (van der Elst, 1981). The list is practically endless, with new relationships being continually discovered, particularly within highly diverse, biologically controlled biotopes such as coral reefs.

The taxonomist and the ecologist define a species differently; the former uses various methods including morphology, colour and behaviour, whereas the ecologist defines a species according to its niche and its reproductive potential. This principal taxonomic unit below generic level is difficult to define, but species form groups of living organisms consisting of similar individuals, capable of exchanging genes or interbreeding and producing fertile offspring. Reproductive isolation is maintained by morphological differences, manifold in the differently shaped male organs which transfer the spermatophores, whether a petasma in penaeoids or gonopods in crabs, as well as in the shape of the recipient female organs, such as the thelycum. Breeding isolation is also maintained by various sympatric decapod populations breeding at different times of the year, or is maintained spatially, such as by *Chaceon*, which undergoes an inshore breeding migration (Melville-Smith, 1987a, b), as do various spiny lobster populations. In the more advanced semi-terrestrial ocypodids such as *Uca*, *Ocypode* and *Macrophthalmus*, which often co-exist on beaches and mudbanks, reproductive signalling is employed through colouration and different chela-waving methods which are highly visual (Crane, 1975; Kitaura et al., 2002). Other breeding strategies are used, such as different dromiids living offshore on the shelf opting for producing either few, large, yolky, lecithotrophic eggs, or many smaller planktotrophic eggs (Barnard, 1950; McLay, 1993).

Various agencies are used to delineate a species, such as morphology, how similar its DNA is or what its ecological niche is. Elton was the first to attribute an ecological function or niche to the various species in a community, particularly in terms of food chains. There are many definitions for a species, usually about reproductive isolation, but Colinvaux (1986) defined a species in terms of competition as “a number of related populations, the members of which compete more with their own kind than with members of other species”. This competition for food, space or other resources drives speciation through processes such as resource partitioning which increase fitness. Whereas the Darwinian approach was the survival of the individual, the population level for a species was promoted through increased gene frequencies for any particular niche or environmental circumstance. Thus a species can be circumscribed by where it lives in terms of niche, habitat, zone, biogeography, its position in the food web, its ecophysiology and what has equipped it to *survive, thrive and breed* in that environment through both larval and adult behaviours, which are unique to that species, allowing it to successfully reproduce and maintain a viable population.

A species can be viewed at species, population, community and ecosystem levels, as well as species, genus, family, superfamily and order levels. Within the food web, *survival* in the Darwinian sense means *not being eaten* (as well as not succumbing to disease and being able to successfully pass on your genes) and decapods have evolved various strategies around this central theme, such as camouflage, burrowing, being poisonous, pretending to be poisonous (aposematism), possessing spines or living in a protected habitat such as a shell, giant anemone, holothurian or giant sponge (Guinot & Wicksten, 2015). Camouflage comes in many and varied forms, from using bivalve shells, to sand dollars to leaves as cover, such as is done by the dromiid *Conchoecetes artificiosus*, dorippids and ethusids such as *Medorippe lanata* (Kalk, 1985) or homolids (Wicksten, 1985). Most dromiids use sponges or zoanths as cloaks such as *Platydromia spongiosa* (MacLay, 1993; Branch et al., 2010), while inachids and epialtids such as *Inachus guentheri*, *Macropoda falcifera* and *Acanthonyx dentatus* stick bits of sponge, hydroids, bryozoans, serpulids or algae on their carapace and legs which may also be eaten (Woods & McLay, 1994). *Acanthonyx* can change colour like a chameleon using a colour-mediated crypsis strategy whereby pigments and chemical defences are derived from the seaweed that is ingested (Hay et al., 1990; Guinot & Wicksten, 2015). Stripes, spots and bands of colour often break the outline of the shrimp, as with the galatheid *Allogathea elegans* or coral shrimp *Pontonides unciger* (King & Fraser, 2014). The pilumnid *Zebrida adamsii* has a striped and jagged outline, which is indistinguishable from the urchin spines on which it lives (Jones, 1997). Many species of hippolytid, such as *Tozeuma*, mimic the shape and colour of the elongated seagrass blade or black coral on which they live. Translucency is a useful strategy which is widely used by shrimps such as the pontonids like *Urocaridella antonbruunii*, *Cuapetes tenuipes* or various species of *Periclimenes*, which have see-through bodies (Debelius, 2001; King & Fraser, 2014). Bathypelagic shrimp such as acanthephyrids are bright red to crimson as red wavelengths do not penetrate deeply so they will appear black like the background and thus invisible (Bauer, 2004). Mesopelagic shrimp such as oplophorids are red to transparent and have photophores which direct blueish bioluminescence downwards making them invisible from below against the down-welling gloom (Herring, 1976, 1985).

Burrowing in the substrate is an excellent strategy, not only for escaping predators, but also for using the cover to ambush prey themselves (Guinot & Wicksten, 2015). This strategy is widespread and evolved very early in decapod evolution (*Callianassa* for example has over 150 fossil species [Schweitzer et al., 2010]), with it having been adopted by many

families, such as the calocaridids, micheleids, laomediids, upogebiids, axiids, callianassids, alpheids, nephropids, calappids, matutids, goneplacids, gecarcinids, portunids, ovalipids, sesarmids and ocypodids.

Many intertidal and reef dwelling crabs can be poisonous, especially xanthids such as *Actaeodes tomentosus* (Llewellyn, 1997) and species of *Atergatis* (Holthuis, 1968) as well as eriphiids such as *Eriphia sebana* (Holthuis, 1968). Pretending to be poisonous or distasteful using aposematic colouration as a strategy is also found in sesarmids such as *Neosarmatium africanum* (Cott, 1930). Spinination is found when species are exposed on the seabed and where burrowing or disguise is not an option through size. This is widely seen in continental shelf palinurids such as *Palinustus mossambicus* (Barnard, 1926) and *Palinurius gilchristi* (Berry & Plante, 1973), inchids such as *Pleistacantha ori* (Ahyong & Ng, 2007) and majids such as *Maja cornuta* (Ng & Richer de Forges, 2015).

Protected habitat strategy has been widely adopted by decapods. Hermit crabs (diogenids) use a wide range of shells which are common where gastropods thrive such as inshore reefs, but offshore on the seabed where they are rare, hermit crabs (mainly parapagurids such as *Sympagurus dimorphus*) use a pseudoshell or gelatinous cavity of zoanthids (Lemaitre, 1996). Many decapods have exploited the protection offered by the stinging nematocysts of a giant anemone, as exploited by the porcellanid *Neopetrolisthes maculatus* (Debelius, 2001; King & Fraser, 2014) and the pontoniid *Periclimenes ornatus* (Bruce, 1969; Davie, 2002a); by the cloaca of a holothurian, as used by *Lissocarcinus orbicularis* (Edmondson, 1954; Crosnier, 1962; Jones, 1997; Debelius, 2001); or by the cavity of a giant sponge, as protects the sponicolid shrimp *Spongicola robustus* (Saito & Komai, 2008).

All environmental factors are important as, for example, a crab or shrimp which osmoregulates effectively can live in a low salinity estuarine system, or the light of a certain wavelength and intensity, together with adequate nutrition, can promote shrimp ovarian development by mobilising lipid reserves from the hepatopancreas to the ovaries (ecophysiology). One species of shrimp may feed on diatoms and another co-existing species might opt for another food resource to minimise competition (resource partitioning), while, when resources are plentiful, many co-existing species may live on similar resources, with overlap in food type. Different species of mesopelagic shrimp, for example, often feed on similar resources, but time their diel migrations, so their populations are separated both spatially and temporally (Omori, 1974; Cartes, 1993a, b, d, 1995, 1998).

Each species is exquisitely tailored to the environment in which it lives and survives—whether it burrows in the substrate, whether it is a filter-feeder, omnivore or predator—and this shapes its morphology—possession of filter-feeding appendages or the large eyes and chelae of a predator—as well as its physiology (predators for example having proteases to digest animal protein). However, although some decapods might look similar, they may be unrelated. A good example is coral-dwelling crabs where the *Trapezia*-like shape has evolved separately at least four times: twice in the Trapezoidea (Trapeziidae and Tetraliidae), once in the Cymoinae (Xanthidae) and once in the Tanaochelidae (Pilumnoidea) (Lai et al., 2009). Similarly *Lambrachaeus ramifer* was initially thought to be a majid as it looks superficially like a spider crab, but careful examination has shown that it is actually a modified parthenopid and is at the extreme end of a morphological cline (Tan & Ng, 2007). While such adaptation to the environment has probably evolved over millions of years, work by Mathews & Anker (2009) has shown both an ancient as well as a recent radiation within an alpeid species-complex.

In mangrove ecosystems, guilds of various species of co-existing ocypodid crabs, such as *Macrophthalmus* and *Uca*, share the intertidal. They do this by sharing the various resources available to them, such as space and food, by having slightly different zonation, substrate preferences and behaviour (Crane, 1975). Different species of *Uca* exhibit preference for overlapping, but slightly different combinations of sand, mud and silt, which are found naturally in different zones. Although some of their diets also overlap, the mouthparts of each species have been shown to be equipped with different arrays of spoon-tipped hairs which are used to remove microalgae and organic particles from the substrate (Icely & Jones, 1978; Kalk, 1995; Weis & Weis, 2004). Decapod species such as the sand prawn *Callichirus kraussi* are known as ecosystem engineers, as they change the physical nature of the substrate through sediment turnover and bioturbation, which influences other species through non-trophic and non-competitive exclusion (Branch & Pringle, 1987; Siebert & Branch, 2006; Pillay et al. 2007b; Branch et al., 2010). Similarly in the Kariega, E Cape, the small, but extremely numerous *Danielita edwardsii* is responsible for a large percentage of this estuary's total organic carbon flux through bioturbation (Taylor & Allanson, 1993). The abundant crab *Parasesarma catenatum* is also important in temperate southern African estuaries for its production of frasse and particulate carbon which is exported to the nearshore (Els, 1982; Baird et al., 1987; Heymans & Baird, 1995; Allanson & Winter, 1999). Because of its central importance in the carbon flow of estuaries, this crab has been used as an indicator species

(Morant & Quinn, 1999). The red mangrove crab *Neosarmatium africanum* is also regarded as a keystone species or ecosystem engineer due to its ecosystem function in leaf processing, sediment turnover, energy flow and nutrient recycling (Kristensen, 2008; Cannicci et al., 2008; Nicholson, 2009). Similarly it has also been suggested that the fiddler crabs, *Uca*, are also ecosystem engineers within mangrove systems on the E Coast of Africa (Penha-Lopes et al., 2009). Ghost crabs such as *Ocyropsis ceratophthalmus* have also been used as bioindicators of human and vehicle disturbances on beaches (Barros, 2001; Schlacher et al., 2007; Yong & Lim, 2009; Lucrezi et al., 2009).

The concept of adaptation to a niche can best be exemplified under extreme conditions such as at hydrothermal vents where shrimps such as *Rimicaris exoculata* and crabs such as *Bathymodiulus thermophilus* live and thrive in a narrow, but fruitful niche between searing heat and the abyssal cold. These sulphurous vents are highly toxic, yet they have adapted not only physiologically, but also trophically, behaviourally, reproductively and in many other ways (Van Dover, 2000).

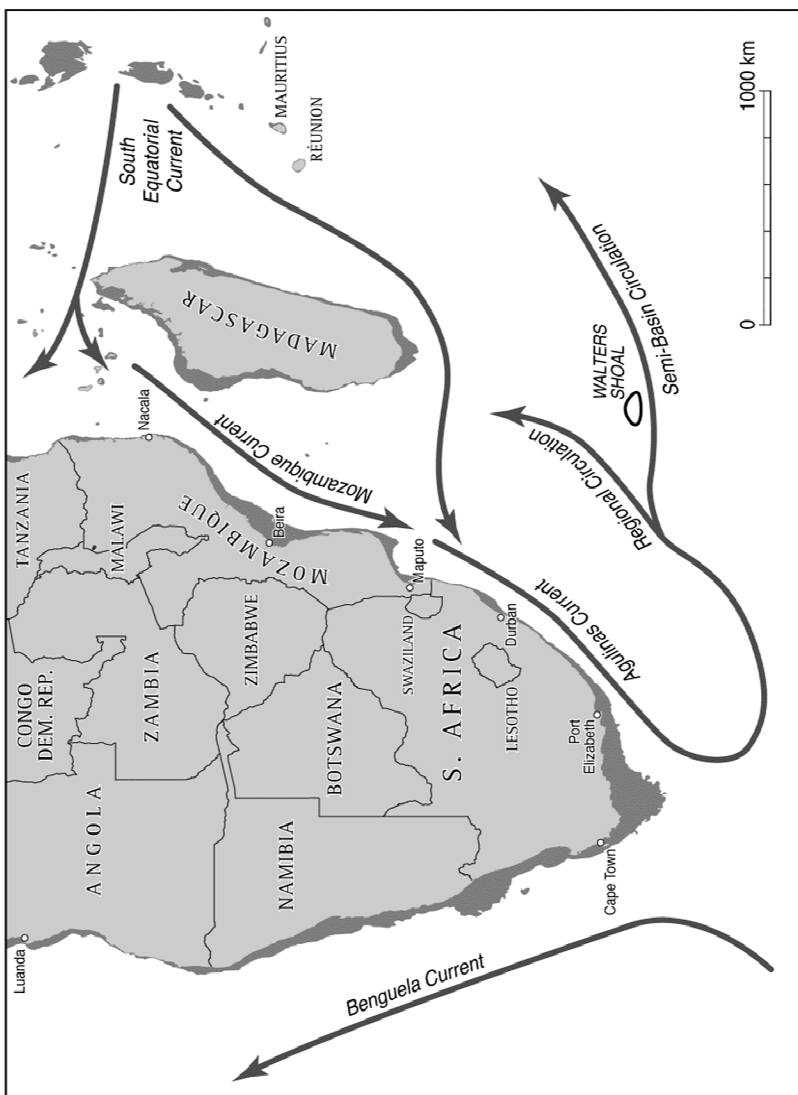
Thus decapod species, and indeed all species, should not be seen as morphological entities, but should equally be referenced according to their ecology, how and why they survive where they do and their relative positioning in the habitat and ecosystem in which they have evolved and become adapted. Their survival and reproductive strategies are existentially important in order that their genes can survive a hostile world. The purpose of this book, therefore, is to provide an updated guide to the decapods that live in and around Namibia, southern Africa and Mozambique, to bridge the gaps between taxonomy, ecology and the fossil record, and hopefully to stimulate interest in this fascinating group of crustaceans by asking and hopefully answering such questions as what those species are, where they live, what they eat, who eats them, how they are adapted to the habitat in which they live and how they evolved through time. Inter-relationships such as commensalisms, proto-cooperation, mutualism, competition, co-existence, position in the food web, behaviour and energetic relationships such as biomass, production and energy flow need to be understood.

Why are decapods so important? Their size often belies their trophic importance. Humans are not the only species to consume decapods (de Boer & Prins, 1992, 2002; de Boer et al., 2002; Pedersen et al., 2003); they form the diet of over 90% of fish in southern Africa (van der Elst, 1981; Compagno et al., 1989) and are an intrinsic component of most food webs as they provide a link between producers (leaves, phytoplankton or chemosynthetic bacteria in hydrothermal vents or cold seeps), leftover



production (detritus or “marine snow”), other invertebrates, and consumers (fish, squid and octopus, sea birds and sea mammals such as dolphins and whales) (Ryan, 1991; Hopkins et al., 1994; Van Dover, 2000; Somers, 2000; Cartes et al., 2007). Most fishermen will vouch that prawn, crayfish and ghost or mole crab make excellent bait organisms, and therein lies their importance, as key linking organisms in the various aquatic food webs. Decapods are an important basal link in biomes and ecosystems such as rocky shore, sandy beach, estuary, inshore, open ocean and fresh water.

Most importantly, I sincerely hope that this book generates interest, for without interest there can be no meaningful research and deeper understanding of the position and importance of decapods in nature. I would also hope that the reader will emerge with a new perspective on these lowly yet interesting and important crustaceans after having shared their world during the journey through the pages which follow.



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**Fig. 2-1.** A map of the southern African sub-continent showing important current systems. Dark grey areas represent the continental shelf down to the 200m isobaths (Kensley, 1981; Branch et al., 1983; Richmond, 1997).

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**Table 2-1.** The emergence and dominance of major decapod groups. Geological time scale according to the International Stratigraphic Chart (after Schweitzer & Feldmann, 2015).

Mya	Era	Period	Epoch	Stage/Age	Emergence-Dominance	
65–0	Cenozoic	Neogene (23–2.6)	Holocene	Holocene	thoracotremes dominant	
				Pleistocene		
			Paleogene (66–23)	Oligocene	Pliocene	
					Miocene	
				Eocene	Messinian	
					Tortonian	
					Serravalain	
					Langhian	
					Burdigalian	
					Aquitainian	heterotremes dominant
					Chattian	oldest freshwater crab?
					Rupelian	
			Palaeocene	Preabonian		
				Bartonian		
252–66	Mesozoic	Cretaceous (145–66)	Late	Lutetian		
				Ypresian		
			Jurassic (201–144)	Early	Thanetian	
					Selandian	freshwater crabs emerge?
				Middle	Danian	thoracotremes emerge
					Maastrichian	podotremes dominant
					Campanian	
					Santonian	
					Coniacian	
					Turonian	
					Cenomanian	
					Albian	oldest scyllarid
			Aptian	earliest raninid		
			Triassic (252–201)	Late	Barremian	
Hautervian	heterotremes emerge					
Early	Valanginian					
	Berriasian	gebiids emerge				
	Tithonian					
	Kimmeridgian					
541–251	Palaeozoic	Permian (299–252)	Lopingian	Oxfordian	axiids emerge	
				Callovian	clawed lobsters dominant	
		Carboniferous (359–299)	Middle	Bathonian		
				Bajocian		
			Early	Aalenian		
				Toarcian		
		Devonian (419–359)	Late	Pliensbachian	podotremes emerge	
				Sinemurian		
			Early	Hettangian		
				Rhaetian	pleocyemata-anomura emerge	
Upper	Middle	Norian				
		Camian	early polychelids			
	Early	Ladinian	shrimp dominant			
		Anisian	first achelate lobster			
Famnenian	Olenekian					
	Induan	clawed lobsters emerge				
Chaghhsingian						

# HISTORY OF DECAPOD RESEARCH IN SOUTHERN AFRICA

Both Barnard (1950) and Kensley (1981a) gave details on the history of decapod collecting and research in southern Africa. One of the earliest collections of Crustacea from southern Africa was made by Dr Andrew Smith who was the founder and first curator of the South African Museum in Cape Town. When he returned to England in 1837 he left his collection to William MacLeay and published the first report on southern African decapods, “Annulosa of South Africa”, which appeared in *Illustrations of the Zoology of South Africa* (MacLeay, 1838). MacLeay emigrated to Australia during 1839 and he took the collection with him. There it remained “lost” for nearly a century. In 1937, M. Ward wrote to K. H. Barnard at the SA Museum from Sydney to inform him that he had found the Smith Collection. This collection is now known as the MacLeay Collection and is housed in the University of Sydney, Australia (Ng & Ah Yong, 2001).

Dr Frederick Krauss spent the years from 1838 to 1840 collecting in southern Africa, and published “Die Sudafrikanischen Crustaceen” in 1843 (Fig. 3-1). Other early collections were made by the US Exploring Expedition (1838–1842), the US North Pacific Exploration Expedition (1853–1856, published by Stimpson, 1858), the *Challenger* (1837), the *Gazelle* (1874), the *Valdivia* (1898, published by Doflein, 1904) and the *Gauss* (1901, 1903, published by Lenz & Strunck, 1914), but these visits were short. The Prussian zoologist Arnold Ortmann (1894b) assembled his decapod collection from the southern African shoreline, while on the west coast Odhner (1923) collected decapod material from Angola down into southern Africa. Other early collectors in this region were Bianconi (1969) and Peters whose collection was published by Hilgendorf (1879).

The first major offshore collection locally was using the *SS Pieter Faure* (1898–1907) and was published by the Rev. T. R. R. Stebbing during the period 1910 to 1924 (Fig. 3-1). Stebbing gathered all the disseminate records together and added another 150 new species in the first “Catalogue of South African Crustacea” in 1910. However, much of the *Faure* material was never submitted to Stebbing. The Union Government vessel *Pickle* made several collections during the 1920s and

the material was examined by Stebbing, Calman and Barnard. Other research vessels used to collect offshore material were the *John D. Gilchrist* and the *Thomas B. Davie* which belonged to the University of Cape Town.

A major contributor to southern African carcinology was Dr Keppel H. Barnard who published the second descriptive catalogue during 1950 in the form of an 837 page monograph in which about 500 species were reviewed (Fig. 3-1). Barnard later added to this list with publications in 1954, 1955 and 1958 as a result of collections made by the Universities of Cape Town and Witwatersrand. His descriptive catalogue was reprinted in 1972 and still remains the single major authority for southern African decapods.

After Barnard, Dr Brian Kensley took over at the South African Museum and began publishing on SA decapods in 1968 (Fig. 3-1). Among his many publications is a guide to the shrimps and prawns published in 1972. A comprehensive collection of pelagic and deep water decapods was made in southern African waters, and subsequently published, using research vessels including the *Africana II* and the *r. v. Meiring Naude* (Kensley, 1968, 1969, 1971a, b, 1975, 1977a, b, 1978, 1980a, b). Kensley, in association with Dr Perez Farfante, published an important review of the world penaeoid and sergestoid shrimp in 1997.

From the seventies onwards there was a general swing away from pure taxonomy to ecologically-based research where ecosystems such as kelp beds, coral reefs, mangroves, rocky shores, sandy shores and estuaries were investigated functionally and energetically, rather than individual species being investigated in isolation. Examples of contributions to the ecology of southern African decapods, which are by no means exhaustive, include the works of Macnae & Kalk (1958, 1962a, b) and Macnae (1963, 1968) on mangrove and coral reef decapods; Day (1974) and Branch et al. (2010) on common southern African decapods; Hughes (1966a, b, 1970), Cockcroft (1985), Cockcroft & McLachlan (1986a, b), de Freitas (1979, 1980, 1984, 1985, 1986a) and Macia (1990, 2004a, b) on penaeoids; Hart (1980a, 1981) on atyids; Emmerson (1984a, 1985a, 1986), Robertson (1984), Read (1982, 1983a, b, 1985a, b) and Bickerton (1989) on palaemonids; Heydorn (1965, 1968, 1969a, b), Berry (1969b, 1970, 1971a, b, 1973, 1974a, b, 1979), Berry & Plante (1973), Pollock (1973, 1979, 1981b, 1982, 1986, 1989, 1990, 1991, 1992, 1993, 1995c), Groeneveld (1997, 2000, 2002, 2003, 2005), Groeneveld et al. (1995, 2006a, c, 2012) and Groeneveld & Branch (2001, 2002) on palinurids; Berry (1969a) on nephropids; Hill (1967, 1971), Forbes (1973, 1977, 1978, 1979), Hanekom (1980), Hanekom et al. (1988), and Hanekom & Erasmus (1989) on

callianassid and upogebid prawns; Hughes (1966b, 1973), McLaughlin (1980), Emmerson (1994a) and Litulo (2004b, c, 2005f, g, h, i, j, k, 2006) on ocyropodid crabs; Alexander & Ewer (1969), Pereyra-Lago (1987, 1989, 1993a, c), Emmerson (1994b, 2001), Paula et al. (2003) and Litulo (2007) on sesarmids; Hill (1975, 1976, 1978, 1979a, b, 1980, 1994), Du Preez (1983, 1984), Du Preez & McLachlan (1984a, b, c, d) and Robertson (1996) on portunids; Melville-Smith (1983a, b, 1985, 1986, 1987b, 1988a, b, 1989) on geryonid crabs; and Owen (1998, 2003, Owen et al., 2000) on camptantriid crabs.

Because of the enormous commercial potential of decapods, research on penaeoid culture was undertaken in KwaZulu-Natal by Colvin (1976a, b), Emmerson (1980a, b, 1983, 1984b), Read & Caulton (1980) and Read (1981). Similarly, the large mud crab *Scylla serrata* was also cultured (Davis et al., 2004, 2005a, b).

Other important contributors to our knowledge of southern African decapods include Forest (1954) on hermit crabs; Hayashi & Miyake (1968) on stylodactylids; Griffin (1966) on majid crabs; Grindley (1961) on KZN crabs; Hayashi (1975b) on processids; McLaughlin (1988, 1997) on pagurids and hermit crabs; Lemaitre (1989, 1990, 2004b) on parapagurids; Macpherson (1983, 1984, 1988a, 1988b, 1990b, 1991) on nephropids, lithodids, galatheids and Namibian decapods; Serène (1984) on xanthids; and Manning & Holthuis (1988) on geryonids. Taxonomic revisions of other groups elsewhere also often include southern African species, such as the dromiids (McLay, 1993), trapeziids (Castro, 1999a; Castro et al., 2004), palicid crabs (Castro, 2000), latreillid crabs (Castro et al., 2003), ethusid crabs (Castro, 2005), goneplacid crabs (Castro, 2007), euryplacid crabs (Castro & Ng, 2010) and parthenopids (Tan & Ng, 2007a, b). The contributions of French and Italian carcinologists such as Fourmanoir (1954), Guinot (1961, 1962, 1967a), Crosnier (1962, 1965), Serène (1972), Vannini (1975a, b, 1976a, b, c, 1980, 1987), Vannini et al. (1989, 1995, 1997, 2001, 2003), Vannini & Innocenti (2000), Cannicci et al. (1995, 1996a, b, c, 1997, 1998, 1999, 2000, 2002), Gherardi & McLaughlin (1994), Gherardi et al. (1990, 1999, 2002a, b), Fratini et al. (2000a, b), Poupin (2003a, 2008) and Poupin et al. (2012) are equally pertinent, as the distribution of many Indo-Pacific, Madagascan and Indian Ocean Island decapod species extends down into southern African waters.

More recent taxonomic work now uses genetic sequencing to uncover cryptic species such as in potamonautids (e.g., Stewart, 1997a; Daniels et al., 2003; Gouws et al., 2000), the *Hymensoma* complex (Edkins et al., 2007) and spiny lobsters (Groeneveld et al., 2012). Although the Spanish have been using bottom trawls for scientific collections since the 1980s on